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Tancrede Alméras, Delphine Jullien, Shengquan Liu, Caroline Loup, Joseph Gril, et al.. The diversity of radial variations of wood properties in European beech reveals the plastic nature of juvenile wood. 2024. hal-04133248v4

HAL Id: hal-04133248

<https://hal.science/hal-04133248v4>

Preprint submitted on 12 Nov 2024

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The diversity of radial variations of wood properties in European beech reveals the plastic nature of juvenile wood

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Keywords

Beech; Wood properties; Variability; Radial variation; Juvenile transition; Ontogenetic juvenility; Adaptive juvenility

Abstract (401 words)

The long-term radial variation of wood properties from pith to bark are largest in the young ages of the tree (internal core). This so-called juvenility reflects both cambium ageing (ontogenetic juvenility) and adaptation to the changing mechanical constraints during secondary growth (adaptive juvenility). Ring width (*RW*), specific gravity (*SG*) and specific modulus (*SM*) are important parameters for each new wood layer, needed for the study of mechanical stability of a standing tree. They should be sensitive to the mechanical adaptation of growth. They were measured on diametrical boards (North/South direction) issued from 86 trees from several high forest stands in European countries. Analysis of variance showed very significant influence of position within the tree (core/external), of trees within a plot and of plots, but not for North/South orientation. The share of variance was similar for *SG* and *SM* (importance of tree effect) but different for *RW* (importance of plot effect). The occurrence of red heartwood in the core on some trees had a significant influence, mostly on *SM*, but the differences between white and red wood was very small. Globally the variability is high for *RW*, rather small for *SM* and very small for *SG*. Accordingly, the variations of the modulus of elasticity (product of *SG* and *SM*) were much more influenced by *SM* than by *SG* for beech. The radial variations of each parameter were fitted by both a linear (2 coefficients: zero value and mean slope) and a parabolic curve (3 coefficients: zero value, initial slope and curvature). They were used to classify types or radial profile in terms of flat, up & down and straight, convex & concave. Median values of coefficients per plot (or total) were used to draw median profiles for each parameter per plot and at the global level. The median global profiles differ from the typical radial pattern (TRP) of juvenility for plantation softwoods for *SG* (down concave instead of up concave) and *SM* (convex as TRP but with a clear decrease in the mature wood). The main result was the very large variability of profiles between trees or even between plots. Even if there is a part of ontogenetic influence in the juvenile patterns for *RW*, *SG* and *SM*, the results suggest that the influence of mechanical constraints in the tree growth (adaptive juvenility) dominates largely.

44 **Notations and abbreviations**

45	<i>CV</i>	coefficient of variation
46	<i>D</i>	density
47	<i>L, L</i>	longitudinal direction, specimen length in L direction
48	<i>R, R</i>	radial direction, specimen length in R direction
49	<i>RW</i>	ring width
50	<i>SG</i>	specific gravity (ratio of <i>D</i> over water density)
51	<i>SM</i>	specific modulus (squared value of sound speed in L direction)
52	<i>T, T</i>	tangential direction, specimen length in T direction
53	TRP	typical radial pattern
54	<i>W</i>	specimen weight

55 **1. Introduction**

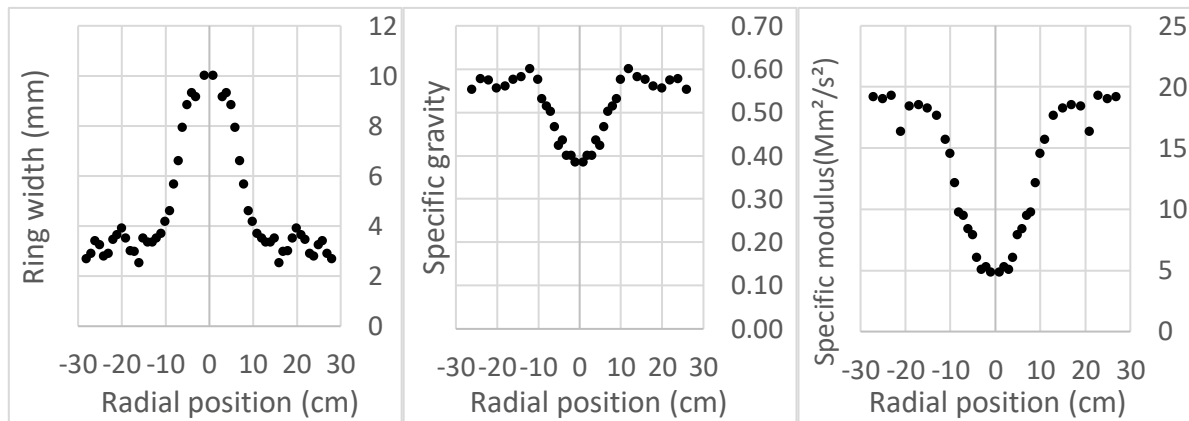
56 Wood is an adaptation to the competition for height growth in the terrestrial environment, which
 57 is submitted to tremendous physical constraints such as gravity, wind and drought. The
 58 functions of wood (mechanical support, conduction and storage) respond these constraints, and
 59 are fulfilled by different cell types (fibres or tracheids, vessels and parenchyma). In tree species,
 60 the bulk of wood material is generally made of fibres, which have mainly a mechanical function.
 61 Despite their major importance for tree functioning and survival, other cell types generally
 62 represent only a small part of wood in terms of biomass investment. Actually, most of terrestrial
 63 biomass is in the form of fibres (Bar-on et al 2017). This massive investment in fibres points to
 64 the major significance of the mechanical constraint for trees. The viewpoint that we will adopt
 65 here is that wood production quantity and quality are mainly responses to the mechanical
 66 requirement of the tree to face the two major constraints that are wind and gravity.

67 Trees are built through wood growth (Thibaut 2019) including simultaneously primary growth
 68 by elongation or creation of twigs and secondary growth by thickening of existing axes.
 69 Secondary growth is performed by living wood cells in the cambial zone: stem cells of cambium
 70 itself and daughter cells (Raven et al 2007, Savidge 2003, Déjardin et al 2010, Thibaut 2019).
 71 It consists of the following successive steps: division of the cambium stem cells into daughter
 72 cells; expansion of daughter cells until the end of primary wall formation; thickening of the
 73 fibre (or tracheid) cell walls until the end of secondary wall formation; lignification of the whole
 74 cell wall, including the compound middle lamella; programmed fibre and vessel cell death.

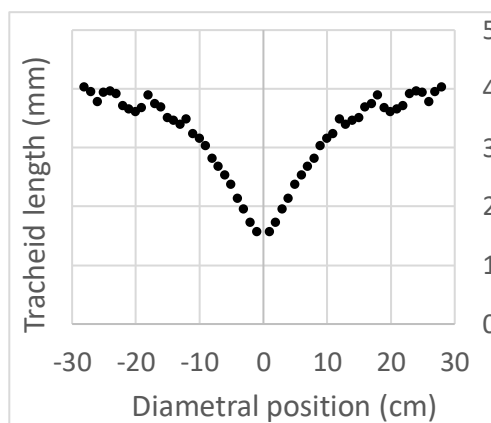
75 During this cambial activity, wood features are achieved. They can be described by ring width
 76 (*RW*), result of combined cell division and expansion, specific gravity (*SG*) resulting from the
 77 ratio between cell wall thickening and expansion, and specific modulus (*SM*) mainly
 78 determined by the organisation of the secondary cell wall (micro-fibril angle of the S2 layer)
 79 (Cave 1969). These three features determine most parameters involved in the adaptation to
 80 mechanical constraints. For a trunk of a given height, the rigidity against lateral wind forces
 81 depends on trunk diameter (related to *RW*) and on wood modulus of elasticity (MOE) which is
 82 the product of *SG* and *SM* (Fournier et al. 2013). For a given biomass investment, there is a
 83 trade-off between *RW* (large growth rate) and *SG* (large density). The flexibility of the trunk
 84 depends inversely on diameter, and positively on wood deformability (equal to the ratio of
 85 strength to modulus of elasticity, which is negatively correlated to *SM* as can be seen on wood
 86 database, e.g. Ross 2010). The mechanical stability of the tree depends on its diameter, modulus
 87 of elasticity (product of *SG* by *SM*), and inversely on its green density (correlated to *SG*, Dlouha
 88 et al 2018). The postural control (Alméras & Fournier 2009) depends on the asymmetry in radial
 89 growth rate (related to *RW*), modulus of elasticity, and maturation strain (often correlated to
 90 *SM*, Alméras et al 2005). Mechanical adaptation is therefore a matter of fine-tuning of wood
 91 properties, accounting for the trade-offs between them.

