

Tree growth stresses, in situ measurement and properties of normal and reaction woods

Bernard Thibaut, Joseph Gril

Review

I was expecting this paper to be a synthesis of tree growth stresses in angiosperms and gymnosperms and how these are related to reaction wood and their role in tree alignment. However, it was not such a paper and I found it to be full of interesting information but without a unifying “narrative”.

My major criticisms of the paper are as follows:

1. There is no “story” holding the whole paper together. There is a discussion about the relationships between green and dry wood properties, a discussion on growth stress indicators and the role of growth stresses in trees, and descriptions of different types of wood including reaction wood. But these are not brought together in a coherent way. What is the purpose of the paper?
2. The language needs some work. I have made a few suggestions in the annotated version of the paper that is uploaded. I also found it difficult to follow the arguments put forward in many places. I could not understand the logic.
3. There are no hypotheses put forward and tested. So it appears to be more a review paper or a data paper. It is not clear.
4. The choice of standing trees was unclear. Why these species? Also there is only one tree from each species so each tree is essentially an experimental unit. Becomes very difficult to do any statistical analysis.
5. There were lots of graphs but the quality was not publication quality. Need redrawing.
6. The text was mixed up with text in Results that should have been in Materials and Methods and text in Discussion that should be in Results.

Other comments and questions are in my annotated version of the paper, which is attached.

Title:

Tree growth stresses, in situ measurement and properties of normal and reaction woods.

Running title: Tree growth stresses

Bernard Thibaut ^{(1), (*)}

Joseph Gril ^{(2), (3)}

⁽¹⁾ LMGC, Univ Montpellier, CNRS, Montpellier, France

bernard.thibaut@umontpellier.fr

^(*) Corresponding author

⁽²⁾ Université Clermont Auvergne, CNRS, Sigma Clermont, Institut Pascal, Clermont-Ferrand, France

⁽³⁾ Université Clermont Auvergne, INRAE, PIAF, Clermont Ferrand, France

Highlight

Experimental study of growth stains on trees restoring their verticality after some accidental inclination combined to measuring of wood properties at the same position allows to discuss the functions of forces created by living wood within trees in pre-stressing the woody skeleton on one side, allowing verticality restoration on the other side.

Abstract

Living wood in the tree performs a kind of muscle action generating forces at the sapwood periphery and thus residual strains in the dead sapwood fibres. Dissymmetric force generation around tree trunk is a kind of motor system useful for movement, posture control and tree reshaping after accidents.

Rather young trees are able to restore the verticality of their trunk after accidental rotation of the soil-root system due to wind or some landslide, leading to typical basically curved stems shape. The very high dissymmetry of forces for the motor action is associated with the occurrence of reaction wood on one side of the inclined stem during many successive years.

A selection of 17 such trees coming from 15 different species (13 different families), tropical or temperate, hardwoods or softwoods, were selected and peripheral residual strains were measured in situ before felling, on 8 positions for each stem. Associated wooden rods were sawn and measured for their mechanical and physical properties at green and dry state, allowing the estimation of tree growth stresses i.e. forces created by the living wood.

Thanks to the wide range of wood types, species and basic densities, simple and highly significant formulas are found for the relationship between green and dry wood properties such as density, longitudinal modulus of elasticity, specific modulus and two shearing modulus of elasticity. It was also possible to build easy to use conversion coefficients between growth stress indicator (GSI), measured in situ by the single hole method, and growth strain and growth stress with the knowledge of basic density and green longitudinal elastic modulus.

38 Growth strains, specific modulus and longitudinal shrinkage are indicators of the fibre wall
 39 properties independent from basic density. Combined to density, they offer a good set of
 40 variables in order to study growth strategy (strains and stresses) and important wood
 41 properties. Compression wood, normal wood and tension wood describe a continuum for
 42 growth strains but do not appear as a continuum for their relationships with the tree
 43 indicators. There should be other basic differences separating these wood types, in the
 44 chemical composition of the matrix and the ultrastructure of cellulose microfibrils.

45 Apart from compression wood, density, specific modulus and longitudinal shrinkage are
 46 largely inefficient for the prediction of growth stresses and a large experimental study is
 47 needed, at first on normal wood only, to investigate chemical determinants of growth stains.

48 **Keywords**

Not following the argument

49 Force genesis; growth strains; modulus of elasticity; wood shrinkage; tree biomechanics;
 50 wood

51 **Abbreviations and notations**

52	MOE, MOE	modulus of elasticity in L direction
53	E_g	green MOE
54	E_d	air-dry MOE
55	E, E_L	Longitudinal modulus
56	G, G_{TL}, G_{RL}	Shear modulus
57	ρ	density
58	BD	basic density
59	DD	dry density
60	k	factor for shear contribution (5/6 for rectangular cross section)
61	SM, SM	specific modulus
62	SM_b	basic SM
63	E_L/ρ	SM in L direction
64	$E_L/G_{TL}, E_L/G_{RL}$	anisotropy factor
65	GSI	growth stress indicator
66	α_m	maturation strain
67	σ_m	maturation stress
68	ϕ	conversion factor α_m/GSI
69	ψ	conversion factor σ_m/GSI
70	L, R, T	longitudinal, radial, tangential directions
71	L_k, R_k, T_k	dimension in L, R, T direction for condition k
72	M	mass

73	DP_x	distance to pith
74	RH	relative humidity
75	MC, MC	wood moisture content
76	VS, LS	volumetric, linear shrinkage
77	FSP	fibre saturation point
78		

Language needs work

79 Introduction

80 Tree biomechanics deal with the analysis of mechanical problems encountered by living trees,
 81 including multiphysical couplings between the deformations and movements due to external
 82 forces and the biology of cell formation and growth. A typical case is the classical experiment
 83 of inclining a young tree at the beginning of cambial activity in Spring (Thibaut et al 2001,
 84 Thibaut 2019). In agreement with the physics of viscoelastic materials, the immediate
 85 response is a downward elastic flexure followed by a slow downward creep flexure during the
 86 first 24 hours. But 5 days later the terminal shoot straightens vertically and 3 months later,
 87 apart from a significant growth in length at the apical side, the existing stem shows a change
 88 of curvature (restoration of verticality) opposite to the physical model prediction. The
 89 biological process of wood growth, both in length (primary growth) and in diameter
 90 (secondary growth) should be added to the physical model through appropriate biological
 91 state variables complementing the physical state variables. Based on the functions of living
 92 wood during the three successive phases of cell division, cell wall expansion and cell wall
 93 thickening, three sets of biological variables can be set, in relation to geometrical changes,
 94 mass changes and force generation.

95 Geometrical and mass changes are rather well documented in the literature on tree growth
 96 (Trouvé et al 2015, Fourcaud et al 2008, Deleuze & Houillier 1997, Chave et al 2005). Their
 97 related variables depend on time, genetic growth patterns (architectural model and wood
 98 anatomy) and adaptation to environment (climate, tree spacing ...). Forces are needed to
 99 enhance bending strength through pre-stressing (Alméras et al 2018, Gril et al 2017, Thibaut
 100 et al 2001) and to create motor systems (Alméras et al 2005b, Alméras & Clair 2016, Coutand
 101 et al 2007) allowing posture control (vertical or inclined growth) or tree shape restoration
 102 after accidents (apex breaking, rotation of root system ...). They are generated during fibre (or
 103 tracheid) wall thickening (Mellerowicz et al 2001, Plomion et al 2001, Gorshkova et al 2012)
 104 and their level is adapted to the mechanical needs of the tree: high level for slender trees
 105 (Loup et al 2013), with a clear asymmetry between two opposite faces of the wooden axis
 106 when a motor action is needed (Alméras et al 2005b, Moulia et al 2006, Fournier et al 2014).
 107 In the most asymmetrical situation, one side is made of the so-called reaction wood (Gardiner
 108 et al 2014), that differs from normal wood in terms of cell wall ultrastructure and chemical
 109 composition (Côté & Timell 1969, Dadswell & Wardrop 1955, Timell 1986, Yeh et al 2005, Yeh
 110 et al 2006, Ruelle et al 2007, Fagerstedt et al 2014) for the same tree. This is illustrated in
 111 Table 1 for the case of softwoods, with normal wood - comprising opposite wood, lateral wood,
 112 juvenile wood, mature wood or flexure wood - clearly distinct from any type of compression
 113 wood.

This section is not very clearly written. The point the authors want to make is not clear

- ① What is the "physical model prediction"
- ② Why not illustrate this for the reader

114 Table 1 Lignin content for different softwood types

Author	Species	Origin	NW	OW	FW	JW	CW	mCW	sCW	JCW
Brennan et al 2012	Radiata pine		29	27.6	28.7		34.8			
Nanayakkhara et al 2009	Radiata pine	R3+4		27.9				32.9	38.6	
Nanayakkhara et al 2009	Radiata pine	R10		27.3				31.4	35.4	
Nanayakkhara et al 2009	Radiata pine	R15+16		27.1				31.3	35.6	
Nanayakkhara et al 2009	Radiata pine	R1		30			31.6			
Nanayakkhara et al 2009	Radiata pine	R2		27.7			34.9			
Nanayakkhara et al 2009	Radiata pine	Trunk		27			37			
Nanayakkhara et al 2009	Radiata pine	Branch		30.7			39.6			
Funda et al 2020	Scot's pine	Trunk	27.6			27.7				
Yeh et al 2005	Loblolly pine	T. Control	29.4							
Yeh et al 2005	Loblolly pine	T. Windy		28.9			36			
Yeh et al 2005	Loblolly pine	T. Bent		29.1			36.6			
Yeh et al 2006	Loblolly pine	T. Top				29.6				
Yeh et al 2006	Loblolly pine	T. Bottom	27.4			28.5				
Yeh et al 2006	Loblolly pine	T. Middle		28.4		28.6	37.4			37.5
115 Mean			28.4	28.3	28.7	28.6	36.0	31.9	36.5	37.5

116 Rx: ring number from pith; T.: trunk
 117 NW: normal wood; OW: opposite wood; FW: flexure wood; JW: juvenile wood
 118 CW: compression wood; mCW: mild compression wood; sCW: severe compression wood;
 119 JCW juvenile compression wood
 120 Bold characters: different lignin content in CW

121 Three parameters can be adjusted during cell wall thickening to fulfil the biomechanical needs
 122 of the tree: final cell wall thickness, orientation of cellulosic reinforcements, chemical
 123 composition of cell wall polymers. As a result of this adaptation, variations of physical and
 124 mechanical properties can be observed in the wood produced by the tree. In this project, trees
 125 from various species and exhibiting active biomechanical movements were selected.
 126 Laboratory tests on standard wood specimens sawn from the felled log were related to in-situ
 127 residual strain measurements that characterize the biomechanical action of the formed wood,
 128 covering as large a range of situations as possible.

129 **Material and methods**

① What do you mean. Range of climate, slope, tree age

130 *Selection of standing trees*

131 Biomechanical studies (Yoshida et al 2000, Jourez et al 2001b, Thibaut et al 2001, Coutand et
 132 al 2007, Gril et al 2017) proved that young trees artificially inclined at angles above 20° restore
 133 progressively their verticality through the production of reaction wood (RW), either tension
 134 wood (TW) on the top or compression wood (CW) on the bottom of the inclined stem. Wood
 135 produced on other sides of the stem after inclination, either laterally or opposite, has quite
 136 similar features both for anatomy and chemical composition. While restoring verticality, the
 137 trees share a common type of bottom geometry with a basal curvature (Clair et al 2006). In
 138 natural conditions, accidental inclination of the whole tree by root system rotation due to
 139 strong wind or landslide can be observed, mostly for young trees. When these trees restore
 140 verticality in the following years they share the same type of bottom geometry (Fig. 1). They

② Share with what?

141 can be considered as natural experiments, and all trees were firstly selected based on this
 142 criterion.

143 To observe a wide diversity of situations, eleven trees were first selected in a tropical rain
 144 forest of French Guiana with the help of the botanical expert M.F. Prévost, each from a
 145 different family - one tree per species and one species per family. Three poplar trees and three
 146 conifer trees (spruce and pines) from temperate forest in France and China were added to the
 147 sampling in order to widen the selection (Table 2). For the spruce tree, two logs corresponding
 148 to two *GSI* measurement levels (see below) where used, at 1m distance from each other. The
 149 mean diameter at breast height of these 17 trees was 26.5 cm.

