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2 **Relationship between tree morphology and growth**
3 **stress in mature European beech stands.**

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12 **(ii) Abstract**

13 Aims: In European Beech (*Fagus sylvatica* L.) large growth stresses lead to severe log end
14 splitting that devalue beech timber. Our study aimed at detecting relationships between growth
15 stress and some morphology parameters in trees.

16 Methods: Growth stress indicators were recorded for 440 mature trees in 9 stands from 5 European
17 countries, together with morphology parameters.

18 Results: Most trees displayed an uneven distribution of growth stress around the trunk. Moreover,
19 growth stress intensity varied largely between individual trees. Geometry of the trunk was a poor
20 predictor of growth stress intensity. Crown asymmetry resulted in a larger stress dissymmetry
21 within trees. Trunk inclination was not correlated to mean or tension stress, contrary to what is
22 usually found in younger trees. In the case of small inclination, growth stress was close to
23 expected from biomechanics of restoring verticality. Trees exhibiting a larger inclination probably
24 evolved a different mechanical solution: a rather large crown, lower tree slenderness and a
25 sufficient asymmetry in growth stress as to prevent a higher inclination due to growth.

26 Conclusion: A large slenderness is the best accurate predictor of a large growth stress, although
27 variations in the ratio Height/DBH explained only 10% of the variability of growth stress. A large
28 crown surface was the best predictor of a low level of growth stress. A large spacing between trees
29 seems a good solution to lower the risk of growth stress in mature Beech.

30 **(iii) Introduction**

31 European Beech (*Fagus sylvatica* L.) is an important tree species, with a rather large distribution
32 in western and central Europe (Alvarez-Gonzalez et al. 2010). Besides firewood, beech is mainly
33 used for furniture, packaging, plywood and decorative veneer.

34 Two main defects in standing trees have important consequences on timber value in industry
35 (Knoke et al. 2006): red heart colour (Liu et al. 2005) and high level of growth stresses leading to
36 log end splitting in veneer industry and board warping in sawmills (Saurat and Gueneau 1976;
37 Archer 1986; Kübler 1987).

38 Three main types of forest management are applied to beech stands in Europe: pure coppice for
39 firewood, high stand, even aged forest, for sawing and veneer industries, coppice-with-standards:
40 middle forest combining coppice and mature trees, for mixed uses. Sometimes coppice and
41 coppice-with-standards were transformed in high stand forest more than one century ago.

42 Growth stresses are always present in trees, (Archer 1986; Kübler 1987; Fournier et al. 1994a;
43 Thibaut and Gril 2003; Jullien and Gril 1996 and 2008).

44 Strictly speaking, the term growth stress should describe the whole stress field in a trunk resulting
45 from tree growth. On one side there are the stresses accumulated as a result of self weight
46 increasing, called “support stresses”. On the other side there are the stresses resulting from the pre-
47 stressing phenomena occurring in each new wood layer at the end of the fibre differentiation
48 process, during cell wall lignifications, called “maturation stresses” (Fournier et al 1994a). Usually
49 this stress field is described on a transverse section of the bottom of the trunk, where it is supposed
50 to be the highest.

51 Support stress field in a continuously growing structure is not usual. Let us consider that a beech
52 tree can be assimilated to a vertical column, perfectly cylindrical which dimensions are R and H,
53 radius and height of the column (assuming that the weight of branches compensate the loss of stem
54 diameter as we go from bottom to top of the tree). A simple rule of allometry is used to link h(t)
55 and r(t) all along tree growth: $h(r) = H(r/R)^{2/3}$.

56 If the column is built classically by piling successive elements of radius R and thickness T, until
57 reaching the height H (Fig. 1), there will be a uniform compressive stress field all over the section
58 with the stress magnitude: $\sigma_0 = \rho g H$, where ρ is the density of the material ($\rho = 1000 \text{kg/m}^3$ for
59 green beech wood), g is the gravitational field, ($g = 10 \text{m/s}^2$). For a 30m height column made of
60 green wood, σ_0 will have a uniform low value of 0,3MPa.

61 In a growing column, each new wood layer starts to be loaded only after it is formed, so we have
62 an incremental problem. From the moment that it has been produced at the distance r from the pith
63 until the final growth of the tree at radius R, the wood layer situated at r position will support an
64 increase of compressive stress due to each new layer deposition. So the final stress will be highest
65 near the pith (the first growth ring will support all the successive increase of compressive stress

66 due to growth). On the contrary, the last growth ring, being just elaborated will not support any
67 stress from what happen before its birth.

68 In the studied case, the solution of the incremental calculation of stress level at each r position in
69 the bottom section is very simple: $\sigma(r) = -4\sigma_0(1-(r/R)^{2/3})$, where $\sigma_0 = \rho gH$. In this case,
70 compressive stress is zero at periphery and 4 times greater than the uniform case value σ_0 (Fig.
71 1). This maximum value is only 1.2 MPa anyway, which means that compressive support stress is
72 very low compared to wood resistance to axial compression (around 50 MPa for green beech
73 wood).

74 The same remark can be applied to a cantilever beam. For a classic beam anchored at one end after
75 the making of the beam, there is maximum tensile stress $+\sigma_m$ at the top of the beam, at anchorage
76 level, and a maximum compressive stress $-\sigma_m$ at the bottom (Fig. 2).