92 The secondary growth descriptors (*RW*, *SG*, *SM*) display spatial variation within a portion of
 93 trunk, in the 3 cylindrical directions: transversely across radii (*Tar*), around the perimeter (*Ap*)
 94 and longitudinally along the stem (*Las*), called variation “*TarApLas*” within the tree by Savidge
 95 (2003). The variations around the perimeter in a given ring are related to posture control
 96 (Alméras and Fournier 2009), either due to trunk inclination (Alméras et al 2005, Dassot et al.
 97 2015) or to orientation change of the branches after apex death (Loup et al 1991). The variations
 98 along the stem deal with primary growth: i) succession of connected zones and free-from-
 99 branching portions of the axis and ii) ageing of the terminal bud in the successive growth units.
 100 Apart from the vicinity of the branching zones, these variations are rather slow (Savidge 2003).
 101 Radial variations from pith to bark at a given height can be divided in two types: i) intra-ring
 102 short distance changes mostly due to seasonal effects and ii) variations of mean ring properties,
 103 reflecting adaptations to changes in mechanical constraints during ontogeny. These mechanical
 104 constraints change according to the size of the tree (Fournier et al. 2013). The biggest variations
 105 in dimensions and environment occur during the young ages, and so are the variations of wood
 106 properties showing higher radial gradients in the inner part of the axis, called *juvenile wood* or
 107 core wood depending on the authors (Lachenbruch et al 2011).

108 A good description of that is given in Bendtsen & Senft (1986). Loblolly pine (Fig. 1 and Fig.
 109 2) is an example of the typical radial pattern (TRP) of juvenility (Lachenbruch et al 2011):
 110 initial increase of tracheid length, specific gravity (*SG*) and specific modulus (*SM*), initial
 111 decrease of ring width (*RW*). The initial increasing or decreasing portion called juvenile wood
 112 is followed by a more or less constant value called mature wood. This is the general case in
 113 softwood plantation trees (Cown & Dowling 2015, Larson et al 2001).



114 Fig. 1. Juvenility for mechanical indicators (typical radial patterns), after Bendtsen & Senft (1986).
 115 Ring width in mm; specific modulus in 10⁶ m²/s
 116



117 Fig. 2. Juvenility for tracheid length (after Bendtsen & Senft 1986)
 118

119 Variations in tracheid or fibre length always share the same initial positive gradient for all trees
 120 (Fig. 2), whether softwood or hardwood (Koubaa et al 1998, Larson et al 2001, Bhat et al 2001,
 121 Bao et al 2001, Kojima et al 2009). This parameter is important for paper industry (Koubaa et
 122 al 1998) but is not cited as a factor influencing wood mechanical properties (Kollmann & Côté
 123 1968, Kretschman 2010).

124 The variation of parameters characterizing wood structure and properties depends on tree
 125 ontogeny and adaptation to changing constraints during its life. *Juvenility* describes the
 126 evolution of wood parameters during the early years of the stem. An important question is to
 127 separate the genetically programmed changes in properties with ontogeny (here termed
 128 *ontogenetic juvenility*) from the plastic adaptation to changing constraints (here termed *adaptive*
 129 *juvenility*). The systematic nature of juvenile gradients in fibre length suggest that they are
 130 consequence of cambium ageing (ontogenetic juvenility). Here we aim at investigating whether
 131 juvenile variations in 3 functional wood properties (*RW*, *SG* and *SM*) depend on plastic
 132 adaptation or on prescribed ontogenetic changes.

133 The data obtained on a large panel of beech trees will be exploited to characterize the patterns
 134 of radial variations of wood mechanical indicators in beech. Hypotheses that will be discussed
 135 are the following: i) most of the variation are similar all around the trunk (profile symmetry),
 136 ii) all the trees share the same radial pattern (ontogenetic juvenility) within the different growing
 137 conditions.

138 In healthy beech trees, heartwood and sapwood can scarcely be distinguished. A so-called “red
 139 heartwood”, which is a kind of chemical discoloration, is often observed (Liu et al 2005) and it
 140 affects the commercial value of the products (Trenčiansky et al 2017). The hypothesis that red
 141 wood occurrence does not affect mechanical parameters will also be tested.

142 2. Material and methods

143 2.1. Material

144 Nine plots representative of forest management in Western Europe (Becker & Beimgraben
 145 2001, Jullien et al 2013) were selected (Table 1). The objective was not to study the role of
 146 forest management but to have a sufficient diversity of growth history. Up to ten trees per plot
 147 (86 in total) were selected for the measurement of wood properties (Table 1). All trees were
 148 dominant or co-dominant and their mean diameter at breast height was around 60 cm (Table 2).

149

Table 1. Characteristics of the studied plots

	age (years)	Plot								
		1	2	3	4	5	6	7	8	9
Forest:	Nb trees	10	10	10	10	10	8	10	10	8
Even-aged	100-130	o		o	o	o	o			
Even-aged (mountain)	120-150		o						o	
Uneven-aged	60-120							o		
Middle to even- aged forest	60									o
Height	m	32.6	32.1	35.5	36.1	36	38.3	34	39.2	35.3
Slenderness	m/m	58.3	65	58.9	64	64.9	61.7	60.2	68	47.6
DBH	cm	56	49.4	60.7	56.6	55.4	62.5	56.9	58.2	74.5

150

Table 2. Geometric description of the 86 selected trees

86 trees	Mean	Min	Max	CV
Height (m)	35.4	23.7	42.6	10.1%
Slenderness (m/m)	61.3	41.0	80.4	13.2%
Diameter (cm)	58.5	47.0	84.5	13.2%

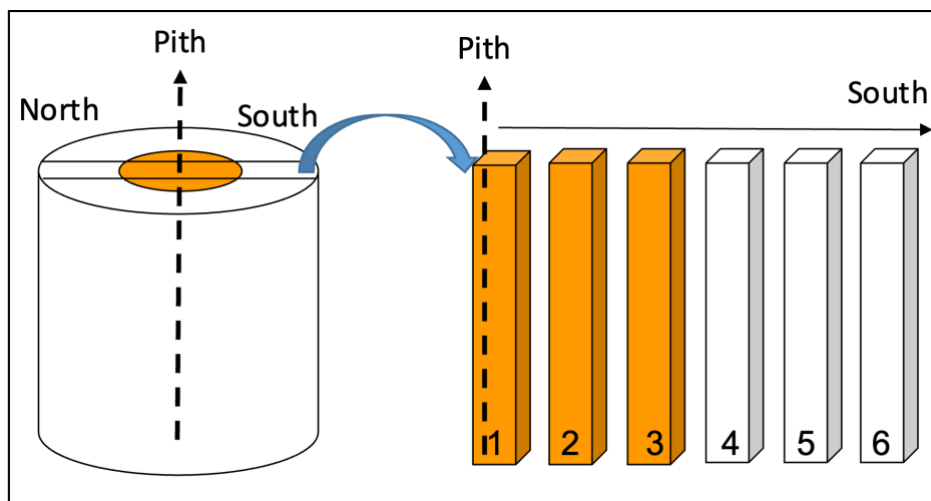
151

Min: minimum value; max: maximum value; CV: coefficient of variation

152

153 One small log of 50 cm length was cut at a height of 4 m for each tree. Each small log was cut
 154 into radial boards, through the pith, from North to South (North direction was carved in the log
 155 bark). These boards were air-dried to an average moisture content of 13.5 % and cut into 1259
 156 rods of 20 mm in radial, 20 mm in tangential and 360 mm in longitudinal direction, from the
 157 pith outwards (Fig. 3). The rods with irregularities or cracks were discarded.