150 Table 2 List of trees used in the study

Code	Family	Genus	Species	DBH	RW
1	Melastomataceae	Miconia	fragilis	23.6	GL
2	Meliaceae	Carapa	procera	23.4	GL.
3	Lecythidaceae	Eschweilera	decolorens	23.8	LGL
5	Vochysiaceae	Qualea	rosea	30.3	LGL
7	Cecropiaceae	Cecropia	sciadophylla	25.3	GL
8	Lauraceae	Ocotea	guyanensis	30.9	GL.
9	Flacourtiaceae	Laetia	procera	29.4	GLc.
11	Bignoniaceae	Jacaranda	copaia	21.7	NGL
12	Myristicaceae	Virola	surinamensis	20.4	NGL.
14	Cesalpiniaceae	Eperua	falcata	27.9	GL.
15	Simaroubaceae	Simaruba	amara	27.7	NGL.
16	Salicaceae	Populus	hybrid	38.3	GL
17	Salicaceae	Populus	hybrid	34.8	GL
18	Salicaceae	Populus	hybrid	25.4	GL
E1	Pinaceae	Picea	abies	24.9	CW
E3	Pinaceae	Picea	abies	24.9	CW
PM	Pinaceae	Pinus	pinaster	20.1	CW
PS	Pinaceae	Pinus	sylvestris	23.0	CW
	Mean			26.4	

So they were selected to have approximately the same dbh

151
 152 DBH: diameter at breast height of the trees in cm
 153 RW, reaction wood type: GL= tension wood (TW) with gelatinous layer, LGL = TW with a lignified G
 154 layer, GLc= TW with a multilayer G layer, NGL= TW with no G layer, CW= compression wood

155 *In situ measurements of maturation strain*

156 According to elastic models of residual strain field inside the trunk (Fournier et al 1994a,
 157 Fournier et al 1994b), the peripheral longitudinal strain locked in recently formed wood is
 158 directly associated to the maturation force just before fibre death (Thibaut 2019). This
 159 "maturation strain" α_m is related to the "maturation stress" σ_m by Hooke's law $\sigma_m = MOE * \alpha_m$,
 160 where *MOE* is the modulus of elasticity (*MOE*) of mature wood in the longitudinal direction.
 161 Several techniques exist for in situ estimation of maturation strain at periphery (Yoshida &
 162 Okuyama 2002) Clair et al 2013, Yang et al 2005). Here the CIRAD single-hole method was
 163 used. Two pins are inserted in the trunk surface in longitudinal alignment at 45mm distance
 164 (Jullien 2013). This distance is measured with a linear displacement transducer before and
 165 after drilling a hole of diameter 20mm and depth about 20mm in the middle between the two
 166 pins. The difference in μm between after and before drilling is called growth stress indicator

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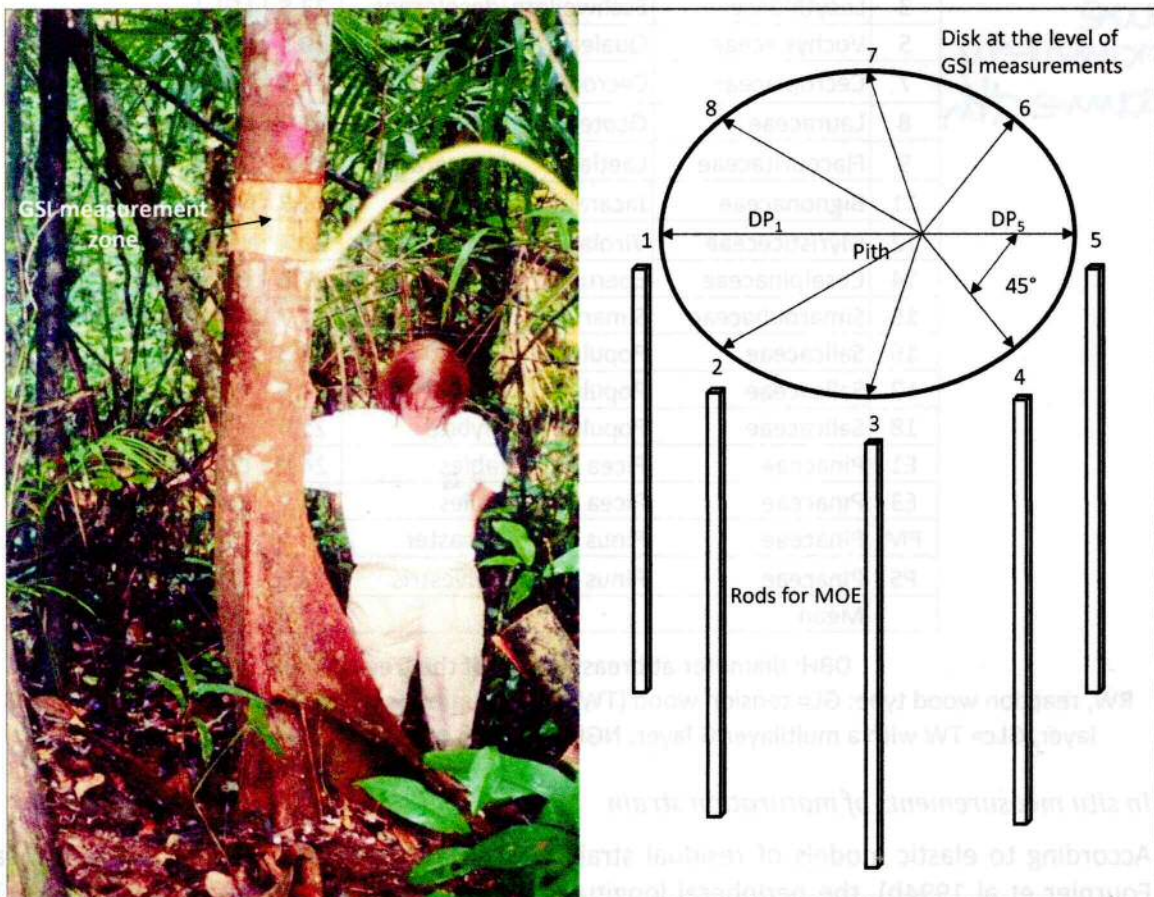
167 (GSI); it is positive for a tension force and negative for a compression force. Eight GSI
 168 measurements are performed on each tree or tree level, equally spaced around the
 169 circumference, beginning by the top of the inclined trunk for hardwoods, where tension wood
 170 is expected, or by the bottom for softwoods, where compression wood is expected.

171 GSI is theoretically (Archer 1984) related to maturation strain α by the relationship:

172
$$\alpha_m = \phi * GSI, \alpha \text{ in microstrain } (\mu\epsilon = 10^{-6}), GSI \text{ in } \mu\text{m}, \phi \text{ in } \mu\epsilon/\mu\text{m}$$

173 where the calibration factor ϕ is calculated by modelling the drilling of an anisotropic material
 174 occupying a half plane, though a complex equation using wood elastic constants and
 175 geometrical factors (distance between pins and hole diameter), see Annex. For various species
 176 Baillères (1994) found ϕ values ranging from - 10 to - 15 $\mu\epsilon/\mu\text{m}$, and Jullien (2013) used - 12.9
 177 $\mu\epsilon/\mu\text{m}$ for beech.

178 *Wood specimens for physical and mechanical properties measurements.*



179 Fig. 1 Tree measured in French Guiana, wooden disk and rods sawn for each tree
 180
 181 DP_x : distance to pith from the x GSI point

182 Just after cutting each tree, a disk (2cm thick) was crosscut at the level of GSI measurements
 183 (Fig. 1). Distance from pith to bark (DP_x) for each GSI measurement position was measured.
 184 Eight longitudinally oriented rods were sawn just above the disk, at the 8 GSI positions, the
 185 closest possible to the bark, few days after tree falling, in CIRAD worksp in Kourou. The
 186 dimensions of the rods were 500mm (L, longitudinal direction) x 25mm (R, radial direction) x
 187 25mm (T, tangential direction) and they were kept in green state, wrapped in food-grade

①. This is only for the tropical wood

188 transparent cellophane, until the measurement of green MOE (E_g). A total of 144 rods were
189 prepared.

190 A smaller rod (50mm x 25 mm x 25 mm) was cut from these long rods for shrinkage study
191 after E_g measurement.

192 The remaining long rods (430mm x 25 mm x 25mm) were air dried in the conditioned chamber
193 at 65 % air relative humidity (RH) and 20°C temperature until equilibrium, corresponding to
194 wood moisture content (MC) around 13%. The MOE was again measured on the air-dry rods
195 as such giving a "crude" air-dry MOE. Rods were then planed on four sides to get standard air-
196 dry rods (400mm x 20mm x 20mm) and standard air-dry MOE (E_d) was measured again.

197 MOE measurements

198 The flexure free-free vibration method analysed with Timoshenko model (Bordonné 1989,
199 Brancheriau & Baillères 2002) was used for all measurements. Dimensions in the 3 directions
200 (L, R, T) and mass (M) of the rods was measured with a good precision (0.1%). The rod was put
201 on 2 thin wires at the first vibration mode positions and tapped at one end, successively on
202 the radial (TL) and tangential (RL) face, corresponding to the RL and TL hitting plane,
203 respectively. The resonant frequency f_i was measured for the three first vibration modes (f_1 ,
204 f_2 , f_3). Using the approximate solution of free vibration theory of Timoshenko, Bordonné
205 (1989) proved that two useful variables x_i and y_i can be built from f_i frequencies, theoretically
206 linked by the expression:

$$207 \quad y_i = E/\rho - x_i * E / (k * G)$$

208 where E is the axial MOE of the rod (the MOE in L direction), G the shear modulus in the hitting
209 plane (G_{TL} or G_{RL} , depending on the orientation of the rod on the wires), ρ the rod density and
210 k a fixed factor. The 3 frequencies (f_1 , f_2 , f_3) give 3 points of coordinates (x_i , y_i) allowing to fit
211 the equation of a straight line with a regression coefficient that should be very close to 1.0.
212 The slope, the most sensitive to defects, and the intercept of the regression line are $-E/(k * G)$
213 and E/ρ , respectively. E/ρ is the specific modulus (SM) and equals to the square of sound
214 speed in L direction (unit m^2/s^2) while the ratio E/G (E_L/G_{TL} or E_L/G_{RL}) describes elastic
215 anisotropy and is useful for the calculation of ϕ . Density is calculated as mass to volume ratio
216 $\rho = M / (L * R * T)$ and MOE by the formula $E = SM * \rho$. Then G can be derived from E and $E/k * G$,
217 with $k=5/6$ for this geometry (Brancheriau & Baillères 2002).

218 Basic density and shrinkage measurements.

219 Wood density depends on wood moisture content (MC). Basic density (BD), the ratio between
220 anhydrous mass and green volume, is a well-defined parameter characterizing wood
221 honeycomb structure. Wood volume remains constant for green wood until the beginning of
222 drying, while green moisture content (MC_g) can vary widely, typically between 30% and 80%.

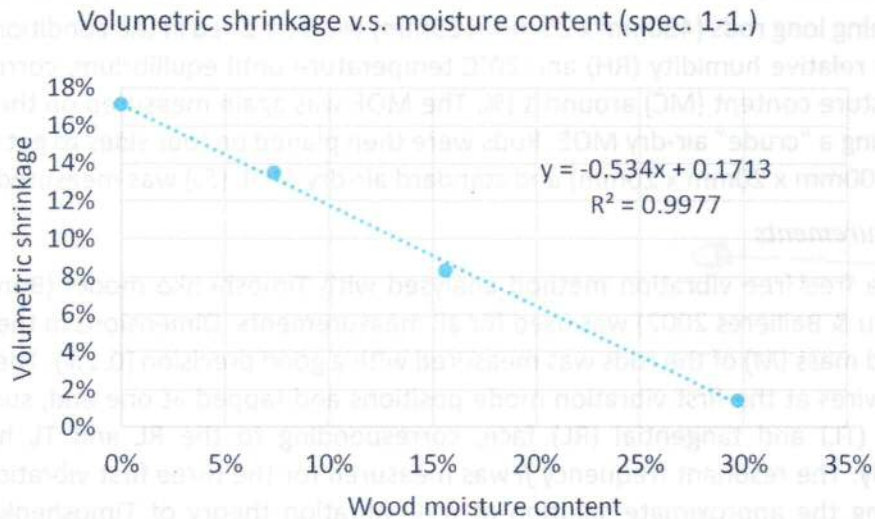
223 Shrinkage behaviour of wood (Glass & Zelinka 2010) is necessary to establish relationships
224 between BD and dry density at a given moisture content (12% for example). This shrinkage
225 begins at a reference MC called fibre saturation point (FSP) and is maximum for anhydrous
226 state ($MC_0 = 0\%$). In order to measure FSP and shrinkage rate, the small rod ($L=50mm$ x
227 $R=25mm$ x $T=25mm$), initially green, is positioned successively in 3 conditioned chambers at
228 decreasing RH ($RH = 80\%$, 65% , 30%) and room temperature ($T=20^\circ C$), then finally in an oven
229 at $103^\circ C$ to obtain the anhydrous state. For each five conditions, mass (M_k) and dimensions
230 L_k , R_k , T_k are measured. The moisture content is calculated as $MC_k = (M_k - M_0) / M_0$ where $k=0$

- ① Dynamic MOE is always higher than that obtained by bending
② Varies with time of year.