77 For a growing anchored beam, the incremental solution is very different, because, again, the last
78 growth ring should have a zero stress all around the beam. The calculus shows that the tensile and
79 compressive stresses are maximum not far from the pith, with a much higher level than σ_m (Fig.
80 2).

81 For a slightly inclined column, the support stress field at bottom is the sum of the compressive
82 stress field calculated for a vertical beam and the flexure stress field obtained by multiplying the
83 values for a horizontally anchored beam by the beam inclination (TI) in %. For TI = 5%, the
84 compressive stress field is negligible as compared to the flexure one (Fig. 3).

85 But we know that the growth ring, just produced at distance r from the pith is in fact pre-stressed
86 in tension with a rather high value ($\sigma_{mat} = 10$ MPa for example in this case). This pre-stressing
87 leads to a global force F_{mat} on this ring that values $2\pi r(dr)\sigma_{mat}$, dr being the thickness of the
88 incremental new ring produced at r position. In order to counterbalance this force F_{mat} there will
89 appear a uniform compressive stress σ_{comp} in the existing core which radius is r : $\sigma_{comp} = F_{mat} / (\pi r^2)$.

90 The calculus of this increment from the first ring to the periphery gives the classical “Kubler
91 model” of growth stress which we call the maturation stress field.

92 At the end, the growth stress field is the sum of these 3 distributions (Compression + Flexure +
93 Maturation) (Fig. 3).

94 For a vertical, straight, equilibrated tree, the growth stress field is practically equal to the
95 maturation stress field. For more or less inclined or unbalanced trees, the stress field is no more
96 symmetrical. Any dissymmetry in maturation stress between two sides of the trunk will also
97 change a lot the stress field (Fournier et al 1994a) but the stress value at tree periphery is always
98 the maturation stress in the last ring.

99 So it should be kept in mind that measurement of maturation strains at tree periphery is just a
100 picture of the present pre-stressing action of the last grown wood in the tree.

101 Previously inclined young trees in the process of vertical recovery have trunks curved upwards
102 with tension wood on the upper part of the trunk (Almeras et al 2005). But this might not be true
103 for old mature trees with big diameters

104 Because maturation strain is the driving phenomena leading to very important problems in forest
105 industries using beech wood (accidents due to log end splitting, severe loss in sawmills or veneer
106 industry), it is of uttermost importance to try and understand what are the main factors influencing
107 the level of maturation strains in beech tree, in order to improve both forest management and log
108 use.

109 The objective of this paper is to examine whether growth stress level in beech could be anticipated
110 from observations on standing trees, as trunk inclination and sinuosity, crown size, position and
111 symmetry or tree slenderness. Moreover using plots from very different silvicultural treatment was
112 a way to confirm on a broad scale the former results on the influence of forest management on
113 growth stress in beech.

114 **(iv) Materials and methods**

115 **1. Stand selection**

116 The stands have been selected to emphasize similarities and differences between the growth stress
117 levels of trees under well-defined growing conditions. In total nine stands in the following five
118 countries were used for the study: Austria, Switzerland, Germany, Denmark and France.

119 Six stands are classical high stand forest, the following list contains stand designator, site, altitude
120 and average tree age:

- 121 • Aa = Purkersdorf, Austria (alt. 400m, about 150 years)
- 122 • Ab = 30 km of Salzburg, (alt. 900m, about 140 years)
- 123 • Dk = Ravnsholte, Denmark (alt. 120m, about 120 years)
- 124 • Fa = Moyeuve, France (alt. 320 m, about 110 years)
- 125 • Sa = Baden, Switzerland (alt. 450 m, about 110 years)
- 126 • Sb = Le Fahy, Switzerland (alt. 500m, about 170 years)

127 Two stands are middle forest type management:

- 128 • Fb = Ecouves, France (alt. 200m, about 150 years)
- 129 • Fc = Sasse, France (alt. 250 m, about 130 years)

130 The trees of the German stand were first grown under a middle forest management system. The
131 treatment of this stand was later on given up and replaced by a high forest management system.

- 132 • G = Schefflenz, Germany (alt. 270m, about 190 years)

133 **2. Tree selection**

134 Out of the nine stands, 50 trees per stand were selected for detailed investigations. Trees were
135 chosen with a mean diameter at breast height of at least 45 cm and without branches up to a height
136 of at least 4,5 meters. Trees with obvious damages of the bark, wavy grain or rotten trunks were
137 not selected.

138 **3. Tree morphology**

139 The total height of the tree (H) and the diameter at breast height (DBH) were systematically
140 measured. Slenderness was calculated as the ratio between total height and diameter at breast
141 height (H/DBH). The trunk inclination at the base of the tree (TI) was estimated by measuring the
142 distance between the trunk and a 2 meters long “plumb line”.

143 Eight sticks were placed vertically below eight points describing the crown periphery. The
144 position of the eight sticks was registered by their orientation in relation to the North direction and

145 their distance to the trunk of the referenced tree. The area of the crown projection (*CS*) was
146 deduced from these measurements, as well as the geometrical centre of the crown projection which
147 is very similar to the projection of crown centre of gravity (Barbacci et al 2009). The distance
148 between the centre of the crown projection and the trunk (*CE*) gives an indication of crown
149 eccentricity related to tree base. Photos and drawings of most of the trees have been made in two
150 different directions in order to show trunk inclination and curvature, branches orientation or
151 abundance, fork presence and disposition.

