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A van Rooij, Eric Badel, Jean-François Barczi, Yves Caraglio, Tancrede Almeras, et al.. Modelling the growth stress in tree branches: eccentric growth vs. reaction wood. Peer Community Journal, 2023, 10.24072/pcjournal.308 . hal-03748026v4

**HAL Id: hal-03748026**

**<https://hal.science/hal-03748026v4>**

Submitted on 13 Jan 2023 (v4), last revised 21 Nov 2023 (v6)

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# Modelling the growth stress in tree branches: eccentric growth *vs.* reaction wood

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## Abstract

This work aims to model the mechanical processes used by tree branches to control their posture despite their increasing weight loading. The two known options for a branch to maintain its orientation are the asymmetry of maturation stress, including reaction wood formation, and eccentric radial growth. Both options can be observed in nature and influence the stress distribution developed in the branch each year. This so-called "growth stress" reflects the mechanical state of the branch. In this work, a growth stress model was developed at the cross-section level in order to quantify and study the bio-mechanical impact of each process. For illustration, this model was applied to branches of two 50-year-old trees, one softwood *Pinus pinaster* and one hardwood *Prunus avium*, both simulated with the AMAPSim finite element software. The computed outputs enlightened that, for both *Prunus avium* and *Pinus pinaster*, eccentric radial growth is less efficient than the formation of reaction wood to counter increasing gravity stress applied to the branch. For the pine, although eccentric growth does not necessarily act as a relevant lever for postural control, it greatly modifies the profile pattern of mechanical stress and could provide mechanical safety of the branch. This work opens experimental perspectives to understand the biomechanical processes involved in the formation of branches and their mechanical safety.

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## 24 Abbreviations and notations (in order of occurrence)

NW, TW, CW	Normal Wood, Tension Wood, Compression Wood
$(x, y, z)$	Local reference coordinates associated with the section
$O$	Centre of the section
$r, R$	Radial polar coordinate and Radii of the cross section (m)
$e(R), \bar{e}(R)$	Eccentricity at the stem radius R, integrated eccentricity up to $r = R$
$(x', y', z')$	Local reference coordinates associated with the section, centred on the pith
$\sigma$	Stress (MPa)
$\sigma_0$	Induced maturation stress (Mpa)
$S$	Cross section area ( $m^2$ )
$N, M$	Loads (N): normal force parallel to $z'$ and bending moment around $y'$
$E$	Module of elasticity in L direction (GPa): MOE
$\mu$	Induced maturation strain
$\epsilon, a, b$	Strain, at the center, local curvature
$K_i$	Structural stiffness of the cross-section
$F_i$	External coefficients (maturation and load)
$\theta$	Circumferential position in section (rad)
$\sigma_0(\theta)$	Maturation strain in the new ring at circumferential position $\theta$
$\alpha$	Mean maturation stress in the new ring
$\beta$	Differential stress in the new ring
$R_{x'y'}$	Radius of the cross section at the instant of appearance of the point $(x', y')$
$\lambda_N, \lambda_M, \nu_M, \nu_N$	Load power law: allometric coefficient
$\lambda_b, \nu_b$	Change of curvature power law: allometric coefficient
$\sigma_{NW}, \sigma_{TW}, \sigma_{CW}$	Maturation stress in the normal wood, tension wood and compression wood
$\mu_{NW}, \mu_{TW}, \mu_{CW}$	Maturation strain in the normal wood, tension wood and compression wood
$\vec{N}_n, \vec{M}_n$	Loads of growth unit n: normal force and bending moment around $y$
$N_z, M_x, M_y, M_z$	Loads of growth unit n: projection of $\vec{N}_n$ on $\vec{z}$ and bending moment $\vec{M}_n$ around $\vec{x}, \vec{y}, \vec{z}$
$m_n$	Mass of the growth unit n (kg)
$g$	Gravity constant: $g = 9.8 \text{ m.s}^{-2}$
$G_n$	Centre of gravity of the growth unit n
$E_d, E_g$	Air-dry, green MOE
$\rho$	Density
$\mu\text{strain}$	$1/10^6$
$D_n, D_{n+1}$	First and second diameter the growth unit n
$D_f$	Deflection of a growth unit
$L_n$	Length of the growth unit n

## 27 Introduction

28 From a mechanical point of view, wood in tree fulfils three major functions: construction of the tree  
 29 architecture, postural control of trunk and branches and breaking resistance to external stimuli [Thibaut  
 30 (2019)]. These three functions are provided by the way wood cells differentiate and accumulate during wood  
 31 formation process. Each axis of a tree can be considered as an inclined beam, consisting of a succession  
 32 of conical growth units [Barthélémy and Caraglio (2007)]. It is built in two steps: first, primary growth  
 33 resulting in new growth units that increase the length of the initial axis; and secondary growth resulting  
 34 in thickening of already existing units by addition of annual rings. These two interactive and additional  
 35 processes lead to a specific pattern of mechanical stress, called 'growth stress', which can be analysed as  
 36 the superposition of support stress and maturation stress [Archer (1976); Fournier et al. (1991a)]. The

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37 support stress results from the continuous increase of the weight supported by the axis over the years.  
38 It reaches maximal levels in the core of the stem and vanishes near stem periphery, where the recently  
39 formed wood contributes to the support of recently produced biomass only. Maturation stress is set up  
40 at the end of the cell-wall maturation process, when molecular components such as lignin polymerise,  
41 generating growth forces by small dilatation or contraction restrained by the rigidity of the previously  
42 formed wood cells [Alméras and Clair (2016)]. An evaluation of the maturation stress can be obtained  
43 by measuring the strain associated to stress release at stem periphery, where no support stress is present  
44 [Nicholson (1971); Yoshida and Okuyama: (2002); Yang et al. (2005)]. The circumferential heterogeneity  
45 of this peripheral stress is needed to regulate stem curvature. In most cases, a tensile maturation stress is  
46 produced in the newly formed 'normal wood' (NW). But observations on inclined trunks [Alméras et al.  
47 (2005); Coutand et al. (2007); Thibaut and Gril (2021)], seedlings [Hung et al. (2016)] and branches [Fisher  
48 and Stevenson (1981); Huang et al. (2010); Tsai et al. (2012); Hung et al. (2017)] have evidenced a clear  
49 difference between hardwood and softwood behaviour. Hardwoods are able to produce 'tension wood'  
50 (TW) inducing a much higher tensile stress on one side, while for softwood a compressive stress is induced  
51 in 'compression wood' (CW). The first pulls, the second pushes. In the most usual case of inclined stems  
52 restoring their vertical orientation, TW is formed on the upper side while CW is formed on the lower side  
53 of the trunk. But other situations can be encountered depending on the biomechanical requirements of  
54 the tree [Wang et al. (2009b)]. In addition to their participation in the postural control of tree stems,  
55 these two types of so-called 'reaction wood' (RW) are characterised by specific anatomical pattern (not  
56 discussed here) and specific physical and mechanical properties.

57  
58 As an alternative to complex experimental approaches, growth stress modelling plays an important  
59 role in the understanding of the phenomena involved in the orientation process of a stem. The history of  
60 biomechanical models began with Kübler (1959) who proposed an analytical formulation of growth stress  
61 for a perfect cylinder made of a homogeneous and transversally isotropic wood. Later, Archer and Byrnes  
62 (1974) took into account an asymmetry of the maturation stress, and Fournier et al. (1991a,b) proposed a  
63 semi-incremental version of these models, allowing to take into account a potential gradient of mechanical  
64 parameters (stiffness, maturation).

65 By associating their previous model to the loading induced by the tree weight, Fournier et al. (1994)  
66 made the connection between growth stress and stem orientation. This model has been adopted and  
67 developed by several authors in order to study the orientation process of stems. Yamamoto et al. (2002)  
68 added a primary shoot and returned to curvature calculations. Alméras and Fournier (2009) introduced  
69 the notion of gravitropic performance (capacity of the tree to correct the bending moment induced by  
70 its weight) and proposed criteria of long-term stability. Huang et al. (2005) and Alméras et al. (2005)  
71 improved the model by introducing a secondary growth asymmetry and its resulting pith eccentricity, as  
72 well as stiffness heterogeneity, allowing to quantify the effectiveness of eccentricity, maturation, stiffness  
73 gradient and initial radius in the curvature regulation process. They enlightened that the main factor in  
74 the gravitropic process is the spatial distribution of the maturation stress. Still in line with Fournier's 1994  
75 model, Alméras et al. (2018) recently developed analytical models of longitudinal growth stress, taking  
76 into account different configurations, like eccentricity or maturation gradient, and evolution laws, like  
77 evolution of stiffness per additional layer. Finally, based on the same philosophy as established by Kübler,  
78 tree-scale and finite-element models have emerged [Fourcaud et al. (2003); Ancelin et al. (2004)].

79 Huang et al. (2010)'s model has been used to understand how eccentric growth and RW are involved in  
80 branch orientation [Wang et al. (2009a); Huang et al. (2010); Tsai et al. (2012); Hung et al. (2017)], but  
81 all these studies were based on the current state of the branch, without consideration of the previous  
82 history: although some of them quantified the roles of maturation and eccentricity in the regulation of  
83 curvature, none did evaluate their capacity to ensure a given growth scenario.

84 Unlike trunks, which usually seek verticality, after the first stages of growth, branches tend to grow in a  
85 stationary way at a fixed angle to the vertical. Therefore, in this framework, we focus on understanding

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86 how branches can control their orientation, through the study of two growth parameters: eccentric growth  
87 and RW. The aim is to check by calculation what option is mechanically possible and safe for the branch.  
88 For this purpose, we developed a semi-incremental biomechanical model of growth stress at the cross  
89 section level that takes into account the eccentricity and maturation gradients during the construction of  
90 branches. Using the digital models of one softwood *Pinus pinaster* and one hardwood *Prunus avium*, the  
91 impact of each of these two growth parameters on the stress state was evaluated.

## 92 Material and methods

### 93 Numerical model

#### 94 General hypotheses

95 The problem was set in the framework of the beam theory. From a geometrical point of view, branches  
96 generally show profiles that suit to this type of analytical framework: a slender shape and no important  
97 diameter variations. The shape effects due to twigs and other local biological phenomena (cavity, nodes,  
98 etc.) were neglected. The same set of hypotheses as in Alméras et al. (2018) was adopted. In this study,  
99 we focused on the behaviour in the longitudinal direction (parallel to the main axis). Horizontal bending  
100 and torsion loads were not considered. Only the vertical bending moment (caused by the weight) was  
101 considered; these hypotheses on the loading modes are discussed later.

