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Tissue tension and axial growth of cylindrical structures in plants and elastic tissues

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Abstract – In many cylindrical structures in biology, residual stress fields are created through differential growth. In particular, if the outer and inner layers of a cylinder grow differentially, parts of the cylinder will be in a state of axial compression and other parts will be in tension. These tissue tensions change the overall material properties of the structure. Here, we study the role of tissue tension in the overall rigidity and stability of the cylinder. A detailed analysis, based on nonlinear elasticity, of the effect of tissue tension on the mechanical properties of growing cylinders reveal a subtle interplay between geometry, growth, and nonlinear elastic responses that help understand some of the remarkable properties of stems and other biological tissues.

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Introduction. – In many biological tissues, due to a combination of genetic, chemical, and mechanical factors, different parts of the tissue experience different growth rates. The net result of this *differential growth* is that the tissue may be under stress even when unloaded. These *residual stresses* are believed to play an important role in morphogenesis and in changing effective material properties. Following the work of Fung [1] on arteries, physiologists have established that arteries are residually stressed. A small disk of artery would naturally open when cut transversally, and the "opening angle" of the sliced disk is a central experimental and theoretical feature of arterial mechanics for which the associated stresses are known to play a fundamental role in the regulation of transmural tractions [2]. While the role of transverse differential growth (along the cross-section) in cylindrical structures is well appreciated, many such structures experience also axial differential growth.

The effect of axial differential growth on the mechanical properties of a cylindrical structure is the main focus of this letter. It can be illustrated by a simple experiment with a stalk of rhubarb (*Rheum rhabarbarum*) and a kitchen peeler. If you carefully peel a strip of the stalk's outer layer and attempt to place it in its original position, you may notice that the strip has shrunk in length by a noticeable amount. If you peel the other outer layers, you may realize that the inner part (the *pith*) is extending in length. This simple experiment shows that the outer wall is in a state of axial tension while the pith is in a state of axial compression (see fig. 1). The possible mechanical role of these stresses and combination of tissues can be appreciated by realizing that the peeled rhubarb has lost most of its rigidity; so much so that it now buckles under its own weight. Similarly if the rhubarb is cut along its axis, it will tend to bend outwards as part

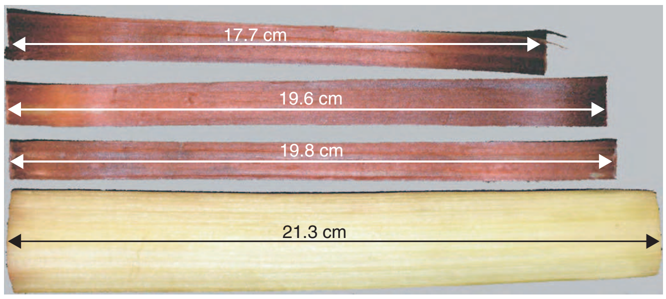

Fig. 1: Tissue tension in rhubarb. The middle segment of a long stalk of rhubarb was cut. This segment, of initial length 20 cm, was then peeled. The peeled strips are now shorter (by about 2–4%) and the pith is longer (by about 6%). The mutual tissue tensions between inner and outer layers have been relieved.

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of the elastic stress is relieved when the pith elongates and the outer tissues shorten by curving. The mutual tension between outer and inner tissues in rhubarb and its possible role in plant mechanics was understood as early as 1848 by Brucke, in 1857 by Sachs, and explored in detail by Hoffmeister in 1867: "We have here the case of an elastic stiff body consisting of two parts, each in a high degree flexible and by no means stiff; only in their natural connection do the epidermal tissue and internal tissues together form an elastic rigid body" ([3], p. 216). Following these early works, tissue tension became a central topic of interest in plant physiology and played an important role in the discovery of auxin as a growth hormone [4] through the so-called "curvature pea-test". As auxin acts differently on different tissues, the respective growth of the epidermis and pith of *Pea hypocotyl* can be controlled by varying the auxin concentration and explicitly tested by slicing the pea along its axis and measuring the resulting stem curvature. However, with the advent of genetics and biochemistry, mechanical aspects of plant development fell out of fashion. In recent years, the study of tissue tension has regained interest [5] and the role of tissue tension in growth regulation has become a controversial topic [6]. Note also that demonstrating the existence of residual stresses in a growing plant structure does not indicate conclusively the origins of these stresses. Here, following many authors [7–9], we attribute these stresses to the differential extension of the cell walls in outer and inner layers, creating an irreversible change in the resting lengths of both tissues. The fact that these resting lengths may evolve after a cut has been made depending on the solute concentration of a bath in which the tissues are immersed clearly indicate that there is also a hydraulic component to the problem. However, from an analysis standpoint, the origin of these stresses is not directly relevant to our conclusions.

