Implementation of elasticity in sensory-growth rod-like organs

Intorduction

This paper describes how to combine our formalism of active reorientations of growing rods with M. Gazzola's Cosserat filament integrator (see *Gazzola RSOS 2018*). To do so, we separate growth and elasticity, following the mathematical formalism presented in A. Goriely's book (*The Mathematics and Mechanics of Biological Growth, Springer 2017*). The mathematical decomposition of growth and elastisity originates from a distinct separation of timescales: the timescale of growth processes in plants is in the order of 10^4 seconds, while their elastic relaxation times are of the order of $1 - 0.01$ seconds. We can therefore assume that the dynamics of a growing plant are in the quasi-static regime, in which the organ reaches its mechanical steady state for every growth step.

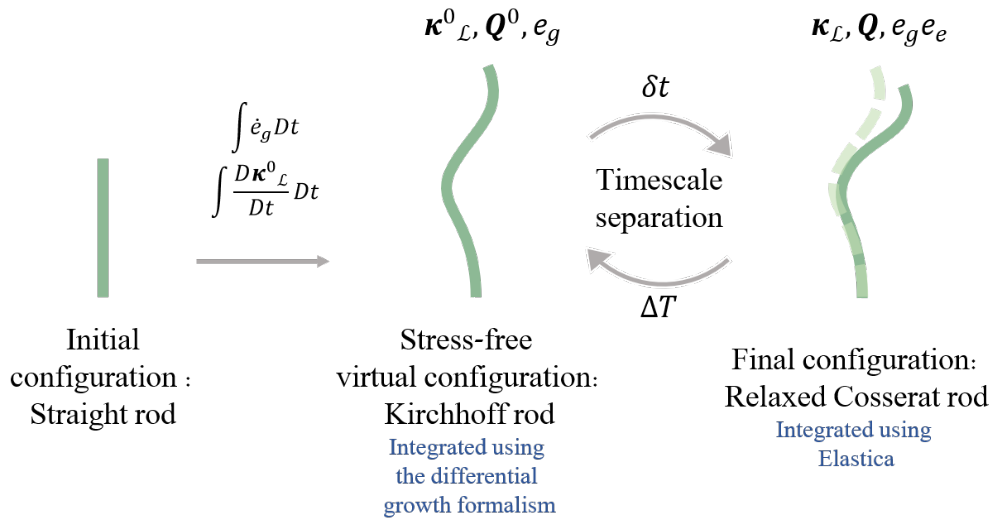

Figure 1: Integration scheme. Strating from a straight rod, growth is implemented by updating the rest lengths and rest curvature vectors of the Cosserat rod according to the active growth model. One can think of rest lengths and curvatures as describing a referential stress-free virtual rod, as done in Goriely's boof. Then, the Cosserat rod relaxes into its new stable mechanical state using Elatsica.

Update growth

The basic principle is to decompose the total stretch in the organ into growth stretch (e_g) and an elastic stretch (e_e):

$$e = e_e \cdot e_g \tag{1}$$

Referring to the re-scaling of segment properties in Gazzola's 2018 paper, the growth stretch e_g does not change the area or curvature of the segment, and adds mass to the segment. Therefore, the following relations hold:

$$ds = e \cdot d\hat{s} = e_e \cdot e_g d\hat{s}\ ,\ R = \frac{\hat{R}}{\sqrt{e_e}}\ ,\ A = \frac{\hat{A}}{e_e}\ ,\ I = \frac{\hat{I}}{e_e^2}\ ,\ B = \frac{\hat{B}}{e_e^2}\ ,\ S = \frac{\hat{S}}{e_e}\ ,\ \kappa_{\mathcal{L}} = \frac{\hat{\boldsymbol{\kappa}}_{\mathcal{L}}}{e_e} \tag{2}$$

The mass of the segment will be:

$$dm = \rho\pi R^2 ds = e_g \rho\pi \hat{R}^2 d\hat{s} \tag{3}$$

Quasi-static integration: There a distinct separation of timescales in our problem: the timescale of growth processes in plants is in the order of 10^4 seconds, while their elastic relaxation times are of the order of $1 - 0.01$ seconds. We can therefore assume that the dynamics of a growing plant are in the quasi-static regime, in which the organ has reaches the steady state for every step of growth. One can thus choose to implement growth either by growing the plant in time-steps which are dictated by the elastic relaxation process (that is, growth takes place when the energy minimizes to a certain minimal threshold), or continuously growing the organ at a very slow rate.