152 Crown shapes were visually separated in 2 classes: “symmetrical” (*S*) and “asymmetrical” (*AS*).
153 For trunk shape four classes have been defined: straight (more or less inclined) trunk (*T1*), trunk
154 curved at base (*T2*), trunk with one big curve (*T3*), sinuous trunk with more than one curve (*T4*)
155 (Tab. 1).

156 Table 1 indicates the number of trees (with a complete set of measurement) for each stand in each
157 category of crown and trunk shape. The symmetric crown category is a little less represented than
158 the dissymmetric one (194 compared to 246). The trunk category *T1* corresponding to straight
159 trunks is much more represented than the sinuous trunks *T2*, *T3* and *T4* (251 compared to 48, 81,
160 60).

161 **4. Growth stress description**

162 Eight values of growth stress indicator were measured on stem periphery, at breast height. Each
163 indicator is obtained by the single-hole method (Fournier et al. 1994b; Yang et al. 2005). It
164 consists in debarking a circumferential part of the trunk, fixing pins to the wood at two points
165 which are aligned in the longitudinal direction of the trunk at a 45 mm distance, drilling a 20 mm
166 diameter hole between the two pins and measuring the relative displacement of the pins due to the
167 drilling. This displacement, being referred to as growth stress indicator (*GSI*) in μm is positive
168 each time the growth stress is a tensile stress (a negative value would indicate compression wood).
169 *GSI* value is proportional to the local longitudinal maturation strain (ϵ_M) through formula (1)
170 (Baillères 1994).

$$171 \quad \epsilon_M = 12.9 \cdot 10^{-6} \cdot GSI \quad (1)$$

172 Maturation stress σ_G can be deduced from maturation strain ϵ_M by formula (2) where E is the
173 longitudinal modulus of elasticity of beech wood in the measurement zone.

$$174 \quad \sigma_G = \epsilon_M \cdot E \quad (2)$$

175 For angiosperms, E does not vary so much between tension and normal wood (Alméras et al.
176 2005). So GSI is a good proxy of growth stress at stem periphery of one tree. Between beech trees,
177 E can vary at a maximum by a factor of two, thus strictly speaking, GSI is a better proxy for
178 maturation strain than for maturation stress.

179 The *GSI* was measured at eight points that were evenly distributed along the circumference of each
180 trunk and the position of the points was defined in reference to the north direction as it is shown in
181 (Fig. 4).

182 The *minimum (Min)*, *maximum (Max)*, *mean (Mean)* value of the 8 indicators per tree and the
183 *difference between the maximum and the minimum values (Range = Max-Min)* were calculated for
184 each tree in order to obtain 4 growth stress tree parameters for the analysis.

185 **(v) Results**

186 **1. Global results**

187 In table 2 an overview of all relevant *GSI* and dendrometric parameters for all trees is given.
188 Variations are rather low for *DBH*, height and tree slenderness but very high for crown area,
189 crown off-centering and trunk inclination, and high for all GSI tree parameters.

190 The distribution of all *GSI* measurements (8 per tree, Online Resource 1) is classical with a clear
191 peak around 45 μm (0,058% strain value), and a long trail for tension wood zones values. It is
192 comparable to what was found for other hardwood species (Fournier et al. 1994; Alméras et al.
193 2005).

194 There was a clear correlation between the direction of leaning of a given tree and the direction of
195 the maximum stress measurement at the circumference (Becker and Beimgraben 2001).

196 Assuming a mean value of 12 GPa for beech green wood MOE, the mean growth stress value σ_G
197 over all trees is 9.64 MPa.
198 The differences between low stressed and highly stressed trees are important (more than a 4 times
199 ratio between the 5% higher and lower percentile) for all the GSI tree parameters (Fig. 5). 45% of
200 the trees have a range of growth stress higher or equal to 15 MPa, and only 15% lower than 8 MPa
201 (around 50 μ m for *GSI* value).

202 **2. Mean results by stand, trunk and crown type**

203 In Online Resource 2 and 3 the mean values of GSI and morphological parameters measured on
204 standing trees, by stand, trunk and crown type are shown.
205 Differences are much higher between stands than between trunk or crown types (Tab. 3). There are
206 significant differences between stands at 0.1% level for all GSI and dendrometrical parameters.
207 Trunk type never gives significant difference except for trunk inclination. Crown asymmetry leads
208 to significant differences for all dendrometrical parameters (higher for *DBH*, crown parameters
209 and trunk inclination), but only for Max-Min GSI (at 1% level).

210 **3. Correlation between parameters**

211 In Table 4 the coefficients of correlation for measured growth stress and tree morphology data for
212 all straight trees (trunk type 1, 251 trees) are indicated. However, the results are fairly identical if
213 these values for all 440 trees (inclined and not inclined) are being correlated.
214 There are strong significant positive correlations among *GSI* parameters (except for Min and
215 Range) and also among tree dimension parameters (*DBH*, Height, crown surface). Parameters
216 expressing the disequilibrium of the tree (trunk inclination and crown eccentricity) are not
217 significantly related to tree dimension except for trunk inclination and total height.
218 All GSI parameters have strong significant correlation at the 0.1% level with slenderness (always
219 positive) and crown surface (always negative). The influence of *DBH* is very similar to that of
220 crown surface and height to slenderness (same sign, but lower level of significance if any). It
221 should be noted that slenderness of trees explains only 10% of GSI max variability (Fig. 6).