With
micrometer?

the

231 denote the anhydrous state. The volume is derived from the rod dimension using the formula:
 232 $V_k = L_k * R_k * T_k$, and volumetric shrinkage (VS) at each moisture content is calculated by the
 233 formula: $VS_k = (V_g - V_k) / V_g$. All the points of coordinates (MC_k, VS_k) are aligned along a straight
 234 line of equation $y = VS - x * VS / FSP$ (Fig. 2) where VS is the total volumetric shrinkage.



235 Fig. 2 Measurement of volumetric shrinkage and fibre saturation point

236

237 Spec. 1-1.: specimen taken at the first GSI position for species Miconia fragilis
 238 The intercepts between this straight line and y and x axes are the values of VS and FSP,
 239 respectively. The total linear shrinkage in direction L (LS) is calculated by the formula: $LS = (L_g -$
 240 $L_0) / L_g$, L_g and L_0 being the length of the rod in green and anhydrous state, respectively.

241 **Results**

242 *Relationships between green and dry properties*

243 Because there are more published data on dry than green wood, it is interesting to look at
 244 relationships between values of useful properties for tree biomechanics (green state) and
 245 wood mechanics (dry state). Concerning the green state, MC_g was on average 89%, ranging
 246 from 38% to 182% (39% to 155% as tree average) and was strongly dependant on wood
 247 density. The dry state, here, refers to the condition of the specimens after a long storage in a
 248 room controlled for temperature ($T = 21^\circ C$) and air relative humidity ($RH = 65\%$). The
 249 corresponding equilibrium MC (MC_d) ranged from 12% to 16% depending on the species and
 250 wood type within the species.

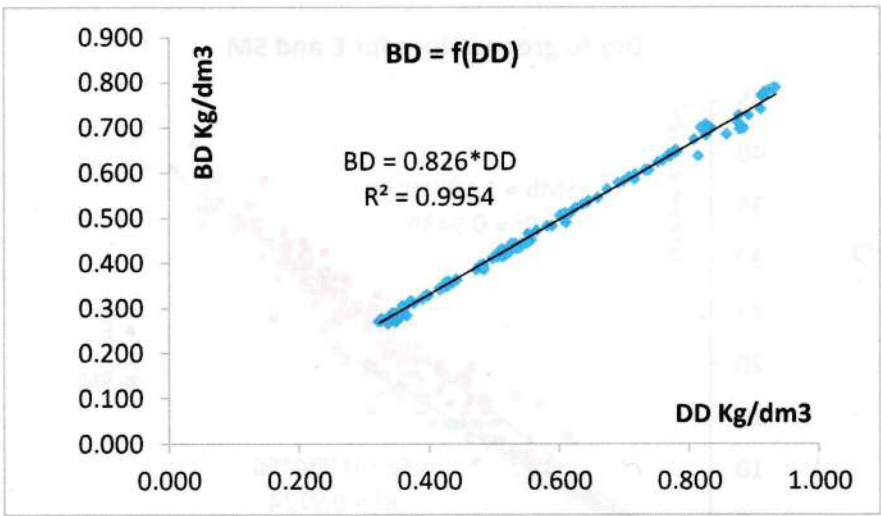
251 For density, green density depending strongly on the seasonal variations of free water content
 252 in the xylem, BD is mostly used instead. The usual proportional relationship, with a very high
 253 coefficient of determination, was observed between BD and dry density (DD) for this sampling
 254 (Fig 3). The proportionality coefficient (BD/DD) had a mean of 0.826 and ranged from 0.77 to
 255 0.86. It depended mainly on the total volumetric shrinkage (VS) (Fig 4).

256

How do you obtain FSP from this graph italic's

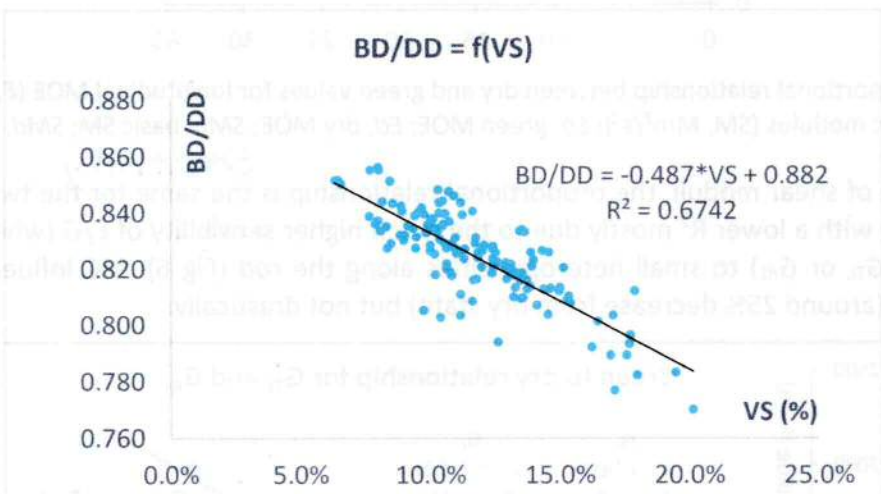


Graphs are not publication quality



257
258

Fig. 3 Proportional relationship between dry and basic density



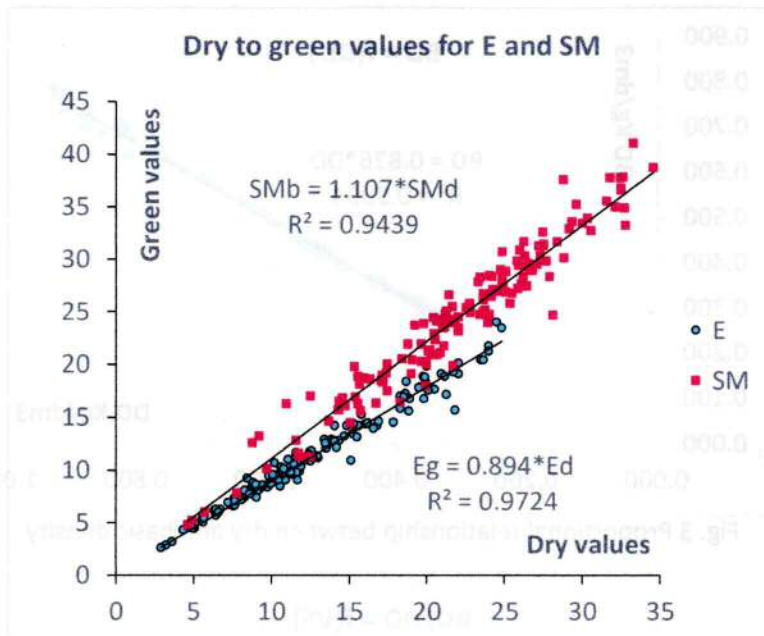
259
260

Fig. 4 Dependence of the basic to dry density ratio to the total volumetric shrinkage.

261 For longitudinal elastic modulus (E), specific modulus (SM) and shear moduli (G_{TL} and G_{RL}),
262 there is also a proportional relationship between green and dry values. The determination
263 coefficient (R^2) is very high for E and SM (Fig. 5) and the influence of MC is relatively small
264 (around 10% decrease from dry state).

What is the purpose of these comparisons?

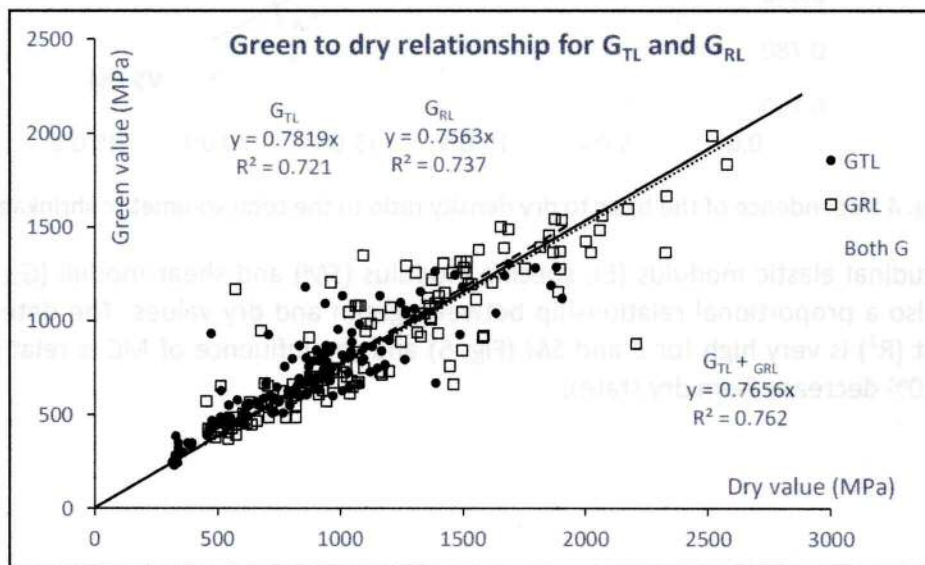
Specific modulus?
 $SM = E/g$



265
 266
 267

Fig. 5 Proportional relationship between dry and green values for longitudinal MOE (E , MPa) and specific modulus (SM , Mm^2/s^2); E_g : green MOE; E_d : dry MOE; SM_b : basic SM; SM_d : dry SM.

268 In the case of shear moduli, the proportional relationship is the same for the two directions
 269 (TL and RL) with a lower R^2 mostly due to the much higher ^{Sensitivity} sensitivity of E/G (where G stands
 270 for either G_{TL} or G_{RL}) to small heterogeneities along the rod (Fig 6). MC influence is more
 271 important (around 25% decrease from dry state) but not drastically.



272
 273

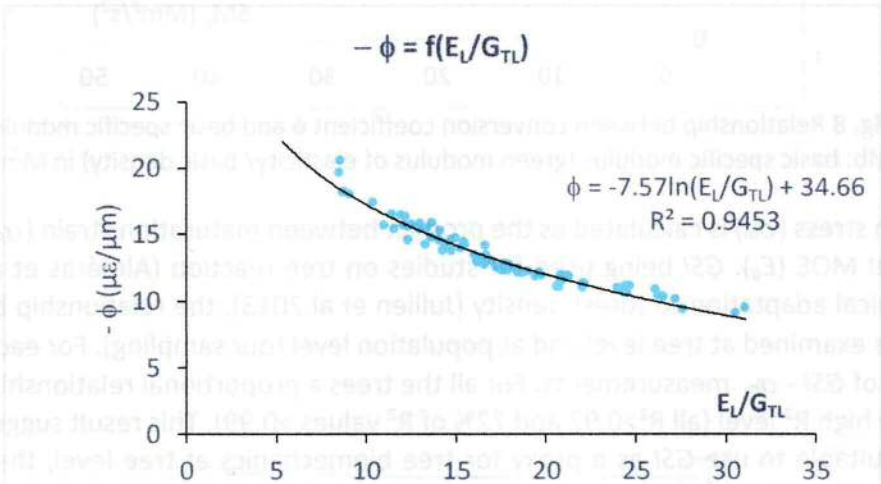
Fig. 6 Proportional relationship between dry and green shear moduli

274 Estimation of maturation strains and stresses
 275 Using the single hole method to estimate residual strains in an orthotropic material requires
 276 the calculation of the conversion parameter ϕ as described in Archer (1984). Baillères in his
 277 PhD thesis (1994) used this calculation for 13 different species. Using elastic orthotropic
 278 constants coming from statistical models built by Guitard and El Amri (1987), he obtained ϕ
 279 values ranging from - 9.1 to - 14.9 $\mu\epsilon/\mu m$. However, special wood types such as RW were not

① Should not be in Results. Should be in Materials + Methods

280 considered. Besides, we do not have the 9 elastic constants for the different species and wood
 281 types (NW and RW) of this study. From Guitard and El Amri and other literature we have built
 282 a data collection of the 6 diagonal moduli (E_L , E_T , E_R , G_{LT} , G_{LR} , G_{TR}) for different species with
 283 known densities. We estimated the non-diagonal constants (ν_{LT} , ν_{TL} , ν_{LR} , ν_{RL} , ν_{RT} , ν_{TR}) using
 284 Guitard's statistical models and then made the whole calculus of ϕ values for these 96 cases
 285 (Excel sheet in annex 1). In order to make that calculus, we have to find the 2 solutions of a
 286 second degree equation, which is not possible if the determinant is negative. That happens
 287 for a few cases (8 with very low E/G values). There was a very high correlation level between
 288 ϕ and the ratio E/G_L and a logarithmic equation gives a very high R^2 (Fig.7). This equation: $-\phi$
 289 $= -77.57 \cdot \ln(E/G) + 34.665$ can be used to calculate ϕ with only one anisotropic ratio.