From a mechanical perspective, experiments clearly establish that the outer tissue plays a substantial role in the overall rigidity (accounting for as much as 70% of the rigidity for less than 10% of the cross-sectional area [10]). This property could be attributed to the large difference in stiffnesses between the outer and inner layers (whose ratio is in excess of 30 [11]) and not to residual stresses [12]. Similarly, many other cylindrical structures, such as tree trunks, roots, and arteries [13] also develop axial tissue tension whose effect on the mechanics is not yet understood. In particular, for trees, apart from primary vertical growth, a secondary cambial radial growth takes place. One of the mechanical function of cambial growth is to allow branches and trunks to gain in girth but also to allow the overall tree structure to attain a mechanical balance. Aside from mechanical balance, even a straight trunk, containing only regular formed wood, is highly pre-stressed. The net mechanical effect of this combined growth is a rather complicated stress field with a combination of tension and compression wood [14]. The mechanism generating residual stresses during the differentiation process of the wood cells and its mechanical function remain elusive. The purpose of this letter is to study the development of residual stress in differential axial growth of biological cylindrical structures and to elucidate its possible mechanical role in modifying material properties.

Model. – We model the biological structure as a cylindrical shell composed of two material layers with different growth and elastic properties. We are trying to understand the specific effect of axial growth, therefore, we neglect the possible effect of fiber reinforcement and anisotropy by assuming that the material is hyperelastic, incompressible, homogeneous, isotropic and subject to growth along the axial direction (taken to be the z-axis). Since typical elongations or compressions can be as much as 40% of the original length [15], the material should be considered as being in large deformation and a correct description requires therefore the machinery of nonlinear elasticity. Growth is included in the model as a multiplicative decomposition of the growth tensor [16]. Since the emphasis here is on the mechanical consequences of growth and not on the regulation of growth, we take growth as a *fait accompli* by postulating that each cylindrical shell has grown axially by a given amount. We can then use the stability analysis of the resulting residually stressed cylindrical shell to obtain an effective Young modulus and explain the observed rigidity of the structure.

More precisely, the deformation of each cylindrical shell is given by $\mathbf{x}_{i,o} = \boldsymbol{\chi}_{i,o}(\mathbf{X}_{i,o})$, where $\mathbf{X}_{i,o} = (R_{i,o}, \Theta_{i,o}, Z_{i,o})$ and $\mathbf{x}_{i,o} = (r_{i,o}, \theta_{i,o}, z_{i,o})$ describe the material cylindrical coordinates of a point in the reference and current configurations, and the subscripts i, o denote the inner cylinder (whose initial radii are A and B) and the outer cylinder (with initial radii B and C). Let $\mathbf{F}_{i,o} = \mathrm{Grad}(\boldsymbol{\chi}_{i,o})$ be the *geometric* deformation gradient. We assume that the gradient tensor is the product of a growth tensor $\mathbf{G}_{i,o} = \mathrm{diag}(1, 1, \gamma_{i,o})$, describing a constant axial growth in cylindrical coordinates, by an elastic tensor $\mathbf{A}_{i,o}$ so that $\mathbf{F}_{i,o} = \mathbf{A}_{i,o} \cdot \mathbf{G}_{i,o}$.

