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# 1 Relationships between growth stress and wood properties in Poplar

## 2 I-69 (*Populus deltoides* Bartr. cv. "Lux" ex I-69/55)

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7 Running title: **Growth stress versus Poplar wood properties**

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13  
14 **Abstract** - Six inclined poplar I-69 (*Populus deltoids* cv. I-69/55) trees were collected for studying the influence  
15 of growth stress level on wood properties. Growth stress indicator (GSI) was measured at 8 positions around the  
16 periphery of each trunk at breast height and corresponding wood samples were obtained. Wood anatomical,  
17 physico-mechanical and chemical characteristics were measured including cell diameter, fibre length, double  
18 wall thickness *excluding gelatinous layer*, lumen diameter *after gelatinous layer removal*, proportion of wood  
19 tissues, basic density, FSP, MOE, compressive strength, shrinkage and chemical composition. Each property  
20 was regarded in relation to the growth stress level to be discussed.

21 **Key-words:** *populus deltoids* cv. I-69/55, poplar, tension wood, growth stress, wood property

## 22 23 1. INTRODUCTION

24 Trees control the shape and orientation of the main trunk or the predetermined angle of a branch,  
25 search for light or react to stronger loading, such as a strong dominant wind, through the generation of  
26 growth stresses during the process of wood formation. This is usually obtained by production of  
27 so-called reaction wood. While gymnosperms produce compression wood in the lower face of stems,  
28 angiosperms produce tension wood generating high tensile stresses on their upper face [23, 55].

29 We will focus here on poplar tension wood, exhibiting important changes of the cell-wall structure  
30 compared to normal wood [42]. In many species such as beech, poplar, oak or chestnut, tension wood  
31 contains fibres with a special morphology and chemical composition due to the development of the  
32 so-called gelatinous layer (G-layer) [42] replacing S<sub>3</sub> and a part or the whole of the S<sub>2</sub> layer [48]. The  
33 G-layer is known to have high cellulose content with a high degree of crystallinity [15, 39] and to  
34 contain microfibrils oriented along the axis of the cell [25].

35 The distinctive anatomical characteristics and chemical composition of tension wood directly cause  
36 the changes of physical and mechanical properties, which refer to technological problems, such as  
37 distortion of solid wood during sawing due to the release of high longitudinal growth stresses [7, 35,  
38 40, 59], defects during drying due to its high longitudinal shrinkage [4, 19, 28, 42], severe woolly  
39 surface during sawing and rotary cutting [43] due to G-fibres, as well as bad quality of paper made of

40 G-fibres [44].  
41 Poplar, an important fast-growing plantation tree for plywood, solid wood and paper manufacture, is  
42 well known to be very sensitive to the stimuli responsible for tension wood formation [27]. Studies at  
43 the microscopic level evidenced gradual changes of anatomical features from normal wood to severe  
44 tension wood, with corresponding variations of macroscopic behaviour [20, 21]. The aim of this work  
45 was to study the gradual changes of poplar I-69 (*Populus deltoids* cv. I-69/55) properties resulting  
46 from tension wood severity as quantified by growth strain assessment.

## 47 **2. MATERIALS AND METHODS**

48 Six poplar trees (*Populus deltoids* cv. I-69/55) were collected in 2004 in the Islet beach of Yangtze  
49 River in Anqing city, Anhui province, China. The trees were planted in 1986. Their characteristics are  
50 given in Table 1. Anatomical and chemical data were obtained in China, physical and mechanical data  
51 in France.

### 52 **2.1. Growth Stress Indicator (GSI)**

53 The “single hole” drilling method developed by CIRAD [24] was used to estimate the longitudinal  
54 growth stress close to trunk surface on the standing tree. The value in  $\mu\text{m}$ , termed Growth Stress  
55 Indicator (GSI), relates to the longitudinal growth stress at the trunk periphery by a proportional factor  
56 depending on the mechanical anisotropy of the species. Hence GSI value is a good indicator of relative  
57 longitudinal growth stress magnitude within trees of the same species [12].

58 GSI measurements were performed on the 6 standing trees at 8 points around the circumference of  
59 trunks at breast height. The points on the top upper sides of leaning trunks were noted as position 1  
60 and then the other 7 points were positioned every  $45^\circ$  on circumference and numbered orderly from 2  
61 to 8, so the lowest side was 5 (Fig. 1).

62 After GSI measurements, trees were felled and 8 directions corresponding to GSI measurements  
63 positions were marked on the trunk surfaces for the further studies. Moreover, transverse section  
64 corresponding to each position was prepared for visual assessment of G-fibre occurrence by  
65 microscopic observation.

### 66 **2.2. Anatomical properties**

67 For each tree, close to positions No.1 (upper side), No. 3 and 7 (lateral side) and No.5 (lower side),  
68 two samples each were taken (Fig. 1). One was used for preparing a transverse section, the other for  
69 measurements of isolated elements after maceration. Transverse sections ( $20\ \mu\text{m}$  thick) were obtained  
70 with a microtome with disposable blades, and double stained with safranin and Fast Green. Safranin  
71 stains all tissues and Fast Green replaces safranin where purely cellulosic G layers of tension wood  
72 are present. This double staining technique is used to detect and confirm tension wood occurrence  
73 (Fig. 2).

