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Submitted on 15 Nov 2008

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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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Running title: Growth stress versus Poplar wood properties

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2008, Annals of Forest Sciences, 65, 307

Abstract - Six inclined poplar I-69 (*Populus deltoides* 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 periphery of each trunk at breast height and corresponding wood samples were obtained. Wood anatomical, 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 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.

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

1. INTRODUCTION

Trees control the shape and orientation of the main trunk or the predetermined angle of a branch, search for light or react to stronger loading, such as a strong dominant wind, through the generation of growth stresses during the process of wood formation. This is usually obtained by production of 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 compared to normal wood [42]. In many species such as beech, poplar, oak or chestnut, tension wood contains fibres with a special morphology and chemical composition due to the development of the so-called gelatinous layer (G-layer) [42] replacing S1 and a part or the whole of the S2 layer [48]. The 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].

The distinctive anatomical characteristics and chemical composition of tension wood directly cause 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, 40, 59], defects during drying due to its high longitudinal shrinkage [4, 19, 28, 42], severe woolly surface during sawing and rotary cutting [43] due to G-fibres, as well as bad quality of paper made of
G-fibres [44].

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 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 from tension wood severity as quantified by growth strain assessment.

2. MATERIALS AND METHODS

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

2.1. Growth Stress Indicator (GSI)

The “single hole” drilling method developed by CIRAD [24] was used to estimate the longitudinal 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 longitudinal growth stress magnitude within trees of the same species [12].

GSI measurements were performed on the 6 standing trees at 8 points around the circumference of 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).

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 corresponding to each position was prepared for visual assessment of G-fibre occurrence by microscopic observation.

2.2. Anatomical properties

For each tree, close to positions No.1 (upper side), No. 3 and 7 (lateral side) and No.5 (lower side), two samples each were taken (Fig. 1). One was used for preparing a transverse section, the other for measurements of isolated elements after maceration. Transverse sections (20 µm thick) were obtained 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 (Fig. 2).

Sections were observed with an optical microscope linked to an image analysis system equipped with a colour CCTV camera (WV-CP460/CH, Panasonic). The sectioning method used caused the
 detachment and swelling of G-layer [11, 14, 21], rendering 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 cell wall thickness excluding G-layer, the lumen diameter after G-layer removal and cell diameter were measured. 30 measurements per sample were done. The proportion of vessel and ray was 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 acid. After maceration the measurement of fibre length was undertaken with a projection microscope.

2.3. Physical and mechanical properties

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

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 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 provide nominal equilibrium moisture content (EMC) of 17% (30°C, 80% RH), 12% (20°C, 65% R.H.) and 8% (20°C, 30% R.H.), respectively, then in an oven at 103°C to obtain an EMC of 0%. At each stage, after constant weight was reached, samples were weighted and measured. Basic density (BD, g/cm$^3$) 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.

2.3.2. MOE, specific MOE and compressive strength

Samples (20mm in R, 20mm in T and 300mm in L direction) were taken in the vicinity of GSI measurement positions (Fig. 1). Samples were kept in a controlled chamber with temperature of 20°C, humidity of 65% until the moisture content reaches 12%. MOE and specific MOE were measured using free vibration and Fast Fourier Transform analysis (FFT). After dimensions and weight 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 (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.

The test of compressive strength parallel to grain was carried out following standard NF B 51-007 [1] (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 $\sigma_{12}$ (in MPa) was estimated using a correction valid for an EMC ranging between 7% and 18% [1]:

where $\sigma_w$ (MPa) is the compressive strength at the EMC of the test, $P_{\text{max}}$ (N) the maximum force applied, a and b the sample dimensions in R and T directions, respectively. This correction was

\[
\sigma_w = \frac{P_{\text{max}}}{a \times b}
\]

\[
\sigma_{12} = \sigma_w \times [1 + 0.04 \times (EMC - 12)]
\]
required as the experiment was performed outside the conditioning room.

2.4. Chemical composition

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 HNO$_3$-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 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 Populus euramerica 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 ± 3.9 μm.

The average length of fibres and standard deviation around the periphery of trunk at breast high in this study was 1347 ± 198 μm. 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 (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 (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 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 [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 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 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 [9, 27, 42, 47, 55], except for Kaeiser and Boyce [29] and Kroll et al. [34] who reported opposite 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 proportion of ray but inconclusive. 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 proportion increased. Theses results can be used to explain the increased wood basic density, see below.