It is important to comment here about this multiplicative decomposition. The deformation is decomposed into two parts that can be understood as follows. First, a virtual growth deformation takes place where each cylinder is allowed to grow without constraint. This leads to an unstressed configuration where the two grown cylinders may have different lengths and can interpenetrate each other. With our particular choice of growth tensor the new length of the cylinders are, respectively, $L\gamma_{i,o}$ in this new unstressed configuration. For $\gamma_i \neq \gamma_o$, the integrity of the body is not preserved during this deformation. Second, we apply an elastic deformation from this new incompatible configuration to a final configuration where the boundary conditions between the cylinders and on the cylinder faces are satisfied. Essentially, we stretch one cylinder and compress the other one. The overall deformation $\mathbf{F}$ is compatible (in the sense that it is the gradient of a map $\boldsymbol{\chi}$) but individually $\mathbf{A}$ and $\mathbf{G}$ are incompatible. Within this modeling approach of growth, this incompatibility is directly related to the residual stress (the stress necessary to preserve the body integrity during the deformation). Note also that the elastic deformation takes the body from the virtual grown configuration to its final configuration. This deformation is fully determined by the tensor $\mathbf{A}$ and as a consequence, the formulation of the elastic energy and the stresses are in terms of $\mathbf{A}$.

Each material is characterized by a strain energy function $W_{i,o} = W_{i,o}(\mathbf{A}_{i,o})$. Here, following existing models for arteries [13] and the data available for stem properties [11], we adopt a model where the inner cylinder is a neo-Hookean material and the outer layer is a Fung material with strain-stiffening properties

$$W_i = \frac{\mu_i}{2}(I_1 - 3), \quad W_o = \frac{\mu_o}{2\nu}\left[e^{\nu(I_1-3)} - 1\right], \tag{1}$$

where $I_1 = \alpha_r^2 + \alpha_\theta^2 + \alpha_z^2$ is the first principal invariant of the Cauchy-Green strain tensor, the principal stretches α_r, α_θ, α_z are the square roots of the principal values of $\mathbf{A}\mathbf{A}^{\mathrm{T}}$, and ν controls the strain-stiffening property of the outer layer (with neo-Hookean limit as $\nu \to 0$) which relates elastic deformation to the Cauchy stress tensor $\mathbf{T} = (t_r, t_\theta, t_z)$ by

$$\mathbf{T}_{i,o} = \mathbf{A}_{i,o} \cdot \frac{\partial W_{i,o}}{\partial \mathbf{A}_{i,o}} - p_{i,o}\mathbf{1}, \tag{2}$$

where $p_{i,o}$ is the Lagrange multiplier associated with the incompressibility constraint. The parameters $\mu_{i,o}$ are elastic moduli. They define the overall stiffness of the material. For small deformation, $\boldsymbol{\alpha} \to 1$, these elastic moduli can be related to the Young moduli of each cylinder by $E_{i,o} = 3\mu_{i,o}$. However, such identification does not hold in large deformation where the stiffness depends on the size of the deformation itself.

The equation for mechanical equilibrium is given by $\mathrm{div}(\mathbf{T}_{i,o}) = 0$, where the divergence is taken in the current configuration. The boundary conditions are: zero normal traction on the inner and outer boundaries $r = a, c$ and equal but opposite traction at $r = b$. The top and bottom have resultant load [17], $N = 2\pi \int_a^c r t_z(r) \mathrm{d}r = 0$.

Before we consider the stability and rigidity of the cylindrical shell, we compute explicitly the residual stresses created through growth by assuming that in the deformation, the cylinder retains its cylindrical symmetry, that is

$$\mathbf{F}_{i,o} = \mathrm{diag}\left(\frac{\mathrm{d}r_{i,o}}{\mathrm{d}R}, r_{i,o}/R, \lambda_{i,o}\right) \tag{3}$$

in cylindrical coordinates and the elastic tensor is

$$\mathbf{A}_{i,o} = \mathrm{diag}(1/(\alpha_{i,o}\beta_{i,o}), \alpha_{i,o}, \beta_{i,o}). \tag{4}$$

