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Relationships between growth stress and wood properties in Poplar

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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- 14 **Abstract -** Six inclined poplar I-69 (*Populus deltoids* cv. I-69/55) trees were collected for studying the influence
- 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
- 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
- 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

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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,
- angiosperms produce tension wood generating high tensile stresses on their upper face [23, 55].
- 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
- so-called gelatinous layer (G-layer) [42] replacing S_3 and a part or the whole of the S_2 layer [48]. The
- 33 G-layer is known to have high cellulose content with a high degree of crystallinity [15, 39] and to
- 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
- 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
- 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
- tension wood, with corresponding variations of macroscopic behaviour [20, 21]. The aim of this work
- 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 . Anatomical and chemical data were obtained in China, physical and mechanical data
- 51 in France.

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

- 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 µm, termed Growth Stress
- Indicator (GSI), relates to the longitudinal growth stress at the trunk periphery by a proportional factor
- 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
- and then the other 7 points were positioned every 45° on circumference and numbered orderly from 2
- to 8, so the lowest side was 5 (Fig. 1).
- 62 After GSI measurements, trees were felled and 8 directions corresponding to GSI measurements
- 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.

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 µm thick) were obtained
- 70 with a microtome with disposable blades, and double stained with safranine and Fast Green. Safranine
- stains all tissues and Fast Green replaces safranine where purely cellulosic G layers of tension wood
- 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

- detachment and swelling of G-layer [11, 14, 21], rending impossible any correct measurement of the
- 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.
- 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.

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
- 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
- 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/cm³) was calculated as the ratio between the ovendry weight and the saturated volume. FSP
- was obtained by calculating the intercept of shrinkage variation with moisture content change. Total T,
- R and L shrinkage, from saturated to ovendry, 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
- accompanying the bending vibrations resulting from a small kick on one end with a little iron stick.
- 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
- difficult to avoid some defects like knot, crack and bend, finally only 21 samples were used for MOE
- measurement.

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- 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
- extracted from the samples used for MOE measurements (Fig. 1). Before measuring the compressive
- strength, the precise sample dimensions were measured. After the test the EMC of the sample during
- test was measured. Compressive strength parallel to grain at 12% EMC σ_{12} (in MPa) was estimated
- using a correction valid for an EMC ranging between 7% and 18% [1]:
- where σ_w (MPa) is the compressive strength at the EMC of the test, P_{max} (N) the maximum force

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

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

required as the experiment was performed outside the conditioning room.

2.4. Chemical composition

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- Disc used for chemical composition measurements was shown in Figure 1. Wood powder of 42-60
- mesh was prepared from samples got near the positions 1, 3, 5 and 7. The lignin content was
- determined by the Klason method [8, 31]. Cellulose content was determined by HNO₃-ethanol method.
- Holocellulose content was determined by chlorite method and hemicellulose content was calculated as
- the difference of holocellulose content and cellulose content.

3. RESULTS AND DISCUSSION

3.1. Growth Stress distribution around the trunk

- GSI value was used in this study to estimate longitudinal growth stress on the surface of standing
- trunk. In poplar, growth stress is a good indicator of tension wood "severity", i.e. G-fibre proportion
- and G-layer thickness in species which can produce G-fibres [20, 21].
- Figure 3 shows the GSI variation along trunk periphery at breast height of the 6 trees. In all 6 trees, the
- upper side values (position 1, Fig. 1) placed at 180° on the graph, were significantly higher than those
- of the lower sides (position 5, Fig. 1), corresponding here to 0° or 360°. Other GSI values mostly
- distributed between those of upper and lower sides. The change of upper side GSI value among 6 trees
- did not show a significant trend with the lean angle. Except for position 180°, 135° and 225°, the GSI
- value varied very little, excluding the point 270° of tree PC2 which was abnormally high. The
- transverse section corresponding to each GSI measurement position was checked with microscopy,
- moreover, the visual assessment of the transverse sections of each position showed that all high GSI
- values were associated with a high proportion of G-fibres, except for that abnormal value where few
- G-fibres were observed. So in the further statistical analysis of this study, this value will be replaced
- by the mean value (170 µm) of the adjacent two values.