#### 102 Geometrical settings

103 The object of study was the cross-section of a branch, placed within a plane locally orthogonal to the pith.  
104 The local reference frame of the section is  $(\vec{x}, \vec{y}, \vec{z})$ , with  $\vec{z}$  the longitudinal direction of the axis, and  $\vec{x}$   
105 placed in a vertical plane and facing upwards (Fig 1). The shape of the cross-section was assumed to be  
106 circular at any stage of development, described by the successive depositions of wood rings. The term of  
107 'ring' refers here to the volume occupied by wood cells produced by the cambium during a certain duration  
108 of time, not necessarily annual: it must be taken in a numerical meaning. These rings possibly could  
109 present an eccentricity resulting from asymmetry of secondary growth. Since the model only takes into  
110 account vertical bending, the eccentricity was set along the  $x$  axis, as expressed by the following equation:

$$O(t) = \int_0^{R(t)} e(r)dr = \bar{e}R(t) \quad (1)$$

111 with  $O(t)$  the position of the geometrical centre and  $R(t)$  the radius of the section at time  $t$ ,  $e(r)$  the  
112 eccentricity when the stem radius was  $r$  and  $\bar{e}$  the integrated eccentricity up to  $r = R$ . The eccentricity can  
113 vary in the interval  $[-1, 1]$ . A zero eccentricity corresponds to a centred section, while  $-1$  or  $1$  corresponds  
114 to maximum eccentricity resulting from secondary growth only on the lower or the upper side of the  
115 section, respectively. In the following, the position  $x'$  in the pith reference frame is needed. By calling  $x$   
116 the vertical position in the geometrical reference frame, we deduce from equation (1):

$$x = x' - \bar{e}R \quad (2)$$

#### 117 Computation of the mechanical behaviour

118 We developed a radial incremental method. For each radial increment, the longitudinal stress was computed  
119 in order to satisfy the static equilibrium of the cross section:

$$\begin{cases} \int_S \delta\sigma dS + \int_{\delta S} \sigma_0 dS = \delta N & (3a) \\ \int_S \delta\sigma x dS + \int_{\delta S} \sigma_0 x dS = -\delta M & (3b) \end{cases}$$

120 where  $S$  is the cross-section area,  $\delta S$  is its increment,  $\delta\sigma$  is the increment of stress  $\sigma$  in the already formed  
 121 wood, in response to the maturation stress  $\sigma_0$  generated in the new wood layer.  $\delta N$  and  $\delta M$  are respectively  
 122 the increment of external force  $N$  and bending moment  $M$ , that are applied on the cross-section. For  
 123 illustration, the geometric situation for  $K$  rings and an increment of stem radius  $\delta R$  is proposed in Fig 1.

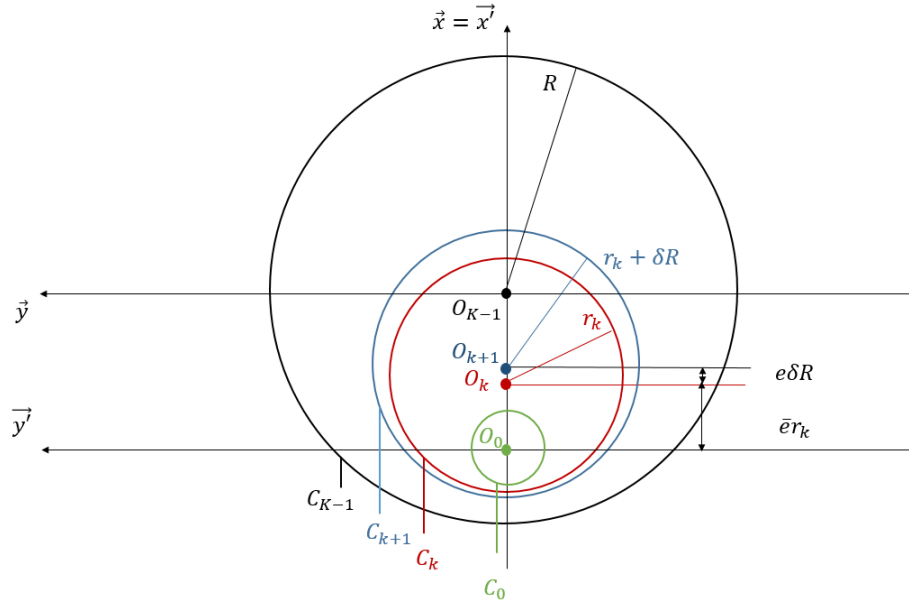


Figure 1: Geometrical representation of a section with  $K$  numerical rings and a radial increment  $\delta R$  between rings  $(k - 1)$  and  $k$ .

124

125 The stress  $\sigma$  is linked to the strain  $\epsilon$  by a classical pre-stressed Hooke's law:

$$\sigma = E(\epsilon - \mu) = E\epsilon + \sigma_0 \quad (4)$$

126 where  $E$  is the longitudinal Young's modulus,  $\mu$  is the maturation strain and  $\sigma_0$  is the maturation stress.  
 127 In the context of the beam theory, the planar cross-sections remain so (Euler-Bernouilli assumption). The  
 128 strain field is then described by the deformation  $a$  at the centre of the pith and the curvature  $b$  relative to  
 129 the  $y$ -axis, as follows:

$$\delta\epsilon = \delta a + x\delta b \quad (5)$$

130 where  $\delta\epsilon$ ,  $\delta a$ ,  $\delta b$  are the increments of  $\epsilon$ ,  $a$ ,  $b$ , respectively. The stress increment  $\delta\sigma$ , in the already formed  
 131 wood, where no maturation occurs anymore, can then be deduced:

$$\delta\sigma = E\delta\epsilon = E(\delta a + x\delta b) \quad (6)$$

From these considerations, the system (3) becomes (details of the calculation are given in Appendix A):

$$\begin{cases} K_0\delta a + K_1\delta b = \delta F_0 \\ K_1\delta a + K_2\delta b = \delta F_1 \end{cases} \quad (7a)$$

$$\begin{cases} K_1\delta a + K_2\delta b = \delta F_1 \end{cases} \quad (7b)$$

132 with

$$K_0 = E\pi R^2, \quad K_1 = E\pi\bar{e}R^3, \quad K_2 = E\pi R^4 \left( \bar{e}^2 + \frac{1}{4} \right) \quad (8)$$

$$\delta F_0 = - \int_{\delta S} \sigma_0 dS + \delta N, \quad \delta F_1 = - \int_{\delta S} \sigma_0 x dS - \delta M$$

133 The calculation of the coefficients  $\delta F_0$  and  $\delta F_1$  depends on the formulation of the maturation stress. The  
 134 maturation stress was assumed to vary circumferentially as follows:

$$\sigma_0(\theta) = \alpha + \beta \cos \theta \quad (9)$$

where the mean stress  $\alpha$  and differential stress  $\beta$  were defined differently in softwood and hardwood species:

$$\left\{ \begin{array}{l} \text{Hardwood: } \alpha = \frac{\sigma_{TW} + \sigma_{NW}}{2}; \beta = \frac{\sigma_{TW} - \sigma_{NW}}{2} \\ \text{Softwood: } \alpha = \frac{\sigma_{CW} + \sigma_{NW}}{2}; \beta = \frac{\sigma_{NW} - \sigma_{CW}}{2} \end{array} \right. \quad (10a)$$

$$\left\{ \begin{array}{l} \text{Hardwood: } \alpha = \frac{\sigma_{TW} + \sigma_{NW}}{2}; \beta = \frac{\sigma_{TW} - \sigma_{NW}}{2} \\ \text{Softwood: } \alpha = \frac{\sigma_{CW} + \sigma_{NW}}{2}; \beta = \frac{\sigma_{NW} - \sigma_{CW}}{2} \end{array} \right. \quad (10b)$$

$\sigma_{TW}$  (resp.  $\sigma_{CW}$ ) being the maturation stress in the TW (resp. CW), and  $\sigma_{NW}$  that in the opposite wood (NW). One gets :

$$\left\{ \begin{array}{l} \delta F_0 = -\pi R (2\alpha + e\beta) \delta R + \delta N \\ \delta F_1 = -\pi R^2 (3\alpha e + e^2\beta + \beta) \delta R - \delta M \end{array} \right. \quad (11a)$$

$$\left\{ \begin{array}{l} \delta F_0 = -\pi R (2\alpha + e\beta) \delta R + \delta N \\ \delta F_1 = -\pi R^2 (3\alpha e + e^2\beta + \beta) \delta R - \delta M \end{array} \right. \quad (11b)$$

135 From equations (8), (11a) and (11b), the components of the system (7) are known. By inversion,  $\delta\alpha$  and  
 136  $\delta b$  can be obtained according to the following equations (see details in Appendix B):

$$\left\{ \begin{array}{l} \delta a = \frac{4}{ER} \left[ \left( 3e\bar{e} - 2e^2 - \frac{1}{2} \right) \alpha + \left( \bar{e}e^2 - e\bar{e}^2 + \bar{e} - \frac{e}{4} \right) \beta \right] \delta R + \frac{4}{E\pi R^3} \left[ \bar{e}\delta M + \left( \bar{e}^2 + \frac{1}{4} \right) R\delta N \right] \\ \delta b = \frac{-4}{ER^2} \left[ (3e - 2\bar{e}) \alpha + (e^2 - e\bar{e} + 1) \beta \right] \delta R - \frac{4}{E\pi R^4} (\delta M + \bar{e}R\delta N) \end{array} \right. \quad (12a)$$

$$\left\{ \begin{array}{l} \delta a = \frac{4}{ER} \left[ \left( 3e\bar{e} - 2e^2 - \frac{1}{2} \right) \alpha + \left( \bar{e}e^2 - e\bar{e}^2 + \bar{e} - \frac{e}{4} \right) \beta \right] \delta R + \frac{4}{E\pi R^3} \left[ \bar{e}\delta M + \left( \bar{e}^2 + \frac{1}{4} \right) R\delta N \right] \\ \delta b = \frac{-4}{ER^2} \left[ (3e - 2\bar{e}) \alpha + (e^2 - e\bar{e} + 1) \beta \right] \delta R - \frac{4}{E\pi R^4} (\delta M + \bar{e}R\delta N) \end{array} \right. \quad (12b)$$

137 Once  $\delta a$  and  $\delta b$  are known, the stress increment  $\delta\sigma$  at any position given by  $(x', y')$  can be obtained from  
 138 equation(6). The stress distribution at this position can be obtained as the sum of the initial maturation  
 139 stress and all the stress increments undergone by the material point since its creation.

$$\sigma(x', y', R) = \sigma_0(x', y') + \sum_{k=k_{x'y'}}^K \delta\sigma_k \quad (13)$$

140 where  $\delta R_k = r_k - r_{k-1}$  for a succession of ring radii  $0 < r_0 < \dots < r_k < \dots < r_K = R$ ,  $\delta\sigma_k$  is the  
 141 corresponding increment, and  $k_{x'y'}$  designates the ring containing the point.