The three diagonal entries of $\mathbf{A}$ correspond to α_r, α_θ and α_z. For computational convenience, we have introduced two variables $\alpha_{i,o}$, $\beta_{i,o}$, which denote, respectively, the angular and axial stretch or compression from the unstressed grown state to the final state. Since both materials are assumed to be incompressible, the deformation in the radial direction is specified by the condition $\det(\mathbf{A}_{i,o}) = 1$. Note that since $\mathbf{F} = \mathbf{A} \cdot \mathbf{G}$, the elastic variables α, β and the geometric variables r, λ are not independent and we have

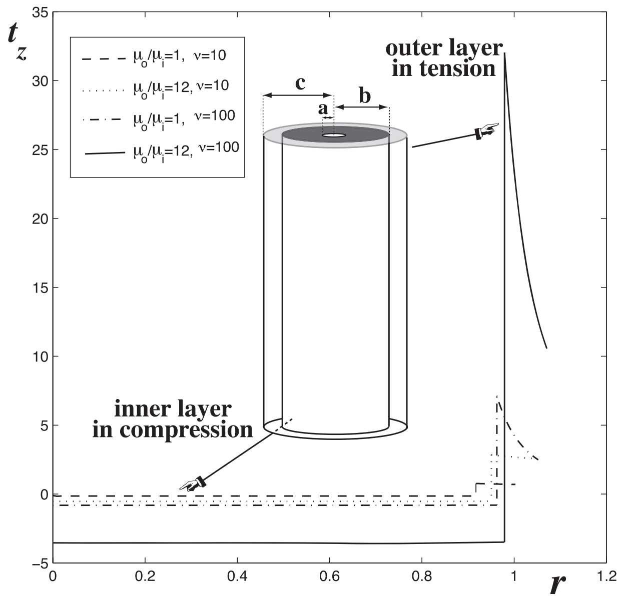

Fig. 2: Tissue tension in cylindrical shells.

$$\alpha_{i,o} = r_{i,o}/R, \quad \lambda_{i,o} = \gamma_{i,o}\beta_{i,o}. \tag{5}$$

The radial stress is given by

$$t_r(R) = \begin{cases} \displaystyle\int_A^R \frac{\partial \widehat{W}_i}{\partial \alpha_i} \frac{1}{\beta_i \alpha_i R} \mathrm{d}R, & R \leqslant B, \\ \displaystyle -\int_R^C \frac{\partial \widehat{W}_o}{\partial \alpha_o} \frac{1}{\beta_o \alpha_o R} \mathrm{d}R, & B \leqslant R \leqslant C, \end{cases} \tag{6}$$

where $\widehat{W}_{i,o}(\alpha_{i,o}) = W_{i,o}(1/(\alpha_{i,o}\beta_{i,o}), \alpha_{i,o}, \beta_{i,o})$. The axial stress is $t_z(R) = t_r + \beta W_3 - W_1/(\alpha\beta)$, where W_1 and W_3 are the derivative of W with respect to its first and third variables and the two free parameters a and λ are obtained, for a given axial load N, by solving simultaneously the two remaining boundary conditions

$$t_r(C) = 0, \quad \text{and} \quad N = 2\pi \int_a^c r t_z(r) \mathrm{d}r = 0. \tag{7}$$

It is particularly interesting to consider the stresses created in the material in the absence of loads, $N = 0$ for various ratio of stiffnesses. In fig. 2, we show the axial stress profile and overall inner layer stretch for various ratio of stiffnesses and different strain stiffening properties. As the strain-stiffening ν is increased, we note that large stress gradients are created in the outer layer.