74 Sections were observed with an optical microscope linked to an image analysis system equipped with  
75 a colour CCTV camera (WV-CP460/CH, Panasonic). The sectioning method used caused the

76 detachment and swelling of G-layer [11, 14, 21], rendering impossible any correct measurement of the  
 77 real G-layer thickness and the real lumen diameter of G-fibres. Therefore, in this study only the double  
 78 cell wall thickness excluding G-layer, the lumen diameter after G-layer removal and cell diameter  
 79 were measured. 30 measurements per sample were done. The proportion of vessel and ray was  
 80 measured by image analysis, allowing the calculation of the fibre proportion.  
 81 The other sample was macerated with mixed solution of half 10% nitric acid and half 10% chromic  
 82 acid. After maceration the measurement of fibre length was undertaken with a projection microscope.

### 83 **2.3. Physical and mechanical properties**

#### 84 **2.3.1. Basic density, fibre saturation point (FSP) and shrinkage**

85 Samples, 20mm in radial (R), 20mm in tangential (T) and 50mm in longitudinal (L) directions, were  
 86 cut in the vicinity of GSI measurement positions (Fig. 1). Sample length in R, T and L directions were  
 87 measured with a digital micrometer accurate to 0.001mm. Following initial green weight and  
 88 dimensions measurements, all samples were placed in three successive conditioning chambers set to  
 89 provide nominal equilibrium moisture content (EMC) of 17% (30°C, 80% RH), 12% (20°C, 65%  
 90 R.H.) and 8% (20°C, 30% R.H.), respectively, then in an oven at 103°C to obtain an EMC of 0%. At  
 91 each stage, after constant weight was reached, samples were weighted and measured. Basic density  
 92 (BD, g/cm<sup>3</sup>) was calculated as the ratio between the oven-dry weight and the saturated volume. FSP  
 93 was obtained by calculating the intercept of shrinkage variation with moisture content change. Total T,  
 94 R and L shrinkage, from saturated to oven-dry, will be analyzed in this study.

#### 95 **2.3.2. MOE, specific MOE and compressive strength**

96 Samples (20mm in R, 20mm in T and 300mm in L direction) were taken in the vicinity of GSI  
 97 measurement positions (Fig. 1). Samples were kept in a controlled chamber with temperature of 20°C,  
 98 humidity of 65% until the moisture content reaches 12%. MOE and specific MOE were measured  
 99 using free vibration and Fast Fourier Transform analysis (FFT). After dimensions and weight  
 100 measurement, the wood sample was placed on two rubbers under a microphone that registers the noise  
 101 accompanying the bending vibrations resulting from a small kick on one end with a little iron stick.  
 102 The values were interpreted according to Bordonné method [6], yielding the modulus of elasticity  
 103 (MOE), density as well as specific MOE defined as MOE / density. As the samples were long, it was  
 104 difficult to avoid some defects like knot, crack and bend, finally only 21 samples were used for MOE  
 105 measurement.

106 The test of compressive strength parallel to grain was carried out following standard NF B 51-007 [1]  
 107 (conform to the international standard ISO 3787). Samples 20mm (R), 20mm (T) and 60mm (L) were  
 108 extracted from the samples used for MOE measurements (Fig. 1). Before measuring the compressive  
 109 strength, the precise sample dimensions were measured. After the test the EMC of the sample during  
 110 test was measured. Compressive strength parallel to grain at 12% EMC  $\sigma_{12}$  (in MPa) was estimated  
 111 using a correction valid for an EMC ranging between 7% and 18% [1]:

112 where  $\sigma_w$  (MPa) is the compressive strength at the EMC of the test,  $P_{max}$  (N) the maximum force

$$\sigma_{12} = \sigma_w \times [1 + 0.04 \times (EMC - 12)] \dots \dots \dots (2)$$

113 applied, a and b the sample dimensions in R and T directions, respectively. This correction was

$$\sigma_w = \frac{P_{max}}{a \times b} \dots \dots \dots (1)$$

114 required as the experiment was performed outside the conditioning room.

## 115 **2.4. Chemical composition**

116 Disc used for chemical composition measurements was shown in Figure 1. Wood powder of 42-60  
117 mesh was prepared from samples got near the positions 1, 3, 5 and 7. The lignin content was  
118 determined by the Klason method [8, 31]. Cellulose content was determined by HNO<sub>3</sub>-ethanol method.  
119 Holocellulose content was determined by chlorite method and hemicellulose content was calculated as  
120 the difference of holocellulose content and cellulose content.

## 121 **3. RESULTS AND DISCUSSION**

### 122 **3.1. Growth Stress distribution around the trunk**

123 GSI value was used in this study to estimate longitudinal growth stress on the surface of standing  
124 trunk. In poplar, growth stress is a good indicator of tension wood “severity”, i.e. G-fibre proportion  
125 and G-layer thickness in species which can produce G-fibres [20, 21].

126 Figure 3 shows the GSI variation along trunk periphery at breast height of the 6 trees. In all 6 trees, the  
127 upper side values (position 1, Fig. 1) placed at 180° on the graph, were significantly higher than those  
128 of the lower sides (position 5, Fig. 1), corresponding here to 0° or 360°. Other GSI values mostly  
129 distributed between those of upper and lower sides. The change of upper side GSI value among 6 trees  
130 did not show a significant trend with the lean angle. Except for position 180°, 135° and 225°, the GSI  
131 value varied very little, excluding the point 270° of tree PC2 which was abnormally high. The  
132 transverse section corresponding to each GSI measurement position was checked with microscopy,  
133 moreover, the visual assessment of the transverse sections of each position showed that all high GSI  
134 values were associated with a high proportion of G-fibres, except for that abnormal value where few  
135 G-fibres were observed. So in the further statistical analysis of this study, this value will be replaced  
136 by the mean value (170 µm) of the adjacent two values.