This is not results



290
291

Fig. 7 Relationship between conversion coefficient ϕ and anisotropic ratio (E/G_{TL}).

292 However, reliable shear moduli data are not always available, so that an alternative method
 293 to estimate ϕ is needed. Using the previous formula for the 144 GSI measurements, it appears
 294 that the calculated ϕ was also very well related ($R^2 = 0.81$) to the basic specific modulus (SMB),
 295 the ratio between Eg and BD (Fig. 8). The higher dispersion around the regression line can be
 296 explained by higher uncertainty of G measurement as compared to E . Finally, this last formula:
 297 $-\phi = -0.4811 \cdot SMB + 25.45$, was used for all specimens. For the very large range of specific
 298 modulus (from 4.6 to 34.6 Mm^2/s^2 for a sampling including RW instead of the usual range
 299 between 15 to 30 Mm^2/s^2 corresponding to NW only) the range of ϕ values is rather large, -
 300 5.8 to - 23 $\mu\epsilon/\mu m$ instead of - 9.1 to - 14.9 $\mu\epsilon/\mu m$ in Baillères (1994).

So you estimate ϕ and then correlate it with something you can measure?

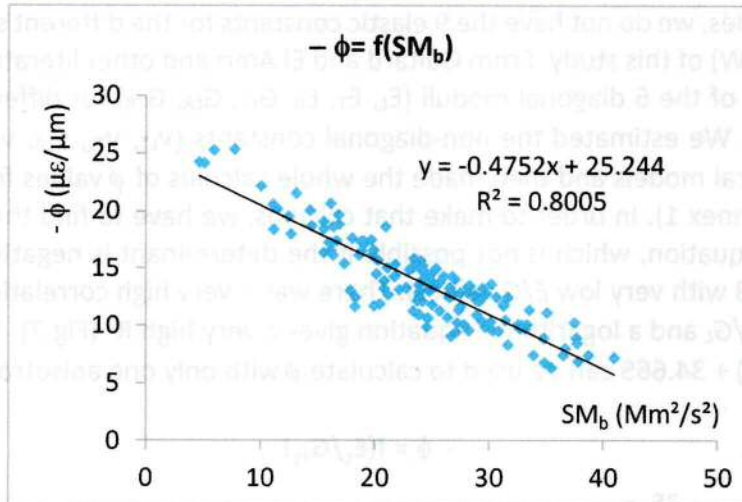


Fig. 8 Relationship between conversion coefficient ϕ and basic specific modulus. SMb: basic specific modulus (green modulus of elasticity/ basic density) in Mm^2/s^2

301
302
303

304 Maturation stress (σ_m) is calculated as the product between maturation strain (α_m) and green
305 longitudinal MOE (E_g). *GSI* being used for studies on tree reaction (Almérás et al 2005b) or
306 biomechanical adaptation to forest density (Jullien et al 2013), the relationship between *GSI*/
307 and σ_m was examined at tree level and at population level (our sampling). For each tree there
308 are 8 pairs of *GSI* - σ_m measurements. For all the trees a proportional relationship was found
309 with a very high R^2 level (all $R^2 > 0.97$ and 72% of R^2 values > 0.99). This result suggests that it is
310 perfectly suitable to use *GSI* as a proxy for tree biomechanics at tree level, the conversion
311 factor $\psi = \sigma_m / \text{GSI}$ (in $\text{MPa}/\mu\text{m}$) ranging from 0.064 to 0.259 depending on the species (Table
312 3).

313

Table 3 Mean values of parameters per tree

Genus	Species	BD	SMb	Eg	ψ	R^2
Miconia	fragilis	0.71	26.92	19.0	0.232	0.9997
Carapa	procera	0.61	24.87	15.2	0.203	0.9941
Eschweilera	decolorens	0.78	25.92	20.2	0.259	0.9996
Qualea	rosea	0.56	21.29	12.1	0.199	0.9936
Cecropia	sciadophylla	0.35	34.95	12.3	0.107	0.9788
Ocotea	guyanensis	0.46	27.20	12.7	0.156	0.9903
Laetia	procera	0.66	21.97	14.4	0.218	0.9979
Jacaranda	copaia	0.42	22.14	9.2	0.132	0.9916
Virola	surinamensis	0.29	36.89	10.8	0.084	0.9954
Eperua	falcata	0.70	22.99	16.1	0.234	0.9975
Simaruba	amara	0.30	28.40	8.4	0.096	0.9976
Populus	hybrid	0.29	28.04	8.2	0.110	0.9724
Populus	hybrid	0.34	29.19	9.8	0.114	0.9903
Populus	hybrid	0.38	19.37	7.4	0.128	0.9823
Picea	abies	0.51	20.61	10.0	0.152	0.9933
Picea	abies	0.49	18.10	8.4	0.142	0.9989
Pinus	pinaster	0.42	10.68	11.4	0.064	0.9793
Pinus	sylvestris	0.45	15.88	4.1	0.108	0.9882

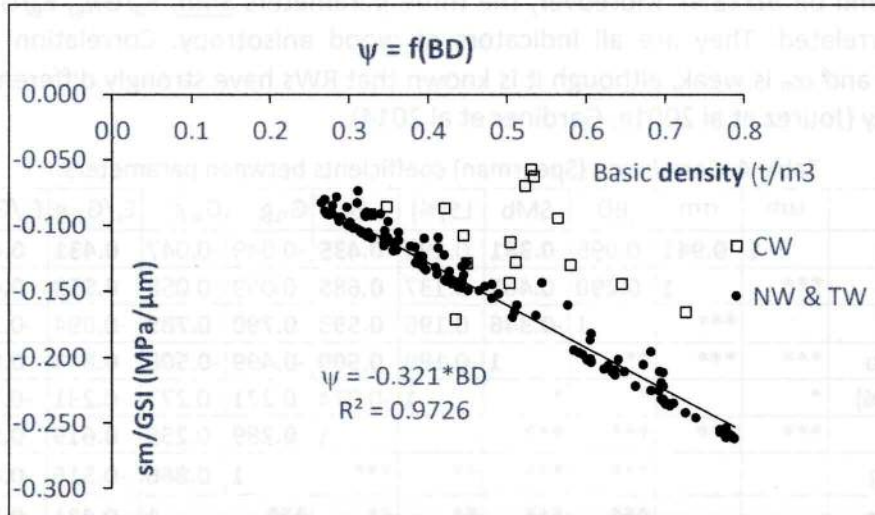
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BD: basic density (Kg/dm^3); SMb: basic specific modulus (Mm^2/s^2); Eg: green elastic modulus (GPa);

- ①. *GSI* is not a proxy for tree biomechanics. It is a measure of growth stresses
- ② No measure of uncertainty! Is this because there was only one tree per species?

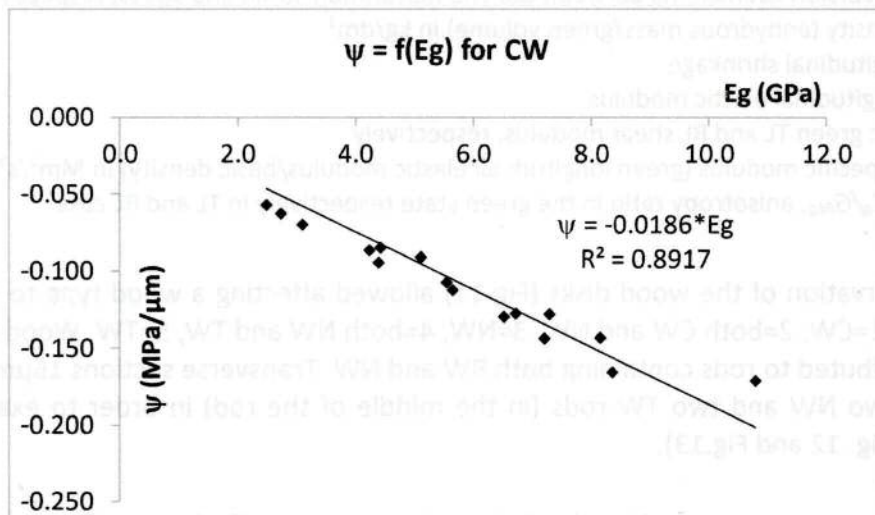
316 ψ : conversion coefficient for maturation stress (in MPa/ μm); R^2 regression coefficient of the
 317 proportional relationship between σ_m and GSI within the tree.

318 The global relationship between the conversion coefficient and BD , for all positions in all trees,
 319 shows a very good proportional relationship ($R^2=0.97$) when rods containing compression
 320 wood are excluded (Fig. 9). When no measurement of green elastic modulus is available, basic
 321 density can be used to calculate the basic specific modulus and then have a good estimation
 322 of the coefficient factor for maturation strain, this simple formula: $\sigma_M = -0.321 * BD * GSI$ (σ_M in
 323 MPa, BD in kg/dm^3 and GSI in μm) can be used for all cases when there is no compression
 324 wood in the measurement zone.



325
 326 Fig. 9 Relationship between conversion coefficient for maturation stress (ψ) and basic density (BD).
 327 ψ : conversion coefficient for maturation stress (MPa/ μm); BD : basic density (Kg/dm^3);
 328 CW: compression wood; NW: normal wood (hardwood & softwood); TW: tension wood

329 This is not true for positions with compression wood. A very good proportional relationship
 330 ($R^2=0.89$) appears between the conversion coefficient and the modulus of elasticity (Fig. 10),
 331 but when the green elastic modulus is available, together with basic density, it is possible to
 332 use the conversion coefficient ϕ for maturation strain and then calculate σ_M .



333
 334 Fig. 10 Relationship between conversion coefficient for maturation stress
 335 and green modulus of elasticity, for compression wood

① How identified? Visually?

336 ψ : conversion coefficient for maturation stress (MPa/ μm)
 337 E_g : longitudinal modulus of elasticity at green state (GPa)

338 *Force generation and longitudinal wood properties*

339 The maturation stress σ_m is the force created by the living wood per unit surface. It is the
 340 product of the maturation strain (α_m) and the green L MOE (E_g), itself the product of basic
 341 density (BD) and basic specific modulus (SM_b). BD , SM_b and α_m are the parameters resulting
 342 from the activity of the living wood until fibre death.

343 A correlation analysis (Table 4) shows that σ_m is mostly dependant on α_m ($R^2=88\%$) then on
 344 SM_b (22%) and on BD (8%). Moreover, the three parameters SM_b , E_g/G_{TLg} , E_g/G_{RLg} are very
 345 strongly correlated. They are all indicators of wood anisotropy. Correlation coefficients
 346 between LS and α_m is weak, although it is known that RWs have strongly different values for
 347 this property (Jourez et al 2001a, Gardiner et al 2014).