Body forces ramp: The code should run smoothly and simulate quasi static growth after an initial relaxation to external forces. Since the initial state of the organ is assumed to be a straight rod, the initial relaxation to gravity may take a while due to oscillations and their damping by dissipation. This relaxation initialization can be reduced by adding the external forces in a quasi-static manner.

Segment division: For a constant profile of growth rates along the organ, after long periods of time the growth stretch e_g will inevitably reach high values (for example around the apex), for which the discrete segments approximation is no longer be valid. Therefore, a "segment division" should be implemented above a certain threshold of local growth stretch e_g. In this division, the segment is to be split in half, while both halves should retain all of its properties but its length:

$$ds_i = ds_{i,1} + ds_{i,2} \tag{4}$$

The propagation of the local coordinates should be updated accordingly.

Current plan: write a code (and a wrapper?) that:

- Implements various growth rate functions $\dot{e}_g(s,t)$ (exponential, apical flat and apical Gaussian).
- Limits growth time-step by maximal growth velocity (apical velocity): $v_{\max} = \int_0^{L(t)} \dot{e}_g(s,t)ds$
- Divides segments that elongate over a certain threshold ($d\hat{s} > ds_{\max}$). This includes the calculation of the local coordinate system (Q) of the two parts of the divided segments, and will probably require recalculations of the Voronoi regions.
- Propagates intrinsic curvature (and twist) according to the active growth model.

Element division

In a growing rod, if an element (or an edge) grows above a certain threshold, we need to divide it into two distinct elements. Using the code of Gazzola's lab, the division can be implemented by breaking down the element, $\boldsymbol{\ell}_i = \boldsymbol{r}_{i+1} - \boldsymbol{r}_i$, into two new elements (see Fig. **??**):

$$\boldsymbol{\ell}_i = \boldsymbol{\ell}_{i,1} + \boldsymbol{\ell}_{i,2} \tag{5}$$

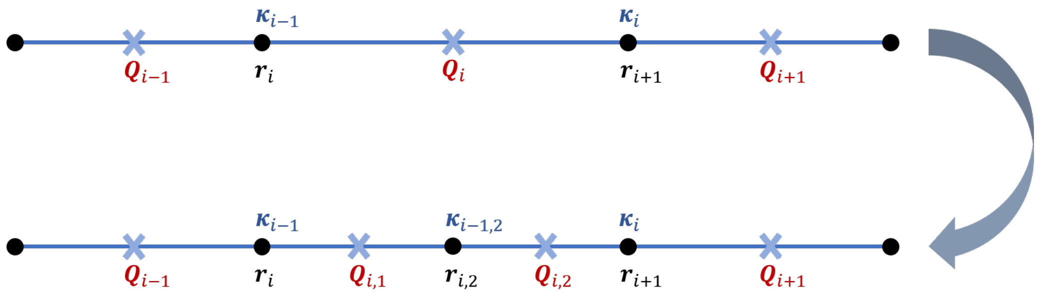

Figure 2: Segment division. One must demand continuity in $\boldsymbol{r}$, $\boldsymbol{Q}$ and $\boldsymbol{a}$ in order to find the corrects values for the characteristics of the new "daughter" elements.

Each segment has a variety of local variables, that are defined either pointwise on the vertices, for example the segments physical location $\vec{r}_i$ and mass m_i, as an edge property, such as the tangent vector $\boldsymbol{t}$ or strain $\hat{\boldsymbol{\sigma}}^i_{\mathcal{L}}$, or on the interior vertex, for example the inextensible curvature $\hat{\boldsymbol{\kappa}}_{\mathcal{L}}$. For simplicity, we assume that the rest length of the segment splits to two equal lengths, or:

$$\hat{\ell}_{i,1} = \hat{\ell}_{i,1} = \frac{1}{2}\hat{\ell}_i \tag{6}$$

and that the elastic stretch e_i and the shear vector $\vec{\sigma}_i$ remain constant on the two "daughter" segments:

$$e_{i,1} = e_{i,2} = e_i \quad , \quad \boldsymbol{\sigma}^{i,1}_{\mathcal{L}} = \boldsymbol{\sigma}^{i,2}_{\mathcal{L}} = \boldsymbol{\sigma}^{i}_{\mathcal{L}} \tag{7}$$