3.2. Growth stress / anatomical properties

- Dadswell and Wardrop [19] have stated that in the fresh state, before any drying has occurred, tension
- 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
- 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
- narrower than the opposite wood fibres observed on cross section. Onaka [42] and Scurfield and
- Wardrop [51] reported a larger tangential diameter of tension wood fibre in some species. In this study
- negative correlation (r = -0.462, significant at 1% level) was found between cell diameter (no attention
- was paid on the radial or tangential direction) and GSI value (Fig. 4a). As high GSI values were
- observed on the upper sides of trunks, where high proportion of tension wood is expected, and low
- ones on lower sides containing opposite wood (Fig. 3), this result is more or less in accordance with

- some of the previous ones. The mean cell diameter and standard deviation was $19.8 \pm 3.9 \,\mu m$.
- 150 The average length of fibres and standard deviation around the periphery of trunk at breast high in this
- study was $1347 \pm 198 \mu m$. There is no agreement in the literatures regarding the length of tension
- wood fibres in comparison that of normal fibres. Compared to normal fibres tension wood fibres were
- reported sometimes as being longer [9, 27, 42], sometimes as being shorter (Giovanmi 1953 [cited in
- Zimmermann [61]]) and sometimes as no marked difference [19, 51]. In this study a very significant
- 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
- tension wood, fibres become longer and longer.
- The formation of tension wood is usually associated with the occurrence of eccentricity, with wider
- ring at the upper side of stem where tension wood is produced [2]. Eccentric radial growth either
- results from an increased duration of division or from a higher division rate in the cambium [54, 55].
- As in normal wood formation the fibre length is inversely related to the growth rate [22, 30, 33]. If
- eccentricity of tension wood arouse from an increased division rate in the cambium, then the tension
- wood fibres would be expected to be shorter [54, 55]. Thus for the case in this study, eccentricity of
- tension was suspected to be the result of increased duration of division. Furthermore, it has been
- 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]]).
- In this study, the double cell wall thickness excluding G-layer was measured for samples with different
- 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
- 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
- excepting G-layer) thickness decreased while G-layer became thicker.
- A very slight and not significant positive correlation existed in this study between GSI value and the
- diameter of cell lumen, after G-layer removal when present (Fig. 4d). As described above the cell
- diameter decreased with an increase of GSI. Since, on the other hand, we shown [20] that the G-layer
- 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
- become bigger with the increase of growth stress level. The unapparent relationship found here could
- be partially explained by the decreased cell diameter related to the increased growth stress level.
- 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
- increased growth stress level. This study gave a very significant negative correlation (r = -0.786,
- significant at 1% level) between vessel proportion and GSI value (Fig. 5a). In the previous studies,
- 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
- concentration. According to Aloni [3], the rate of vessel differentiation is determined by the amount of
- auxin obtained by the differentiating cell, while tension wood forms in the region with less IAA
- concentration [17, 38].
- No apparent relationship was found between ray proportion and GSI (Fig. 5b). Onaka [42] and Jourez

- et al. [27] also reported that ray proportion did not vary with wood type, normal or tension wood. A
- 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
- with increased GSI value (r = 0.429, significant at 5% level, Fig. 5c). This result is in accordance with
- Fang et al. [21]. Furthermore, they reported that with the increased growth stress level G-fibre
- 197 proportion increased. Theses results can be used to explain the increased wood basic density, see
- 198 below.