### 137 **3.2. Growth stress / anatomical properties**

138 Dadswell and Wardrop [19] have stated that in the fresh state, before any drying has occurred, tension  
139 wood fibres appeared to be in cross-section of exactly the same diameter as normal wood fibres. But  
140 Chow [9] reported that tension wood fibres were narrower than those of normal wood in beech on  
141 isolated fibres. Similarly Wardrop [55] and Jourez et al. [27] reported that in poplar (*Populus alba* and  
142 *Populus euramericana* cv ‘Ghoy’, respectively), in the radial direction, the G-fibres were relatively  
143 narrower than the opposite wood fibres observed on cross section. Onaka [42] and Scurfield and  
144 Wardrop [51] reported a larger tangential diameter of tension wood fibre in some species. In this study  
145 negative correlation ( $r = -0.462$ , significant at 1% level) was found between cell diameter (no attention  
146 was paid on the radial or tangential direction) and GSI value (Fig. 4a). As high GSI values were  
147 observed on the upper sides of trunks, where high proportion of tension wood is expected, and low  
148 ones on lower sides containing opposite wood (Fig. 3), this result is more or less in accordance with

149 some of the previous ones. The mean cell diameter and standard deviation was  $19.8 \pm 3.9 \mu\text{m}$ .

150 The average length of fibres and standard deviation around the periphery of trunk at breast high in this  
151 study was  $1347 \pm 198 \mu\text{m}$ . There is no agreement in the literatures regarding the length of tension  
152 wood fibres in comparison that of normal fibres. Compared to normal fibres tension wood fibres were  
153 reported sometimes as being longer [9, 27, 42], sometimes as being shorter (Giovanmi 1953 [cited in  
154 Zimmermann [61]]) and sometimes as no marked difference [19, 51]. In this study a very significant  
155 positive correlation ( $r = 0.751$ , significant at 1% level) was found between fibre length and GSI values  
156 (Fig. 4b). It indicates that with the increase of growth stress, i.e. from normal wood to mild and severe  
157 tension wood, fibres become longer and longer.

158 The formation of tension wood is usually associated with the occurrence of eccentricity, with wider  
159 ring at the upper side of stem where tension wood is produced [2]. Eccentric radial growth either  
160 results from an increased duration of division or from a higher division rate in the cambium [54, 55].  
161 As in normal wood formation the fibre length is inversely related to the growth rate [22, 30, 33]. If  
162 eccentricity of tension wood arise from an increased division rate in the cambium, then the tension  
163 wood fibres would be expected to be shorter [54, 55]. Thus for the case in this study, eccentricity of  
164 tension was suspected to be the result of increased duration of division. Furthermore, it has been  
165 evidenced that the duration of cambial activity is greater on the side of stems forming tension wood  
166 (Wardrop [54]; Priestley and Tong 1927 [cited in Wardrop [55]]).

167 In this study, the double cell wall thickness excluding G-layer was measured for samples with different  
168 growth stress levels and a significant negative correlation ( $r = -0.812$ , significant at 1% level) was  
169 found between them (Fig. 4c). It means from normal wood to mild and severe tension wood the  
170 thickness of cell wall excluding G-layer decreased. This result was also confirmed in a recent study  
171 [20] who reported that with the increase of growth stress the other cell wall layers (all cell wall layers  
172 excepting G-layer) thickness decreased while G-layer became thicker.

173 A very slight and not significant positive correlation existed in this study between GSI value and the  
174 diameter of cell lumen, after G-layer removal when present (Fig. 4d). As described above the cell  
175 diameter decreased with an increase of GSI. Since, on the other hand, we shown [20] that the G-layer  
176 thickness increased with an increase of growth stress level, the real cell lumen diameter (G-layer not  
177 removed) should be negatively related with GSI. And when the G-layer is removed, the lumen should  
178 become bigger with the increase of growth stress level. The unapparent relationship found here could  
179 be partially explained by the decreased cell diameter related to the increased growth stress level.

180 Many researchers have reported the comparison of vessel proportion between tension and normal  
181 wood or between upper-side wood and lower-side wood, but not on vessel proportion variation along  
182 increased growth stress level. This study gave a very significant negative correlation ( $r = -0.786$ ,  
183 significant at 1% level) between vessel proportion and GSI value (Fig. 5a). In the previous studies,  
184 there was a general agreement that tension wood contained lower vessel proportion than normal wood  
185 [9, 27, 42, 47, 55], except for Kaeiser and Boyce [29] and Kroll et al. [34] who reported opposite  
186 results. The decreased vessel proportion in tension wood could partially explained by the auxin  
187 concentration. According to Aloni [3], the rate of vessel differentiation is determined by the amount of  
188 auxin obtained by the differentiating cell, while tension wood forms in the region with less IAA  
189 concentration [17, 38].

190 No apparent relationship was found between ray proportion and GSI (Fig. 5b). Onaka [42] and Jourez

191 et al. [27] also reported that ray proportion did not vary with wood type, normal or tension wood. A  
192 different result was reported by Chow [9] who observed that tension wood contained a larger  
193 proportion of ray but inconclusive.

194 Considering the results discussed above it is easy to get the conclusion that fibre proportion increased  
195 with increased GSI value ( $r = 0.429$ , significant at 5% level, Fig. 5c). This result is in accordance with  
196 Fang et al. [21]. Furthermore, they reported that with the increased growth stress level G-fibre  
197 proportion increased. These results can be used to explain the increased wood basic density, see  
198 below.