348 Table 4: Correlation (Spearman) coefficients between parameters.

	α_m	σ_m	BD	SM_b	$LS(\%)$	E_g	G_{TLg}	G_{RLg}	E_L/G_{TLg}	E_L/G_{RLg}
α_m	1	0.941	0.095	0.381	0.196	0.435	-0.049	-0.047	0.431	0.422
σ_m	***	1	0.290	0.467	0.137	0.685	0.059	0.058	0.559	0.495
BD		***	1	-0.346	0.196	0.593	0.790	0.783	-0.094	-0.178
SM_b	***	***	***	1	-0.189	0.500	-0.499	-0.508	0.843	0.828
$LS(\%)$	*		*	*	1	-0.074	0.271	0.277	-0.231	-0.175
E_g	***	***	***	***		1	0.289	0.255	0.619	0.534
G_{TLg}			***	***	**	***	1	0.866	-0.516	-0.473
G_{RLg}			***	***	**	**	***	1	-0.421	-0.587
E_L/G_{TLg}	***	***		***	**	***	***	***	1	0.877
E_L/G_{RLg}	***	***	*	***	*	***	***	***	***	1

349
 350 Bold characters: correlation significant at 0.001

351 ***: correlation significant at 0.001 **: correlation significant at 0.01

352 *: correlation significant at 0.05

353 α_m : maturation strain in micro-deformation; σ_m : maturation stress in MPa

354 ϕ and ψ : conversion coefficients between GSI and maturation strain and stress, respectively

355 BD : basic density (anhydrous mass/green volume) in kg/dm^3

356 LS : total longitudinal shrinkage

357 E_g : green longitudinal elastic modulus

358 G_{TLg} and G_{RLg} : green TL and RL shear modulus, respectively

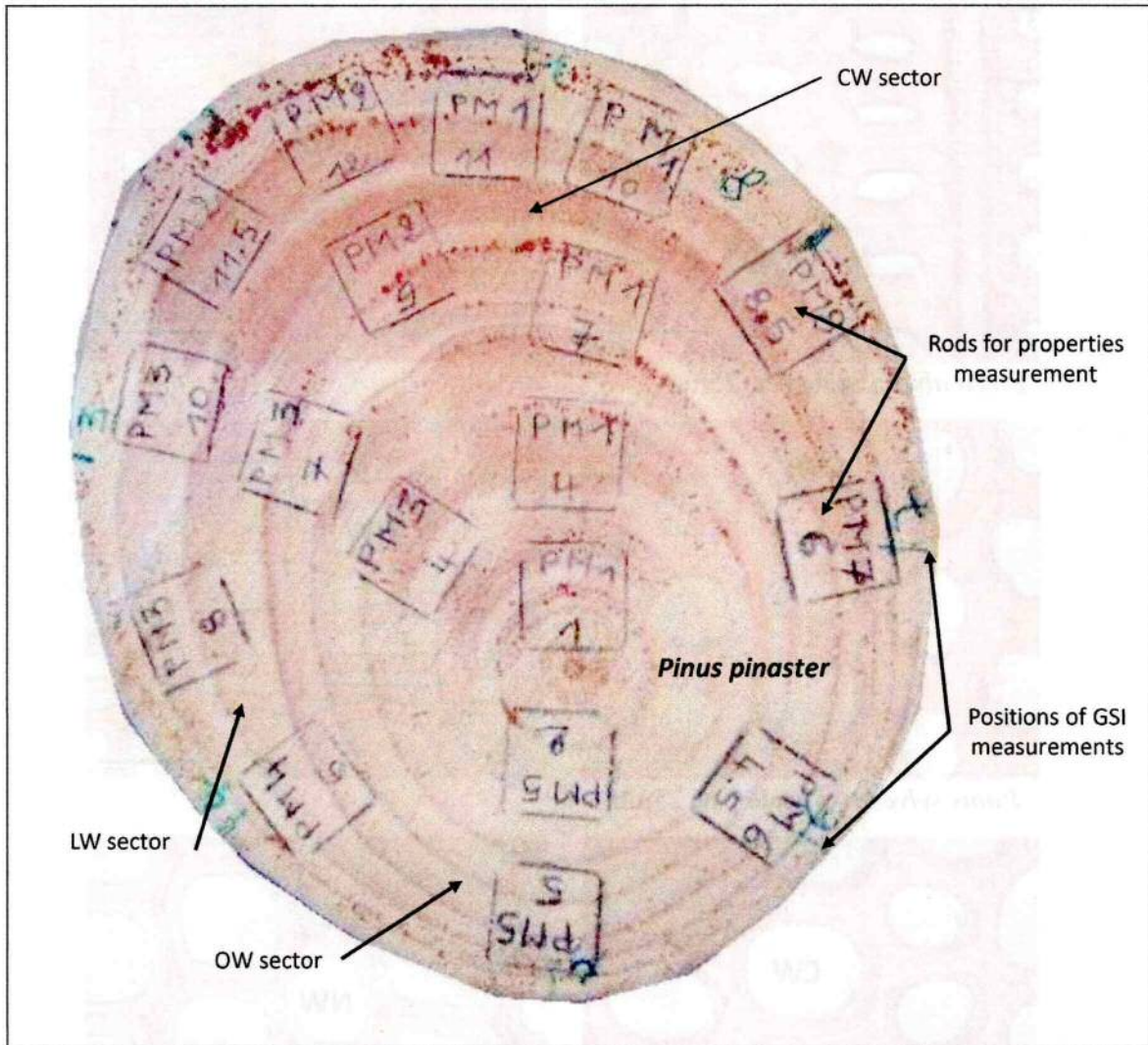
359 SM_b : basic specific modulus (green longitudinal elastic modulus/basic density) in Mm^2/s^2

360 E_g/G_{TLg} and E_g/G_{RLg} : anisotropy ratio in the green state respectively in TL and RL case

361

362 Visual observation of the wood disks (Fig 11) allowed affecting a wood type to each tested
 363 specimen: 1=CW, 2=both CW and NW, 3=NW, 4=both NW and TW, 5=TW. Wood types 2 and
 364 4 were attributed to rods containing both RW and NW. Transverse sections $15\mu\text{m}$ thick were
 365 cut from two NW and two TW rods (in the middle of the rod) in order to examine wood
 366 anatomy (Fig. 12 and Fig.13).

① Are you suggesting green LMOE is NOT a basic property of the wood



367
368
369
370

Fig. 11 Image of the section of *Pinus pinaster* tree with the positions of measurements
 CW: compression wood, OW: opposite wood, LW lateral wood
 The tree is young hence all wood can be considered as juvenile wood (JW)

What height on tree

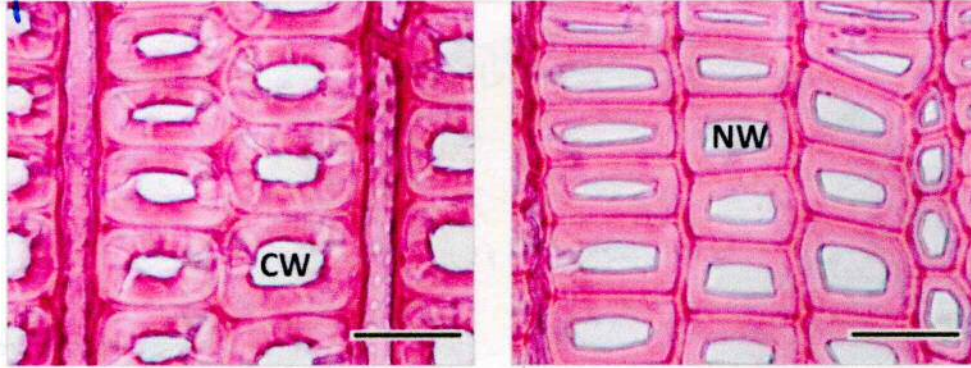
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Fig. 12 Comparative anatomy of compression wood and normal wood for the winter species
 LW: normal wood, CW: compression wood

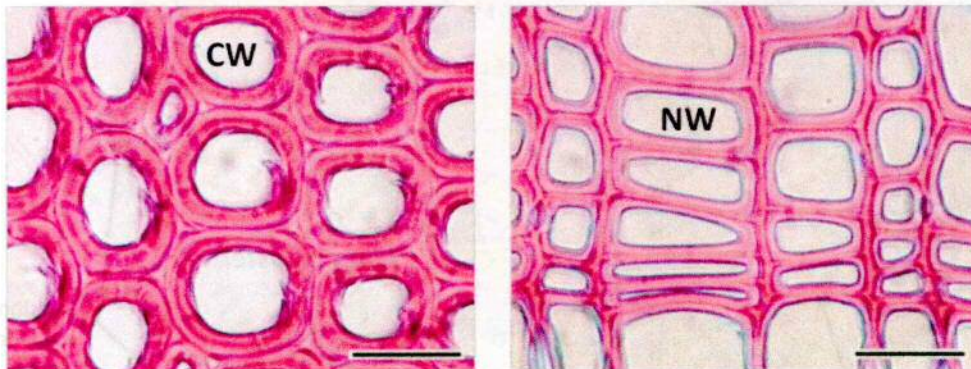
For contrast, the difference between CW and NW is classical (Kuehnle 2014). The mean microfibrillar angle (MFA) is always high for CW, and globally lower for NW but with some overlap around 30-35° (Bridg and et al 2013). The fibres were rather young (Fig. 11) so most of the NW can be considered as juvenile wood (JW).

But in this study we have a different situation
 Growth of wood in winter

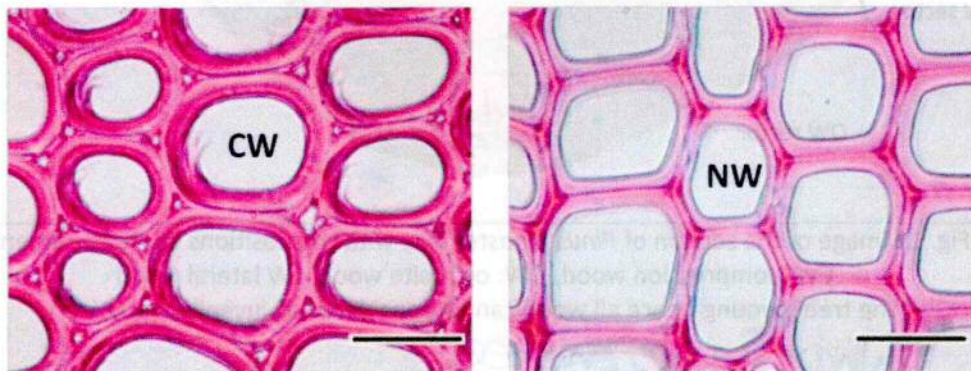
Why do we start discussing a single *Pinus pinaster* disk at this point?



Picea abies; Scale bar: 25 μ m



Pinus sylvestris; Scale bar: 25 μ m



Pinus pinaster; Scale bar: 25 μ m

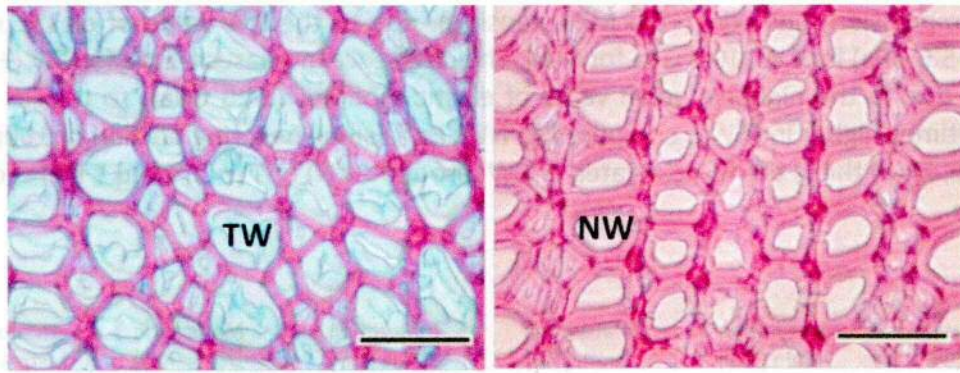
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Fig. 12 Comparative anatomy of compression wood and normal wood for the conifer species
NW: normal wood; CW: compression wood

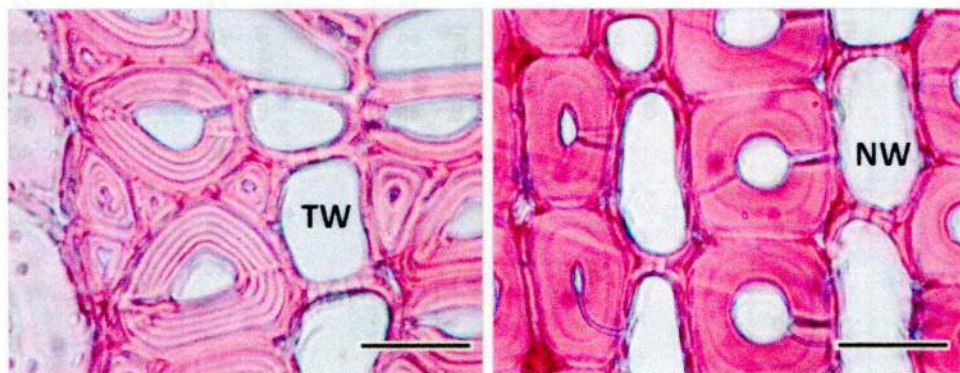
374 For conifers, the difference between CW and NW is classical (Ruelle 2014). The mean
375 microfibrillar angle (MFA) is always high for CW, and globally lower for NW but with some
376 overlap around 30-35° (Brémaud et al 2013). The trees were rather young (Fig. 11) so most of
377 the NW can be considered as juvenile wood (JW).