Stability analysis and stem rigidity. – We can now determine the overall rigidity of our grown cylinder. Since the cylinder is in large deformation and supports residual stress, the traditional notion of Young modulus does not apply directly and an explicit computation of the rigidity is not possible. However, we can perform the following thought experiment to obtain an *effective Young modulus*. Consider the grown cylinder and measure all its initial geometric parameters (inner and outer radii a_0 and c_0 and length l_0 being the geometric parameter for zero load) and subject it to a normal load N until it buckles at N_{crit}. This critical value of the axial stress $P_{\text{crit}} = N_{\text{crit}}/\pi(c_0^2 - a_0^2)$ can be used to compute the effective Young modulus, defined as the Young modulus of an equivalent homogeneous elastic cylinder with no residual stress and buckling with the same axial stress, that is

$$E_{\text{eff}} = \frac{4P_{\text{crit}}}{\pi^2\sigma^2}, \tag{8}$$

where $\sigma = \sqrt{c_0^2 + a_0^2}/l_0$ is the inverse of the slenderness ratio. This definition is valid as long as the cylinder is sufficiently slender (σ sufficiently small), so that the Euler buckling formula is valid (see below). Therefore, in order to obtain an estimate of the cylinder rigidity through an effective Young modulus, one needs to obtain the critical buckling load, that is to compute the stability of the grown cylinder under applied loads. To do so, we consider perturbation around the grown cylindrical solution $\boldsymbol{\chi}^{(0)}$. That is, $\boldsymbol{\chi} = \boldsymbol{\chi}^{(0)} + \epsilon\boldsymbol{\chi}^{(1)}$, where $\boldsymbol{\chi}^{(1)} = (u(r,\theta,z), v(r,\theta,z), w(r,\theta,z))$. In terms of the geometric deformation tensors, we have $\mathbf{F} = (\mathbf{1} + \epsilon\mathbf{F}^{(1)}) \cdot \mathbf{F}^{(0)}$, with $\mathbf{F}^{(1)} = \text{grad}(\boldsymbol{\chi}^{(1)})$ and $\mathbf{A} = (\mathbf{1} + \epsilon\mathbf{A}^{(1)}) \cdot \mathbf{A}^{(0)}$. Similarly, we expand the Cauchy stress $\mathbf{T} = \mathbf{T}^{(0)} + \epsilon\mathbf{T}^{(1)} + \text{O}(\epsilon^2)$. The expansion of the constitutive equation leads to [18]

$$\mathbf{T}^{(1)} = \mathcal{L} : \mathbf{F}^{(1)} + \mathbf{F}^{(1)} \cdot \mathbf{A}^{(0)} \cdot W_{\mathbf{A}}^{(0)} - p^{(1)}\mathbf{1},$$
$$\mathcal{L} : \mathbf{F}^{(1)} = \mathbf{A}^{(0)} \cdot W_{\mathbf{AA}}^{(0)} : \mathbf{F}^{(1)} \cdot \mathbf{A}^{(0)},$$

where $\mathbf{T}^{(0)}$ is the Cauchy stress associated with the solution $\boldsymbol{\chi}^{(0)}$, $p = p^{(0)} + \epsilon\, p^{(1)}$, $\mathcal{L}$ is the instantaneous elastic moduli tensor (given explicitly in ([19], p. 412)), and $W_{\mathbf{A}}^{(0)}$, $W_{\mathbf{AA}}^{(0)}$ are the first and second derivatives of W with respect to $\mathbf{A}$ evaluated on $\mathbf{A}^{(0)}$. The stability analysis proceeds by solving $\text{div}(\mathbf{T}^{(1)}) = 0$ together with the first-order incompressibility condition, $\text{tr}(\mathbf{F}^{(1)}) \equiv u_r + (u + v_\theta)/r + w_z = 0$, and the boundary conditions obtained as the expansions to first order of the global boundary conditions (not shown explicitly here). This leads to a set of eight partial differential equations for the eight variables $u_{i,o}, v_{i,o}, w_{i,o}, p_{i,o}^{(1)}$ in the inner and outer layers which can be further simplified to a boundary-value problem for a set of differential equations in the variable r by Fourier expanding the dependance in θ and z, that is: $u = f(r)\cos m\theta \cos\eta z$, $v = g(r)\sin m\theta\cos\eta z$, $w = h(r)\cos m\theta\sin\eta z$, $p^{(1)} = k(r)\cos m\theta\cos\eta z$. For each mode m, the solution of this boundary-value problem is possible only for a particular combination of parameters $N_{\text{crit}} = N_{\text{crit}}(m, a, c)$. These values give the load necessary for the existence of the m-th mode. Numerically, these values are obtained by the determinant method for the n-th order linear boundary-value problems [18,20]. As a test of the method, we compute the bifurcation curves for a neo-Hookean two-layer cylindrical model. In the case where both layers have the same moduli $\mu_i = \mu_o$, we can compare (see fig. 3, dashed curve) the solution with the Euler buckling formula (dashed line), by identifying the moduli with Young's moduli $\mu_{i,o} = E_{i,o}/3$. Three features are of interest: first we see that for slender structures, Euler's formula provides an excellent description of the critical stress value for buckling. Second, in the case where Euler's formula cannot be applied, the graph of P_{crit} as a function of σ becomes linear for σ small enough and therefore, this bifurcation analysis provides a valid method to define an effective Young modulus. Third, note that barreling modes ($m \neq 1$) require a short cylinder and these modes are not relevant for the situation at hand and will not be studied here.