158 The rods were numbered according to their position in the board, their distance to pith was
 159 measured, and their orientation (North or South) was noted. At the same time, the number of
 160 rings at both ends of the samples was recorded and the mean annual ring width of the rod (RW)
 161 was calculated as the ratio of the mean radial dimension to the number of rings. Each sample
 162 located at a distance lower than 10 cm from the pith was considered as a “core” sample. The
 163 presence of red heartwood was also noted for the rods located in the core, in relation to a
 164 previously published work (Liu et al 2005).



165

166 Fig. 3. Diagram of the sawing of the rod after the sawing of a North-South diametrical board.

167 Numbering both for Northern and Southern parts of the board start with pith position. The coloured

168 parts evoke the case of red heartwood occurrence.

169 2.2. Measurement of properties.

170 The density (D) was calculated by measuring the weight (W) and the dimensions R , T , L of the
 171 rod in direction R , T , L , respectively: $D = W/(R.T.L)$. The specific gravity (SG) was the ratio
 172 between D and water density.

173 To measure the specific modulus (SM , $10^6\text{m}^2/\text{s}^2$), each rod was positioned on fine wires and set
 174 in free vibration by a hammer stroke. The analysis of the sound vibration by fast Fourier
 175 transform gave the values of the three highest resonance frequencies, which were interpreted
 176 using Timoshenko solution (Brancheriau & Baillères 2002).

177 **2.3. Statistical analyses**

178 2.3.1 Correlations and basic statistics

179 Basic statistical analyses were performed using XLSTAT software. The data description table
 180 included the number of data, the minimum, maximum and mean values for each parameter, as
 181 well as the coefficient of variation (CV). The normality of the distribution was verified by
 182 Shapiro-Wilk test. A Pearson correlation analysis was used in the case of a normal distribution,
 183 and a Spearman correlation analysis in the case of a non-normal distribution, which was the
 184 majority of cases.

185 2.3.2 Analysis of variance and variance components

186 Analyses of variance (ANOVA) and variance components analyses (VCA) were carried out
 187 using R software (R Core Team 2018). A first set of analyses tested the effect of the different
 188 factors on the three measured variables (*RW*, *SM* and *SG*), using a nested ANOVA design where
 189 a random “tree” factor was nested within the “plot” factor, and the “core” factor nested within
 190 the “tree” factor. Sample orientation (North or South) was accounted for through an
 191 independent “orientation” factor.

192 Another set of ANOVA and VCA was carried out to test the effect of red heartwood on wood
 193 properties. This analysis was based only on core specimens, as red heartwood occurs only on
 194 these specimens. As both the measured properties and the occurrence of red heartwood were
 195 correlated to the distance to the pith (red heartwood occurs more often in inner parts of the
 196 core), its effect was tested with a two-ways ANOVA, with specimen number and red heartwood
 197 occurrence (Red) as two independent factors. A VCA was carried out on this model to quantify
 198 the share of variance of each factor.

199 2.3.3 Quantitative analysis of radial profiles

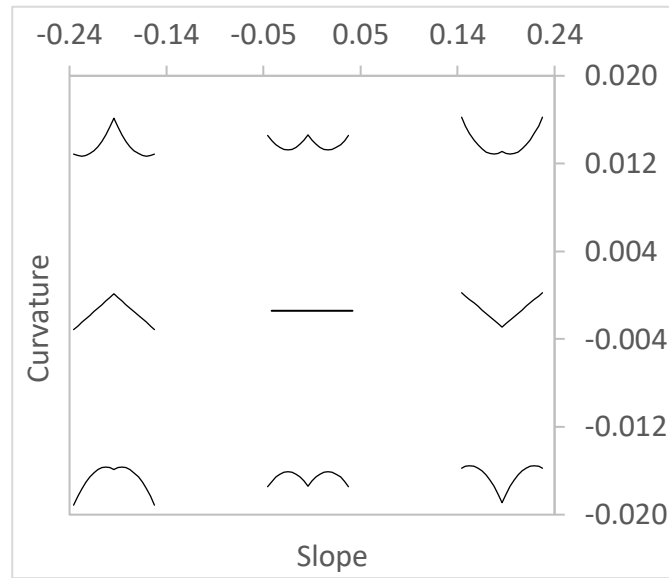
200 North and south radial profiles were analysed together, yielding 172 profiles on which the three
 201 variables (*RW*, *SG* and *SM*) have been quantified as a function of the distance to the pith. We
 202 built a Microsoft Excel file to view and analyse these profiles (see Suppl. Mat.). The purpose
 203 of this analysis was the quantification of the shapes of these profiles, and how they correlate
 204 between properties or vary between plots. To achieve this, we considered two main indicators
 205 of each profile’s shape: the slope, and the curvature.

206 The slope of the particular radial profile was computed as the coefficient of the linear regression
 207 between the considered property and the distance to the pith. It indicates whether the property
 208 is globally increasing, decreasing, or staying constant. The curvature was computed as the
 209 coefficient of quadratic term of a second-degree polynomial regression. A positive value
 210 corresponds to a convex shape, where the local slope increases outward, whereas a negative
 211 value corresponds to a concave shape, where the slope decreases outward. All combinations of
 212 slope and curvature can exist. Thus, each profile could be represented as a dot on a
 213 slope/curvature graph, corresponding to a particular shape. The correspondence between
 214 parameter’s values and profile shapes is illustrated on Fig. 4, where the ‘icons’ illustrate the
 215 symmetric shape corresponding to their position on the graph.

216 The correlations between quantitative parameters of the profiles were studied through a PCA
 217 (carried out using R) taking into account the following 15 variables for each of the 172 radial
 218 profiles: the mean value of the property (*RW_m*, *SG_m*, *SM_m*), the global slope (*RW_s*, *SG_s*,
 219 *SM_s*) obtained from the linear regression, the initial value of the property (*RW_{a0}*, *SG_{a0}*,
 220 *SM_{a0}*), the initial slope of the property (*RW_{a1}*, *SG_{a1}*, *SM_{a1}*) and the curvature (*RW_{a2}*,
 221 *SG_{a2}*, *SM_{a2}*), obtained as the coefficients of the second-degree polynomial regression.

222 At the plot level, we computed the median and the interquartile range of each parameter (slope
 223 and curvature) on each variable (*RW*, *SG* and *SM*), to appreciate whether there were systematic

224 differences in profile shapes between plots. An ANOVA was used to test the effect of the plot
 225 factor on each parameter.



226
 227 Fig. 4. Illustration of the correspondence between profile parameters (slope and curvature) and shape
 228 of a symmetric profile (“flying bird” icons).
 229

230 The 172 profiles were then classified according to two criteria: they were classified as “Flat”,
 231 “Up” or “Down” according to a threshold on the slope, and as “Straight”, “Convex” or
 232 “Concave” according to a threshold on the curvature. We used a criterion based on the
 233 magnitude of the effect of each parameter rather than on its statistical significance. Indeed, in
 234 many cases the significance of the slope (or curvature) was found high (low P-value) although
 235 the magnitude of the effect was weak when compared to the overall range of variation of the
 236 parameter. The threshold values were set at an arbitrary 50% of the overall standard deviation
 237 of each variable, scaled by the mean distance to the pith (10 cm) for the slope, and by its square
 238 for the curvature. At the tree level, the diametral profiles (including both north and south
 239 profiles) were classified as symmetric (“Sym”) if parameters of the North and South profiles
 240 differed less than a threshold defined consistently with above (see suppl. mat.).