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 ± 0.02 g/cm³.
- 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
- tension wood. Washusen et al. [57] stated a positive correlation between microdensity and tension
- wood fibre percentage. Similar results were also reported by Kroll et al. [34] and Clair et al [12], while
- Arganbright et al. [4] and Lowell and Krahmer[37] did not observe a significant effect of lean or side
- on wood density. A lower density in tension wood was also reported in Tilia [43]. Basic density of
- samples located at different growth stress levels were compared in this study and a significant but
- 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
- were found (Fig. 5c), and furthermore increased G-fibre proportion and G-layer thickness [21], the
- increased basic density with increased growth stress level can be easily explained.
- Mean and standard deviation of FSP were $30.3 \pm 1.4\%$. A significant but weak negative correlation
- 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
- study, see below, and also reported by Furuya et al. [26]. Furthermore, in the tension wood the G-layer
- has very high crystallinity [15, 39] which leading to low affinity for water.
- A significant positive correlation (Pearson r = 0.671, significant at 1% level) was found between MOE
- and GSI value (Fig. 7a). Similar results were reported by Coutand et al. [16] that the Young's modulus
- 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
- percentage [9, 50]. Increased MOE with increased GSI value could be explained to some extend by the
- 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 S₂ 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.
- With the increase of GSI value, a decreased compressive strength was found here (Pearson r = -0.466,
- 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
- below), longer and thinner fibre (see above), as suggested by Frey-Wyssling (1936, cited in Wardrop
- and Dadswell [56]) that when a compressive stress is applied on a fibre the micelles tend to buckle
- because of their great length as compared with their lateral dimensions. Thus, in an unlignified fibre
- similar to that of tension wood, buckling could occur easily, giving rise to the formation of slip planes
- 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.
- 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
- shrinkage and GSI value (Fig. 9a). High longitudinal shrinkage in tension wood can be explain by the
- evidence of the longitudinal shrinkage in G-layer itself [13]. But the L shrinkage of G-layer remains
- 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
- with the one observed on 20-µm-thick sections of poplar in our previous study where T and R
- 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
- even though massive wood, not section, was studied.

3.4. Chemical composition

- 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
- 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
- presented in Figure 11. The cellulose content (Fig. 11a)rose to a maximum in the upper sides of all 6
- trees where highest GSI values were measured (Fig. 3) and paired (by different trees) samples t-test
- showed it was significant higher in the upper side than than in the other sides, but no significant
- difference existed between lower and lateral sides (Tab. II). A contrary result was found for the lignin
- 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].

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:

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- The highest GSI values were located in the upper sides of the inclined trunks. Other GSI values
 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
- stress, i.e. from normal wood to mild and severe tension wood, fibres become longer and longer
- and the thickness of cell wall excluding G-layer decreased. A very significant negative correlation
- between vessel proportion and GSI value. No apparent relationship was found between ray
- 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.
- With the increase of GSI value, MOE increased, compressive strength decreased, L shrinkage
- increased and T and R shrinkage decreased.
- 292 The cellulose content rose to a maximum in the upper sides where highest GSI values were
- measured. A contrary result was found for the lignin content. 4 out of 6 trees showed the lowest
- hemicellulose content located in the upper sides but the differences among different sides were not
- significant.
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REFERENCES

- 305 [1] AFNOR, French standard NF B 51007, approved in February 1942, No. 85365, 1985.
- 306 [2] Almeras T., Thibaut A., Gril J., Effect of circumferential heterogeneity of wood maturation strain, modulus
- of elasticity and radial growth on the regulation of stem orientation in trees, Trees, Structure and function 19 (2005) 457-467.
- 308 19 (2005) 457-467.
- 309 [3] Aloni R., Vascular differentiation within the plant, in: Roberts L.W., Gahan P.B., Aloni R. (Eds.), Vascular differentiation and plant growth regulators, Springer-Verlag, Berlin, 1988, pp. 39-59.
- 311 [4] Arganbright D.G., Bensend D.W., Manwiller F.G., Influence of gelatinous fibers on the shrinkage of silver maple., Wood Sci. 3 (1970) 83–89.
- 313 [5] Barefoot A.C., Selected wood characteristics of young yellow-poplar. Part II: Shrinkage of normal and abnormal wood., For. Prod. J. 13 (1963) 443-448.