### 199 **3.3. Growth stress / physico-mechanical properties**

200 The average basic density and standard deviation of outmost samples at breast height of poplar I-19  
201 (*Populus deltoides* Bartr.cv. "Lux" ex I-69/55) in this study were  $0.39 \pm 0.02 \text{g/cm}^3$ .

202 Chow [9], Lenz [36] Panshin and de Zeeuw [43] and Jourez et al. [28] compared tension wood and  
203 normal wood without considering the severity of tension wood and reported a higher basic density of  
204 tension wood. Washusen et al. [57] stated a positive correlation between microdensity and tension  
205 wood fibre percentage. Similar results were also reported by Kroll et al. [34] and Clair et al [12], while  
206 Arganbright et al. [4] and Lowell and Krahmer[37] did not observe a significant effect of lean or side  
207 on wood density. A lower density in tension wood was also reported in *Tilia* [43]. Basic density of  
208 samples located at different growth stress levels were compared in this study and a significant but  
209 weak positive correlation (Pearson  $r = 0.326$ , significant at 5% level) between them was found (Fig.  
210 6a). As with increased growth stress level decreased vessel proportion and increased fibre proportion  
211 were found (Fig. 5c), and furthermore increased G-fibre proportion and G-layer thickness [21], the  
212 increased basic density with increased growth stress level can be easily explained.

213 Mean and standard deviation of FSP were  $30.3 \pm 1.4\%$ . A significant but weak negative correlation  
214 was found between FSP and GSI value (Fig. 6b). This could be explained by a difference in cell wall  
215 hygroscopicity between normal and tension wood. The hygroscopicity is depended on the chemical  
216 compositions of cell wall, cellulose crystallinity, cell wall density, extractives contents. Among  
217 chemical components in cell walls, of the three major materials (lignin, hemicelluloses and cellulose)  
218 lignin has the lowest affinity for water and hemicelluloses the highest. The affinity of cellulose for  
219 water is between these two [10]. A lower hemicelluloses content in tension wood was found in this  
220 study, see below, and also reported by Furuya et al. [26]. Furthermore, in the tension wood the G-layer  
221 has very high crystallinity [15, 39] which leading to low affinity for water.

222 A significant positive correlation (Pearson  $r = 0.671$ , significant at 1% level) was found between MOE  
223 and GSI value (Fig. 7a). Similar results were reported by Coutand et al. [16] that the Young's modulus  
224 of tension wood, green or dry, is higher than that of normal wood with the three points bending test  
225 method. While some other authors did not find any relation with growth stress level or with G-fibre  
226 percentage [9, 50]. Increased MOE with increased GSI value could be explained to some extend by the  
227 increased density (Fig. 6) [16], but it still increased with the increase of GSI value even after  
228 normalising for density (i.e. specific MOE) (Fig. 7b). This could be explained by the difference of  
229 microfibrillar angle between  $S_2$  and G-layers, as has been observed and modelled for softwoods [32,  
230 49], but also by differences in chemical composition or other structural features. A comprehensive  
231 model relating the macroscopic behaviour in L direction to the parameters of cell wall composition

232 (e.g., [60]) would be required to analyses these relationships more deeply.  
233 With the increase of GSI value, a decreased compressive strength was found here (Pearson  $r = -0.466$ ,  
234 significant at 1% level) (Fig. 8a). Similar relation was reported by Ruelle [46] on 3 tropical species.  
235 The lower compressive strength in tension wood could be explained by the lower lignin content (see  
236 below), longer and thinner fibre (see above), as suggested by Frey-Wyssling (1936, cited in Wardrop  
237 and Dadswell [56]) that when a compressive stress is applied on a fibre the micelles tend to buckle  
238 because of their great length as compared with their lateral dimensions. Thus, in an unligified fibre  
239 similar to that of tension wood, buckling could occur easily, giving rise to the formation of slip planes  
240 and minute compression failures. However, in a lignified fibre, lignin, packed between the micelles,  
241 resists the tendency of the micelles to buckle. This could explain the common occurrence of slip  
242 planes and minute compression failures in the cell walls of tension wood observed by Wardrop and  
243 Dadswell [18, 19, 56].  
244 Specific compressive strength was also presented (Fig. 8b). It is easy to understand the negative  
245 correlation with GSI value because of the decreased compressive strength and increased density.  
246 Similar result was reported by Onaka [42].  
247 There is no bifurcation on the higher L shrinkage of tension wood than that of normal wood [12, 19,  
248 28, 56, 60]. This was further confirmed in this study by the significant positive correlation between L  
249 shrinkage and GSI value (Fig. 9a). High longitudinal shrinkage in tension wood can be explain by the  
250 evidence of the longitudinal shrinkage in G-layer itself [13]. But the L shrinkage of G-layer remains  
251 paradoxical and its mechanism is still unknown.  
252 Few studies have been done on the transverse shrinkage of tension wood and the results are  
253 contradictory. Washusen and Ilic [58], Clair et al. [12] reported a higher transverse shrinkage in  
254 tension wood, while Barefoot [5], Arganbright et al. [4] and Fang et al. [20] observed a lower one. In  
255 this study T and R shrinkages were found strongly and weakly, respectively, correlated negatively with  
256 GSI value and both correlations were significant (Fig. 9b, c). This result was completely accordant  
257 with the one observed on 20- $\mu\text{m}$ -thick sections of poplar in our previous study where T and R  
258 shrinkages at both mesoscopic (section) and microscopic levels were discussed and an explanation for  
259 the lower transverse shrinkage of tension wood was given [20]. That explanation could be used here  
260 even though massive wood, not section, was studied.