241 **3. Results**

242 **3.1 Structuration of variance at the within-tree, between-tree and between-plot levels**

243 ANOVA was highly statistically significant on each of the three measured variables (*RW*, *SG*
 244 and *SM*). Plot, tree within plot and core within tree were all very highly significant factors ($P <$
 245 10^{-6}) for the three variables, while orientation was a significant factor only for *SM* ($P =$
 246 0.00012). The share of variance of each factor for each variable is displayed in Table 3, together
 247 with the statistical significance of each factor. For *RW*, the core factor (inner 10 cm radius,
 248 compared to the outer zone) represented the largest part of variance, followed by the plot and
 249 tree factors. For *SG* and *SM*, the tree factor was the largest part of variance. The orientation
 250 factor was statistically significant only for *SM* with a very low share of variance and a very low
 251 difference in mean value for North (637 rods; mean value = $22.1 \cdot 10^6 \text{ m}^2/\text{s}^2$) and South (622
 252 rods; mean value = $22.4 \cdot 10^6 \text{ m}^2/\text{s}^2$).

253 Table 3. Results of the variance component analysis of the effect of Plot, Tree, Core and Orientation
 254 factors on the properties of all specimens: share of variance for each factor (%) and significance
 255 of the factors

Factor	<i>RW</i>	<i>SG</i>	<i>SM</i>
Plot	21.9***	14.0***	15.4***
Plot/tree	9.2***	36.4***	28.6***
Plot/tree/core	29.5***	18.2***	14.6***
Orientation	ns	ns	0.8***

256 *** $P < 10^{-3}$; ns $P > 0.05$; *RW*: ring width; *SG*: specific gravity; *SM*: specific modulus

257 The effect of red heartwood on wood properties was tested on core specimens only, accounting
 258 for the distance to the pith (specimen number) as an independent factor. The results (Table 4)
 259 show that the distance to the pith was always a significant factor while red heartwood was non-
 260 significant for *RW* and *SG*.

261 Table 4. Results of the variance component analysis of the effect of red heartwood occurrence (Red)
 262 and specimen number (Num, indicating the distance to the pith) on the properties of core specimens:
 263 share of variance for each factor (%) and significance of the factors

Factor	<i>RW</i>	<i>SG</i>	<i>SM</i>
Num	2.5**	2.7***	3.0***
Red	ns	ns	8.6***

264 *** $P < 10^{-3}$; ** $P < 10^{-2}$; ns $P > 0.05$; *RW*: ring width; *SG*: specific gravity; *SM*: specific modulus

265 **3.2. Correlations between properties at different levels**

266 Ring width, specific gravity and specific modulus play a role in stem construction and are linked
 267 to the 3 successive phases of living wood cells in the cambial zone: cell division, cell expansion
 268 and cell-wall thickening. Each phase is influenced by the mechanical and hydraulic constraints
 269 on the tree during wood growth. So, it is rather doubtful that the variation of the three
 270 mechanical parameters are independent. Distribution of properties and correlations between
 271 them can be computed at each level (between rods, between trees and between plots). It is
 272 expected that the variability of properties decreases between the rod, tree and plot levels.

273 **3.2.1. Rod level**

274 Table 5 shows descriptors of the distribution of properties for all samples (1259 rods). The
 275 variation of *SG* between samples was very low (coefficient of variation 6.2%) compared to that
 276 of *SM* (10.9%) and *RW* (35%).

277 Table 5. Parameter description for all rods

1259 rods	<i>RW</i>	<i>SG</i>	<i>SM</i>
Minimum	0.67	0.55	11.08
Maximum	6.67	0.83	27.49
Mean	2.30	0.69	22.22
Max/min	10.00	1.51	2.48
C.V.	35.0%	6.2%	10.9%

278 *RW*: ring width (mm); *SG*: specific gravity; *SM*: specific modulus ($10^6 \text{m}^2/\text{s}^2$)

279 Table 6. Correlation table for all rods (Spearman)

1259 rods	<i>RW</i>	<i>SG</i>	<i>SM</i>
<i>RW</i>	1	0.16***	-0.33***
<i>SG</i>	0.16***	1	0.12***
<i>SM</i>	-0.33***	0.12***	1

280 *RW*: ring width; *SG*: specific gravity; *SM*: specific modulus

281

282 *SG* and *SM* were correlated positively (Table 6). *RW* was correlated positively with *SG* and
 283 negatively with *SM*. These correlations were very significant (below the 0.1% level) although
 284 they were quantitatively rather weak, explaining only 5% to 10% of variance.

285 3.2.2. Tree level

286 Table 7 shows the descriptors of the distribution of mean values of properties per tree.
 287 Variability at the tree level, as quantified by the coefficients of variation, was significantly
 288 lower than for the rod level, and notably low for *SG*. This result was consistent with the fact
 289 that a substantial part of the variance was at the within-tree level (Table 3, “Core” factor).

290 At the between-tree level, only the negative correlation between *RW* and *SM* remained
 291 significant (Table 8), showing that trees with higher growth rates (higher mean *RW*) had lower
 292 *SM*. Note that the correlation between these properties was even higher in magnitude at the tree
 293 level (-0.40) than at the rod level (-0.33).

294 Table 7. Parameter description for tree mean values

86 trees	<i>RW</i>	<i>SG</i>	<i>SM</i>
Minimum	1.29	0.63	17.6
Maximum	4.78	0.78	25.6
Mean	2.28	0.70	22.4
Max/min	3.70	1.24	1.46
C.V.	24.9%	4.8%	7.6%

295 *RW*: ring width (mm); *SG*: specific gravity; *SM*: specific modulus (10⁶m²/s²)

296 Table 8. Correlation table for all trees (Spearman)

86 trees	<i>RW</i>	<i>SG</i>	<i>SM</i>
<i>RW</i>	1	0.08 ^{ns}	-0.40 ^{***}
<i>SG</i>	0.08 ^{ns}	1	0.16 ^{ns}
<i>SM</i>	-0.40 ^{***}	0.16 ^{ns}	1

297 *RW*: ring width; *SG*: specific gravity; *SM*: specific modulus

298 3.2.3. Plot level

299 Table 9 shows the descriptors of the distribution of mean values of properties per plot.
 300 Variability at the plot level, as quantified by the coefficients of variation, was significantly
 301 lower than for the tree level, consistent with the large part of variance at the between-tree level
 302 (Table 3, “Tree” factor).

303 Table 9 Parameter description for the 9 plots mean values

Plot	<i>RW</i>	<i>SG</i>	<i>SM</i>
1	2.06	0.70	21.5
2	1.80	0.71	23.1
3	2.63	0.70	22.2
4	2.50	0.71	21.2
5	2.12	0.68	21.9
6	2.57	0.73	23.7
7	2.84	0.68	22.0
8	1.63	0.68	24.1
9	2.50	0.67	21.7
Maximum	2.84	0.73	24.1
Minimum	1.63	0.67	21.2

Radial variations of beech properties

Mean	2.29	0.70	22.4
C.V.	16.9%	2.6%	4.2%

RW: ring width (mm); *SG*: specific gravity; *SM*: specific modulus ($10^6\text{m}^2/\text{s}^2$)

304

305

306 At the plot level there were no more significant correlation between indicators (Table 10).

307

Table 10. Correlation table for all plots (Spearman)

9 Plots	<i>RW</i>	<i>SG</i>	<i>SM</i>
<i>RW</i>	1	0.18 ^{ns}	-0.17 ^{ns}
<i>SG</i>	0.18 ^{ns}	1	0.23 ^{ns}
<i>SM</i>	-0.17 ^{ns}	0.23 ^{ns}	1