- 315 [6] Bordonné P.-A., Module dynamique et frottement intérieur dans le bois. Mesures sur poutres flottantes en
- vibrations naturelles, Institut National Polytechnique de Lorraine, Nancy, 1989, p. 109 p. + bibliogr. +
- 317 annexes.
- 318 [7] Boyd J.D., Relationship between fibre morphology and shrinkage of wood, Wood Sci. Technol. 11 (1977)
- 319 3-22.
- 320 [8] Browning B.L., Methods of wood chemistry, Interscience, John Wiley & Sons, New York, 1967.
- 321 [9] Chow K.Y., A comparative study of the structure and composition of tension wood in beech (*Fagus sylvatica* L.), Forestry 20 (1946) 62-77.
- 323 [10] Christensen G.N., Kelsey K.E., Die Geschwindigkeit der Wasserdampfsorption durch Holz, Holz als Roh-324 und Werkstoff 17 (1959) 178-188.
- 325 [11] Clair B., Gril J., Baba K., Thibaut B., Sugiyama J., Precautions for the structural analysis of the gelatinous layer in tension wood, IAWA J. 26 (2005) 189-195.
- 327 [12] Clair B., Ruelle J., Thibaut B., Relationship between growth stresses, mechano-physical properties and
- proportion of fibres with gelatinous layer in chestnut (Castanea Sativa Mill.), Holzforschung 57 (2003)
- 329 189-195.
- 330 [13] Clair B., Thibaut B., Shrinkage of the Gelatinous Layer of Poplar and Beech Tension Wood, IAWA J. 22 (2001) 121-131.
- 332 [14] Clair B., Thibaut B., Sugiyama J., On the detachment of the gelatinous layer in tension wood fiber, J. wood sci. 51 (2005) 218-221.
- 334 [15] Côté W.A.J., Day A.C., Timell T.E., A contribution to the ultrastructure of tension wood fibers, Wood Sci. 335 Technol. 3 (1969) 257-271.
- 336 [16] Coutand C., Jeronimidis G., Chanson B., Loup C., Comparison of mechanical properties of tension and opposite wood in Populus, Wood Sci. Technol. 38 (2004) 11-24.
- In [17] Cronshaw J., Morey P.R., The effect of plant growth substances on the development of tension wood in horizontally inclined stems of Acer Rubrum seedlings, Protoplasma 65 (1968) 379-391.
- 340 [18] Dadswell H.E., Wardrop A.B., What is reaction wood, Aust. For. 13 (1949) 22.
- 341 [19] Dadswell H.E., Wardrop A.B., The structure and properties of tension wood, Holzforschung 9 (1955) 342 97-104.
- 343 [20] Fang C.-H., Clair B., Gril J., Almeras T., Transverse shrinkage in G-fibers as a function of cell
- wall layering and growth strain, Wood Sci. Technol. (First online 2007).
- Fang C.-H., Clair B., Gril J., Liu S.-Q., Growth stresses are highly controlled by the amount of G-layer in poplar tension wood, IAWA J. (accepted 2007).
- Fang C.-H., Liu S.-Q., Zhu L.-H., Jin S.-X., Wu W.-Q., Comparative study on the effect of fertilization on wood anatomical features of Poplar I-69 (in Chinese), J. A-H.agric. Univ. 29 (2002) 398-402.
- 349 [23] Fisher J.B., Stevenson J.W., Occurence of reaction wood in branches of Dicotyledons and its role in tree architecture, Bot. Gazette 142 (1981) 82-95.
- 351 [24] Fournier M., Chanson B., Thibaut B., Guitard D., Mesure des déformations résiduelles de croissance à la
- surface des arbres, en relation avec leur morphologie. Observation sur différentes espèces, Ann. Sci. For. 51 (1994) 249-266.
- 354 [25] Fujita M., Saiki H., Harada H., Electron microscopy of microtubules and cellulose microfibrils in secondary wall formation of poplar tension wood fibers, Mokuzai Gakkaishi 20 (1974) 147-156.
- 356 [26] Furuya N., Takahashi S., Miyazaki M., The chemical compositions of gelatinous layer from the tension wood of *Populus euro-americana*, Mokuzai Gakkaishi 16 (1970) 26-30.
- Jourez B., Riboux A., Leclercq A., Anatomical characteristics of tension wood and opposite wood in young inclined stems of popular (populus euramericana cv " ghoy "), IAWA J. 22 (2001) 133-157.