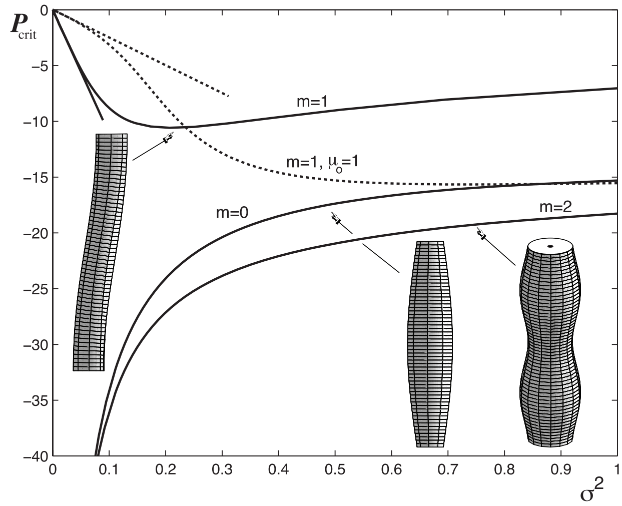

Fig. 3: Bifurcation modes for a two-layer cylindrical shell. The first three modes are shown. The mode $m = 1$ corresponds to Euler buckling mode, whereas the modes $m = 0, 2$ give axisymmetric barreling solutions. The dashed line indicates the prediction given by the Euler buckling formula for a solid cylinder (where $\mu_i = \mu_o = 1 = E/3$). The slope of the solid line gives the effective Young modulus. An increase in μ_o produces an increase in effective Young Modulus (larger slope) for $\mu_o = 12$, $A = 0.0001$, $B = 0.9$, $C = 1$.

Estimates. – The analysis presented in the previous sections is a full three-dimensional large-deformations stability analysis of a residually stressed nonlinear material. What this approach gains in rigor, it loses in its ability to provide simple estimates where the role of each parameter can be established. We use the three-dimensional analysis to establish the validity of an estimate based on simple consideration of elasticity.

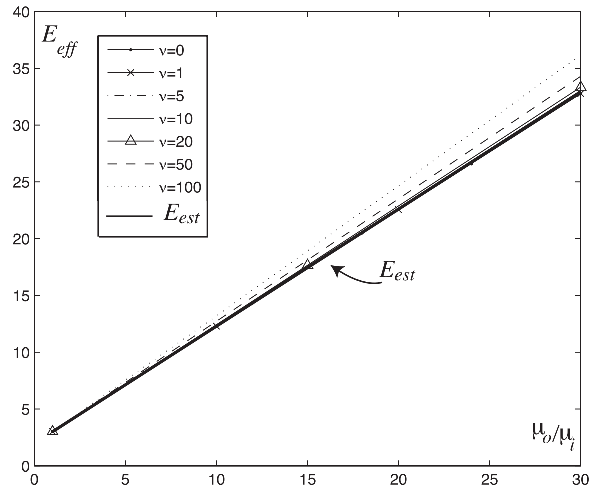

Fig. 4: The effect of outer wall stiffness and strain-stiffening properties on the stability of a two-layer cylinder. $A=0.0001$, $B=0.9$, $C=1$. The solid line corresponds to the estimate (10).