308

RW: ring width; *SG*: specific gravity; *SM*: specific modulus

309

310 3.3. Diversity of radial profiles of properties

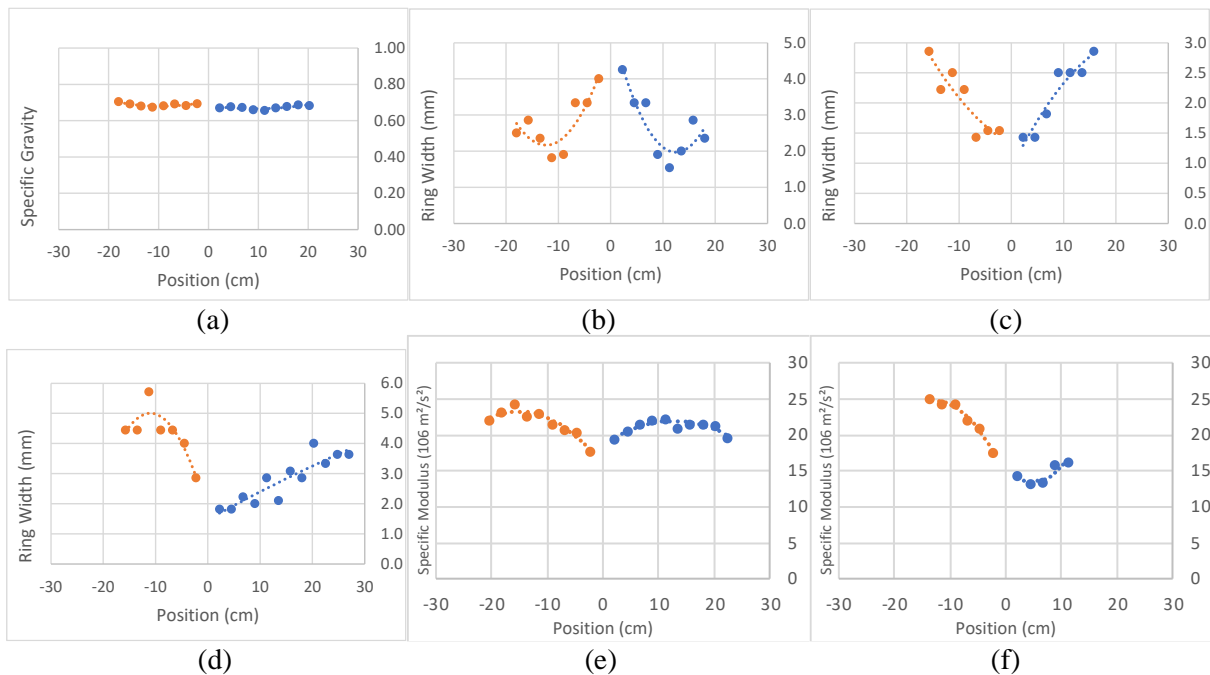
311 3.3.1 Illustration of profile diversity

312 A total of 516 profiles (86 trees x 2 orientations x 3 variables) were observed and analysed. The
 313 mean coefficients of determination (R^2) of the regressions was 0.43 for linear regression, and
 314 0.61 for second-degree polynomial regressions, showing that the quadratic term captured a
 315 large part of profile non-linearity.

316 Examples of typical profiles together with the second-degree fitting are shown in Fig. 5 (all
 317 profiles can be viewed from the file provided as supplementary material). The chosen examples
 318 illustrate the diversity of the diametral profiles, with symmetric profiles (a, b, c, e) as well as
 319 non-symmetric profiles (d, f). The radial profiles were either flat (a), increasing (c, d, e-South,
 320 f) or decreasing (b), and either straight (a, c, d-North), convex (b, f-North) or concave (d-South,
 321 e, f-South).

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Fig. 5. Examples of property profiles: (a) tree 694, plot 6; (b) tree 443, plot 4;
 (c) tree 290, plot 2; (d) tree 1050, plot 9; (e) tree 1025, plot 9; (f) tree 299, plot 2

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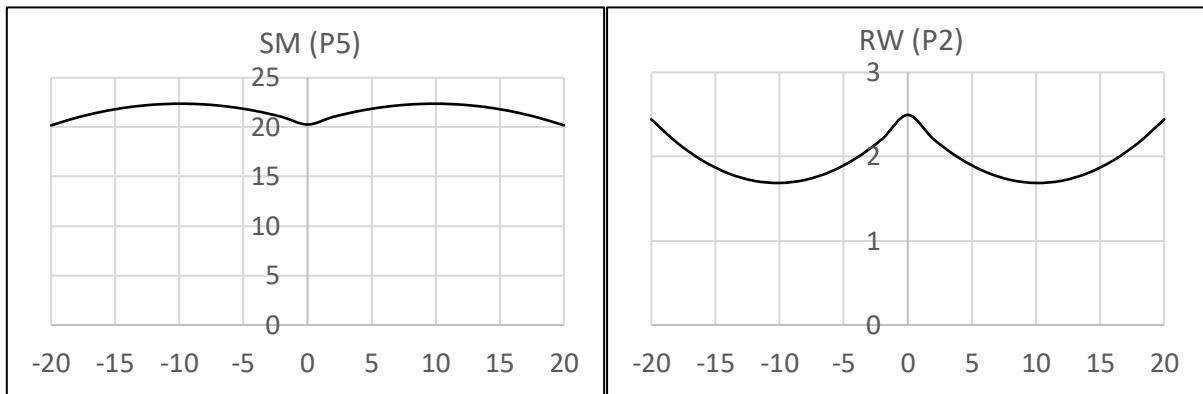
329 3.3.2 Typology of profiles

330 For each of the three studied variables (*RW*, *SG* and *SM*) there was a large diversity of radial
 331 profiles, with instances of all nine possible combinations of slope (“Up”, “Flat”, “Down”) and
 332 curvature (“Convex”, “Straight”, “Concave”). Nevertheless, the frequency of these different
 333 shapes differed (Table 11). The proportion of symmetric profiles (“Sym”) is about one third,
 334 showing that most trees display substantial variations of properties around the periphery.

335 Table 11. Occurrence of profile types for 172 north and south cases

N + S	Sym	Flat	Up	Down	Straight	Convex	Concave
<i>RW</i>	36%	41%	18%	41%	36%	37%	27%
<i>SG</i>	37%	42%	13%	45%	48%	34%	19%
<i>SM</i>	28%	42%	37%	20%	28%	10%	62%

336 The proportion of flat radial profiles was of about 40% for each variable. Most other profiles
 337 were decreasing for *RW* and *SG*, and increasing for *SM*. But less than 50% of flat profiles were
 338 straight, meaning that most flat profiles were either convex (for *RW* or *SG*), or concave (as for
 339 *SM*) (Fig. 6).
 340



341 Fig. 6. Examples of median plot profiles with flat slope: flat-convex (*SM*, P5) or flat-concave (*RW*, P2)
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 343