microfibril

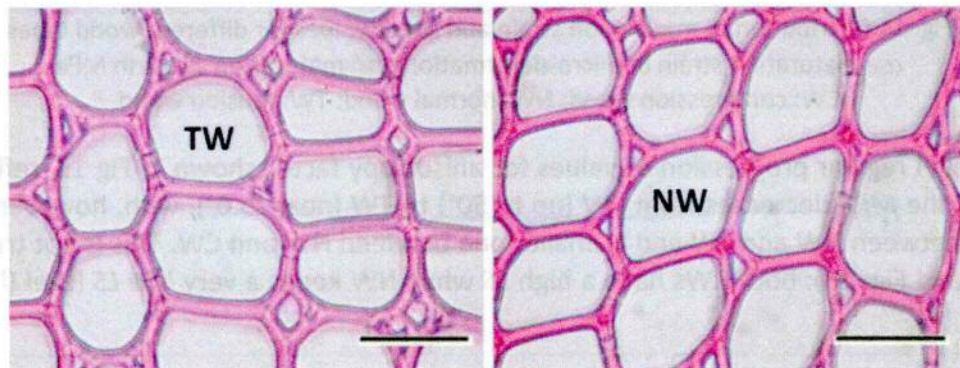
But in Fig 12 there is no information about microfibril angle



Eperua falcata; Scale bar: 25µm



Laetia procera; Scale bar: 25µm



Simarouba amara; Scale bar: 25µm

Fig.13 Comparative anatomy of tension wood and normal wood for three tropical species
NW: normal wood; TW: tension wood

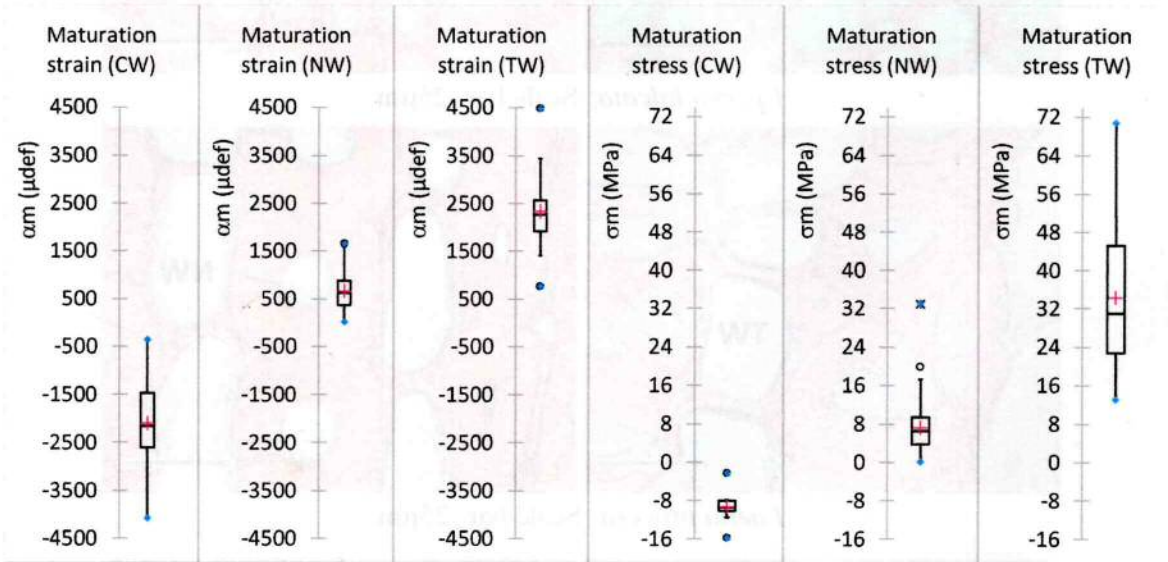
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381 For hardwoods, a majority of G-layer type TW (3 poplars, Miconia, Carapa, Ocotea, Cecropia,
382 *Eperua*) were studied (Table 2), two species had a lignified G layer (*Eschweilera* & *Qualea*),
383 one a peculiar multi-layered G layer (*Laetia*) and three no G layer fibre (*Jacaranda*, *Virola*,
384 *Simarouba*), according to a recent classification based on 242 tropical species (Ghislain et al
385 2019). Measurement of *MFA* on the 3 species represented in Fig. 13 (Ruelle et al 2007) showed
386 lower values for TW (2° to 14°) than for NW (10° to 35°), with some overlap around 10°-14° .

387 The clear distinction between wood types for the parameters describing force generation (Fig.
388 14) results from the very definition of RW as force generator: compression (negative
389 strain/stress) for CW, slight tension for NW, high tension for TW. Median maturation strain is
390 very high, around 2200 µdef (0.22%) in absolute value for both RWs, much lower (620 µdef)
391 for NW. Median maturation stresses are not so different, in absolute value, between CW (-9.5

392 MPa, compression) and NW (+6.6 MPa, tension), due to the low value of elastic modulus
 393 (median 5.5 GPa) for CW (10.2 GPa for NW). The difference increases a little for TW (+31 MPa,
 394 tension) due to the higher median value of elastic modulus (14.5 GPa), so tensile stress is
 395 nearly 5 times higher in TW as compared to NW. For a small new ring portion of 100mm² (50
 396 mm wide, 2mm thick) the force created in CW (around 1 kN) or TW (around 3 kN) sectors are
 397 very high.

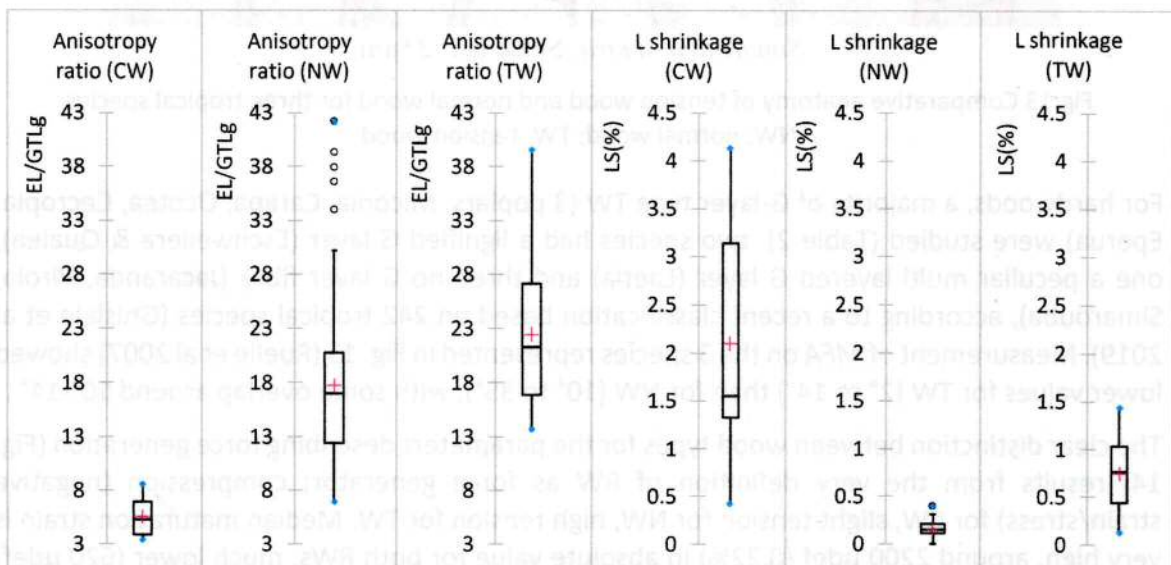
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Fig. 14 Distribution of maturation strain and stress values for different wood types
 α_m : maturation strain in micro-deformation; σ_m : maturation stress in MPa
 CW: compression wood; NW: normal wood; TW: tension wood

403 The parallel regular progression of values for anisotropy factor shown in Fig 15, reflects the
 404 fact that the MFA decreases from CW (up to 50°) to TW (near to 0°), with, however, a large
 405 overlap between NW and TW and a smaller one between NW and CW. This is not true for LS
 406 (Fig. 15 and Fig. 16): both RWs have a high LS while NW keeps a very low LS level (less than
 407 0.4%).



408
 409

Fig. 15 Distribution of L shrinkage (LS) and anisotropy ratio (E/G_{TL}) for different wood types

①. Where are these MFA values presented?
 No statistical analysis to show that they are different.
 Is each tree an experimental unit

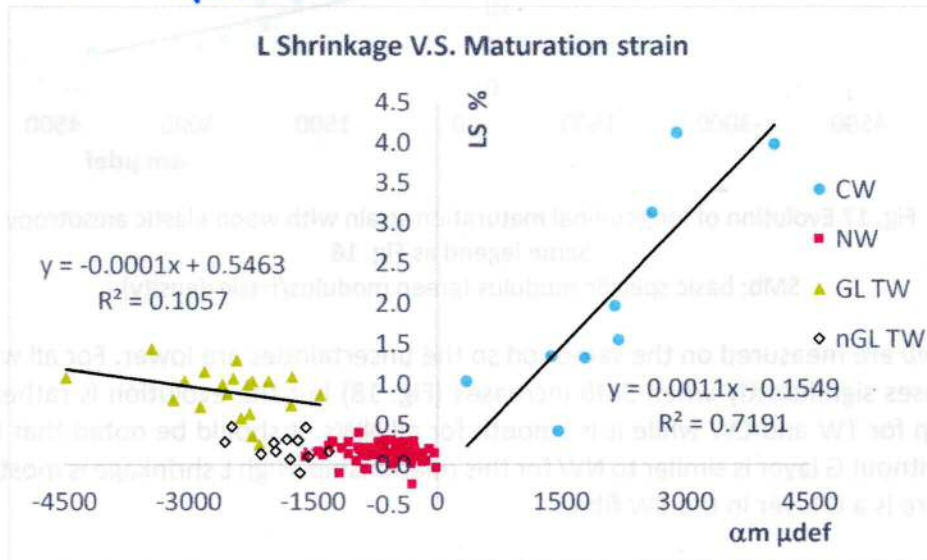
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LS: longitudinal shrinkage, E_g/G_{TLg} : anisotropy ratio at green state.
same legend as Fig. 11

What is this referring to?

412 The relationship between LS and α_m (Fig. 16), α_m and *SMB* (Fig. 17) or LS and *SMB* (Fig. 18)
413 shows evidences of different patterns for NW, CW and TW. It should be noted that α_m and green wood
414 properties (LS and *SMB*) are not strictly measured on the same material and this contributes
415 to lower correlations between them.