222 Trunk inclination has a strong negative significant correlation only with GSI min and GSI mean.
223 This tendency can also be observed on stand level (Online Resource 4 and 5).

224 **(vi) Discussion**

225 Ideally, if equilibrated during its whole life, a straight vertical tree is expected to have an
226 equilibrated level of growth stress along the circumference of its trunk. However, for the trees in
227 this study this was only the case for rather few trees. Most of the trees have a marked asymmetry
228 of GSI corresponding to a response to a mechanical disequilibrium of the tree (mainly tree
229 inclination).

230 Each time there is a need for a strong mechanical reaction, e.g. aiming at changing trunk geometry
231 in order to restore verticality after some accidental leaning the cambium will produce tension
232 wood (Coutand et al. 2007; Jourez et al. 2003; Alméras et al. 2005 and 2009; Wilson et al. 1979
233 and 1996; Moulia and Fournier 2009). The tension wood is being produced on one side of the
234 trunk, usually on an angular section ranging from 90° to 120°. When tension wood occurrence
235 lasts long enough at the same position of the trunk, a tension wood growth layer of a sufficient
236 dimension will develop with the result that the tensile force is much higher at this position of the
237 trunk circumference. This introduces a flexure moment and a change in curvature of the trunk
238 results. The tension wood is positioned on the concave side of the curvature (i.e. on the upper side
239 for an inclined tree restoring its verticality).

240

241 **1. Maturation stresses**

242 Ranging the 8 GSI values from the smallest (min) to the highest (max) in each tree, leads to a
243 typical distribution in two parts (Fig. 7). The four lower values grow linearly with a rather low
244 slope while the four higher ones grow linearly with a slope nearly three times higher. The first part
245 corresponds globally to the sector without any tension wood (opposite wood OW). The second

246 part corresponds to the peak of growth stress where the presence of tension wood TW can be
247 dominant.

248 Max-Min GSI is used as a mechanical indicator for restoration of verticality. Under the
249 consideration that the position of GSI max is very close to the peak of high tension wood sector
250 the difference between this GSI max and the GSI value found on the opposite position (Tension-
251 Opposite GSI) can be calculated. As shown in the relationship between *Max-Min GSI* on one side,
252 *Tension-Opposite GSI* on the other side (Fig. 8) the two values are very similar and very strongly
253 correlated. The width of the strip close to bisector line results from the fact that the “true” peak
254 and the “true” opposite sides can be at plus or minus 45° from what was chosen. Trees strongly
255 outside of the high correlation strip are those with unusual growth stress profile (Fournier et al
256 2004a) for example with two tension peaks.

257 Globally GSI max is a good proxy for tensile side while GSI min is a valuable proxy for the
258 opposite side.

259

260

261 **2. Tree morphology and growth stresses**

262 There are no significant differences between curved and straight trees for growth stresses. This is
263 rather opposite to what is usually found for small diameter trees. It could be suspected that for big
264 trees, highly stressed straight vertical ones are at the end of their verticality restoration phase.

265 It is commonly believed that trunk inclination should be a factor that positively influences growth
266 stress (Wilson et al. 1996), because of tension wood occurrence in order to restore verticality. For
267 the mature beech trees of the present study, there are significant negative correlations between
268 trunk inclination, mean and minimum GSI values (for straight trees as well as for all of them).

269 For a better assessment of this relationship, the straight trees were put into classes of different
270 inclination (Online Resource 6). All classes gather roughly 20 trees except 80 trees for the first
271 class with zero inclination.

272 GSI for opposite wood (GSI min) is slowly decreasing when trunk inclination grows until 2.5%.
273 Then it suddenly drops and continues to slowly decrease after. The same general pattern is shown
274 for GSI mean. GSI max begins to grow until 2.5% inclination, but decreases rather abruptly after
275 that and stays more or less flat until the highest tree leaning, with similar values as vertical trees.
276 GSI Max-Min, is lower for vertical trees but it stays more or less stable in inclined trees because
277 the decrease in GSI min compensate the decrease in GSI max. Looking at dendrometrical
278 parameters, trees with inclination over 2.5% have low H/DBH (below 55) and high crown surface.
279 Based on the results of big beech trees, it seems that a threshold for trunk inclination around 2.5 %
280 exists. Above this value, all GSI values decrease strongly, except for GSI max-min that keeps
281 more or less constant at a value approximately 20% higher than for vertical trees. Straight trees
282 exhibiting high trunk inclination do not use very high maximum GSI values on the tensile side but
283 rather low values on the opposite side so they keep a sufficient asymmetry in GSI in order to
284 prevent more tree leaning. They have bigger crowns and it should be looked more closely whether
285 this crown development contributes to some limitation in the disequilibrium of the tree.
286 Finally, for old mature trees, morphological traits as inclination, straightness or crown symmetry
287 are not good candidates for the prediction of high levels of growth stresses, but they help to predict
288 a higher asymmetry of these stresses.