- 360 [28] Jourez B., Riboux A., Leclercq A., Comparison of basic density and longitudinal shrinkage in tension wood
- and opposite wood in young stems of Populus euramericana cv. Ghoy when subjected to a gravitational
- 362 stimulus, Can. j. for. res. 31 (2001) 1676-1683.
- 363 [29] Kaeiser M., Boyce S.G., The relation of gelatinous fibers to wood structure in eastern cottonwood (*Populus deltoides Marsh.*), Amer. J. Bot. 52 (1965) 711-715.
- 365 [30] Kennedy R.W., Fibre length of fast and slow grown black cottonwood, For. Chron. 33 (1957) 46-55.
- 366 [31] Klason P., Bidrag till narmare kännedom on granvedens kemiska sammansättning, Arkiv för Kemi, 367 Mineralogi och Geologi 3 (1908) 1-20.
- 368 [32] Koponen S., Toratti T., Kanerva P., Modelling longitudinal elastic and shrinkage properties of wood, Wood Sci. Technol. 23 (1989) 55-63.
- 370 [33] Koubaa A., Hernandez R., Beaudoin M., Poliquin J., Interclonal, intraclonal, and within-tree variation in 371 fiber length of poplar hybrid clones, Wood Fiber Sci. 30 (1998) 40-47.
- 372 [34] Kroll R.E., Ritter D.C., Au K.C., Anatomical and physical properties of Balsam poplar (*Populus balsamifera* L.) in Minnesota, Wood Fiber Sci. 24 (1992) 13-24.
- 374 [35] Kubler H., Growth stresses in trees and related wood properties, For. Abstr. 10 (1987) 62-119.
- 375 [36] Lenz O., Le bois de quelques peupliers de culture en Suisse, Ann. Inst. Fed. Rech. For. 30 (1954).
- 376 [37] Lowell E.C., Krahmer R.L., Effects of lean in red alder trees on wood shrinkage and density, Wood Fiber Sci. 25 (1993) 2-7.
- 378 [38] Morey P.R., Cronshaw J., Induction of tension wood by 2,4-dinitrophenol and auxins, Protoplasma 65 (1968) 393-405.
- 380 [39] Norberg P.H., Meier H., Physical and chemical properties of the gelatinous layer in tension wood fibre of aspen (*Populus tremula* L.), Holzforschung 20 (1966) 174-178.
- 382 [40] Okuyama T., Yamamoto H., Iguchi M., Yoshida M., Generation process of growth stresses in cell walls II. 383 Growth stresses in tension wood, Mokuzai Gakkaishi 36 (1990) 797-803.
- 384 [41] Okuyama T., Yamamoto H., Yoshida M., Hattori Y., Archer R.R., Growth stresses in tension wood: role of microfibrils and lignification, Ann Sci For 51 (1994) 291-300.
- 386 [42] Onaka F., Studies on compression and tension wood, Wood research, Bulletin of the Wood research 387 Institute, Kyoto University, Japan 24 (1949) 1-88.
- 388 [43] Panshin A.J., de Zeeuw C., Textbook of Wood Technology, Mc Graw-Hill Book Co., New York., New York, 389 1980.
- 390 [44] Parham R.A., Robinson K.W., Isebrands J.G., Effects of tension wood on Kraft paper from a short-rotation hardwood (*Populus "Tristis No. 1"*), Wood Sci. Technol. 11 (1977) 291-303.
- 392 [45] Pilate G., Chabbert B., Cathala B., Yoshinaga A., Leplé J.-C., Laurans F., Lapierre C., Ruel K., Lignification 393 and tension wood, C. R. Biologies 327 (2004) 889-901.
- 394 [46] Ruelle J., Analyse de la diversité du bois de tension de 3 espèces d'angiospermes de forêt tropicale humide 395 de Guyane Française, Forest and wood science, Université Antilles Guyane, Cayenne, 2006, p. 210.
- 396 [47] Ruelle J., Clair B., Beauchêne J., Prevost M.F., Fournier M., Tension wood and opposite wood in 21 tropical rain Forest species. 2. Comparison of some anatomical and ultrastructural criteria, IAWA J. 27
- 398 (2006) in press.
- 399 [48] Saiki H., Ono K., Cell wall organization of gelatinous fibers in tension wood, Bull. Kyoto Univ. For. 42 400 (1971) 210-220.
- 401 [49] Salmén L., Ruvo A.d., A model for the prediction of fiber elasticity, Wood Fiber Sci. 17 (1985) 336-350.
- 402 [50] Sassus F., Déformations de maturation et propriétés du bois de tension chez le hêtre et le peuplier : mesures 403 et modèles, in: Thibaut B. (Ed.), Thesis de l'ENGREF en Sciences du bois, Montpellier, 1998.
- 404 [51] Scurfield G., Wardrop A.B., The nature of reaction wood. VI. The reaction anatomy of seedlings of woody