416 LS increases with the absolute value of α_m (Fig. 16) for both CW and GL-TW while LS keeps low
417 for all the NWs. Samples

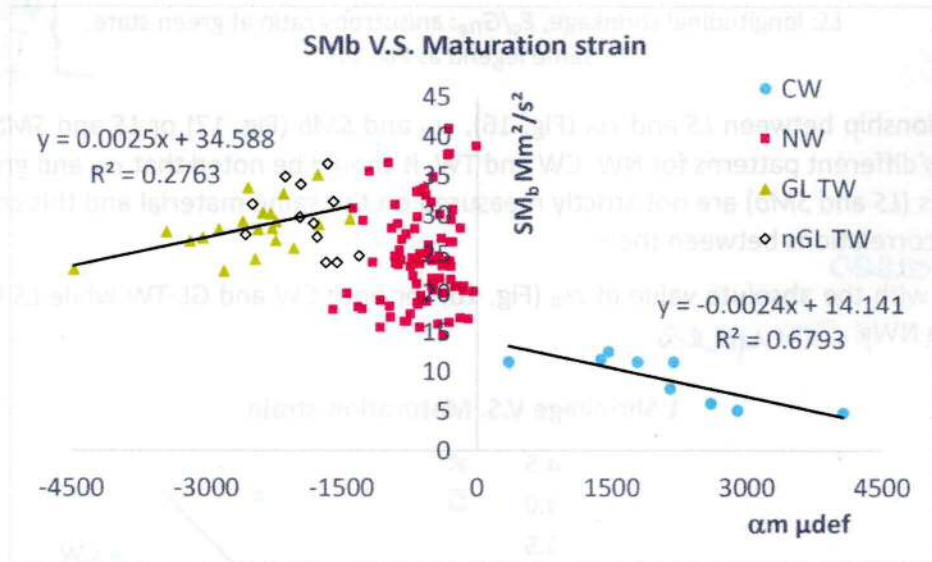


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Fig. 16 Evolution of longitudinal shrinkage with maturation strain

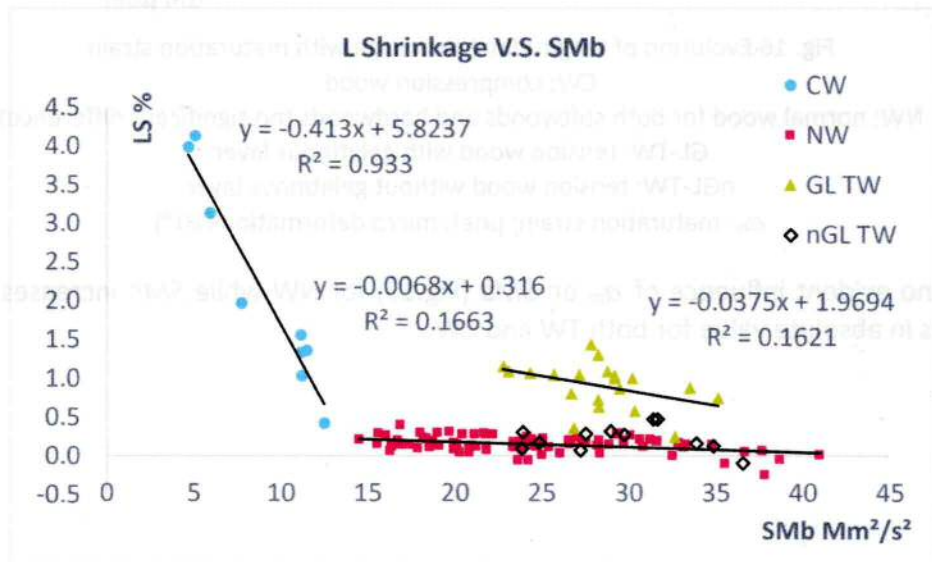
CW: compression wood
NW: normal wood for both softwoods and hardwoods (no significant difference)
GL-TW: tension wood with gelatinous layer
nGL-TW: tension wood without gelatinous layer
 α_m : maturation strain; μdef : micro deformation (10^{-6})

425 There is no evident influence of α_m on *SMB* (Fig.17) for NW while *SMB* increases when α_m
426 decreases in absolute value for both TW and CW.



427
428 Fig. 17 Evolution of longitudinal maturation strain with wood elastic anisotropy
429 Same legend as Fig. 16
430 Smb: basic specific modulus (green modulus/basic density)

431 *LS* and *Smb* are measured on the same rod so the uncertainties are lower. For all wood types
432 *LS* decreases significantly when *Smb* increases (Fig. 18) but the evolution is rather steep or
433 very steep for TW and CW while it is smooth for all NWs. It should be noted that the TW of
434 species without G layer is similar to NW for this relationship. High L shrinkage is mostly present
435 when there is a G layer in the TW fibre.



436
437 Fig. 18 Evolution of longitudinal shrinkage with wood elastic anisotropy
438 Same legend as Fig. 16 & 17

439 Discussion

440 *Green to dry wood properties*

441 *BD* is now commonly used in ecological studies on carbon sequestration in forests. Using the
442 large CIRAD database (4022 trees) a very nice proportional relationship was found between
443 *DD* (12% moisture content) and *BD* with a proportional factor of 0.828 (Vieilledent et al 2018).

① Tested statistically ?

444 Here, with a quite different sampling, a factor of 0.826 was obtained. The very large range of
445 VS due to the presence of CW shows that this proportional factor ranges from 0.78 to 0.86
446 (Fig. 4) with a good prediction of the variation by VS which can be easily measured at the same
447 time as BD.

448 In our study, elastic properties are measured by vibration technique, namely high deformation
449 rate where little viscosity is active (no creep added to the instantaneous elastic strain). The
450 decrease between dry and green state is only around 10% for E and around 25% for G , either
451 G_{RL} or G_{TL} . The Wood Handbook (Gretschman 2010) gives MOE values in the green state and
452 at 12% MC, as means for 64 hardwood species and 37 softwood species, using different rods
453 for each condition in order to measure also rupture strength. A very good proportional
454 relationship is also obtained ($R^2=0.86$ for hardwoods, $R^2=0.95$ for softwoods), as compared to
455 $R^2=0.97$ in this study. The decrease between air-dry and green states is around 20% (22% for
456 hardwoods, 20% for softwoods), which is significantly different (two times greater). A small
457 part of the difference can be explained by a different equilibrium MC (from 12% to 16% for
458 air-dry wood in this study), but the greatest part is likely to originate from the experimental
459 method. In the Wood Handbook the measurements are performed in 3 points bending at slow
460 deformation rate, allowing some initial creep which is more important for green wood than
461 for dry wood.

462 *GSI as a good indicator for growth stresses*

463 The single hole method has the advantage of being quick, easily operable in all field situations
464 and cheap, making it most appropriate for large measurement campaigns such as the
465 "Stresses in beech" EU project where 8,000 GSI data were collected in situ (Jullien et al 2013).
466 It requires, however, the use of a conversion factor (ϕ) from GSI to α_m . The theoretical
467 computation of ϕ , based on an orthotropic elastic model of residual stress (Archer 1984),
468 depends of wood anisotropy near the measurement zone and thus depends on the wood
469 species as well as the wood type. It can be practically estimated from the basic specific
470 modulus (SM_b) that ranges from 5 Mm²/s² for severe compression wood to up to 40 Mm²/s²
471 for resonance wood with high sound speed. The range of resulting maturation strains found
472 in this study is very similar to values in the literature for CW (Yamamoto et al 1991, Huang et
473 al 2001, Yamashita et al 2007) and TW (Yoshida et al 2000, Fang et al 2008, Clair et al 2013),
474 around -4000 to +4000 μ def.

475 The 8 maturation stresses calculated for each tested tree were proportional to GSI values with
476 very high regression coefficients ($R^2>0.97$), so it is possible to use GSI as a proxy of growth
477 stress within a tree, even when it contains severe CW or TW sectors. Furthermore, the
478 conversion coefficient ψ between GSI and maturation stress is proportional to BD with a very
479 good regression coefficient ($R^2=0.97$), except in the case of CW occurrence. This means that
480 for hardwoods, BD is the only parameter needed for the conversion coefficient ψ .

481 *Strain, stress and force generation.*

482 Force generation is one of the functions provided by fibres/tracheids during cell-wall
483 thickening, and force asymmetry between both sides of a wooden axis is the motor of its
484 posture control (Almérás et al 2005b, Almérás et al 2009). The force (F) produced by an
485 angular portion of new living xylem equals the product of the area (A) of that portion,
486 orthogonal to the force, by the maturation stress (σ_m) generated in the xylem tissue during
487 cell-wall thickening: $F=A \cdot \sigma_m$. A depends both on the amount of cell division in the cambium
488 and on the cell expansion until the end of primary wall setting (Cuny et al 2012). σ_m is also the

② No mention in the paper about differences in MOE obtained from dynamic method (speed of sound) + bending method.

- ① What else would it be the result of?
 ② Rather simplified explanation. Can you give some references?

489 residual stress present in the last ring of sapwood after the programmed fibre death, and can
 490 be measured in situ by classical residual stress measurement methods. The existence of this
 491 pre-stress enhances the flexure resistance of wooden axes (Gril et al 2017) and thus
 492 contributes to the skeleton function of wood in the tree.

493 Maturation stress σ_m is associated to maturation strain α_m via Hooke's law: $\sigma_m = E \cdot \alpha_m$, where
 494 E stands here for E_g , the MOE of xylem tissue at the end of the maturation process. α_m is
 495 locked in the wood until stress release, e.g. by cutting. It is largely agreed that α_m , as a result
 496 of the whole lignification process, is the source of σ_m . As the new layer is glued on a solid rigid
 497 core, the "natural" extension or shrinkage of the fibre cannot be expressed, resulting in stress
 498 occurrence.] ②

499 This longitudinal expansion during secondary wall deposition is of the order of 0.1%, much
 500 smaller than the expansion occurring during primary wall building. But, at the end of the
 501 maturation process, the MOE of a xylem portion is very high, of the order of 10 GPa, thousands
 502 of time bigger than the modulus at the end of primary wall expansion. As a result, maturation
 503 stresses have high values allowing to produce large forces (of the order of kN) and large motor
 504 actions (Almérás et al 2005b). ③

505 In the L direction, thanks to the honeycomb-like microstructure of wood with a quasi-parallel
 506 alignment of the wall of fibres or tracheids, wood MOE (E) is directly related to cell-wall MOE
 507 (E_w). Below FSP, when cell cavities (lumens) contain only air and water vapour, wood specific
 508 modulus $SM = E/d$ equals that of the cell-wall $SM_w = E_w/d_w$, where d_w is the cell-wall density;
 509 both being equal to the square of the longitudinal sound of speed (Gibson and Ashby 1999).
 510 Wood MOE can thus be expressed as: $E = d \times SM = d \times SM_w = (d/d_w) \times E_w$. In this expression the
 511 relative density (d/d_w) represents the cell-wall proportion; it is a basic property of the cellular
 512 material, while E_w is a basic property of the cell wall. Both d_w and E_w depend on the properties
 513 of the polymers composing the cell wall; while d_w variation is very small among wood species
 514 and types ($d_w \sim 1.5 \text{g/cm}^3$), E_w is highly dependent on the ultrastructural organisation of the
 515 cell wall such as the orientation of cellulosic microfibrils. The longitudinal maturation strain
 516 α_m , like E_w , depends on cell-wall composition and organization.

517 Wood formation involves three successive processes: cell division, expansion and maturation:
 518 the number of cells produced during a given period of time is controlled by cell division, their
 519 size by cellular expansion and the properties of their wall by cellular maturation (taken here
 520 in a broad sense, including the cell-wall thickening). Wood relative density (d/d_w),
 521 approximately proportional to the ratio between cell-wall thickness and cell diameter, is
 522 controlled both by division and by maturation, while cell-wall MOE (E_w) and maturation strain
 523 (α_m) are mostly controlled by maturation. Wood MOE (E), as the product of E_w and d/d_w , and
 524 maturation stress σ_m , as the product of E and α_m , are both controlled by expansion and
 525 maturation. When a layer of wood is deposited at stem periphery, the force produced by a
 526 portion of that ring, equal to the product of σ_m and the ring thickness, is controlled by
 527 expansion and maturation, and by division - and so is the bending motor force produced at
 528 the stem level, since it amounts, roughly, to the product of the driving forces on the two
 529 opposite faces and the total diameter growth. The regulation of such a scheme is very complex
 530 and is far from being fully understood today. Anyway, this regulation of forces is also, at the
 531 end, a regulation of all wood properties because it affects chemistry, anatomy, and cell-wall
 532 ultrastructure. ④

- ③ Do you mean they can move stems a long way
 ④. Seems more like a chapter out of a textbook.
 Almost no references.

533 *Compression wood, normal wood and tension wood*

534 It is natural and useful to use maturation strain α_m as basic indicator of maturation because it
 535 depends only on this living phase, but it is also the case of E_w as well as of longitudinal
 536 shrinkage (LS), which depend essentially only the composition and structure of the cell wall.
 537 Hence the relationships between these three parameters can provide information on what
 538 happened during secondary wall thickening until programmed cell death.

539 The distinction between wood types is based on α_m : CW produces positive α_m , TW very large
 540 negative α_m and NW very low to rather high negative α_m . All have a muscular action for the
 541 control of stem curvature: NW alone for a moderate action, or combined with RW (either CW
 542 or TW) for a strong action. Many papers highlight that triggering RW mobilise specific genes
 543 (Gardiner et al 2014) and changes strongly the chemical composition of the cell wall matrix as
 544 compared to NW. This is probably what explains the different patterns in the relationships
 545 observed in Fig. 15, 16 & 17.

546 For NW, no significant difference ^{α_m} seems to exist between softwoods and hardwoods in spite
 547 of chemical differences in chemical composition of the matrix, mainly for the hemicelluloses
 548 (Gérard et al 2020). For all NWs there is a wide range of MFA , and consequently, in specific
 549 modulus (Fig. 14), with a large range overlap for TW and a small one for CW (Brémaud et al
 550 2013, Ruelle et al 2007). But no significant relationship was found between α_m and SMB (Fig.
 551 17) although both have large variations. Many papers have described a very significant
 552 relationship between MFA and α_m but they combine NW and RW and the significance comes
 553 from the RW (Yamamoto et al 1991, Okuyama et al 1994, Yamamoto et al 1998).