## 142 Analytical formulations

143 Using equations (12b) and dividing by  $\delta R$ , we get the following equations when  $\delta R$  tends to zero :

$$\left\{ \begin{array}{l} \frac{da}{dR} = \frac{4}{ER} \left[ \left( 3e\bar{e} - 2e^2 - \frac{1}{2} \right) \alpha + \left( \bar{e}e^2 - e\bar{e}^2 + \bar{e} - \frac{e}{4} \right) \beta + \frac{1}{\pi R^2} \left( \bar{e} \frac{dM}{dR} + \left( \bar{e}^2 + \frac{1}{4} \right) R \frac{dN}{dR} \right) \right] \\ \frac{db}{dR} = \frac{-4}{ER^2} \left[ (3e - 2\bar{e}) \alpha + (e^2 - e\bar{e} + 1) \beta + \frac{1}{\pi R^2} \left( \frac{dM}{dR} + \bar{e}R \frac{dN}{dR} \right) \right] \end{array} \right. \quad (14a)$$

$$\left\{ \begin{array}{l} \frac{da}{dR} = \frac{4}{ER} \left[ \left( 3e\bar{e} - 2e^2 - \frac{1}{2} \right) \alpha + \left( \bar{e}e^2 - e\bar{e}^2 + \bar{e} - \frac{e}{4} \right) \beta + \frac{1}{\pi R^2} \left( \bar{e} \frac{dM}{dR} + \left( \bar{e}^2 + \frac{1}{4} \right) R \frac{dN}{dR} \right) \right] \\ \frac{db}{dR} = \frac{-4}{ER^2} \left[ (3e - 2\bar{e}) \alpha + (e^2 - e\bar{e} + 1) \beta + \frac{1}{\pi R^2} \left( \frac{dM}{dR} + \bar{e}R \frac{dN}{dR} \right) \right] \end{array} \right. \quad (14b)$$

144 Using equation (13) and dividing again by a vanishing  $\delta R$ , we obtain the following equation involving the  
 145 partial derivative  $\partial\sigma/\partial R$ :

$$\sigma(x', y', R) = \sigma_0(x', y') + \int_{R_{x'y'}}^R \frac{\partial\sigma}{\partial R}(x', R') dR' \quad (15)$$

146 where  $R_{x',y'}$  is the radius of the section at the instant of appearance of the point with coordinates  $(x', y')$ .

On the other hand, the expressions of axial force  $N(R)$  and bending moment  $M(R)$  are required to compute the evolution of the stress distribution in the cross section. For this purpose, we assumed that both vary as a power function of the radius of the branch. This resulted in the following allometric laws:

$$\begin{cases} N = \lambda_N R^{\nu_N} & (16a) \\ M = \lambda_M R^{\nu_M} & (16b) \end{cases}$$

147 where  $\lambda_{N,M}$  and  $\nu_{N,M}$  are allometric coefficients. The  $\lambda$ -coefficients are directly proportional to the weight  
 148 of the branch part supported by the cross section (the branch itself and the other axes of higher orders).  
 149 The  $\nu$ -coefficients express the kinetics of the secondary growth: a small  $\nu$  refers to an early secondary  
 150 growth while a higher one refers to a later diameter increase.

151

The calculation of  $\sigma$  requires also the knowledge of the temporal variation of the curvature  $b$ . In order to simplify the analyses, we mainly studied stationary cases, i.e. we assumed that the branch maintains its orientation and remains straight. This assumption results in  $\frac{db}{dR} = 0$ . Physiologically, this equation expresses that the branch always compensates its weight increment at each deposition step of a new wood layer, corresponding to an additional weight. However, we can consider two cases for which the branch does not build up in a stationary way: i) the passive bending (under its own weight) case, and ii) the up-righting case (i.e. the action of maturation is stronger than the additional weight). In both cases, the resulting change in curvature has been modelled by Alm eras and Fournier (2009) and Alm eras et al. (2018). It can then be written as follows:

$$\begin{cases} \text{Up-righting:} & \frac{db}{dR} = -4 \frac{\beta}{ER^2} & (17a) \\ \text{Passive bending:} & \frac{db}{dR} = 4 \frac{\lambda_M \nu_M}{E\pi} R^{\nu_M-5} & (17b) \end{cases}$$

152 For the next computations, we used the following general law:

$$\frac{db}{dR} = \lambda_b R^{\nu_b} \quad (18)$$

153 As a remark, even if this equation bears some resemblance to (16), it does not express any notion of  
 154 allometry and is used here only for convenience. Combining (14),(15),(16) and (18), the total stress can  
 155 then be computed as:

$$\sigma^i(x', y', R) = \sigma_0^i(x', y') + S_1 \ln \left( \frac{R}{R_{x',y'}} \right) + \frac{S_2}{S_3} \left( R^{S_3} - R_{x',y'}^{S_3} \right) + \frac{S_4}{S_5} \left( R^{S_5} - R_{x',y'}^{S_5} \right) + \frac{S_6}{S_7} \left( R^{S_7} - R_{x',y'}^{S_7} \right) x' \quad (19)$$

156 where  $S_1 = 4 \left[ \left( 3e\bar{e} - 2e^2 - \frac{1}{2} \right) \alpha + \left( \bar{e}e^2 - e\bar{e}^2 + \bar{e} - \frac{e}{4} \right) \beta \right]$  is driven by the maturation process,  $S_2 =$   
 157  $\frac{\lambda_N \nu_N}{\pi} \left( \bar{e}^2 + \frac{1}{4} \right)$ ,  $S_3 = \nu_N - 2$ ,  $S_4 = \frac{4}{\pi} \lambda_M \nu_M \bar{e}$  and  $S_5 = \nu_M - 3$  by the branch loading (geometric evolution  
 158 of the branch),  $S_6 = E\lambda_b$  and  $S_7 = \nu_b + 1$  by the branch orientation.

159 For each radius  $r$ , the remaining unknowns are the mean stress  $\alpha$ , the differential stress  $\beta$  and the  
 160 eccentricity  $e$ . Equation (14b) can be rewritten as:

$$(3e - 2\bar{e}) \alpha + \left( e^2 - e\bar{e} + 1 \right) \beta = \frac{-1}{\pi r^2} \left( \frac{dM}{dR} + \bar{e}R \frac{dN}{dR} \right) - E \frac{R^2}{4} \frac{db}{dR} \quad (20)$$

161 Thus by fixing two parameters, the third is directly determined. The maturation parameters  $\alpha$  and  $\beta$  are  
 162 determined by the maturation stress  $\sigma_{NW}$  in NW and  $\sigma_{TW}$  or  $\sigma_{CW}$  in RW according to equation (10).

163 We considered two possible configurations for the simulations in next section:



- 
1. First, we applied a constant eccentricity (so that  $\bar{e} = e$ ) and we fixed the stress level in the NW. In that case, the maturation stress of the RW was given by equations (10):

$$\left\{ \begin{array}{l} \sigma_{TW} = \frac{-2}{\pi R^2(1+e)} \left( \frac{dM}{dR} + eR \frac{dN}{dR} \right) + \sigma_{NW} \left( \frac{1-e}{1+e} \right) + \lambda_b \left( \frac{ER^2}{2(1+e)} \right) R^{\nu_b} \\ \sigma_{CW} = \frac{2}{\pi R^2(1-e)} \left( \frac{dM}{dR} + eR \frac{dN}{dR} \right) + \sigma_{NW} \left( \frac{1+e}{1-e} \right) - \lambda_b \left( \frac{ER^2}{2(1-e)} \right) R^{\nu_b} \end{array} \right. \quad (21a)$$

$$\left\{ \begin{array}{l} \sigma_{TW} = \frac{-2}{\pi R^2(1+e)} \left( \frac{dM}{dR} + eR \frac{dN}{dR} \right) + \sigma_{NW} \left( \frac{1-e}{1+e} \right) + \lambda_b \left( \frac{ER^2}{2(1+e)} \right) R^{\nu_b} \\ \sigma_{CW} = \frac{2}{\pi R^2(1-e)} \left( \frac{dM}{dR} + eR \frac{dN}{dR} \right) + \sigma_{NW} \left( \frac{1+e}{1-e} \right) - \lambda_b \left( \frac{ER^2}{2(1-e)} \right) R^{\nu_b} \end{array} \right. \quad (21b)$$

- 164 2. Second, we fixed the maturation parameters and we observed how the eccentric growth could, or not,  
 165 maintain the orientation of the branch. In this configuration, equation (20) became a two degrees  
 166 equation in  $e$  that could be solved numerically.

167 In these two configurations, using data on the support allometries  $\lambda_N, \lambda_M, \nu_M, \nu_N$ , we can calculate the  
 168 stress in the RW and/or the eccentricity with different  $(\lambda_b, \nu_b)$ , then deduce the growth stress profile in  
 169 the section (eq. 19). In the next part, we see how the allometric coefficients can be obtained from data  
 170 generated by growth model.

## 171 Realistic growth data

### 172 Tree architecture modelling

173 Numerical experiments were carried out using two reference models: one softwood *Pinus Pinaster* (pine)  
 174 and one hardwood *Prunus avium* (birch) (Fig 2). Their growth follows the architectural model of Rauh  
 175 [Hallé et al. (1978)]. This implies that the branching is rhythmic, the axes are monopodial and the branches  
 176 are orthotropic. These digital trees were computed with AMAPSim software [Barczi et al. (2007)]. The  
 177 input of this software are architectural parameters which were provided by observations and field studies:  
 178 Coudurier et al. (1993) and Heuret et al. (2006) for *Pinus pinaster*, Caraglio (1996) and Barthélémy et al.  
 179 (2009) for *Prunus avium*. The choice of these species was based on the availability of temperate species in  
 180 AMAPSim database. The two trees were modelled over 50 years in open-growth conditions, which did not  
 181 correspond to the same ontogenic stage of development, but allowed both trees to be considered mature.  
 182 In the final state, the pine (resp. birch) was 18,2 m (resp. 14,1 m) high. The diameter at the base was  
 183 40 cm for both species. The insertion height of the first branch was 14,3 m for pine and 4,6 m for the  
 184 birch. The branches of interest were the main branches; those that were directly attached to the trunk. In  
 185 addition, only branches that were more than 20 years old have been studied, so that they had a consistent  
 186 loading history. Finally, 33 branches for the pine and 45 for the birch were selected. For each of the branch  
 187 groups, the distributions of length  $L$ , radius  $r$  and insertion angle with the trunk  $\theta$  are shown in Table 1.