344 The proportions of each type of profile seemed to differ between plots, as illustrated on Fig. 7.

Radial variations of beech properties

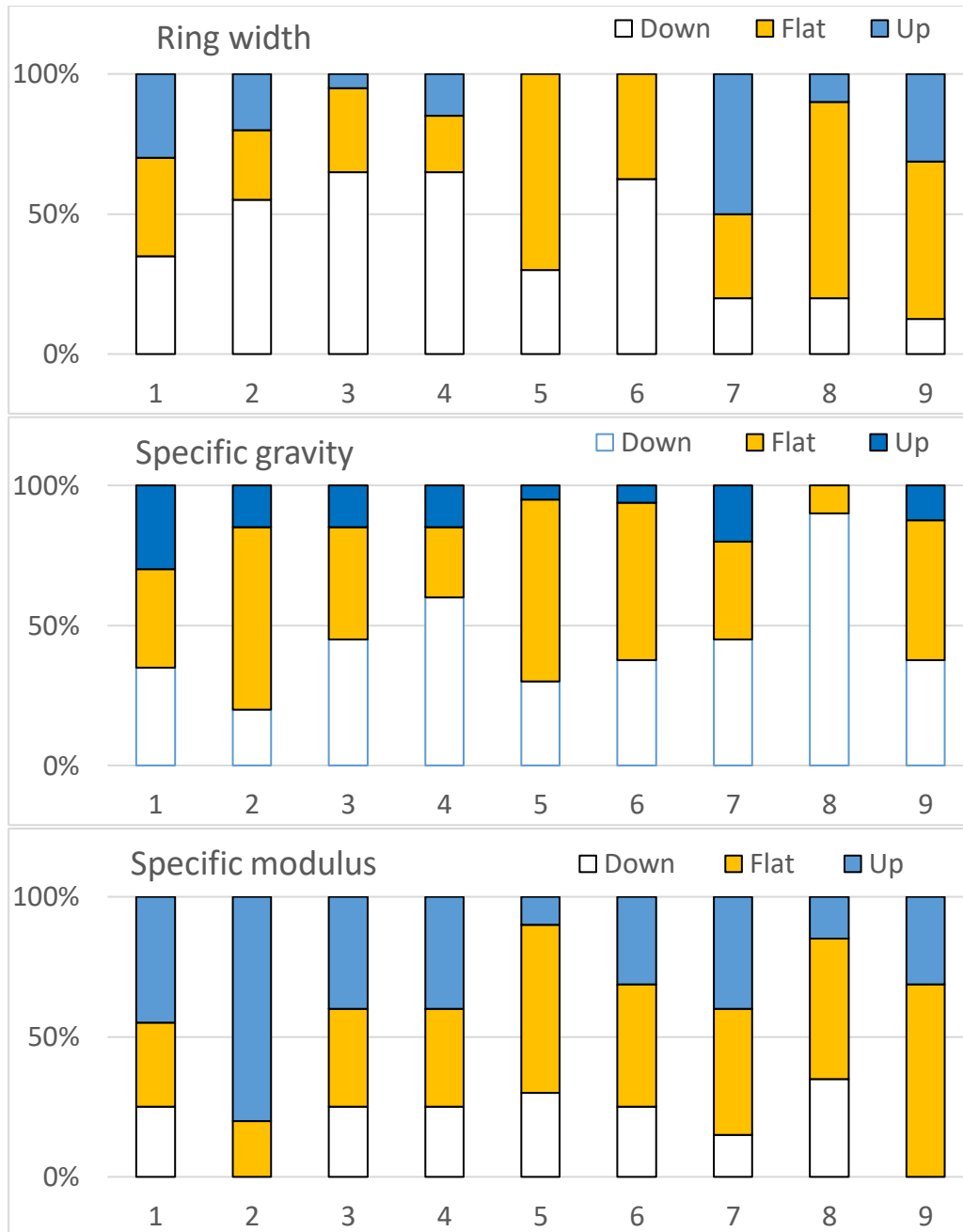


Fig. 7. Distribution of profile types per plot (based on the slope of linear regression)

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350 3.3.3 Distribution of profiles shape parameters

351 The median shape of all radial profiles is illustrated on Fig. 8. These profiles were “down-
 352 convex” for *RW* and *SG*, and “up-concave” for *SM*. The shape of the median profile of each
 353 plot can be viewed from the supplementary material.

354

Radial variations of beech properties

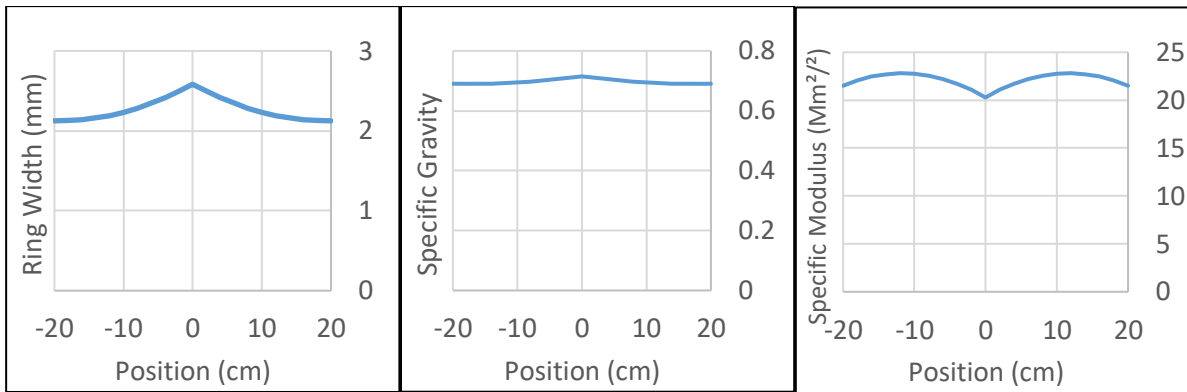


Fig.8 Median profiles over all trees, mixing both orientations in a symmetrical presentation.

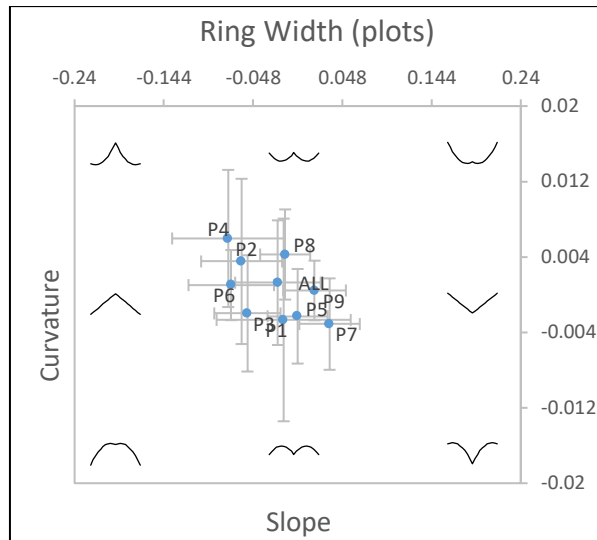
355
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358 The distribution of profile shape parameters is illustrated in Fig. 9. Each figure represents the
359 distribution (median and inter-quartile) of parameters (slope and curvature) for each plot,
360 together with “icons” illustrating the correspondence between the position on the graph and the
361 profile shape. The figures are centred on zero on the X and Y axis, so that the centre of the
362 figure represents the flat straight profile, and each quadrant of the figure represents a type of
363 profile. A similar figure representing the distribution of parameter from individual radial
364 profiles is provided in supplementary material.

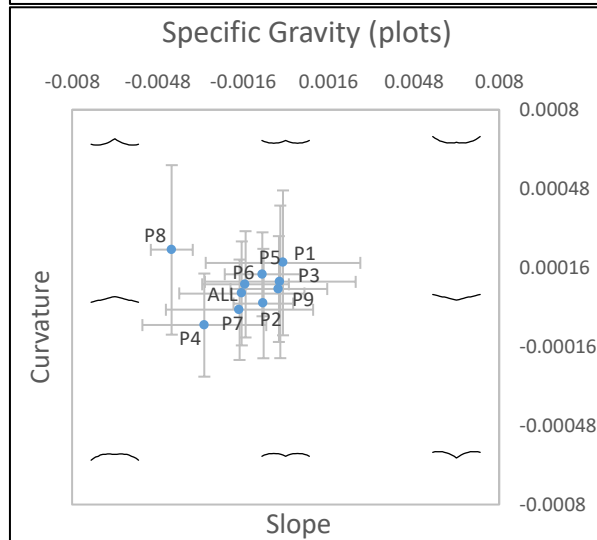
365 It is apparent from Fig. 9 that shape parameters of profiles were not randomly distributed. The
366 plot effect on the slope parameter was found significant for all three variables, while its effect
367 on curvature was found significant only for *SG*.