First, we consider a cylinder made out of two cylinders of different materials in the absence of growth with respective radii A, B and C and length L as before. Then, a classical way to estimate the Young modulus [21] of the assembly is to consider the sum of flexural rigidities, that is

$$E_{\mathrm{est}} I = E_i I_i + E_o I_o, \tag{9}$$

where E_{est} is an estimate for the effective Young modulus provided by the linear theory of elasticity. Explicitly, it reads

$$E_{\mathrm{est}} = 3\frac{\mu_i(B^4-A^4)+\mu_o(C^4-B^4)}{C^4-A^4}. \tag{10}$$

This estimate provides the main linear relationship with respect to changes in the rigidity of the outer layer observed in fig. 4 but fails to provide the correction with the strain-stiffening parameter.

Second, we consider a grown two-layer cylinder with a neo-Hookean material inside and a Fung material outside. We further assume that $a_0 \ll 1$ so that a_0^2, a_0^4 can be neglected. Before we consider an estimate of the flexural rigidity, we need to model the Fung material under extension. To do so, we consider the first approximation that captures both the exponential behavior and the small-deformation limit, that is the axial strain is

$$T_o = 3\mu_o e^{3\nu\epsilon_o\epsilon_o^2}, \tag{11}$$

where ϵ_o is the axial strain, computed with respect to the unstressed grown configuration of the outer cylinder. The apparent Young modulus of the outer cylinder is obtained as the slope of the tangent to this curve as a function of ϵ_o

$$E_o = \frac{\partial T_o}{\partial \epsilon_o} = 3\mu_o(6\nu\epsilon_o^2+1)e^{3\nu\epsilon_o^2}. \tag{12}$$

Similarly, we have, for the inner cylinder $T_i = 3\mu_i\epsilon_i$ and $E_i = 3\mu_i$, where ϵ_i is the strain with respect to the unstressed configuration of the inner cylinder. Next, we compute the rest shape of the grown cylinders, that is, we assume that no net traction is applied at the two caps so that

$$\begin{aligned} N = 0 &= \pi\left[T_o b_0^2 + T_i(c_0^2-b_0^2)\right] \\ &= 3\pi\left[\mu_o e^{3\nu\epsilon_o\epsilon_o^2} b_0^2 + \mu_i\epsilon^i(c_0^2-b_0^2)\right], \end{aligned} \tag{13}$$

where $\epsilon_{i,o} = l_0/\gamma_{i,o} - 1$ and the two cylinders are assumed, without loss of generality, to have height 1 before they start growing. The equation $N=0$ can be solved for l_0 to obtain the residual strain. Since the equation is transcendental in l_0, no useful estimates of l_0 can be obtained, except in the case $\nu = 0$ which is an upper bound, l_{est} for the length l_0

$$l_{\mathrm{est}} = \gamma_i\gamma_o\frac{\mu_i b_0^2 + \mu_o(c_0^2-b_0^2)}{\mu_i\gamma_o b_0^2 + \mu_o\gamma_i(c_0^2-b_0^2)}. \tag{14}$$

We can use again eq. (9) to obtain an estimate:

$$E_{\mathrm{est}} = 3\frac{\mu_i b_0^4 + \mu_o(6\nu\epsilon_o^2+1)e^{3\nu\epsilon_o^2}(c_0^4-b_0^4)}{c_0^4}, \tag{15}$$

where $\epsilon_o = l_{\mathrm{est}}/\gamma_{i,o} - 1$ and b_0, c_0 are obtained by using the assumption $a_0 \ll 1$ and from the conservation of volume of each cylindrical layer, namely $B^2\gamma_i = b_0^2 l_{\mathrm{est}}$ and $(C^2-B^2)\gamma_o = (c_0^2-b_0^2)l_{\mathrm{est}}$. This estimate is compared with the results of the numerical analysis of the stability equation in the next section.