To properly find the curvatures and the local material frames of the new segments, one must demand that the surrounding quantities remain constant, that is, that $\boldsymbol{r}_{i+1}$ and $\boldsymbol{r}_i = \boldsymbol{r}_{i,1}$ don't change, and neither do $\boldsymbol{Q}_{i-1}$ and $\boldsymbol{Q}_{i+1}$.
We start the condition on the local coordinate frames. We notice that one can write the relation between $\boldsymbol{Q}_{i-1}$ and $\boldsymbol{Q}_{i+1}$ using the Rodrigues formula twice (notice that it's not the same formula in the article, a minus needs to be added):

$$\boldsymbol{Q}_{i+1} = \exp\left(-\hat{\mathcal{D}}_i \hat{\boldsymbol{\kappa}}^i_{\mathcal{L}}\right) \boldsymbol{Q}_i = \exp\left(-\hat{\mathcal{D}}_i \hat{\boldsymbol{\kappa}}^i_{\mathcal{L}}\right) \exp\left(-\hat{\mathcal{D}}_{i-1} \hat{\boldsymbol{\kappa}}^{i-1}_{\mathcal{L}}\right) \boldsymbol{Q}_{i-1} \tag{8}$$

Where:

$$\hat{\mathcal{D}}_i = \frac{1}{2}(\hat{\ell}_{i+1} + \hat{\ell}_i) \tag{9}$$

In a similar manner, after the division we have:

$$\boldsymbol{Q}_{i+1} = \exp\left(-\hat{\mathcal{D}}_{i,2} \hat{\boldsymbol{\kappa}}^{i,2}_{\mathcal{L}}\right) \exp\left(-\hat{\mathcal{D}}_{i,1} \hat{\boldsymbol{\kappa}}^{i,1}_{\mathcal{L}}\right) \exp\left(-\hat{\mathcal{D}}'_{i-1} \hat{\boldsymbol{\kappa}}^{i-1}_{\mathcal{L}}\right) \boldsymbol{Q}_{i-1} \tag{10}$$

where we notice that:

$$\hat{\mathcal{D}}_{i-1} = \frac{1}{2}(\hat{\ell}_i + \hat{\ell}_{i-1}) \neq \hat{\mathcal{D}}'_{i-1} = \frac{1}{2}(\hat{\ell}_{i,1} + \hat{\ell}_{i-1}) = \frac{1}{2}(\frac{1}{2}\hat{\ell}_i + \hat{\ell}_{i-1}) \tag{11}$$

Eq. **??** and Eq. **??** give the continuity condition on the local coordinate frame:

$$\exp\left(-\hat{\mathcal{D}}_i \hat{\boldsymbol{\kappa}}^i_{\mathcal{L}}\right) \exp\left(-\hat{\mathcal{D}}_{i-1} \hat{\boldsymbol{\kappa}}^{i-1}_{\mathcal{L}}\right) = \exp\left(-\hat{\mathcal{D}}_{i,2} \hat{\boldsymbol{\kappa}}^{i,2}_{\mathcal{L}}\right) \exp\left(-\hat{\mathcal{D}}_{i,1} \hat{\boldsymbol{\kappa}}^{i,1}_{\mathcal{L}}\right) \exp\left(-\hat{\mathcal{D}}'_{i-1} \hat{\boldsymbol{\kappa}}^{i-1}_{\mathcal{L}}\right) \tag{12}$$

or explicitly:

$$\exp\left(-\frac{1}{2}(\hat{\ell}_{i+1}+\hat{\ell}_i)\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i}\right)\exp\left(-\frac{1}{2}(\hat{\ell}_{i}+\hat{\ell}_{i-1})\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)=$$
$$=\exp\left(-\frac{1}{2}(\hat{\ell}_{i+1}+\frac{1}{2}\hat{\ell}_i)\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,2}\right)\exp\left(-\frac{1}{2}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,1}\right)\exp\left(-\frac{1}{2}(\frac{1}{2}\hat{\ell}_i+\hat{\ell}_{i-1})\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right) \quad (13)$$