Species	$L_m$ (m)	$r_m$ (m)	$\theta_m$ (°)
<i>Pinus pinae</i>	$5.3 \pm 0.4$	$5.2 \pm 0.3$	$70 \pm 0.01$
<i>Prunus avium</i>	$7.9 \pm 1.4$	$8.1 \pm 0.7$	$80 \pm 0.05$

Table 1: Geometric distribution of branches of interest

### 190 Loading scenarii: allometric laws

191 Each tree was composed of axes organised hierarchically according to their order: 1 for the tree seed,  
 192 2 for the trunk, 3 for the main branches, 4 for those attached to them, etc.. Each axis was described  
 193 as a succession of growth units (GU), which were sections of cones, identified by a number (in order of  
 194 appearance), and defined by a parent number, an order, a start and end diameter, the coordinates of the  
 195 centres of both initial and final sections as well as their length (Fig 3). Note that the description provided  
 196 by AmapSim did not include the internal structure of the growth units, such as eccentricity. To avoid



Figure 2: AMAPSim representation of aerial architecture of 50-years old trees. (a) *Prunus avium* and (b) *Pinus pinaster*

197 unnecessary complications, the coordinates of the centres were taken as those of the pith. From the model  
 198 data, the moments and normal forces can be computed in each growth unit, at any time of the tree's  
 199 existence. In addition to a part of its own weight, each unit is subjected to the weight of its offsprings -  
 200 this term referring to any growth unit that would fall if the studied one was cut. The normal force  $\vec{N}_n$   
 201 and bending moment  $\vec{M}_n$  supported by the growth unit  $n$  can be written:

$$\vec{N}_n = \frac{1}{2}m_n\vec{g} + \sum_{\substack{k>n \\ k \text{ offspring}}} m_k\vec{g} \quad (22)$$

$$\vec{M}_n = \overrightarrow{G_n G'_n} \wedge \left( \frac{1}{2}m_n\vec{g} \right) + \sum_{\substack{k>n \\ k \text{ offspring}}} \overrightarrow{G_n G_k} \wedge (m_k\vec{g}) \quad (23)$$

203 where  $G_n$  is the centre of gravity of the current growth unit,  $G'_n$  is the centre of gravity of its second half.  
 204 On the downstream side of  $G_n$ ,  $G_k$  is the centre of gravity of an offspring of number  $k > n$ ,  $m_i$  is the mass  
 205 of growth unit  $i$  and  $\vec{g}$  is the gravity vector. Once  $\vec{N}_n$  and  $\vec{M}_n$  were computed in the absolute coordinates  
 206 used for the description of the whole tree, they were projected in the local coordinates system  $(\vec{x}', \vec{y}', \vec{z})$ ,  
 207 with  $\vec{z}$  of the chosen cross section. In the following, in accordance with the development of the previous  
 208 section,  $N_z$  refers to the projection of  $\vec{N}$  on  $\vec{z}$  and  $M_y$  to the projection of  $\vec{M}$  on  $\vec{y}'$ .

209 Power law regressions were performed to recover the allometric coefficients  $\lambda_M, \lambda_N, \nu_N, \nu_M$ . A summary  
 210 of the analysis process is proposed in Fig 3.

211 For the selected branch groups, the distribution of all allometric coefficients are presented in Fig 4. In *Pinus*,  
 212 there was a large variation in  $\nu$ -coefficient, with  $\nu_M$  varying by almost a factor 2 in the studied sample;  
 213 indicating very variable secondary growth kinetics. In *Prunus*, the range of variation of the allometric  
 214 power coefficients was smaller, which depicted a higher homogeneity of secondary growth kinetics. For  
 215 both species, a great diversity in  $\lambda$ - coefficients was observed, which depicted a significant variability  
 216 in the loading history. This is particularly interesting as the branches showed geometric determinants  
 217 that did not vary over large ranges (Table 1). Also, these coefficients do not appear to vary as a function

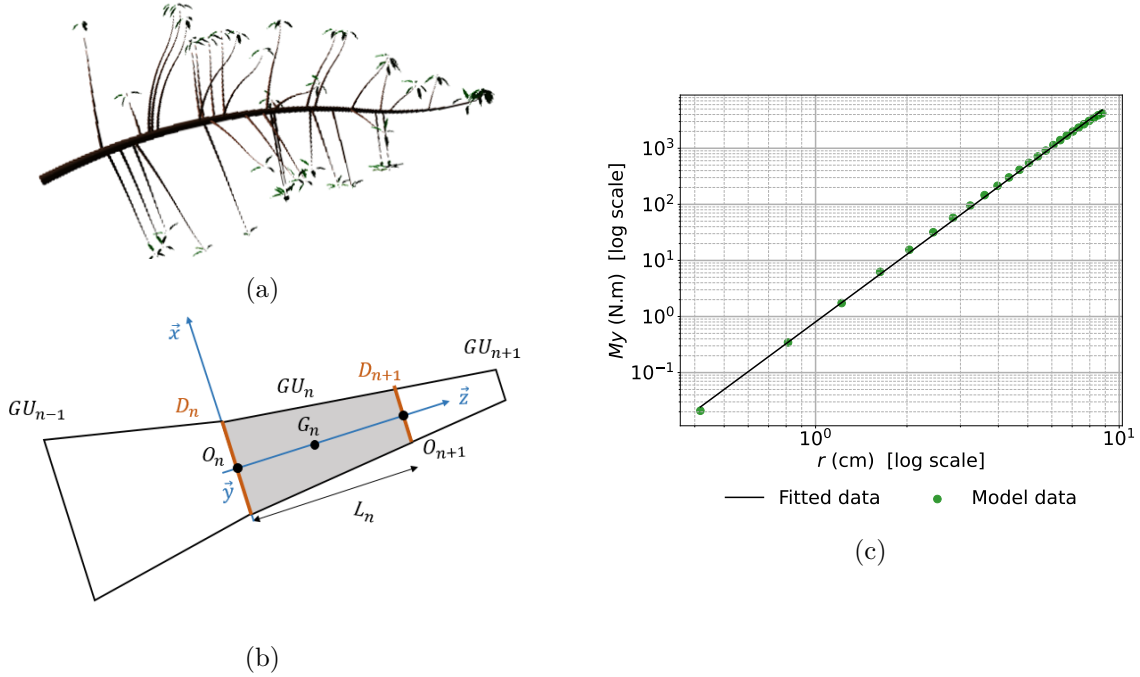


Figure 3: Allometric law of *Prunus avium*. The bending moment is calculated from the geometry of the modelled branch (a) and (b). The graph (c) represents the relationship between the branch diameter and the bending moment. The fitted curve provides the allometric law.

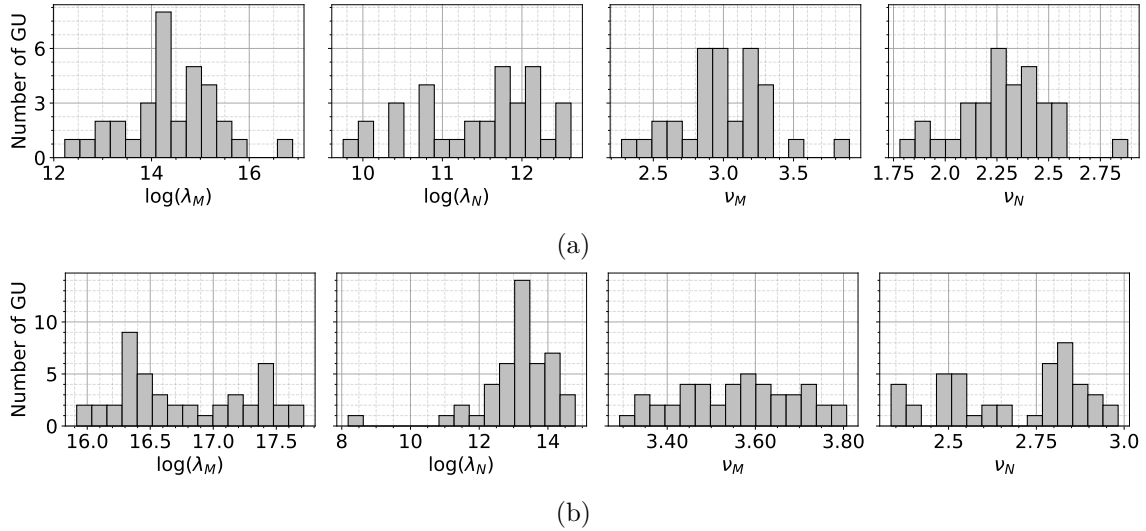


Figure 4: Statistical distribution of allometric coefficients for modelled branches: (a) *Pinus pinaster* (b) *Prunus avium*.  $\lambda_{M,N}$  refers to the weight,  $\nu_{M,N}$  to the kinetic of secondary growth.

218 of geometric parameters. This reflects the complexity of predicting the loading of a branch from the  
 219 determinants of the main axis, and shows the importance of branching. In both cases, these variations in  
 220 the  $\lambda$ -coefficients result in a factor of 4 in the bending load between the lightly loaded and the heavily  
 221 loaded branches.

222 The average values of each allometric and final geometry, indicated in table 2, will be used for the  
 223 simulations.

---

## 224 Material data

225 The stress values in the NW were fixed according to the average maturation strains advised by Thibaut  
226 and Gril (2021). Similarly, the green wood MOE were given by the correlation between dry and green  
227 MOE identified by Thibaut and Gril (2021):  $E_g = 0.89 * E_d$ . Dry MOE were provided by the tropix  
228 database of CIRAD [Gérard et al. (2011)]. The density of green wood was approximated by the density of  
229 water  $\rho = 1000 \text{ kg.m}^{-3}$ . These inputs are summarised in Table 2.

230 In the following section, the case of stationary growth ( $\nu_b = 0$ ) will be considered principally and analysed  
231 thoroughly. Situations of changing curvature will be then considered briefly.

Species	$\lambda_M$	$\lambda_N$	$\nu_M$	$\nu_N$	$r$	$\mu_{NW}$	$E_d$	$E_g$
<i>Pinus pinae</i>	-6.4e6	5e4	3.2	2.5	0.05	410	8.8	7.9
<i>Prunus avium</i>	-2.6e7	9.5e3	3.6	2.7	0.08	712	10.2	9.1

232 Table 2: Mean input characteristics of the branches.  $\lambda_{N,M}$  and  $\nu_{N,M}$  correspond to the allometric evolution  
of the normal load and bending moment,  $r$  (m) is the radius at the basal part of the branch,  $\nu_{NW}$  ( $\mu$ strain)  
is the maturation strain in the NW, and  $E_{d,g}$  (GPa) is the dry and green modulus of the material.

## 233 Results

### 234 *Prunus avium*

235 Fig 5 shows simulation results obtained for *Prunus avium*, when one of the factors (eccentricity or RW) is  
236 set to zero. On Fig 5.a, the stress on the whole section is represented. In this case, the branch maintains  
237 its orientation through the formation of RW only (no eccentric growth). The area near the pith is in  
238 compression (red), while the periphery is in tension (blue), with a higher tension on the upper side,  
239 allowing to maintain the orientation. Fig 5.b shows the interpolation of the stress distribution of Fig 5.a  
240 on the main axis  $y=0$ . The Fig 5.c represents the maturation stress in the TW throughout the growth of  
241 the branch. The larger the branch grew, the higher the needed stress level. The symmetric case, with no  
242 formation of RW but eccentric growth, is presented in Fig 5.d-f. This example illustrates that eccentricity  
243 alone could theoretically provide the orientation control. Fig 5.f shows the evolution of the eccentricity  
244 through the radial growth of the branch. Like the RW stress in the previous case, the needed eccentricity  
245 increased when the branch grew. The pattern of stress distribution of Fig 5.d is quiet similar as in Fig  
246 5.a, with compression near the pith and tension at the periphery, but the section is off-centred and the  
247 tension at periphery is the same all around the section, confirming the absence of RW.