Radial variations of beech properties

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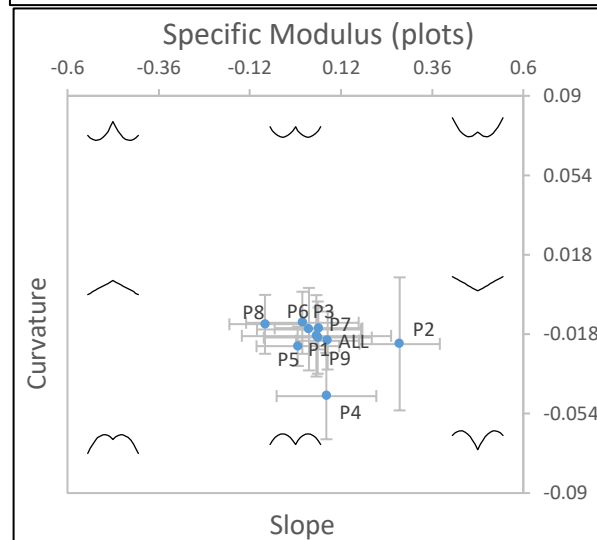


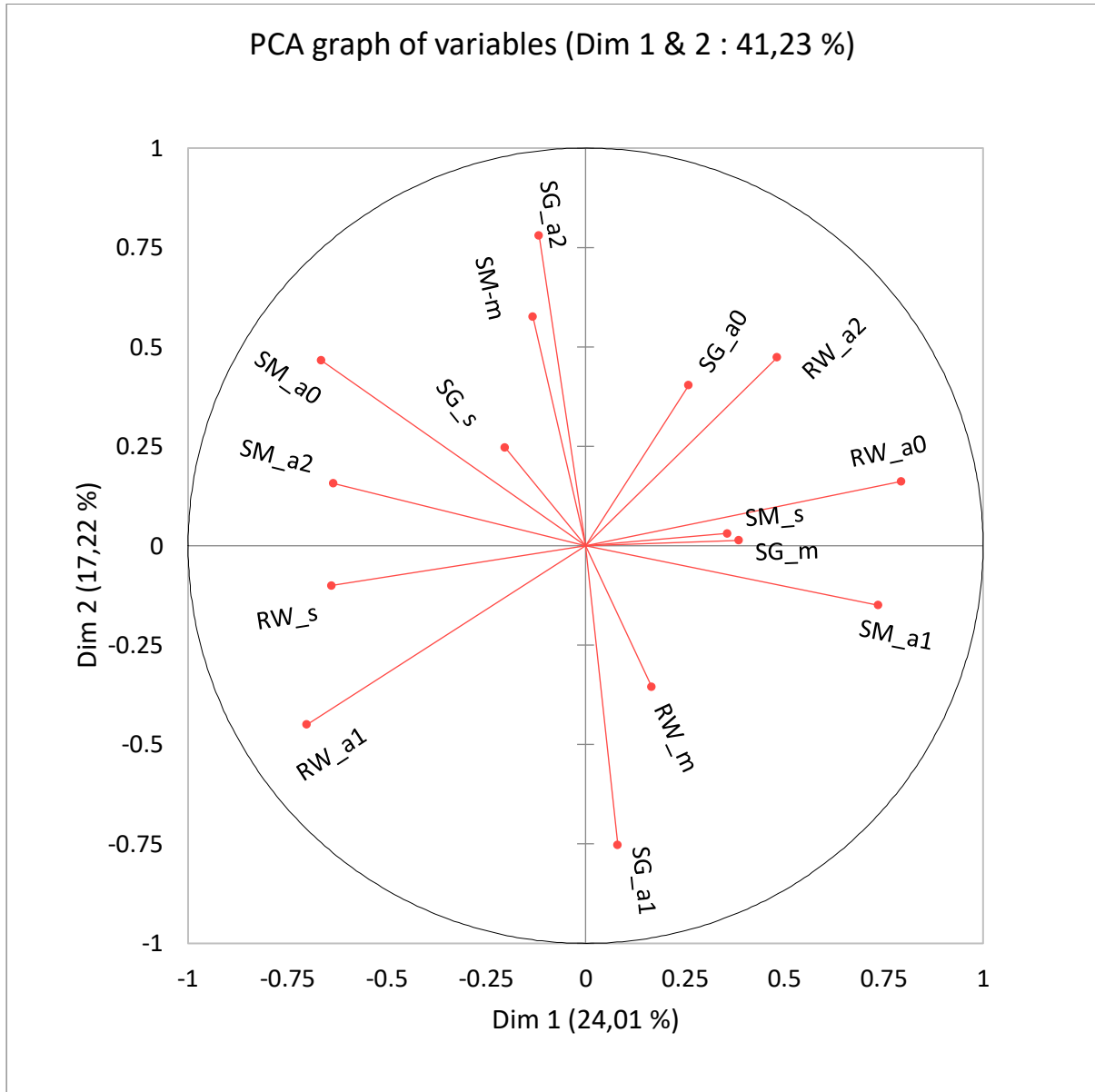
Fig. 9. Distribution of median plot profiles in the slope/curvature plane. Error bars represent the interquartile range of each plot. "Flying-bird" icons represent the shape associated to their position in the figure (see Fig. 4).

375 3.3.4 Correlations between profile shape parameters

376 The correlations between shape parameters of the profiles are illustrated in Fig. 10. The first
 377 axis of this PCA opposed high initial ring width (RW_{a0}) and positive initial slope of specific
 378 modulus (SM_{a1}) to high initial specific modulus (SM_{a0}) and positive slope of ring width
 379 (RW_{a1}). This axis opposed high growth rate to high cell wall stiffness.

380 It is apparent that the initial slope ($_{a1}$) and curvature ($_{a2}$) were negatively correlated for all
 381 three variables, meaning that the more the variable was initially quickly changing, the more this
 382 rate of change was lowered during growth.

383



384

385 Fig. 10. Principal Component Analysis of shape profile parameters.
 386 See §2.3.3 for the meaning of variables.

387

388 4. Discussion

389 4.1. Effect of red heartwood on wood properties

390 Contrary to our expectations, the effect of red heartwood on the specific modulus was found
 391 significant, representing a substantial share of variance (8.6%). Its occurrence is associated to
 392 a lower SM ($-0.67 \cdot 10^6 \text{ m}^2/\text{s}^2$ in average, 3% of the mean value), even when the effect of distance
 393 to the pith was accounted for. Pöhler et al (2006) found significant difference ($p < 0.05$) both for
 394 density and modulus of elasticity. But the two parameters were higher for red heartwood (+3%
 395 and +6% respectively, which means +3% for SM). One reason for the difference could be due
 396 to a modification of cell wall properties during the expansion of red heartwood. Another one
 397 could be that trees with lower SM were more prone to develop red heartwood in our sampling.
 398 Anyway, in both studies, the difference between red heartwood and white heart density and
 399 specific modulus was quite small.

400 4.2. Interpretation of correlations between properties

401 As a result of the large difference of variability between SG and SM (Table 5) the variability of
 402 the modulus of elasticity which is the product of SG and SM , is more dependent on the variations
 403 of SM than on the variations of SG in beech: The R^2 of the linear regression between MOE and
 404 SG is only 0.26, while that of the regression between SG and SM is 0.78.

405 Correlation between RW and both SG and SM were very highly significant, with a positive value
 406 for SG (density is higher for large ring width) and a negative one for SM (specific modulus is
 407 lower for large rings). These results were partly due to covariations along the juvenility gradient
 408 that will be analysed in the next paragraph.

409 There was no significant correlation between SG and SM . This can be interpreted as a global
 410 independence in mechanical adaptation of the two parameters: SG reflects the quantity of cell
 411 wall (cell wall relative thickness), and SM its quality (microfibril angle), and these two
 412 parameters can be regulated independently.

413 4.3. Major importance of within-tree variations in properties

414 The importance of within-tree variations can be deduced from Table 3. Within-tree variation is
 415 the share of variance that is not captured by higher scale factors ("Plot" and "Tree"), so it is the
 416 sum of the "Core" factor, the "Orientation" factor and the "Error" factor (this last factor is not
 417 shown in Table 3, it is the differences between 100% and the sum of all displayed effects).
 418 Within-tree variations represented approximately 65% of variance for RW , 50% for SG and
 419 55% for SM .