### 261 **3.4. Chemical composition**

262 A positive correlation of cellulose content and negative ones of lignin and hemicellulose contents with  
263 GSI value were found in this study (Fig. 10). It should be mentioned however, the samples for  
264 chemical composition measurements were collected at relative big districts near GSI measurement  
265 positions (Fig. 1). Furthermore, at the low scale of GSI values all the three contents varied a lot (Fig.  
266 10). Therefore, the obtained correlation should be considered with some caution.  
267 The distribution of cellulose, lignin and hemicellulose content around trunk of different trees is  
268 presented in Figure 11. The cellulose content (Fig. 11a) rose to a maximum in the upper sides of all 6  
269 trees where highest GSI values were measured (Fig. 3) and paired (by different trees) samples t-test  
270 showed it was significant higher in the upper side than than in the other sides, but no significant  
271 difference existed between lower and lateral sides (Tab. II). A contrary result was found for the lignin  
272 content (Fig. 11b). 4 out of 6 trees showed the lowest hemicellulose content (Fig. 11c) located in the  
273 upper sides but the differences among different sides were not significant after paired samples t-test.



274 Tension wood is generally described as containing a high proportion of cellulose and being less  
275 lignified than normal wood [26, 45, 53]. Our results showed that the studied species of poplar in  
276 general has the similar chemical properties. Similar results were also reported by previous studies on  
277 different species [9, 41, 52, 56].

## 278 4. CONCLUSION

279 In this study a quantitative assessment of growth stress level was used to characterise the wood on 6  
280 inclined poplar I-69 (*Populus deltoids* cv. I-69/55) trees at breast height. Following conclusions are  
281 drawn:

- 282 – The highest GSI values were located in the upper sides of the inclined trunks. Other GSI values  
283 mostly distributed between those of upper and lower sides.
- 284 – Negative correlation was found between cell diameter and GSI value. With the increase of growth  
285 stress, i.e. from normal wood to mild and severe tension wood, fibres become longer and longer  
286 and the thickness of cell wall excluding G-layer decreased. A very significant negative correlation  
287 between vessel proportion and GSI value. No apparent relationship was found between ray  
288 proportion and GSI. Fibre proportion increased with increased GSI value.
- 289 – GSI was significantly but weakly correlated positively with basic density and negatively with FSP.  
290 With the increase of GSI value, MOE increased, compressive strength decreased, L shrinkage  
291 increased and T and R shrinkage decreased.
- 292 – The cellulose content rose to a maximum in the upper sides where highest GSI values were  
293 measured. A contrary result was found for the lignin content. 4 out of 6 trees showed the lowest  
294 hemicellulose content located in the upper sides but the differences among different sides were not  
295 significant.

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428

## 429 FIGURES LEGENDS

430 **Figure 1.** Schematic localization of measurement positions.

431 **Figure 2.** Cross sections of normal (left) and tension wood (right) where G-layers appear green and other layers  
432 appear red after double staining. Scale bar = 50µm.

433 **Figure 3.** GSI variation along trunk periphery at breast height. The upper sides correspond to 180°. Different  
434 lines indicate different trees.

435 **Figure 4.** Relationship between GSI (µm) and (a) cell diameter, (b) fibre length, (c) double wall thickness  
436 *excluding G-layer*, (d) lumen diameter *after G-layer removal*. Error bars shows 95% confidence intervals of  
437 mean.

438 **Figure 5.** Relationships between GSI value (µm) and proportion (%) of wood tissues: (a) vessels; (b)  
439 parenchyma rays; (c) fibres.

440 **Figure 6.** Relationships between GSI (µm) and (a) basic density (g/cm<sup>3</sup>) and (b) FSP (%).

441 **Figure 7.** Relationships of (a) MOE (GPa) and (b) specific MOE (GPa·cm<sup>3</sup>·g<sup>-1</sup>) with GSI (µm).

442 **Figure 8.** Relationships of (a) compressive strength (MPa) and (b) specific compressive strength (MPa·cm<sup>3</sup>·g<sup>-1</sup>)  
443 with GSI (µm).

444 **Figure 9.** Relationships between GSI (µm) and shrinkage (%) of (a) L, (b) T and (c) R.

445 **Figure 10.** Relationships between GSI value (µm) and chemical compositions: (a) cellulose content (%), (b)  
446 lignin content (%) and (c) hemicellulose content (%).

447 **Figure 11.** The distribution of (a) cellulose, (b) lignin and (c) hemicellulose content around trunk at breast height  
448 of different trees. The upper sides locate at 180°. <sup>♠</sup>: PC1; <sup>♣</sup>: PC2; <sup>♢</sup>: PC3; <sup>♣</sup>: PC4; <sup>♠</sup>: PC5; <sup>♠</sup>: PC6.