248 Fig 6 shows the combination of the two factors. For each of them, three different scenarii were proposed.  
249 In Fig 6.a, the RW factor controlled the orientation. Different eccentricities, ranging from -0.5 to 0.5 were  
250 imposed. The resulting stress patterns are represented in Fig 6.a.i : the higher tension on the upper side  
251 maintained the posture. The more hypotrophic the eccentricity, the higher the tension stress at periphery.  
252 This is confirmed by the evolution of RW maturation stress through branch growth in Fig 6.a.ii. The  
253 situations where the eccentricity controlled the posture are shown in Fig. 6.b. Where uniform tension  
254 was imposed ( $\sigma_{TW} = 2\sigma_{NW}$ ,  $\sigma_{TW} = 3\sigma_{NW}$ ), the eccentricity pattern became particular: we observed a  
255 decrease during the first year, followed by an increase (Fig 6.b.ii). This is explained by the growth scenario:  
256 at the beginning of the development, fixing a uniform RW formation tended to right-up the stem, while  
257 a stationary orientation was imposed. Therefore, the eccentricity process counteracted this righting up  
258 movement, leading to the initial decrease. As the branch grew, the effect of the RW decreased and the  
259 branch tended to bend forward: the eccentricity counteracted this trend, leading to the final increase.  
260 This coordination problem may probably be specific to our scenario that imposed a stationary orientation  
261 throughout the entire growth the branch, including the first stages of development.

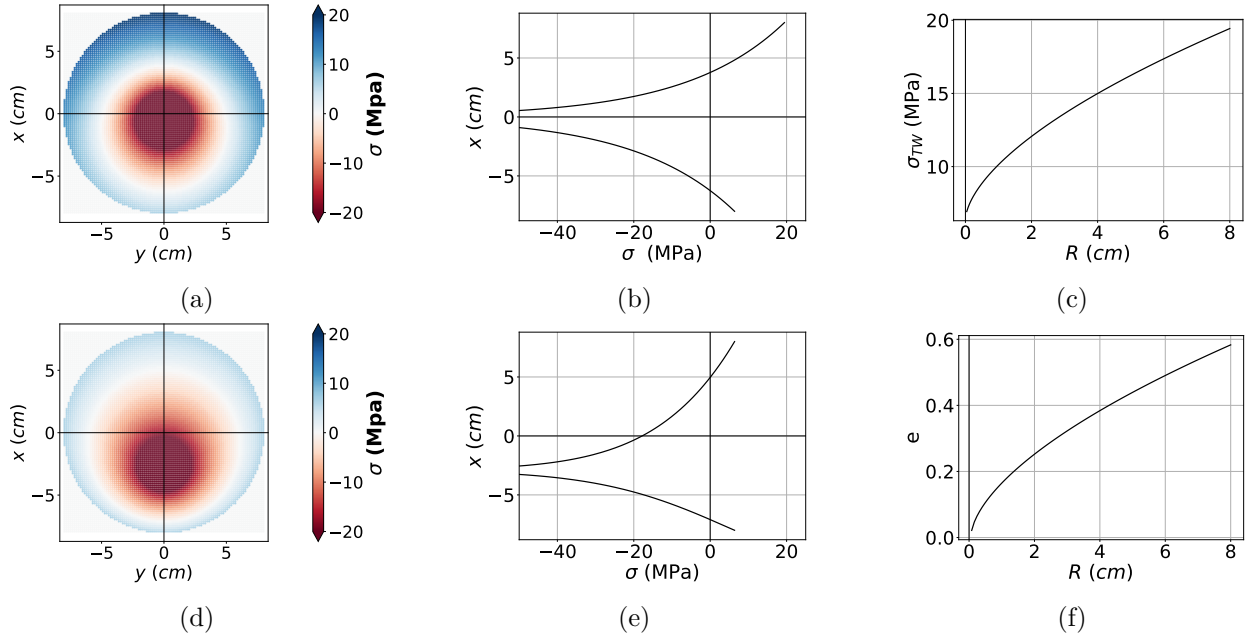


Figure 5: *Prunus avium*: The horizontal orientation of the branch is maintained by the two different processes: (a-c) the maturation stress provided by the formation of RW; (d-f) the eccentric growth; (a,d) 2D visualisation of the growth stress in the whole section; (b,e) Growth stress profile on diameter  $y=0$ . (c,f) Parametric representation of the tropic driver, maturation stress (c) and eccentricity (f).

## 262 *Pinus pinaster*

263 For *Pinus pinaster*, we used the same approach. The set of results is presented in Fig 7 and Fig 8. When  
 264 no eccentricity was involved (Fig 7.a-c), a light compression stress was observed on the lower side of the  
 265 section. When the branch grew, the compression stress increased (Fig 7.c). In case of no RW formation  
 266 (i.e. homogeneous maturation stress), the distributions of growth stress and eccentricity (Fig 7.d-f) were  
 267 quiet similar to the previous example with the birch tree: tension in periphery, compression near the pith,  
 268 and an increasing eccentricity with branch growth.

269 The combination of the two factors is shown in Fig 8. As for *Prunus avium*, different eccentricities were  
 270 imposed (Fig 8.a): the more epitrophic the eccentricity, the higher RW maturation stress. Although the  
 271 different compression stress levels were close, the dynamic of this stress within the growth of the branch  
 272 was different (Fig 8.a.ii). Also, the stress pattern exhibits a difference near the pith (Fig. 8.a.i), with  
 273 some tension in this area for eccentricity  $e = 0.5$ . In case of a uniform RW maturation (8.b), the profile  
 274 remained quite similar to birch tree. We could not impose a too low compression stress because of the  
 275 above-mentioned coordination incompatibility.

## 276 Influence of branch orientation: the stationarity hypothesis

277 In order to evaluate the relevance of the stationarity hypothesis i.e. the branch keeps the same orientation,  
 278 different growth scenarii were considered. For each branch, the case of active up-righting or passive  
 279 bending was modelled (using equation 17). Passive bending was driven by increasing weight, calculated  
 280 on the modelled branches. Up-righting was driven by the maturation gradient, which was set at 400  
 281  $\mu$ strain ( $\sigma \approx 3.2$  MPa) for pine and 700  $\mu$ strain ( $\sigma \approx 6.2$  MPa) for birch (the gradient was of the order of  
 282 magnitude of NW stress). The results are shown in Fig 9. In birch, no major change of the stress pattern  
 283 was observed. In contrast, the pattern changed greatly for pine. For a passive-bending branch, a 'V' profile  
 284 and the absence of CW were observed. For up-righting, the previously-mentioned profile with tension at

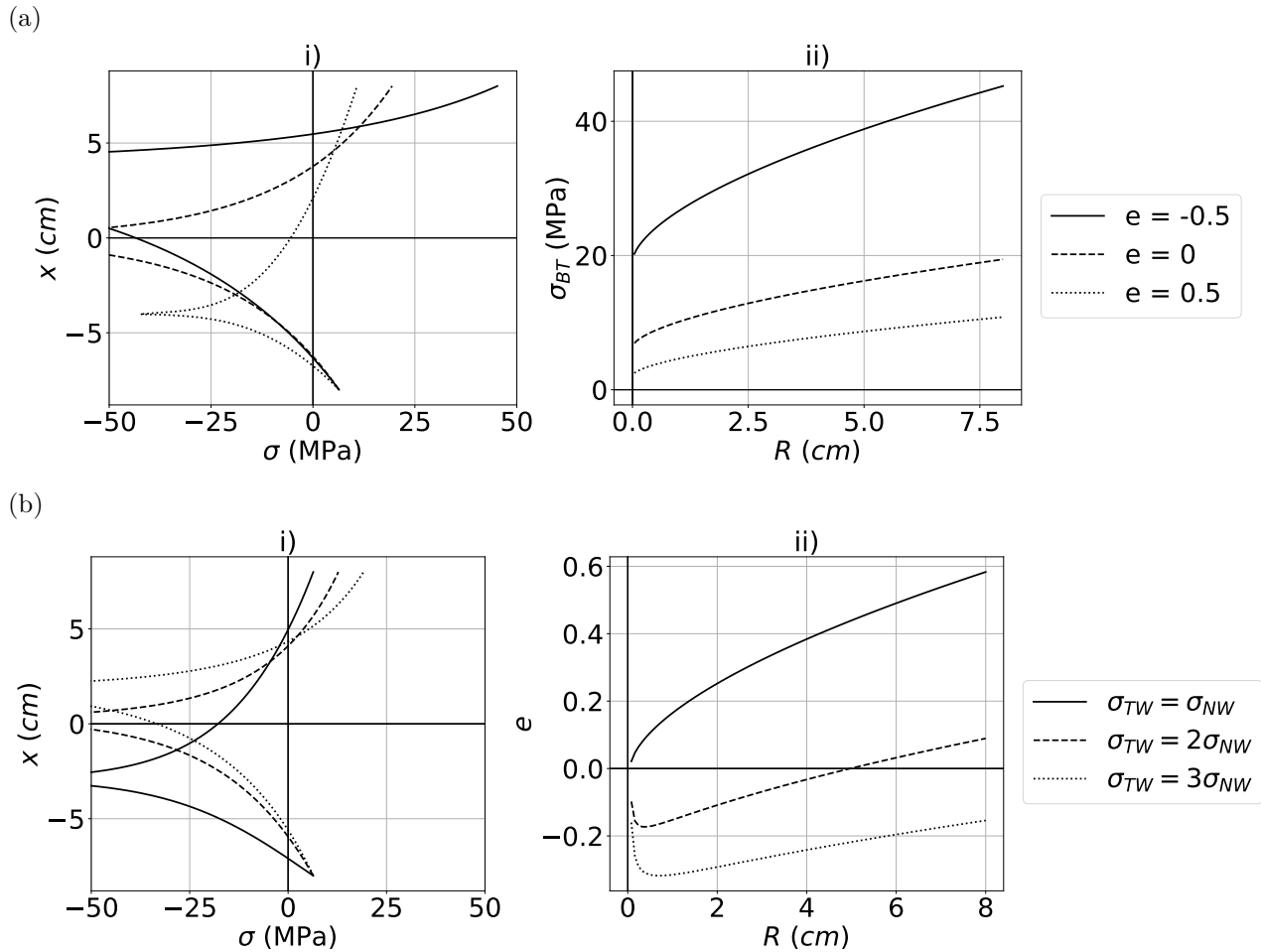


Figure 6: Different possible options to maintain the orientation of *Prunus avium* branches: (a) a constant eccentricity combined with the maturation that becomes the main driver of postural control; or (b) a constant maturation gradient combined with an eccentricity that becomes the main driver of postural control.

285 the pith was observed.