289 **3. Dendrometrical parameters and growth stress**

290 Slenderness (H/DBH) and crown surface (CS) seem to be the best predictors of high or low growth
291 stresses in old beech trees. A high ratio H/DBH is clearly a factor that leads to increased growth
292 stresses. This was also shown by previous studies (Polge 1981; Ferrand 1982; Saurat and Gueneau
293 1976). On the contrary, big crowns (and big diameters DBH) are favourable factors that in general
294 lead to a moderate to low growth stress level.

295 Using classes of values for crown surface and tree slenderness (Online Resource 6) shows that all
296 GSI parameters always decreases when CS increases and the reverse is true for H/DBH .

297 But no more than 10% of GSI variability is explained by H/DBH and crown dimension. On one
298 hand there are differences between trees for the basic level of growth stress without reaction wood

299 (see variations in Min GSI). On the other hand, Max GSI controls the value of Mean and Max-Min
300 GSI, where Max GSI is well linked to the occurrence of tension wood produced by the tree. Not
301 every tree in each stand was subjected to such reaction phases, and the level of reaction is
302 therefore not the same. This explains the high variability in growth stress due to individual tree
303 history, apart from general trends linked to forest management.
304 Part of the negative correlations between growth stress indicators and both, *DBH* and crown
305 surface can be linked to the very high negative correlation between slenderness and these
306 parameters in our stands.

307 **4. Forest management and growth stress.**

308 Stand effect is highly significant both on growth stress indicators and dendrometrical parameters.
309 We can hypothesize that stand effect is strongly linked to forest management, e.g. related to mean
310 number of adult trees per hectare. Upon the assumption of a closed canopy by the gathering of all
311 crowns, the mean crown surface per tree is smaller for a great number of trees per hectare.
312 Crown surface has a very high level of correlation with *DBH* (positive) and slenderness (negative),
313 but not with total height, the latter one is being known to depend more on stand age and soil
314 fertility than on forest management. It has also very significant correlation with all growth stress
315 indicators (Table 4).
316 Looking at the implications to forest management, it can be deduced that low spacing of trees
317 induce small mean crown surface, small mean *DBH* and high slenderness at a given age. Thus
318 higher spacing of trees seems to be a good solution to lower the level of growth stress in high
319 forest beech stands, which confirms findings by (Polge 1981 and Ferrand 1982).

320 **Conclusion**

321 Most of the trees have an uneven distribution of growth stress around the trunk but geometry of
322 the trunk itself was not a good predictor of growth stress level. Trunk inclination is not globally
323 correlated to growth stress indicators. For trunk inclinations higher than 2.5%, it appears a

324 significant drop of maximum, minimum and mean GSI values although the difference between
325 tensile and opposite side is kept more or less constant.

326 High slenderness ratio between total height of the tree and trunk diameter at breast height
327 (H/DBH), is the best predictor of high level of growth stress, although variations in H/DBH
328 explain only 10% of mean and maximum growth stress variability. On the contrary, large crown
329 surface is the best predictor of low level of growth stress. These two descriptors are strongly
330 negatively correlated.

331 Thus large tree spacing is a good solution to lower the risk of high levels of growth stress in
332 Beech, as it appears through the mean values per stand, and as was previously stated by various
333 authors.

334

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410 **(x) Tables**

411
412

Stand	Nb	Crown		Trunk			
		Sym	Assym	T1	T2	T3	T4
Aa	45	14	31	20	6	7	12
Ab	49	17	32	35	6	7	1
Dk	50	34	16	27	7	6	10
Fa	50	14	36	32	4	11	3
Fb	50	20	30	27	3	12	8
Fc	50	28	22	32	1	13	4
G	46	24	22	22	6	13	5
Sa	50	19	31	19	15	4	12
Sb	50	24	26	37	0	8	5
Total	440	194	246	251	48	81	60

Table 1: Repartition of trees of each stand in each morphological category of crown (sym : symmetric; asym: asymmetric) and trunk (T1: straight, T2: curved at base, T3: with one big curve; T4: sinuous with more than one curve)

413

	GSI Min	GSI Max	GSI Range	GSI Mean	DBH	H	H/DBH	CS	TI	CE
	µm	µm	µm	µm	cm	m	cm/m	m ²	%	m
Mean	23,9	122	97,1	62,3	60,2	33,3	56,3	83,7	4,0	1,8
Mediar	21,0	121	95,5	59,4	57,9	33,5	56,6	68,7	3,0	1,6
Sd	15,6	49,8	45,0	25,6	10,6	4,1	9,1	54,9	4,0	1,1
Min	-	21,0	16,0	12,3	42,7	21,0	34,2	14,0	-	0,1
Max	114	295	269	155	113	44,0	83,2	439	23,5	6,6
Nb	440	440	440	440	440	440	440	440	440	440

Table 2: General results at tree level (440 trees)
GSI growth stress indicator; DBH diameter at breast height;
H height; CS crown surface; TI trunk inclination; CE crown eccentricity