- 405 perennials, Aust. J. Bot. 10 (1962) 93-105.
- 406 [52] Sugiyama K., Okuyama T., Yamamoto H., Yoshida M., Generation process of growth stresses in cell walls:
- 407 Relation between longitudinal released strain and chemical compostion, Wood Sci. Technol. 27 (1993) 408 257-262.
- 409 [53] Wada M., Okano T., Sugiyama J., Horii F., Characterization of tension and normally lignified wood cellulose in Populus maximowiczii, Cellulose 2 (1995) 223-233.
- 411 [54] Wardrop A.B., The nature of reaction wood. V. The distribution and formation of tension wood in some species of Eucalyptus, Aust. J. Bot. 4 (1956) 152-166.
- 413 [55] Wardrop A.B., The reaction anatomy of arborescent angiosperms, in: Zimmermann M.H. (Ed.), The formation of wood in forest tree, Academic Press, New York, 1964, pp. 405-456.
- 415 [56] Wardrop A.B., Dadswell H.E., The nature of reaction wood I The structure and properties of tension wood 416 fibres, Australian journal of scientific research, series B, Biological sciences 1 (1948) 3-16.
- 417 [57] Washusen R., Ades P., Evans R., Ilic J., Vinden P., Relationships between density, shrinkage, extractives 418 content and microfibril angle in tension wood from three provenancesof 10-year-old Eucalyptus globulus 419 Labill, Holzforschung 55 (2001) 176-182.
- 420 [58] Washusen R., Ilic J., Relationship between transverse shrinkage and tension wood from three provenances 421 of *Eucalyptus globulus* Labill, Holz als Roh und Werkstoff 59 (2001) 85-93.
- 422 [59] Washusen R., Ilic J., Waugh G., The relationship between longitudinal growth strain and the occurrence of 423 gelatinous fibers in 10 and 11-year-old Eucalyptus globulus Labill, Holz als Roh- und Werkstoff 61 (2003) 424 299-303.
- 425 [60] Yamamoto H., Abe K., Arakawa Y., Okuyama T., Gril J., Role of the gelatinous layer (G-layer) on the 426 origin of the physical properties of the tension wood of Acer sieboldianum, J. wood sci. 51 (2005) 222-233.
- 427 [61] Zimmermann M.H. (Ed.), The formation of wood in forest trees, Academic Press, New York, 1964.
- 429 FIGURES LEGENDS
- Figure 1. Schematic localization of measurement positions.
- 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 = $50\mu m$.
- 433 **Figure 3.** GSI variation along trunk periphery at breast height. The upper sides correspond to 180°. Different
- lines indicate different trees.
- 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)
- parenchyma rays; (c) fibres.
- Figure 6. Relationships between GSI (μm) and (a) basic density (g/cm³) and (b) FSP (%).
- Figure 7. Relationships of (a) MOE (GPa) and (b) specific MOE (GPa·cm³·g⁻¹) with GSI (μm).
- Figure 8. Relationships of (a) compressive strength (MPa) and (b) specific compressive strength (MPa.cm³.g⁻¹)
- 443 with GSI (μ m).
- 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)
- lignin content (%) and (c) hemicellulose content (%).
- Figure 11. The distribution of (a) cellulose, (b) lignin and (c) hemicellulose content around trunk at breast height
- of different trees. The upper sides locate at 180°. *: PC1; *: PC2; *: PC3; *: PC4; *: PC5; *: PC6.

450 TABLES

Table . 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

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

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

456 FIGURES

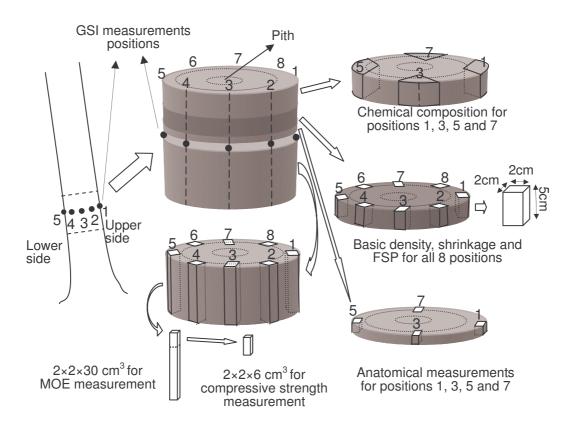


Fig. 1.