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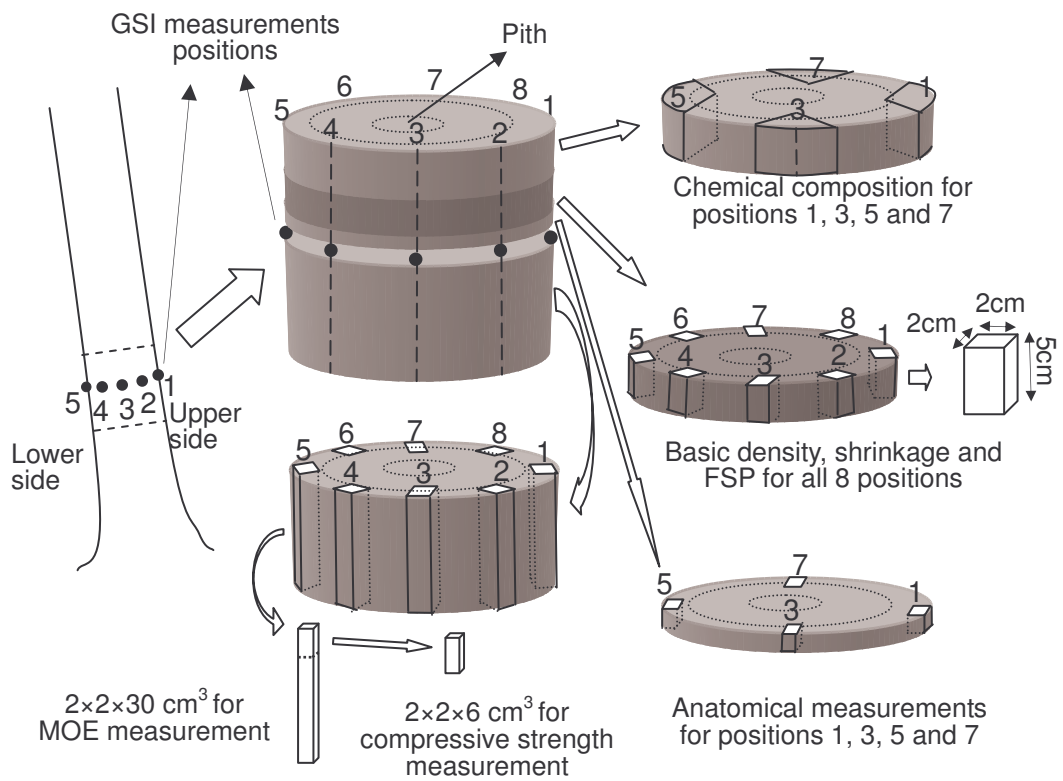
450 **TABLES**

451 **Table I.** Information on the 6 studied trees. DBH means diameter at breast height.

Tree	PC1	PC2	PC3	PC4	PC5	PC6
Lean angle from vertical position ( °)	15.1	17.0	12.2	12.7	18.2	17.2
Height (m)	23.5	23.5	23.6	23.6	23.5	23.5
DBH in lean direction (cm)	29.0	32.0	31.0	28.0	25.5	29.0
DBH in lateral direction (cm)	27.0	30.0	28.0	25.0	25.0	28.5
DBH, average (cm)	28.0	31.0	29.5	26.5	25.3	28.8

452  
 453 **Table II.** Paired (by different trees) samples t-test of chemical compositions differences among upper, lower and  
 454 lateral side. Lateral side value was the mean of position 3 and 7 (Fig. 1). NS = not significant, \* = significant at  
 455 0.05 level, \*\* = significant at 1% level.

	Upper-Lower	Upper-Lateral	Lateral-Lower
Cellulose (%)	*	**	NS
Lignin (%)	*	*	NS
Hemicellulose (%)	NS	NS	NS