414

GSI Min	GSI Max	GSI Range	GSI Mean	DBH	H	H/DBH	CS	TI	CE
µm	µm	µm	µm	cm	m	m/cm	m ²	%	m
***	***	***	***	***	***	***	***	***	***

		**		***	*	**	***	***	***

Table 3: Variance analysis for stand, trunk and crown type effects (440 trees)
GSI growth stress indicator; DBH diameter at breast height
H height; CS crown surface; TI trunk inclination; CE crown eccentricity

415

	Min	Max	Range	Mean	DBH	H	H/DBH	CS	TI %	CE m
Min	1	***		***		**	***	***	***	**
Max	0,492	1	***	***	***	*	***	***		
Range	0,145	0,931	1	***	***		***	***		
Mean	0,779	0,854	0,647	1	**	***	***	***	***	**
DBH	-0,110	-0,247	-0,233	-0,177	1	***	***	***		
H	0,197	0,136	0,075	0,208	0,359	1	***		***	
H/DBH	0,246	0,323	0,266	0,313	-0,666	0,437	1	***		*
CS	-0,236	-0,272	-0,210	-0,253	0,656	0,123	-0,498	1		*
TI %	-0,295	-0,063	0,051	-0,223	-0,087	-0,209	-0,092	0,070	1	***
CE m	-0,196	-0,073	-0,005	-0,177	0,063	-0,075	-0,140	0,149	0,440	1

Table 4 Correlation between parameters for the straight trees (type 1, 251 trees)
*, **, *** respectively significant at 5%, 1% and 0.1% level
Min, Max, Range=Max-Min, Mean: GSI growth stress indicators
DBH diameter at breast height; H height; CS crown surface; TI trunk inclination; CE crown eccentricity

416

417 **(xi) Captions of figures**

418 **Fig. 1** *Compressive support stress distribution at the bottom of a column. Left: built in one*
419 *operation, then erected. Right: built by successive additions of elements glued to the previous ones*
420 **Fig. 2** *Flexure support stress distribution for horizontal beam/branch anchored at one end, subject*
421 *to gravity. Dotted line: stress distribution for a man-made cylindrical beam. Continuous line:*
422 *stress distribution for a growing stem with constant allometry: $H \propto R^{2/3}$*
423 **Fig. 3** *Stress distribution at tree base level for a beech “equivalent tree” of characteristics:*
424 *Diameter 50cm, Height 30m, Trunk inclination 5%, constant peripheral maturation stress: 9,64*
425 *MPa. Flex: Flexure support stress; Comp: Compressive support stress; Mat: Maturation stress*
426 *Total: Growth stress = Flexure support stress + Compressive support stress + Maturation stress*
427 **Fig. 4** *Distribution of GSI values in relation to the cardinal points. In this example (tree G44) the*
428 *tension wood zone stretches fom the North to the East*
429 **Fig. 5** *Distribution of tree Growth Stress Indicator (GSI) parameters*
430 **Fig. 6** *Relationship between Tension-Opposite Growth Stress Indicator and Max-Min Growth*
431 *Stress Indicator for 390 trees*
432 **Fig. 7** *Relationship between maximum growth stress indicator (GSI Max) and tree slenderness*
433 *(H/DBH) for the straight trees*
434 **Fig. 8** *Mean value in each stand of the 8 measurements sorted from the smallest to the highest per*
435 *tree. OW: opposite wood; TW: tension wood; Stands: Aa, Ab, Dk, Fa, Fb, Fc, G, Sa, Sb*

436 **(xii) figures**

437

Fig. 1 Compressive support stress distribution at the bottom of a column

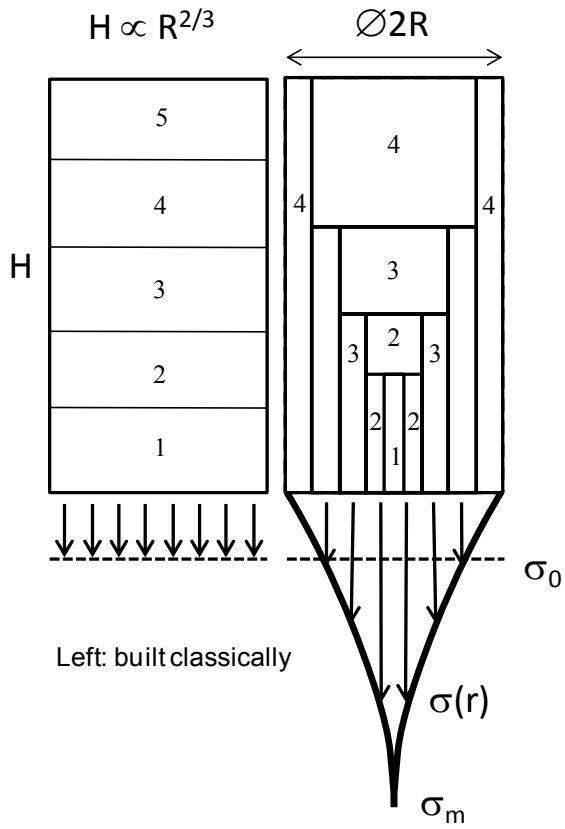
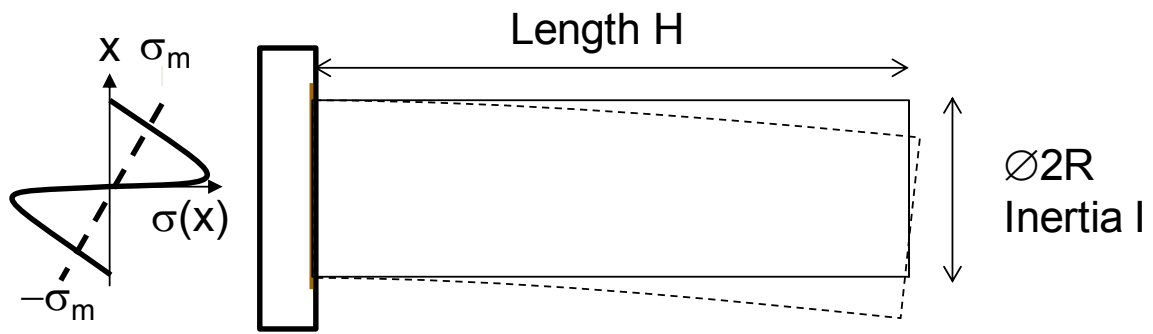