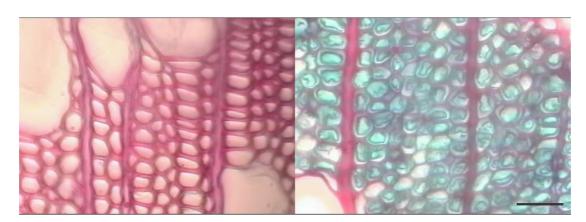


Fig. 2.

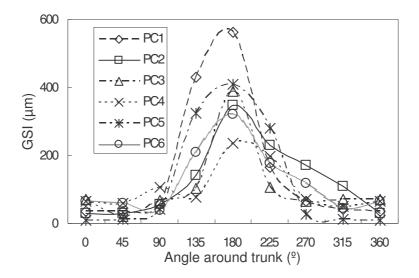


Fig. 3. 467

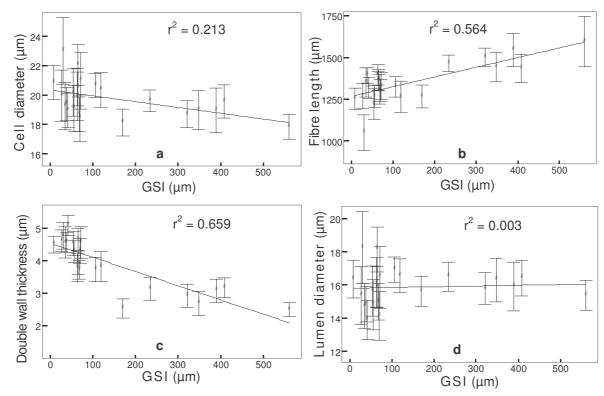


Fig. 4.

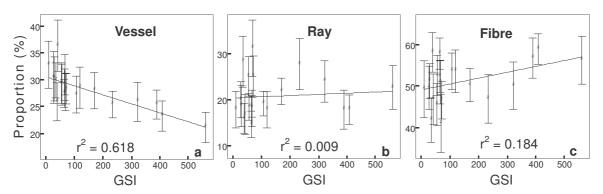
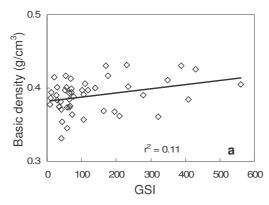


Fig. 5.



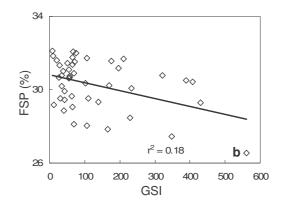
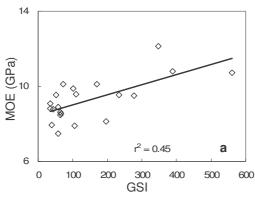


Fig. 6.



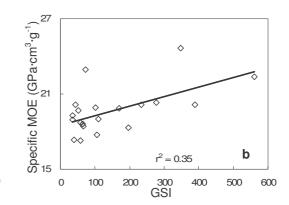
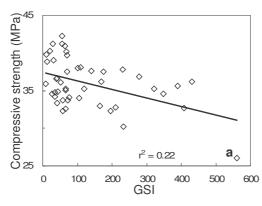


Fig. 7.



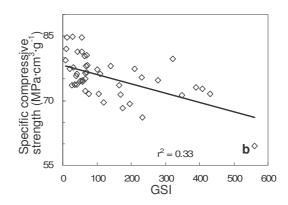


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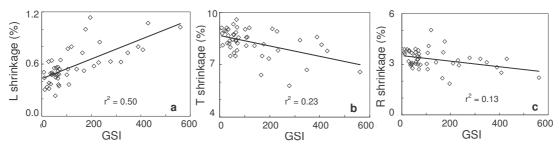


Fig. 9.

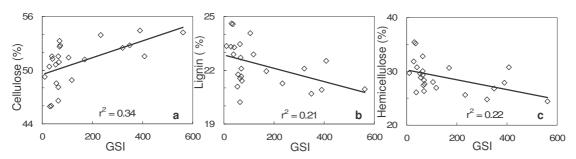


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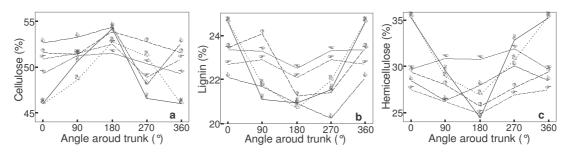


Fig. 11.