420 The within-tree variations of properties originated from both peripheral variations and radial
 421 variations. Peripheral variations were reflected by the frequent occurrence of non-symmetric
 422 diametral profiles: for all 3 studied variables, most trees presented important differences
 423 between North and South profiles (Table 11, Fig. 5). Radial variations were reflected by the
 424 importance of the "Core" effect (Table 3), and by the non-zero values of slope and curvature
 425 parameters of most radial profiles (section 3.3.3).

426 4.4. The frequency of non-symmetric diametral profiles reveals the importance of the gravity 427 constraint and posture control mechanisms.

428 Most diametral profiles were asymmetric (Table 11) despite the fact that the "Orientation"
 429 factor had no systematic effect on wood properties (Table 3). This is because the tree
 430 asymmetry, if any, due to stem inclination (linked to the effect of wind or soil instability),
 431 asymmetric crown (linked to the adaptation to light availability), and/or prevailing winds, had
 432 only few reasons to be North/South. It is thus not surprising to find insignificant systematic
 433 effect of orientation in the sampling.

434 The tree asymmetry induces mechanical constraints in relation to how trees manage gravity.
 435 The growth of an asymmetric tree induces a rapid increase of the bending moment applied by
 436 gravity of the trunk, which tends to bend the tree downwards. To counteract this effect, a
 437 gravitropic reaction is needed (Alméras & Fournier 2009, Gril et al 2017). This reaction is
 438 achieved by a dissymmetry of growth forces on the two sides of the inclined stem: a higher
 439 tensile force on the upper side for hardwood species like beech. The tensile force produced on
 440 each side of the tree during wood maturation process is proportional to ring width, to specific
 441 gravity, to specific modulus and to maturation strain (Alméras et al 2005, Thibaut et Gril 2021).
 442 Increasing the force on the upper side means increasing the local value of any combination of
 443 these four factors, together with decreasing it on the lower side. This leads to asymmetric
 444 profiles of wood properties.

445 Reaction wood occurrence is the typical expression of strong gravitropic reactions, influencing
 446 the asymmetry in *RW*, *SG*, *SM*, and the asymmetry in maturation strains, that results from
 447 macromolecular processes occurring during secondary wall formation (Alméras and Clair 2016,
 448 Thibaut and Gril 2021). However, for small inclination angles (e.g. coppice stems) the
 449 production of tension wood is not necessary: the difference in maturation strain between normal
 450 wood located on lower and upper sides of the growing stem can be high enough to enable
 451 posture control (Thibaut and Gril 2021). Tension wood occurrence is rather easy to detect by
 452 visual observation but variations of maturation strain in normal wood are, until now, impossible
 453 to estimate except by in-situ measurements of residual stress at stem periphery (Jullien et al
 454 2013).

455 ***4.5. Diversity in radial profiles suggests that “adaptive juvenility” is prevailing over***
 456 ***“ontogenetic juvenility”***

457 Most of the papers on mechanical properties of juvenile wood refer to plantation, either of
 458 softwoods or hardwoods (Bensend and Senft 1986, Kojima et al 2009, Bhat et al 2001, Bao et
 459 al 2001). For softwoods, the “typical radial pattern” (TRP) for mechanical factors (Lachenbruch
 460 et al 2011) is always the case for fast-growing plantations. It is characterized by a decrease of
 461 *RW* and an increase of both *SG* and *SM* from pith to bark until a juvenile core limit.

462 For hardwoods this is not always the case, and *SG* can be more or less flat (Bendtsen & Senft
 463 1986), while *SM* can be high near the pith and decrease for trees growing in dense tropical forest
 464 (Mc Lean et al 2011). On *Bagassa guianensis*, a fast-growing secondary forest tree of French
 465 Guiana, Bossu et al (2018) observed a general TRP for microfibril angle and density, very clear
 466 for density (varying from 0.3 to 0.9 along the radius). Plourde et al (2015) studied radial density
 467 variation for 91 tropical species (Costa Rica): 42 over 74 had a net variation in density, 37 with
 468 increasing TRP type and 5 with decreasing “anti TRP” type. Secondary forest species (open
 469 environment in juvenile phase) had the clearest positive variations (low juvenile density),
 470 primary forest species (closed environment in juvenile phase) were the only anti-TRP species,
 471 with a lower variation (high internal density). Beech in this study is rather similar to trees from
 472 the primary forest with an internal density above 0.5 and a decreasing profile. Longuetaud et al
 473 (2017) studied 3 broadleaved trees: oak, beech, sycamore maple and two softwoods: fir and
 474 Douglas fir. The TRP model was valid for maple and Douglas fir, but for oak the density
 475 decreased instead of increasing. For fir and beech, the profile was bell-shaped (beech) or U-
 476 shaped (fir) with slight variations. Purba et al (2021) studied density and microfibril angle in
 477 oak and beech for dominated, small-diameter trees harvested during thinning. Overall, the TRP
 478 applied to both cases.

479 For beech, we have measured parameters describing the juvenility of old trees in managed forest
 480 with a rather large variety of plot environment and management practices. The median profiles

481 for each mechanical parameter (beech radial pattern in Fig. 8) was similar to some hardwood
 482 description in literature for *SG*.

483 In Europe, old growth beech forests can have different forest origins (Ciancio et al 2006): even-
 484 aged (France or Germany) or uneven-aged high forest (Switzerland), coppicing with standards
 485 (France) or conversion of coppice forest into high forest (Germany, France) but are very rarely
 486 the result of plantations (none in the 9 plots). *Fagus* is known for its shade tolerance and ability
 487 to grow very slowly under a closed canopy (Collet et al 2011) and most forest plots undergo
 488 more or less severe thinning before final harvesting, which leads to an increase of *RW* due to
 489 better access to light (Noyer et al 2017). This is reflected in the different mean *RW* radial
 490 patterns for the 9 plots (Fig. 9). For plots 7 (uneven-aged high forest) and 9 (middle forest
 491 transformed in even-aged high forest), a clear increase of *RW* was observed in the young ages,
 492 while the reverse and classical pattern was true for plots 1, 4, 5 and 6 (all even-aged forest in
 493 flat area). Similar results were found on younger beech trees (Bouriaud et al 2004). The low
 494 *RW* values for plots 2 and 8 (even aged, steep terrain) could be expected in a mountainous area,
 495 and the observed increase of *RW* after an initial decrease possibly due to thinning operations.

496 Probably due to the large diversity of plot management, the beech median radial pattern did not
 497 apply to many trees of the sampling. As a result, there was no “universal” juvenile trend for any
 498 of the 3 parameters for all trees. Combining global trend (flat, up, down) and curvature (straight,
 499 convex, concave), there was a large variety of profile occurrence in each of the 9 cross-types
 500 for each plot. This was similar to the large variety of radial patterns found in most of the studied
 501 hardwoods, contrary to the “universal” pattern for fibre (or tracheid length). Even if there is a
 502 part of ontogenetic influence in the juvenile patterns for *RW*, *SG* and *SM*, the results suggest
 503 the main influence of plastic adaptation to mechanical constraints in the tree growth (adaptive
 504 juvenility).

505 **5. Conclusion**

506 Based on the analysis of variance and the analysis of radial profiles, we showed that, for the 3
 507 studied variables (*RW*, *SG* and *SM*) within-tree variations represented the largest part of
 508 variance. These within-tree variations occurred both through peripheral variations (asymmetry
 509 between North and South profiles) and through radial variations (dependence of the property
 510 on the distance to the pith). The patterns of radial variations of the 3 variables were diverse,
 511 including increasing, flat and decreasing patterns, as well as convex, straight and concave
 512 patterns. Overall, these observations demonstrate that juvenile wood in Beech did not obey to
 513 systematic variations (ontogenetic juvenility), but was the result of plastic adaptation (adaptive
 514 juvenility) to variable individual trajectories and associated mechanical constraints.

515 **Acknowledgments**

516 The data were obtained thanks to the support of European Commission through the FAIR-
 517 project CT 98-3606, coordinated by Prof. Gero Becker. The financial support of CNRS K. C.
 518 Wong post-doctoral program and China Scholarship Council must be also acknowledged.

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