Fig. 2 Stress field on the section of the beam at anchorage level
Dotted line: stress distribution for a man-made cylindrical beam
Continuous line: stress distribution for a growing stem with constant allometry: $H \propto R^{2/3}$



Flexure of an anchored beam under its self weight charge

Fig. 3 Support stress, maturation stress and total growth stress

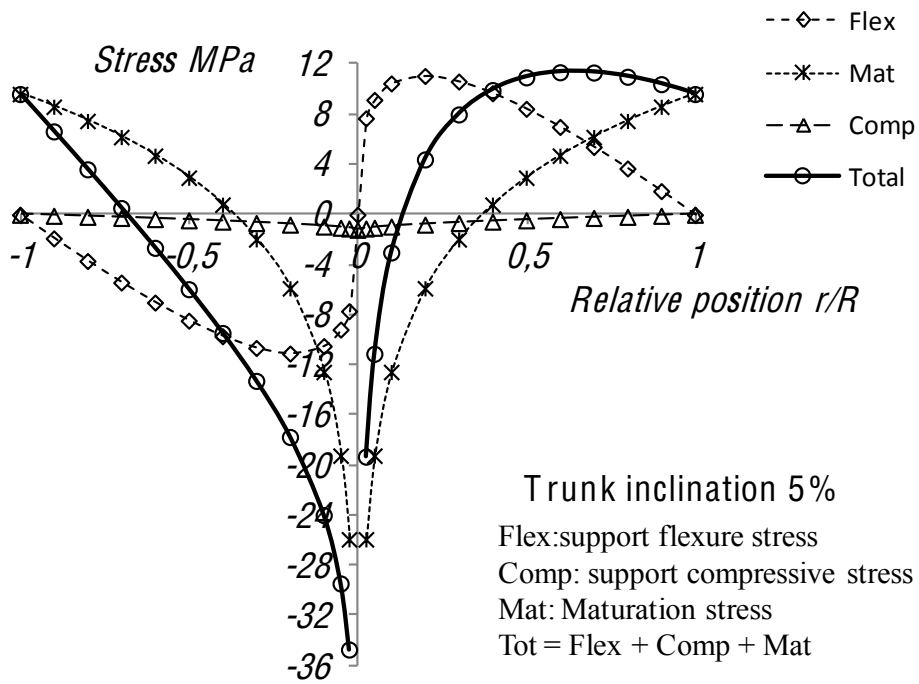


Fig. 4 Distribution of GSI values in relation to the cardinal points.
In this example (tree G44) the tension wood zone stretches from the North to the West