## 286 Discussion

### 287 *Prunus avium*: heavily loaded hardwood

288 Regarding the stress distribution (Fig 5), using either eccentric growth or RW led to realistic orders of  
 289 magnitude (except near the pith, which is an intrinsic limit of our model. This specific point is discussed  
 290 in section *Limits of the model*). In the case with no eccentricity, a tensile strain of  $\mu_{RW} \approx 2140\mu\text{strain}$   
 291 ( $\sigma_{TW} \approx 19.5$  MPa) was obtained, quite similar to literature values, for much smaller branches: on 4 cm  
 292 plagiotropic branches of eight tree species, Tsai et al. (2012) reported an average strain in RW of around  
 293  $2100\mu\text{strain}$ , with some values up to  $\approx 5000\mu\text{strain}$ . When combined with uniform eccentricity (Fig 6.a),  
 294 it seems safer to promote the growth on the upper side: it minimises both high tensile stress and area  
 295 with high compression stress. Interestingly, the worst case (hypotrophic eccentricity  $e = -0,5$ , more, solid  
 296 line in Fig 6.a) led to levels approaching the limits, but previously observed [Huang et al. (2005); Tsai  
 297 et al. (2012)]:  $\mu_{RW} \approx 4970\mu\text{strain}$  ( $\sigma_{TW} \approx 45.4$  MPa)). Note that although for softwoods, there is a  
 298 consensus on the usually observed eccentricity orientation (hypotrophic) [Timell (1986)], the eccentricity

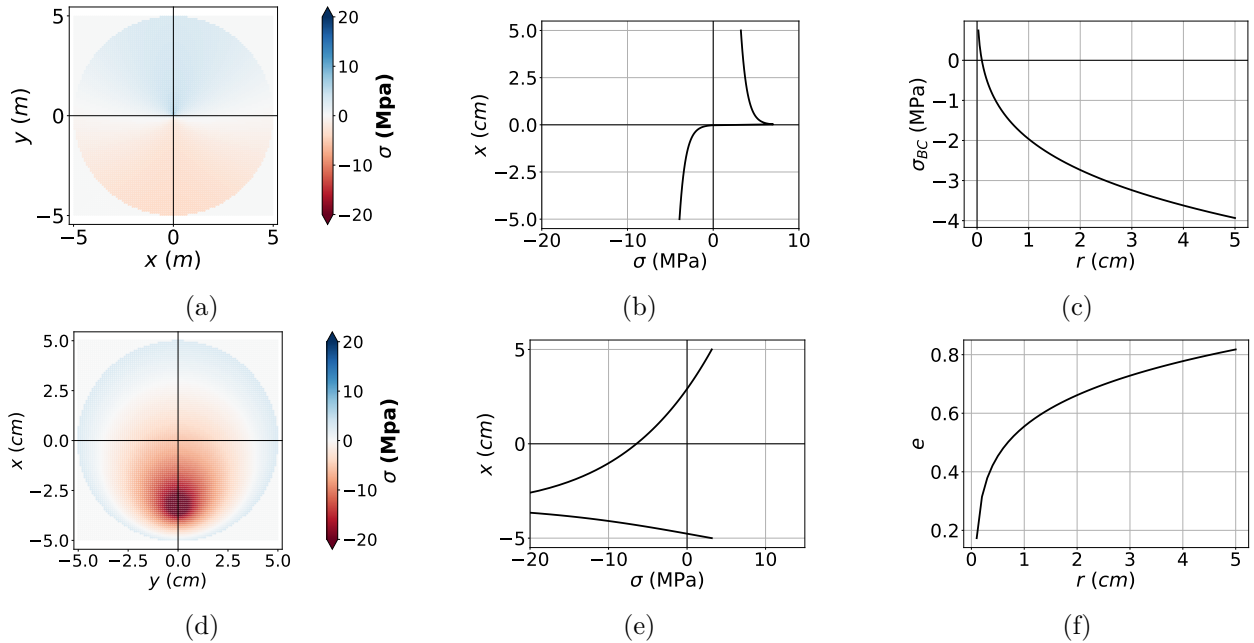


Figure 7: *Pinus pinaster*: The horizontal orientation of the branch is maintained by the two different processes: (a-c) the maturation stress provided by the formation of RW; (d-f) the eccentric growth; (a,d) 2D visualisation of the growth stress in the whole section; (b,e) Growth stress profile on diameter  $y=0$ . (c,f) Parametric representation of the tropic driver, maturation stress (c) and eccentricity (f).

299 has been observed in both directions in hardwood branches [Kucera and Philipson (1977); Wang et al.  
300 (2009b); Tsai et al. (2012)] although not usually in trunk. Therefore, this could be a tropic response for  
301 angiosperms branches, that tend to bend forward. This non-optimal pattern would be the consequence of a  
302 coordination between eccentricity and maturation stress. An extensive measurement campaign on branches  
303 would be needed to clarify this point. In the absence of RW (Fig 5.d-f), the eccentricity alone ensured the  
304 orientation. The maximal value was around 0.6, which seems quite high compared to literature values. For  
305 example, Hung et al. (2017) performed measurements on 10 plagiotropic branches of *Koelreuteria henryi*.  
306 The average radius was 2.6 cm, and the eccentricity had an average value of -0.37, with a maximum at  
307 -0.54. Unpublished data on more than 150 branches from six different temperate species showed very  
308 different patterns, depending from the species, but eccentricity was never below -0.5. This suggests that  
309 eccentricity is a limited driver of postural control. This result is in line with the work of Alm eras et al.  
310 (2005), who showed that eccentricity in leaning stem explains a much lower part of the curvature than the  
311 maturation gradient ( $\approx 29\%$  for eccentricity while  $\approx 66\%$  for maturation gradient).  
312 The combination of radial growth eccentricity with uniform maturation stress showed the same tendency  
313 as the dual combination (uniform eccentricity): a higher maturation stress led to a larger eccentricity.  
314 Comparing all simulations, the most optimal case was a constant positive eccentricity (dotted line in Fig  
315 6.a). However, experimental observation showed that this is not the usual configuration for branches.  
316 It raises interesting question on the main mechanical driver of branch construction. From a biological  
317 point a view, it could be more "costless" to produce TW than eccentricity, but this hypothesis was not yet  
318 investigated. Also, more work is needed to understand how TW and eccentricity are linked in angiosperm  
319 trees: since they may have some uncoordinated action, we can wonder if they have common triggered  
320 factors.

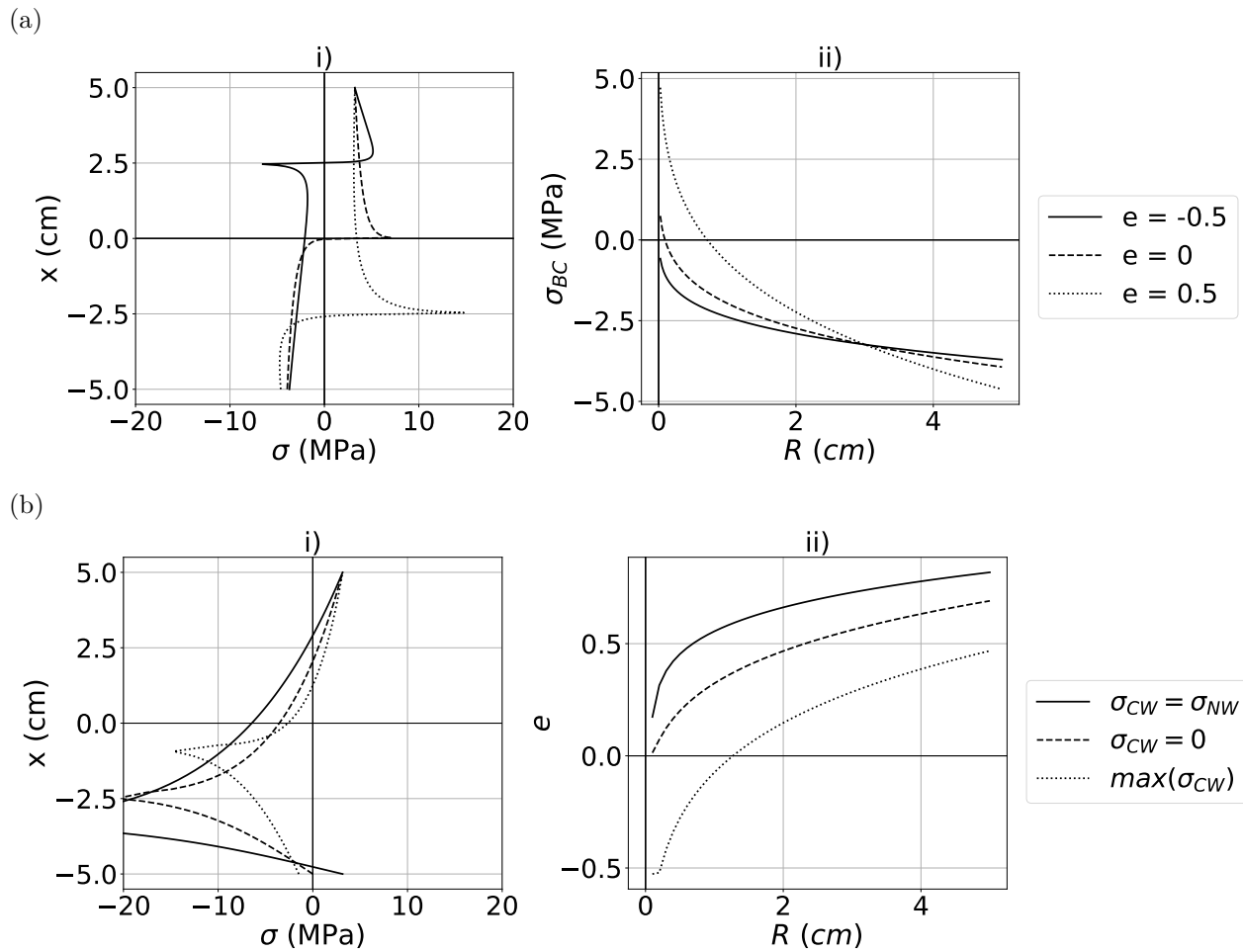


Figure 8: Different possible options to maintain the orientation of *Pinus pinaster* branches: (a) a constant eccentricity combined with the maturation that becomes the main driver of postural control; or (b) a constant maturation gradient combined with an eccentricity that becomes the main driver of postural control.

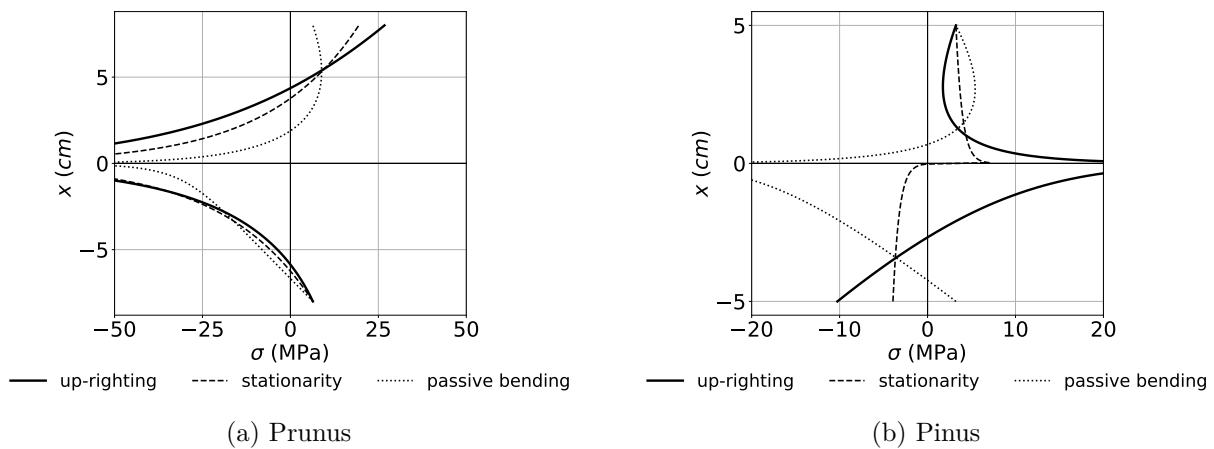


Figure 9: Distribution of growth stresses for different orientation scenarios.