554 For CW there is a strong relationship between α_m and SMB ; this is similar to all results from
 555 the literature and is consistent with models built on the assumption of a bulk shrinkage of cell
 556 wall matrix (Alméras et al 2005a, Yamamoto et al 1988, Guitard et al 1999). The models cannot
 557 be well adjusted to both NW and CW. ②

558 For TW although it is admitted that MFA is always small or very small, the specific modulus is
 559 not as high as for NW with low MFA . A tiny tendency of lower SMB for higher maturation strain
 560 (in absolute value) seems to appear for G-layer TW. MFA cannot explain the high maturation
 561 strain of TW, and there is no clear difference between G-layer, lignified G-layer and no G-layer
 562 types of TW regarding the relationship between SMB and α_m .

563 One clear indication within each tree is the much higher LS for both RWs as compared to the
 564 NW in the same tree (Table 5). But this difference is higher in the case of G-layer TW.

565 Table 5 Differences between normal and reaction wood

Type	α_m NW	α_m RW	RW/NW	LS NW	LS RW	RW/NW	SMB NW	SMB RW	RW/NW
SW	386	-2103	-5.4	0.15	2.10	14.4	21.08	9.01	0.43
HW GL	796	2255	2.8	0.17	0.89	5.3	25.48	28.42	1.12
HW GLc	522	3579	6.9	0.15	1.22	7.9	19.16	24.58	1.28
HW LGL	668	2174	3.3	0.17	0.53	3.0	22.95	29.21	1.27
HW NGL	637	1995	3.1	0.11	0.31	2.9	27.89	32.18	1.15

566 SW: Softwood; HW: hardwood; NW: normal wood; RW: reaction wood

567 GL: gelatinous layer; GLc: multi-layered GL; LGL: lignified GL; NGL: no GL

568 α_m : maturation strain; LS : longitudinal shrinkage; SMB : basic specific modulus

569 RW/NW: ratio between RW and NW values

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Why is this here?

- ① Maybe reference the specific chapter
- ② Do you mean you cannot build a standard model for NW + CW?

571 For conifers, the difference of dependence between LS and SM for NW and RW was described
572 by before (Watanabe & Norimoto 1996).

573 Models for longitudinal shrinkage of wood (Cave 1972, Yamamoto et al 2001) predict a steady
574 growth of LS with growing MFA over 30° and suggest a small inverse situation for small MFA
575 below 30° . Remembering that specific modulus is strongly decreasing (from 30 to $10 \text{ Mm}^2/\text{s}^2$)
576 when MFA increases from 10 to 30° (Cowdrey & Preston 1966, Cave & Hutt 1968, Brémaud et
577 al 2013), LS should increase when SM_b increases in the range 11 to $33 \text{ Mm}^2/\text{s}^2$ (using the
578 conversion factor 1.1 between dry specific modulus and SM_b). In fact, there was a very
579 significant negative correlation between LS and SM_b for NW in that range. The same seems to
580 be true also for TW, but SM_b was supposed to be higher for the low MFA values in TW.
581 Moreover, G-layer TW has a much higher LS than NW for similar values of SM_b .

582 The paradoxical situation of longitudinal shrinkage for G-layer tension wood was described in
583 the literature (Dadswell & Wardrop 1955, Jourez et al 2003, Clair & Thibaut 2014). Many
584 recent papers discuss the role of cellulose nano-fibres organisation within the microfibrils,
585 using both experiments and models (Clair et al 2008, Chang et al 2015, Alméras & Clair 2016,
586 Gorshkova et al 2018). α_m and LS are considered but these models and could be also efficient
587 to predict the specific modulus "anomaly" for G-fibres.

588 *Trade-off between active posture control and passive pre-stressing*

589 The tensile pre-stressing of stem periphery enhances its flexure resistance, thanks to the
590 resistance in tension of wood being typically twice that in compression (Gordon 1978, Thibaut
591 & Gril 2003, Moulia et al 2006). In order to roughly quantify this, the relationship between
592 resistance to compression (CR) and basic density (BD) was examined on the data for green
593 wood in the wood handbook (Kretschmann 2010). CR can be predicted by a proportional
594 formula: $CR = k * BD$, where $k = 52.5$ for softwoods and 46.1 for hardwoods with CR in MPa and
595 BD in kg/dm^3 . The specific resistance to compression (resistance/density) is rather unaffected
596 by microfibril angle (Gindl 2001, Gindl & Teischinger 2002), specifically for CW (Pillow &
597 Luxford 1937, Cockrell & Knudson 1973), and the same ratio can be used for CW and NW.

598 The same database gives also values of green flexure resistance (MOR), roughly twice CR , that
599 can be used as a conservative value for tensile strength (Kretschmann 2010); green wood MOR
600 also can be predicted by a proportional formula: $MOR = k * BD$, where $k = 108$ for both
601 softwoods and hardwoods. According to a smaller database (18 species), associated to the
602 large wood handbook database, the green ultimate tensile resistance is in average 60% higher
603 than green MOR for the same species (Markwardt & Wilson 1935). Published data of green
604 TW resistance are scarce. Clarke (1937) writes that tensile strength of TW is 10% higher than
605 that of NW for beech, while compression strength of TW is much lower, which is consistent
606 with the higher proportion of cellulose microfibrils in TW. It can also be accepted that green
607 tensile strength of TW is around 60% higher than its green MOR .

608 The crude approximation of CR and MOR in the green state, based on BD , was used for all
609 tested rods. Table 6 summarizes, for NW, TW and CW, the mean values of BD , CR and MOR ,
610 together with the maturation stress σ_m . According to the pre-stressing represented by σ_m , in
611 case of tree bending the maximum allowable compressive stress case is equal to the sum of
612 CR and σ_m , while the maximum allowable tensile stress is the difference between MOR and
613 σ_m .

I think focus on what we still don't understand
or what your data clarifies.

Why are these data presented in the Discussion

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Table 6 Pre-stressing and flexure resistance for different wood types

Tree	BD	DPrel	Eg	CR	MOR	σ_m	$\sigma_m + CR$	MOR- σ_m
mean CW	0.56	1.26	5.1	29.5	60.8	-9.3	20.2	70.1
mean NW SW	0.46	0.91	10.9	22.4	46.3	3.8	26.2	42.5
mean NW HW	0.47	0.93	11.4	21.7	50.9	8.1	29.7	42.8
mean TW	0.51	1.16	14.4	23.3	54.8	34.3	57.6	20.5

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BD: basic density (Kg/dm³); Eg: green modulus of elasticity (GPa);

DPrel: ratio between rod distance to pith (DP) and mean DP for the 8 rods of the tree;

CR: longitudinal crushing resistance (MPa); MOR: flexure resistance (MPa)

CW: compression wood; NW SW: normal wood of softwood; NW HW normal wood of hardwood;

σ_m : maturation stress or pre-stress (MPa)

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For a well-balanced tree containing no RW, σ_m is always positive (tension) on both sides of the trunk under wind action, and the wind stress σ is maximum and the same in absolute value, on the two faces: compression downwind, tension upwind. If the maximum wind stress is around 25 MPa for the mean trees of Table 6, the NW will be safe in all wind situations. But for both types of RW the allowable resistance to compression (case of CW) or to tension (case of TW) are similar and lower than a wind stress of 25MPa. Stresses due to strong reacting forces may bring danger in case of wind action either on the compressed side for softwoods or the tensile side for hardwoods.

No references

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As MOR is likely to be much lower than tensile strength, the situation may not be critical for a TW side, but for the higher tensile stresses there may be a small wind stress attenuation by ovalisation of the cross section inducing a growth of the second moment of inertia in the wind direction.

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The compressive stress produced by CW is obviously dangerous in case of strong wind opposite to the CW side. The trade-off between pre-stressing of the skeleton and high force asymmetry for verticality restoration is managed in a rather sophisticated way as can be examined on Fig. 11 and Table 6. For CW, density is higher, MOE is much lower and ring width is much higher - with ovalisation of the cross section. A high compressive force in the newly formed CW is achieved, despite the very low MOE, by higher density and much higher ring width. CR is higher due to higher density and maturation compressive stress is limited by the small value of MOE so that the maximum allowable compression stress is not so low. Moreover, there is a large heterogeneity of MOE within the cross section between CW zone and the rest. The neutral axis in bending under wind action will no more be in the geometric centre of the section. As a result, the strain level at periphery will be 15 to 20% higher in the low modulus portion (the compression wood side) and lower in the other side. As MOE is much lower in the CW side (2 times lower), the compressive wind stress will be lower than expected for a normal tree. Ovalisation of the cross section will bring a small additive security factor and the sum of these compensations should be enough for wind safety in such a case.

No references

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Conclusion

Also tree grows eccentrically so biological centre is not geometric centre

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The combined growth stress evaluation on standing trees and laboratory measurements of wood properties on a large range of situations (different species and densities, NW and RW) bring useful tools for this kind of studies. 1- very good proportional relationships were established for the relationship between green and dry state for density, specific modulus,

① Not sure what you are comparing the 25 MPa with. Is it $\sigma_m + CR + MOR - \sigma_m$?

① A vague statement.

653 longitudinal elastic (MOE) and shearing modulus of elasticity (G_{TL} and G_{RL}). Hence dry wood
654 properties can be used whether there are no green wood data. 2 - a simple conversion
655 coefficient (ϕ) was obtained between growth stress indicator (GSI) coming from the single hole
656 method and maturation strain using the basic specific modulus (ratio between green MOE and
657 basic density BD) and even maturation stress using only basic density for hardwood or
658 softwood normal wood. The proportionality is true within a tree in all cases, hence GSI can be
659 directly used for biomechanical studies at tree level. ①

660 Basic specific modulus (SM_b) and longitudinal shrinkage (LS) as well as maturation strain (α_m)
661 are properties of cell wall material in the longitudinal direction depending only on the last
662 fibre living phase (maturation phase, i.e. secondary wall deposition). Microfibril angle (MFA)
663 in the secondary wall and chemical composition of cell wall polymers are the underlying
664 parameters explaining the variations of these 3 properties. α_m provides a continuum of wood
665 types from CW to TW through NW, but the analysis of SM_b and LS proves that RW cannot be
666 considered as extreme case of NW but specific patterns as suggested by genomic studies.
667 Predictive models should be built separately for the 3 types, but the pertinent combined data
668 on α_m , MFA and chemistry of main polymers is lacking mainly for NW which has an important
669 contribution to muscular function of the living wood, even in posture regulation. For CW (Yeh
670 et al 2005) and for non G-layer TW (Baillères et al 1995) the relative composition in lignin
671 monomers (H/G for softwoods, S/G for hardwoods) was a good predictor of RW. These
672 parameters can be active also within NW without too much changes in lignin content.

673 By creating forces, the living wood generates tensile residual stresses within the internal
674 skeleton, improving its resistance to flexure forces as wind action on the compressive side
675 where the resistance to compression is lower. But high compression pre-stressing on one side
676 or very high tension pre-stressing on the other side by RW will bring dangerous situations in
677 case of strong wind in the axis of RW. There is a necessary trade-off between efficient posture
678 control (by forces) and efficient pre-stressing (by stresses) and compression wood solution
679 (the most dangerous under wind action) is managed by a complex simultaneous regulation of
680 strain, modulus of elasticity (via the MFA), stress (via the density), force (via the ring width)
681 and global geometry (via the anisotropy of second moment of area of the section).

+ Asymmetric growth.

682 References

683 **Alm3ras T, Thibaut A, Gril J.** 2005b. Effect of circumferential heterogeneity of wood
684 maturation strain, modulus of elasticity and radial growth on the regulation of stem
685 orientation in trees. *Trees Structure and function* 19 (4), 457–467. *Trees Structure and*
686 *function*

687 **Alm3ras T, Derycke M, Jaouen G, Beauch3ne J, Fournier M.** 2009. Functional diversity in
688 gravitropic reaction among tropical seedlings in relation to ecological and developmental
689 traits. *Journal of Experimental Botany* 60, 4397–4410.

690 **Alm3ras T, Clair B.** 2016. Critical review on the mechanisms of maturation stress generation
691 in trees. *Journal of The Royal Society Interface* 13(122) , 20160550

692 **Alm3ras T., Jullien D., Gril G.** 2018. Modelling, Evaluation and Biomechanical Consequences
693 of Growth Stress Profiles Inside Tree Stems. Anja Geitmann, Joseph Gril. *Plant Biomechanics.*
694 *From Structure to Function at Multiple Scales*, Springer International Publishing, pp.21-48

② Patterns of what?