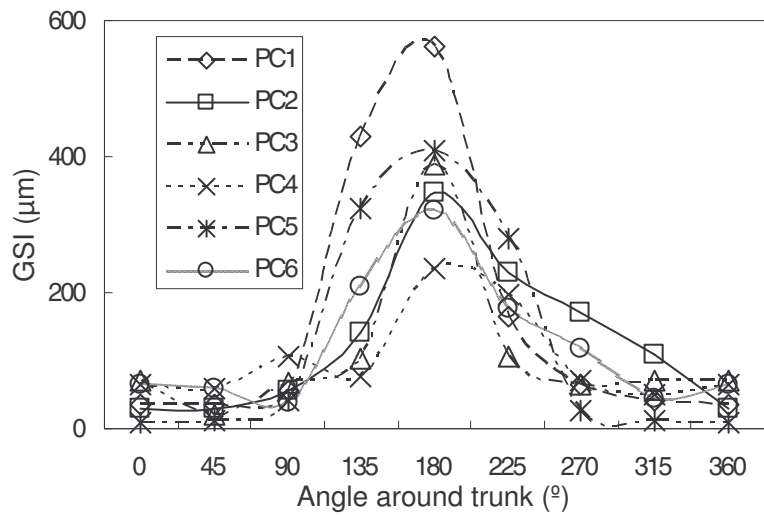


457 **Fig. 1.**

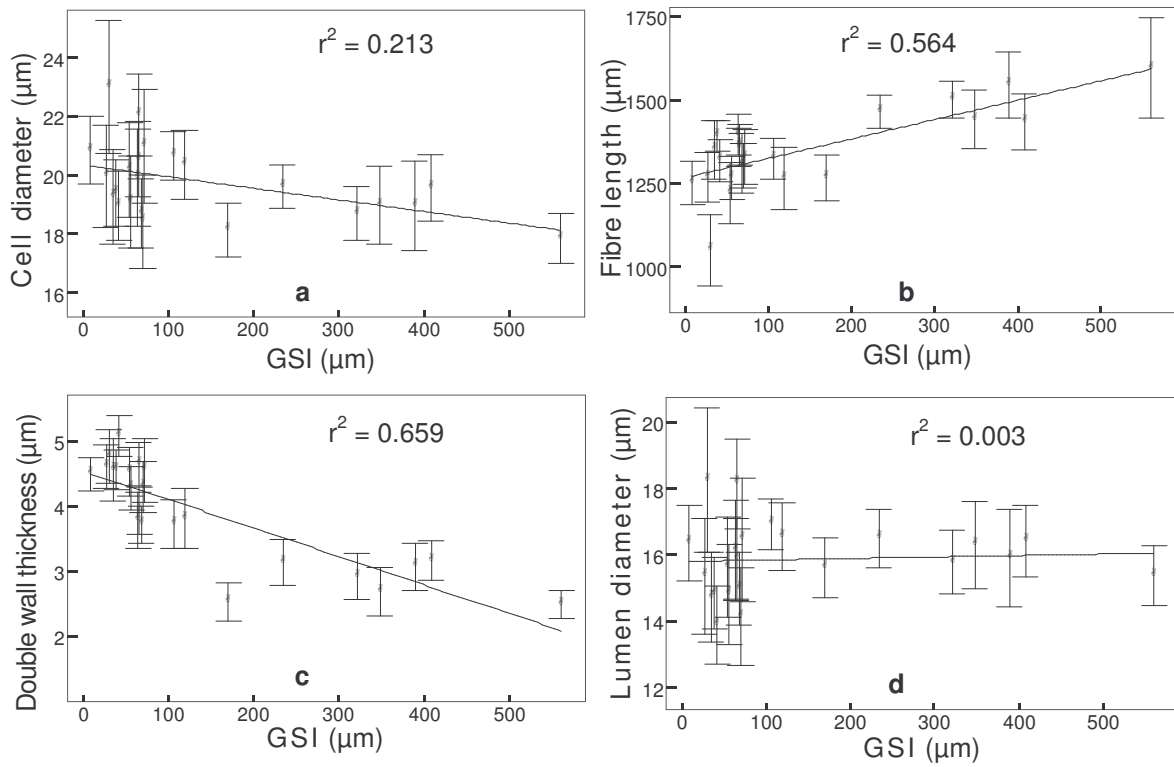


458 **Fig. 2.**

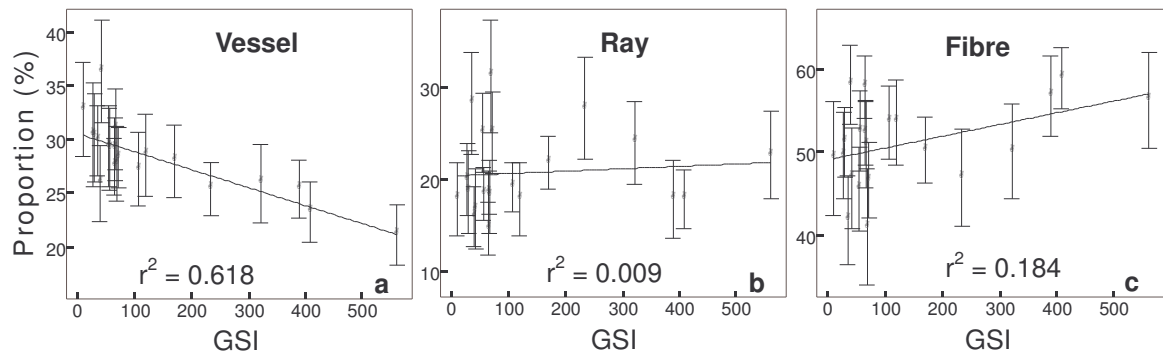
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466 **Fig. 3.**  
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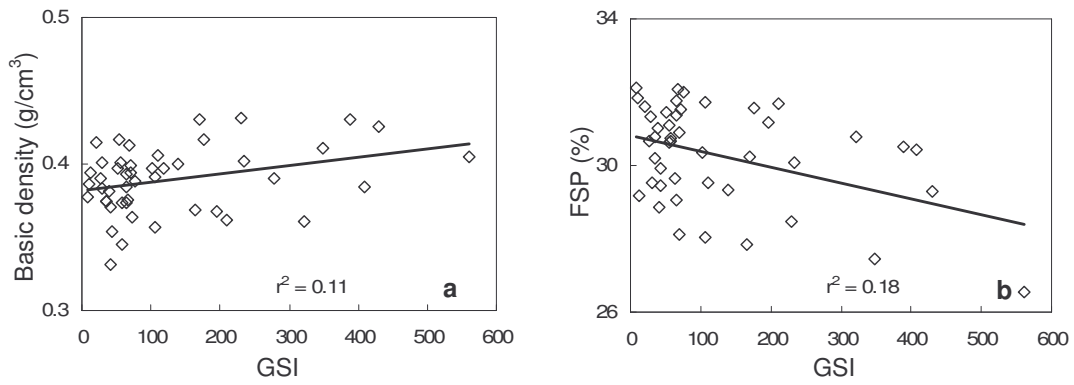