321 ***Pinus pinaster*: lightly loaded softwood**

322 First of all, the values of the stress distribution were much lower than for *Prunus avium*. This was  
 323 explained by the size of the modelled branches: the average bending moment is much higher for birch



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tree than for pine, by a factor roughly 10 (see  $\lambda_M$  and  $\lambda_N$  in Table 2). The effect of each factor alone (Fig 7) suggested that maturation is a much more efficient option than eccentricity. To ensure the same growth scenario, the eccentricity alone rose to about 0.8, which is close to a theoretical limit, whereas maturation alone led to low maturation strains in CW (<500  $\mu$ strain, corresponding to 4 MPa). Besides, this eccentricity was not in the direction of what is commonly observed. This point remains logical, because without CW, the epitrophic eccentricity is the only way to counteract the effect of gravity. A uniform eccentricity combined with RW formation led to quite similar patterns (Fig 8.a): for this range of loading, the eccentricity had little influence on stress distribution. Considering that the density of elastic energy is proportional to the square of the stress, the pattern produced a low level of stored elastic energy, possibly reducing the risk of mechanical failure. Also, although eccentricity did not bring much variations in the value of the maturation stress, it considerably modified the shape of the resulting stress profiles (Fig 8.a.i). Indeed, these profiles can become 'crenellated' (Fig 8.a.i, dashed curve for zero eccentricity, solid curve for  $e = -0.5$ ) or include tension at the pith (dotted line for  $e = 0.5$ ). It seems that before producing tension in the pith, an efficient configuration could be reached by generating compression below the pith and tension above. Ideally, this may be a very relevant option for branches. These results about the mechanical strategies of branches should be confronted to experimental measurements. Otherwise, these pattern changes could also be an optimisation of the residual strength of wood: CW is known to have high compressive strength conferred by its high lignin content and cell wall structure. Generating some tension at the pith allows the branch to create more CW. To answer this question it would be necessary to take into account strength parameters in our stress computation model. Adding a damage-elastoplastic law would also allow to study the effects of stress relaxation and to observe if some profiles, that are here not optimal for maintaining the branch orientation, could possibly become optimal for resisting breakage. Using eccentricity combined to RW formation (Fig 8.b) leads to usual patterns, with compression near the pith, tension on the upper side and compression on the lower one. Eccentricity is epitrophic: this is the opposite to what is usually observed: unpublished data on 20 branches (average radius of 3 cm) of *Pinus nigra* showed an average eccentricity of -0.2. This non-intuitive result is partly explained by our hypothesis of uniform stiffness, as will be discussed later. It is also explained here by the change of sign between NW and CW. In the early stages of growth, as long as the stress in the CW is lower than in the NW, the best option to maintain the orientation is to do epitrophic eccentricity. Once the stress in the CW becomes higher than in the NW, it is more efficient to do hypotrophic eccentricity. Our scenarios do not allow us to reach stress levels in compression that are higher than the stress in normal wood. This is due to the above mentioned incompatibility of our scenario.

### 356 **Influence of the branch's orientation : the stationary hypothesis**

357 In both trees, the orders of magnitude are compatible with a mechanical safety margin for the branches.  
358 Apart from modified tropisms (change of light environment, weight change by loss of part of the branch,  
359 etc.), the maintaining of the orientation is quite common for real branches. However our simulations  
360 suggest that if, for any reason, they need to modify their orientation, they can do it without taking too  
361 much mechanical risk. The hypothesis of branch direction stationarity is totally in accordance with the  
362 long-term mechanical requirements needed during the construction of branches.

### 363 **Vertical bending moment vs horizontal bending and torsion moments**

364 One of the hypothesis of our model was that the vertical bending moment ( $M_y$ ) prevails over the torsional  
365  $M_z$  and horizontal bending  $M_x$  moments. This allowed to consider only one direction of eccentricity and  
366 to avoid all the non-linear terms generated by the torsional components. We evaluated the maximum  
367 values of the three moments for all modelled branches of each species for comparison purpose. The results  
368 are presented in Fig 10. They enlighten that for each species, the vertical moment shows much higher  
369 values than the torsional and horizontal bending moments and validates our initial hypothesis.

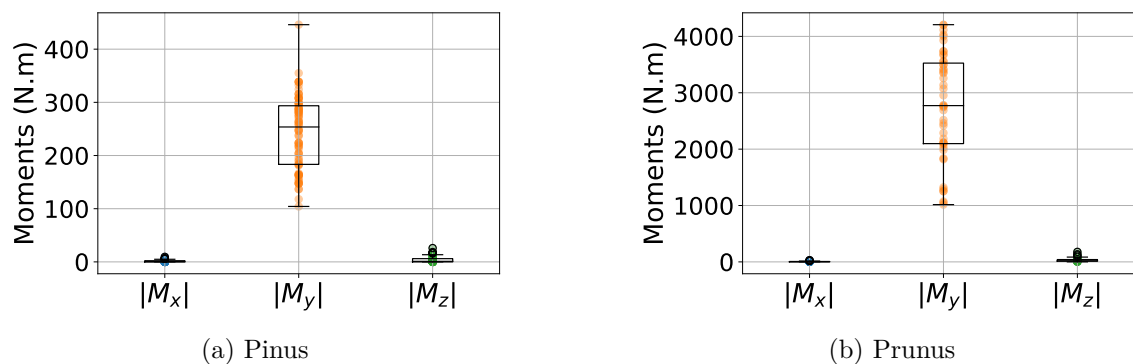


Figure 10: Comparison of maximum moments for modelled branches.  $M_x$ : horizontal moment;  $M_y$ : vertical moment;  $M_z$ : torsional moment.

### 370 Limits of the model

371 The hypothesis of homogeneous wood stiffness in the whole section is questionable. Systematic stiffness  
 372 differences have been observed between wood types (TW or CW vs NW). Alm eras et al. (2005) have  
 373 studied the variation of Young's modulus in the section of leaning stems from 14 angiosperms and 3  
 374 gymnosperms, all coming from different families. For the angiosperms, the average Young's modulus of  
 375 TW was higher than in NW by 15%, while for the gymnosperms, the Young's modulus was 38% lower in  
 376 CW than in NW. This heterogeneity of rigidity plays a role in the postural control of the stems [Alm eras  
 377 et al. (2005); Huang et al. (2010); Hung et al. (2017)]. In our case, either a higher rigidity in TW or a  
 378 lower in CW would make the branch bend upward. In the current formulation of the model imposing an  
 379 homogeneous stiffness, an almost equivalent effect would have been obtained by an initial offset in the  
 380 eccentricity. Calling this offset tentatively 'compensating eccentricity'  $e_c$  (Fig 11), the model computed a  
 381 total eccentricity,  $e$ , combining  $e_c$  and the "real" eccentricity needed to maintain the orientation. Therefore,  
 382 in case in RW formation on one side, the eccentricity displayed need to be offset by  $e_c$  to correspond to  
 383 more realistic situations. This explains, for instance, why the simulations for the softwood resulted in  
 384 hypertrophic eccentricity while it is well-known that inclined softwood stems usually exhibit hypotropic  
 385 eccentricity. Although data are missing to approximate the value of this parameter, and further work is  
 386 needed to assess theoretically the possible equivalence between rigidity variations and eccentricity, the  
 387 available information on relative stiffness of NW and RW suggests a more important effect in gymnosperms  
 388 than in angiosperms.

389 The evaluation of the stress during the first stages of branch development is ano issue of the model. In  
 390 almost every stress profile, a tension or compression peak is generated in the pith. It generally exceeds  
 391 the wood strength, which is not compatible with branch sustainability. This point could be corrected  
 392 in two ways. First, the role of the bark could be taken into account. Its mechanical role for small axes  
 393 has already been studied and its importance in postural maintenance was clearly highlighted [Clair et al.  
 394 (2019); Ghislain et al. (2019)]. Our model could include the mechanical action of bark in the early stages  
 395 of branch development. This improvement would require additional data about the mechanical behaviour  
 396 of the bark but would bring more realistic stress predictions and limit the artefacts at the pith. A second  
 397 exciting perspective would be to take into account the elastoplastic behaviour of wood. By imposing a  
 398 realistic plastic strain limit, the peak at the pith would then disappear; the increments would be spread  
 399 over the middle part of the section, thus modifying the non-realistic patterns previously observed.

400 Finally, modelling the evolution of normal force and bending moment loads by allometric laws was  
 401 questionable. Indeed, the orientation of the branch may vary with time, which implies variations of the  
 402 effect of weight. For example, modelling a constant increase of the normal force is inappropriate if the  
 403 inclination of the branch decreases with time. An improvement of our model could be the construction

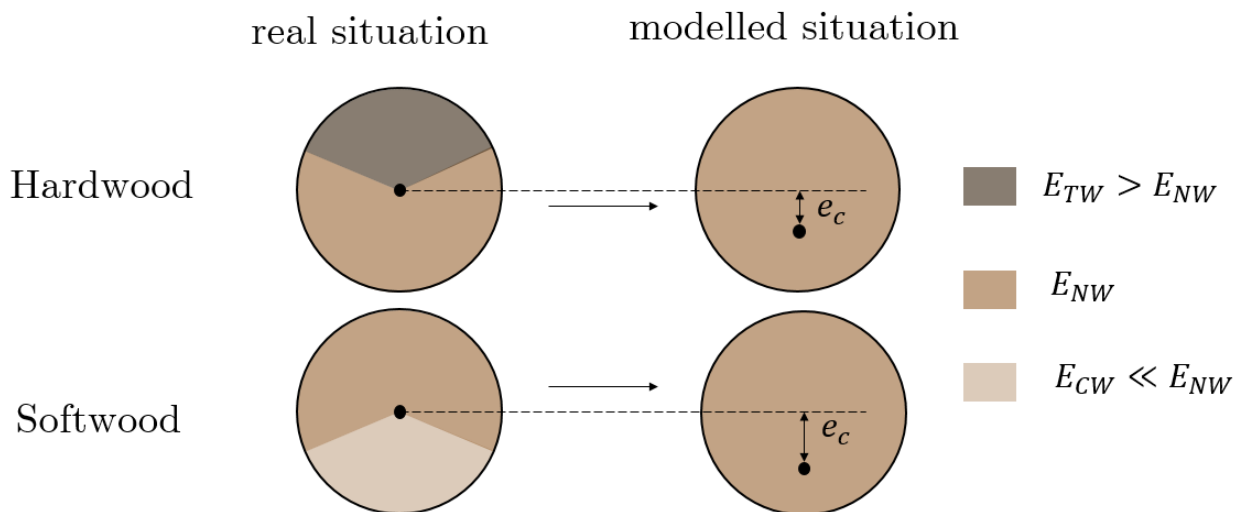


Figure 11: How the hypothesis of a uniform wood stiffness impacts the initial position of the pith.