3.3. Growth stress / physico-mechanical properties

The average basic density and standard deviation of outmost samples at breast height of poplar I-19 $(Populus deltoides Bart.¢v. "Lux" ex I-69/55)$ in this study were $0.39 \pm 0.02$ g/cm$^3$. Chow [9], Lenz [36] Panshin and de Zeeuw [43] and Jourez et al. [28] compared tension wood and 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. 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 hygroscopicity between normal and tension wood. The hygroscopicity is depended on the chemical compositions of cell wall, cellulose crystallinity, cell wall density, extractives contents. Among chemical components in cell walls, of the three major materials (lignin, hemicelluloses and cellulose) lignin has the lowest affinity for water and hemicelluloses the highest. The affinity of cellulose for 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 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 normalising for density (i.e. specific MOE) (Fig. 7b). This could be explained by the difference of microfibrillar angle between $S_2$ and G-layers, as has been observed and modelled for softwoods [32, 49], but also by differences in chemical composition or other structural features. A comprehensive model relating the macroscopic behaviour in L direction to the parameters of cell wall composition
(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. 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 unliignified 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, resists the tendency of the micelles to buckle. This could explain the common occurrence of slip planes and minute compression failures in the cell walls of tension wood observed by Wardrop and Dadswell [18, 19, 56].

Specific compressive strength was also presented (Fig. 8b). It is easy to understand the negative correlation with GSI value because of the decreased compressive strength and increased density. Similar result was reported by Onaka [42].

There is no bifurcation on the higher L shrinkage of tension wood than that of normal wood [12, 19, 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.

Few studies have been done on the transverse shrinkage of tension wood and the results are contradictory. Washusen and Ilic [58], Clair et al. [12] reported a higher transverse shrinkage in tension wood, while Barefoot [5], Arganbright et al. [4] and Fang et al. [20] observed a lower one. In this study T and R shrinkages were found strongly and weakly, respectively, correlated negatively with 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 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 GSI value were found in this study (Fig. 10). It should be mentioned however, the samples for 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. 10). Therefore, the obtained correlation should be considered with some caution.

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 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 upper sides but the differences among different sides were not significant after paired samples t-test.
Tension wood is generally described as containing a high proportion of cellulose and being less lignified than normal wood [26, 45, 53]. Our results showed that the studied species of poplar in general has the similar chemical properties. Similar results were also reported by previous studies on different species [9, 41, 52, 56].

4. CONCLUSION

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

- 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.
- 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.
- 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.
- 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.

Acknowledgements. We want to express thanks to Bernard Thibaut and Anna Thibaut from UMR Ecologie des Forêts de Guyane for the guidance of GSI measurements and samples preparation, Gilles Camp and Sandrine Bardet from Laboratoire de Mécanique et Génie Civil, Université Montpellier 2 for assistance on samples preparation, Qinglong Chen, Chunya Qin and Kaiqing Zhang from Forest Products Department, Anhui Agricultural University for assistance on anatomical measurements and Gilles Calchera from CIRAD - Forêt, Montpellier for assistance on compressive strength measurement. This study was partly supported by the foundation of Anhui science and technology granted by Anhui education administration.

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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 appear red after double staining. Scale bar = 50µm.

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

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

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) with GSI (µm).

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

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 180º. #: PC1; &: PC2; #: PC3; #: PC4; #: PC5; #: PC6.
### TABLES

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

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

**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.

<table>
<thead>
<tr>
<th></th>
<th>Upper-Lower</th>
<th>Upper-Lateral</th>
<th>Lateral-Lower</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cellulose (%)</td>
<td>*</td>
<td>**</td>
<td>NS</td>
</tr>
<tr>
<td>Lignin (%)</td>
<td>*</td>
<td>*</td>
<td>NS</td>
</tr>
<tr>
<td>Hemicellulose (%)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>
Fig. 1. 2×2×6 cm³ for compressive strength measurement

GSI measurements positions

Upper side

Lower side

2×2×30 cm³ for MOE measurement

Pith

Chemical composition for positions 1, 3, 5 and 7

Basic density, shrinkage and FSP for all 8 positions

Anatomical measurements for positions 1, 3, 5 and 7

Fig. 2.
**Fig. 3.**

\[
0 \quad 45 \quad 90 \quad 135 \quad 180 \quad 225 \quad 270 \quad 315 \quad 360
\]

**Fig. 4.**

- **a:** Cell diameter (µm) vs. GSI (µm), \( r^2 = 0.213 \)
- **b:** Fibre length (µm) vs. GSI (µm), \( r^2 = 0.564 \)
- **c:** Double wall thickness (µm) vs. GSI (µm), \( r^2 = 0.659 \)
- **d:** Lumen diameter (µm) vs. GSI (µm), \( r^2 = 0.003 \)
Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.