468 **Fig. 4.**  
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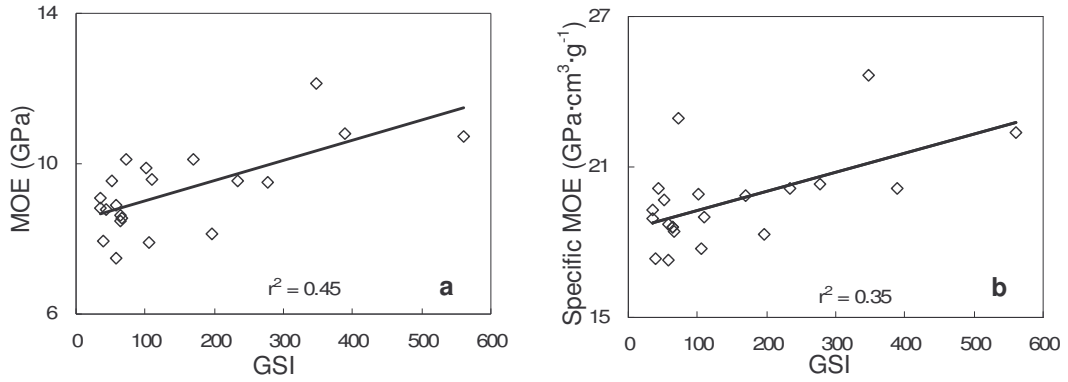


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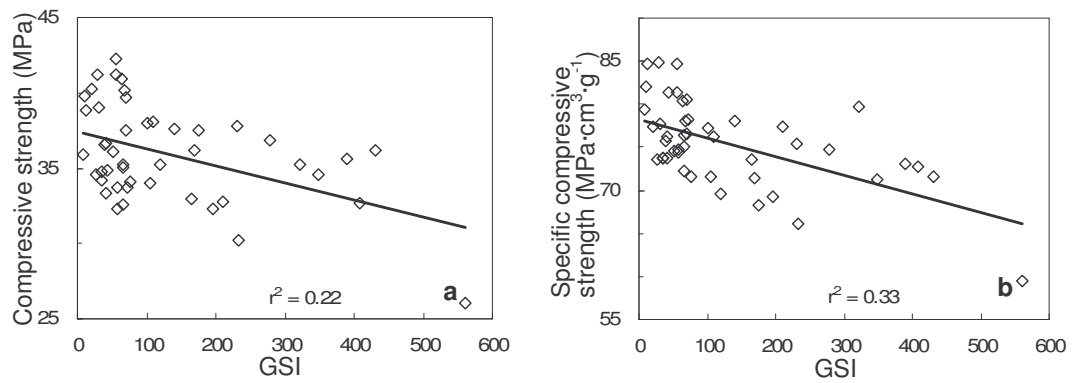
475 **Fig. 5.**



476 **Fig. 6.**

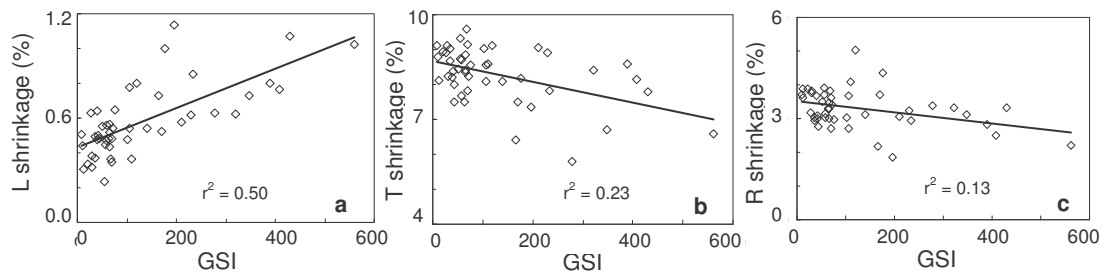


477 **Fig. 7.**

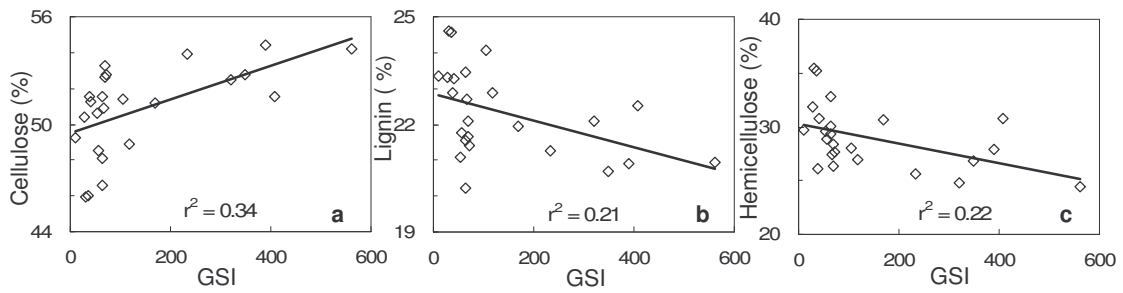


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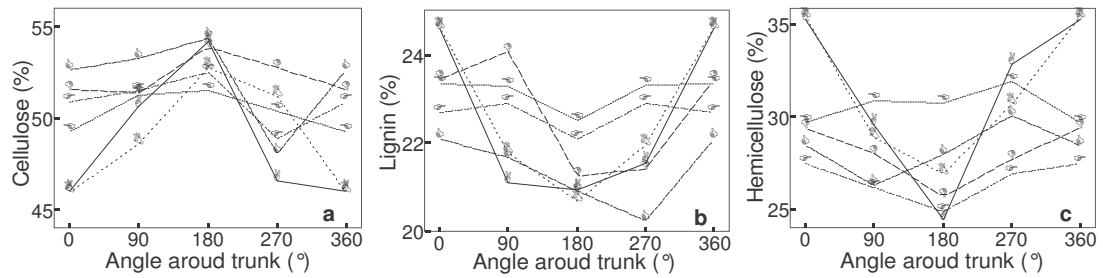




479 **Fig. 9.**



480 **Fig. 10.**



481 **Fig. 11.**