404 of loads based on equivalent length allometries taking into account the mass of the branch, and the  
 405 computation of the loads for each position in the right reference frame.

## 406 Conclusion and perspectives

407 A semi-analytical growth stress model has been developed in the context of branch development. At  
 408 each radius increment, the stress balance is computed in order to fit with a fixed curvature. A first  
 409 novelty of this model is that it takes into account the role of the eccentricity variation over the years.  
 410 A second contribution is the computation of stress distribution in the whole cross-section. We tested  
 411 the effectiveness of two well-known biomechanical processes of woody plants to control the orientation  
 412 of their axes: eccentric radial growth and RW formation. The case of one softwood *Pinus pinaster* and  
 413 one hardwood *Prunus avium* were computed using data provided by AMAPSim software. For both  
 414 trees, growth stress simulations showed that maturation stress was more efficient than eccentric radial  
 415 growth to maintain a fixed orientation (i.e. to counter the increasing gravity constrain applied to the  
 416 growing branch). For the hardwood branches, the computations highlighted that the eccentricity needed  
 417 to maintain orientation did not corroborate the observations reported in literature. This suggests that this  
 418 parameter probably provides another function than the orientation control, like the improved bending  
 419 strength of the branch that provides it a greater mechanical safety. For the softwood branches, although  
 420 the model showed that eccentric radial growth did not play a major role in maintaining the branch's  
 421 orientation, it does modify the shape of the stress profiles in the cross section of the branch. A few odd  
 422 and critical profiles, crenellated or with tension near the pith, have been identified. Their analysis provided  
 423 exciting perspectives for further experimental works to gather real data.

424 Now that a complete model is available, it becomes crucial to start experimental investigations on branches  
 425 in order to compare the outputs with real in situ observations. Especially, we need to evaluate the relevance  
 426 of the different biological processes used by branches to ensure their mechanical sustainability over the  
 427 years.

428 From a biological point of view, a key point for understanding branch sizing is the question of biomass  
 429 costs. Building additional wood on one side or forming RW are carbon sinks with possible trade-offs. In  
 430 order to investigate this point, our model could help by affecting a cost to the production of RW as well  
 431 as to eccentric growth. The resulting computations could then help to understand the relevance of some  
 432 options and would lead to coupling the biomechanical point of view to other biological considerations.

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549 **Appendix A**

550 The calculation of integrals of system (3) requires preliminary elements. The situation of two consecutive  
 551 rings is represented in Fig. 12. Each position  $x$  in the geometrical reference frame is expressed with respect  
 552 to the position  $x'$  in the pith reference frame according to the equation:

$$x = r \cos \theta = x' - \bar{e}R \quad (24)$$

with  $r$  the radius at time  $t$  and  $R$  the radius at the final time.

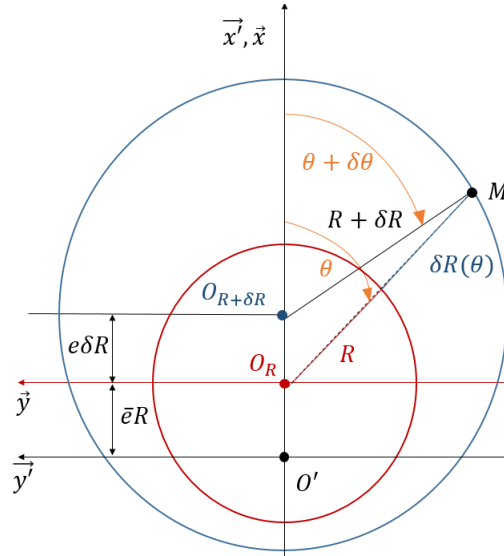


Figure 12: Representation of two consecutive rings and the elements needed to calculate  $\delta R(\theta)$

553

554 The integrals of system (3) are computed as follows:

$$\begin{aligned} \int_s \delta \sigma ds &= \int_s E [\delta a + (x + \bar{e}.R)\delta b] r \delta r d\theta \\ &= E\pi R^2 (\delta a + \bar{e}.R\delta b) \\ \int_s x' \delta \sigma ds &= \int_s [\delta a + (x + \bar{e}.R)\delta b] [x + \bar{e}.R] r \delta r d\theta \\ &= E\pi R^3 \left[ \bar{e}\delta a + R \left( \bar{e}^2 + \frac{1}{4} \right) \delta b \right] \end{aligned}$$

The tangential distribution of the radius increment  $\delta R(\theta)$  is required to compute the maturation terms. Applying  $\overrightarrow{O_R M} - \overrightarrow{O_{R+dR} M} = \overrightarrow{O_R O_{R+dR}}$  (Fig 12):

$$\begin{cases} [R + \delta R(\theta)] \cos \theta - (R + \delta R) \cos (\theta + \delta \theta) = e_R \delta R & (25a) \\ [R + \delta R(\theta)] \sin \theta - (R + \delta R) \sin (\theta + \delta \theta) = 0 & (25b) \end{cases}$$

555 By setting  $\delta \theta \rightarrow 0$ , it comes:

$$\begin{cases} \cos (\theta + \delta \theta) = \cos \theta - \sin \theta \delta \theta & (26a) \\ \sin (\theta + \delta \theta) = \sin \theta + \cos \theta \delta \theta & (26b) \end{cases}$$

556 Substituting (26) into (25), and combining (25a) and (25b),  $\delta R(\theta)$  can finally be written as:

$$\boxed{\delta R(\theta) = \delta R [1 + e_R \cos \theta]} \quad (27)$$

Then:

$$\begin{aligned} \int_{\delta s} \sigma_0^i ds &= \int_{\delta s} \sigma_0^i(\theta) R \delta R(\theta) d\theta \\ &= \int_{\delta s} [\alpha + \beta \cos \theta] [1 + e \cos \theta] R \delta R(\theta) d\theta \\ &= \pi (2\alpha + e\beta) R \delta R \\ \int_{\delta s} x' \sigma_0^i ds &= \int_{\delta s} \sigma_0^i(\theta) (x + e.R) R \delta R(\theta) d\theta \\ &= R^2 \delta R \pi (3\alpha e + \beta e^2 + \beta) \end{aligned}$$

## 557 Appendix B

The matrix system (7) becomes:

$$\begin{cases} \delta a = \frac{\delta F_0 K_2 - \delta F_1 K_1}{K_0 K_2 - K_1^2} & (28a) \\ \delta b = \frac{\delta F_0 K_1 - \delta F_1 K_0}{K_1^2 - K_0 K_2} & (28b) \end{cases}$$

558 Then, numerators and denominators are calculated separately:

$$K_0 K_2 - K_1^2 = E^2 \pi^2 R^6 \left( \bar{e}^2 + \frac{1}{4} \right) - E^2 \pi^2 R^6 \bar{e}^2 = \frac{(E \pi R^3)^2}{4}$$

$$\begin{aligned} \delta F_0 K_2 - \delta F_1 K_1 &= E \pi^2 R^5 \left[ -(2\alpha + e\beta) \left( \bar{e}^2 + \frac{1}{4} \right) + \bar{e} (3\alpha e + \beta e^2 + \beta) \right] \delta R + E \pi R^3 \left[ R \delta N \left( \bar{e}^2 + \frac{1}{4} \right) + \bar{e} \delta M \right] \\ &= E \pi^2 R^5 \left[ \alpha \left( 3e\bar{e} - 2\bar{e}^2 - \frac{1}{2} \right) + \beta \left( \bar{e}e^2 - e\bar{e}^2 + \bar{e} - \frac{e}{4} \right) \right] \delta R + E \pi R^3 \left[ R \delta N \left( \bar{e}^2 + \frac{1}{4} \right) + \bar{e} \delta M \right] \end{aligned}$$

$$\begin{aligned} \delta F_0 K_1 - \delta F_1 K_0 &= E \pi^2 R^4 \left[ -\bar{e} (2\alpha + e\beta) + (3\alpha e + e^2 \beta + \beta) \right] \delta R + E \pi R^2 [\bar{e} R \delta N + \delta M] \\ &= E \pi^2 R^4 \left[ \alpha (3e - 2\bar{e}) + \beta (1 + e^2 - e\bar{e}) \right] \delta R + E \pi R^2 [\bar{e} R \delta N + \delta M] \end{aligned}$$

Putting the calculations together, system (28) becomes:

$$\begin{cases} \delta a = \frac{4}{ER} \left[ \alpha \left( 3e\bar{e} - 2\bar{e}^2 - \frac{1}{2} \right) + \beta \left( \bar{e}e^2 - e\bar{e}^2 + \bar{e} - \frac{e}{4} \right) \right] \delta R + \frac{4}{E\pi R^3} \left[ R \delta N \left( \bar{e}^2 + \frac{1}{4} \right) + \bar{e} \delta M \right] \\ \delta b = \frac{-4}{ER^2} \left[ \alpha (3e - 2\bar{e}) + \beta (1 + e^2 - e\bar{e}) \right] \delta R + \frac{-4}{E\pi R^4} [\bar{e} R \delta N + \delta M] \end{cases}$$



---

## 559 Appendix C

560 The following calculus is based on Fig 3.b. To get the vertical bending moment  $M_y$  of unit n (eq 23), one  
 561 need the calculation of each volume  $V_n$  and center of gravity  $G_n$ . Let name  $D(z)$  the diametral extension  
 562 of the cone. It comes:

$$V_n = \int_0^{L_n} \frac{\pi D(z)^2}{4} dz \quad (30)$$

563 where  $D(z) = D_n + \left(\frac{D_{n+1}-D_n}{L_n}\right)z$ . One gives

$$O_n G_n = \frac{1}{V_n} \int_0^{L_n} \frac{\pi D(z)^2}{4} z dz \quad (31)$$

Setting  $\gamma = \frac{D_{n+1}-D_n}{D_n}$  and  $\xi = \frac{L_n}{z}$ , equations (30) and (31) become:

$$V_n = \frac{\pi D_n^2 L_n}{4} \int_0^1 (1 + \gamma \xi)^2 d\xi = \frac{\pi D_n^2 L_n}{4} \cdot \left(1 + \gamma + \frac{\gamma^2}{3}\right)$$

$$O_n G_n = \frac{1}{V_n} \frac{\pi D_n^2 L_n^2}{4} \cdot \left(\frac{1}{2} + \frac{2\gamma}{3} + \frac{\gamma^2}{4}\right)$$

564 So, finally,  $O_n G_n$  can be written:

$$O_n G_n = \frac{L_n}{2} \left( \frac{1 + \frac{4}{3}\gamma + \frac{1}{2}\gamma^2}{1 + \gamma + \frac{1}{3}\gamma^2} \right) \quad (32)$$