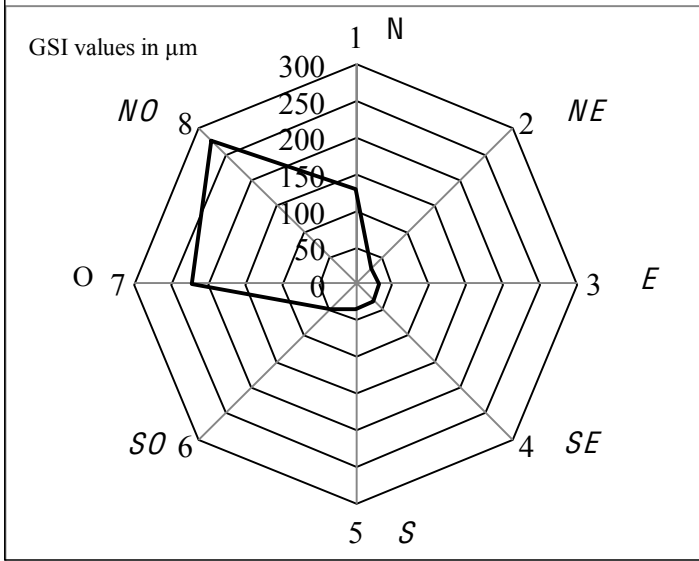


Fig. 5 Distribution of tree Growth Stress Indicator (GSI) parameters
440 trees

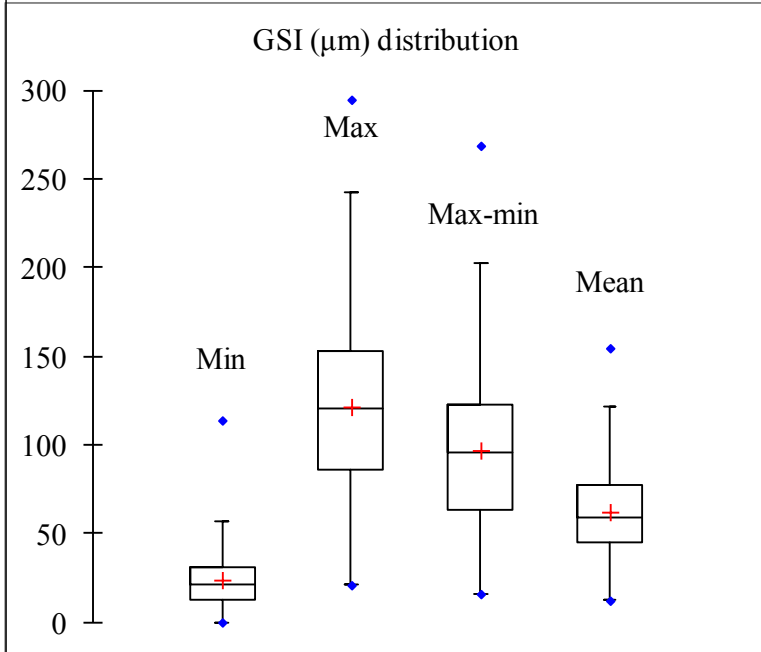


Fig. 6 Relationship between Tension-Opposite Growth Stress Indicator and Max-Min Growth Stress Indicator

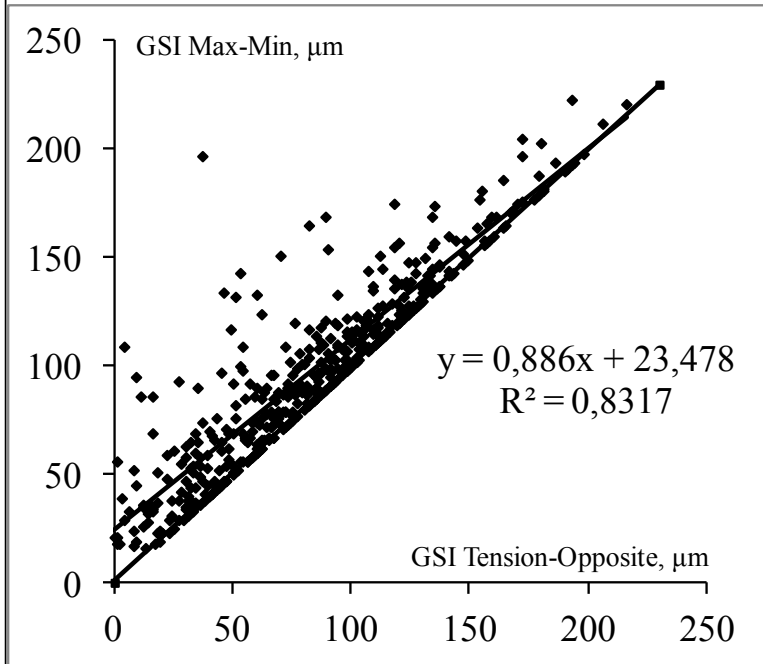


Fig. 7 Relationship between GSI max and H/DBH
251 straight trees

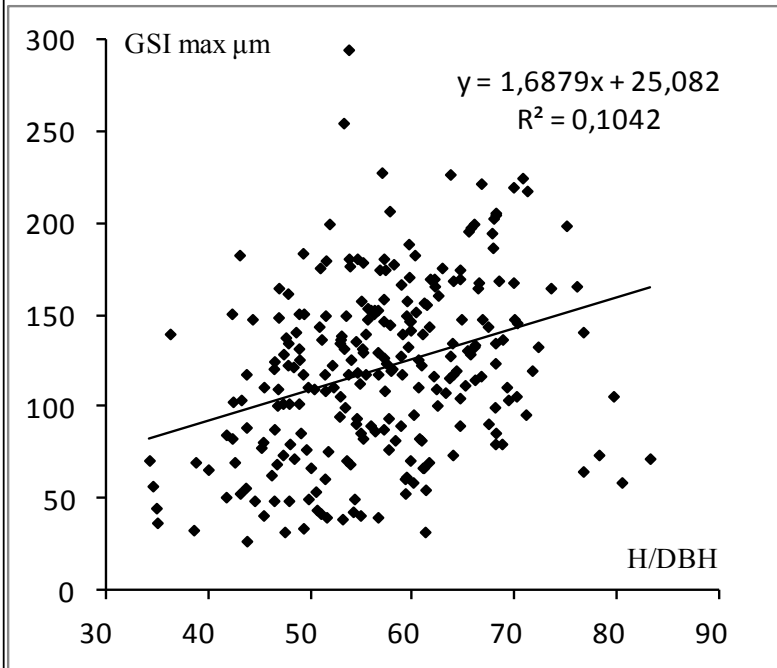


Fig. 8 Eight GSI measurements per tree sorted by value (Mean per stand)
 TW: tensile side; OW opposite side