We can see from Eq. **??** that we have 2 unknowns: $\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,1}$ and $\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,2}$. To find them, we now add the requirement that the spatial vectors $\boldsymbol{r}_{i+1}$ and $\boldsymbol{r}_i=\boldsymbol{r}_{i,1}$ remain unchanged. To do so, we look at the expression for the strain vector:

$$\boldsymbol{\sigma}_{\mathcal{L}}^{i}=\boldsymbol{Q}_i\left(\frac{\partial \boldsymbol{r}_i}{\partial \hat{s}}-\boldsymbol{d}_3^i\right) \quad (14)$$

Multiplying from the left by $\boldsymbol{Q}_i^T$ and integrating by $\hat{s}$ give:

$$\boldsymbol{r}_{i+1}=\left(\boldsymbol{Q}_i^T\boldsymbol{\sigma}_{\mathcal{L}}^{i}+\boldsymbol{d}_3^i\right)\hat{\ell}_i+\boldsymbol{r}_i \quad (15)$$

Or:

$$\boldsymbol{\ell}_i=\left(\boldsymbol{Q}_i^T\boldsymbol{\sigma}_{\mathcal{L}}^{i}+\boldsymbol{d}_3^i\right)\hat{\ell}_i \quad (16)$$

In a similar fashion, we can now write the relation between $\boldsymbol{r}_{i+1}$ and $\boldsymbol{r}_i=\boldsymbol{r}_{i,1}$ after the division:

$$\begin{aligned}\boldsymbol{r}_{i+1}&=\boldsymbol{\ell}_{i,2}+\boldsymbol{\ell}_{i,1}+\boldsymbol{r}_i\\&=\left(\boldsymbol{Q}_{i,2}^T\boldsymbol{\sigma}_{\mathcal{L}}^{i,2}+\boldsymbol{d}_3^{i,2}\right)\hat{\ell}_{i,2}+\left(\boldsymbol{Q}_{i,1}^T\boldsymbol{\sigma}_{\mathcal{L}}^{i,1}+\boldsymbol{d}_3^{i,1}\right)\hat{\ell}_{i,1}+\boldsymbol{r}_i=\\&=\left(\left(\boldsymbol{Q}_{i,2}^T+\boldsymbol{Q}_{i,1}^T\right)\boldsymbol{\sigma}_{\mathcal{L}}^{i}+\boldsymbol{d}_3^{i,2}+\boldsymbol{d}_3^{i,1}\right)\frac{\hat{\ell}_i}{2}+\boldsymbol{r}_i\end{aligned} \quad (17)$$

where in the last equation we used the assumption of a constant strain vector. Equating Eq. **??** and Eq. **??** gives the continuity condition on the rod's position:

$$\boldsymbol{Q}_i^T\boldsymbol{\sigma}_{\mathcal{L}}^{i}+\boldsymbol{d}_3^i=\frac{1}{2}\left(\left(\boldsymbol{Q}_{i,2}^T+\boldsymbol{Q}_{i,1}^T\right)\boldsymbol{\sigma}_{\mathcal{L}}^{i}+\boldsymbol{d}_3^{i,2}+\boldsymbol{d}_3^{i,1}\right) \quad (18)$$

Using the Einstein notation, we notice that:

$$\boldsymbol{Q}^T\boldsymbol{\sigma}_{\mathcal{L}}+\boldsymbol{d}_3=\boldsymbol{Q}_{ij}^T\boldsymbol{\sigma}_{\mathcal{L},j}+\boldsymbol{Q}_{ij}\delta_{i,3}=\boldsymbol{Q}_{ji}\boldsymbol{\sigma}_{\mathcal{L},j}+\boldsymbol{Q}_{ij}\delta_{i,3}=\boldsymbol{Q}_{ij}\left(\boldsymbol{\sigma}_{\mathcal{L},i}+\delta_{i,3}\right) \quad (19)$$

Plugging Eq. **??** into Eq. **??** gives a simplified condition:

$$\boldsymbol{Q}_i=\frac{1}{2}\left(\boldsymbol{Q}_{i,2}+\boldsymbol{Q}_{i,1}\right) \quad . \quad (20)$$