Results. – We now consider a grown two-layer cylinder with a neo-Hookean material inside and a Fung material outside and compute the effective Young modulus as a function of the parameters. Without loss of generality, we take $\gamma_o = \mu_i = 1$. For comparison, we scale the effective Young modulus by the Young modulus of a neo-Hookean one-layer cylinder E_{nh}. In the absence of growth, the stiffness of the outer layer μ_o provides a substantial improvement on the overall rigidity of the structure, which is essentially linear in the ratio and well approximated by the estimate (10) (see fig. 4). Note that the correction due to the nonlinearity of the Fung model cannot be captured since the estimate does not depend on the strain-stiffening parameter ν. However, the strain stiffening property of the outer wall has very little, if any, effect. Essentially, in this regime, the outer layer is in a regime where it behaves as a neo-Hookean material.

We can now fix the value of μ_o and consider the effect of growth. In fig. 5, we first observe that in the absence of strain-stiffening, the effect of growth is to reduce the stability of the structure. Indeed, growth creates a large zone of compression in the inner tissue (see fig. 2) so that the cylinder is pre-compressed due to growth and therefore buckles for a smaller load. Therefore, there is no gain in stiffness due to growth in a homogeneous, isotropic,

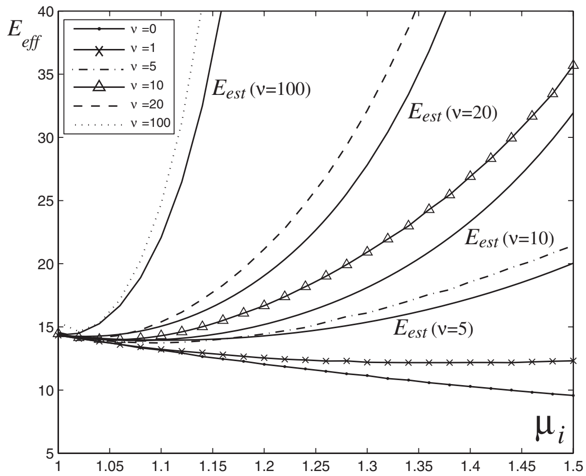

Fig. 5: The effect of axial differential growth on the rigidity of a two-layer cylinder for different strain-stiffening properties (initial size $A = 0.0001$, $B = 0.9$, $C = 1.0$, $\mu_o = 12$). The estimates given by eq. (15) capture most of the exponential increase of the rigidity as the relative growth between outer and inner layer increases.

incompressible, two-layer neo-Hookean cylinder. However, for a strain-stiffening outer layer, the situation is different and even modest differential axial growth has a dramatic effect on the rigidity of the structure. After growth, large stresses are needed for the small changes in strains that would occur on the concave side of the cylinder during bending. The exponential increase of the effective Young modulus is well captured by the estimate (15) that predicts an exponential term of the form $\exp[\kappa\nu(\gamma_i - 1)^2]$, where κ depends on the moduli $\mu_{i,o}$ and the geometric parameters. We conclude that the effect of differential growth is to bring the outside layer in a regime where the nonlinear stiffening response can be fully utilized.

Conclusion. – In order to isolate and understand the effect of differential axial growth, we have neglected important effects necessary to obtain a precise picture of the material properties of specific biological structures, notably, anisotropic response and inhomogeneity. However, the analysis presented here was performed using the general framework of nonlinear elasticity which can be easily generalized to include these effects.

Differential growth is known to be the driving force for many important mechanical material properties and morphogenesis. Since the early work of Brücke, differential growth and tissue tension were believed to play an important role in shaping material properties for plants. Surprisingly, the mechanical advantages of axial tissue tension in cylindrical structures has not been rationally explored despite a large literature devoted to the similar problem of angular residual stress in arteries. Here, we have shown that tissue tension, developed through differential growth, creates a mechanical environment that takes full advantages of the material's elastic properties, revealing a remarkable combination of effects related to growth, stresses, and nonlinear elastic response.

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