Writing both sides of Eq. **??** using $\boldsymbol{Q}_{i-1}$ and the Rodrigues formula gives the relation:

$$\exp\left(-\frac{1}{2}(\hat{\ell}_i+\hat{\ell}_{i-1})\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)=$$
$$=\frac{1}{2}\left(\exp\left(-\frac{1}{2}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,1}\right)\exp\left(-\frac{1}{2}(\frac{1}{2}\hat{\ell}_i+\hat{\ell}_{i-1})\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)+\exp\left(-\frac{1}{2}(\frac{1}{2}\hat{\ell}_i+\hat{\ell}_{i-1})\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)\right) \quad (21)$$

We now remind the reader that if A is a matrix and a,b are scalars, then $e^{aA}e^{bA}=e^{(a+b)A}$. Hence, multiplying Eq. **??** from the right by $\exp\left(\frac{1}{2}(\frac{1}{2}\hat{\ell}_i+\hat{\ell}_{i-1})\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)$ gives:

$$\exp\left(-\frac{1}{4}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)=\frac{1}{2}\left(\exp\left(-\frac{1}{2}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,1}\right)+1\right) \quad (22)$$

which gives us $\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,1}$:

$$\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,1}=-\frac{2}{\hat{\ell}_i}\ln\left(2\exp\left(-\frac{1}{4}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)-1\right) \quad (23)$$

Inserting the resulting $\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,1}$ into Eq. **??** will give us $\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,2}$. We begin by multiplying Eq. **??** from the right by $\exp\left(\frac{1}{2}(\frac{1}{2}\hat{\ell}_i + \hat{\ell}_{i-1})\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)$. This gives:

$$\exp\left(-\frac{1}{2}(\hat{\ell}_{i+1} + \hat{\ell}_i)\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i}\right)\exp\left(-\frac{1}{4}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right) = \\ = \exp\left(-\frac{1}{2}(\hat{\ell}_{i+1} + \frac{1}{2}\hat{\ell}_i)\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,2}\right)\exp\left(-\frac{1}{2}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,1}\right) \tag{24}$$

Inserting Eq. **??** into Eq. **??** gives:

$$\exp\left(-\frac{1}{2}(\hat{\ell}_{i+1} + \hat{\ell}_i)\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i}\right)\exp\left(-\frac{1}{4}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right) = \\ = \exp\left(-\frac{1}{2}(\hat{\ell}_{i+1} + \frac{1}{2}\hat{\ell}_i)\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,2}\right)\left(2\exp\left(-\frac{1}{4}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right) - 1\right) \tag{25}$$

To isolate $\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,2}$, we multiply Eq. **??** by the inverse of the exponentials in the correct order. This gives:

$$\exp\left(\frac{1}{2}(\hat{\ell}_{i+1} + \frac{1}{2}\hat{\ell}_i)\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,2}\right) = \left(2 - \exp\left(\frac{1}{4}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)\right)\exp\left(\frac{1}{2}(\hat{\ell}_{i+1} + \hat{\ell}_i)\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i}\right) \tag{26}$$

or:

$$\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,2} = \frac{4}{2\hat{\ell}_{i+1} + \hat{\ell}_i}\ln\left(\left(2 - \exp\left(\frac{1}{4}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)\right)\exp\left(\frac{1}{2}(\hat{\ell}_{i+1} + \hat{\ell}_i)\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i}\right)\right) \tag{27}$$

Then, the rest curvatures of the new segments are known, and the local coordinate frames can be found using the Rodrigues formula:

$$\boldsymbol{Q}_{i,1} = \exp\left(-\frac{1}{2}(\frac{1}{2}\hat{\ell}_i + \hat{\ell}_{i-1})\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i-1}\right)\boldsymbol{Q}_{i-1} \quad , \quad \boldsymbol{Q}_{i,2} = \exp\left(-\frac{1}{2}\hat{\ell}_i\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,1}\right)\boldsymbol{Q}_{i,1} \tag{28}$$

Special attention should be given to the last element: Since the last node doesn't have a corresponding curvature, only the curvature of the new node is missing. The continuity in $\boldsymbol{r}$ gives us the required $\hat{\boldsymbol{\kappa}}_{\mathcal{L}}^{i,1}$, as expressed in Eq. **??**.
This derivation is true for the real curvature. A parallel calculation must be done for the virtual rod, where the propagation in arc length of the local coordinate frame is done with the intrinsic (rest) curvature rather than the real one.

Growth rate coupling

In real plants, the total growth rate $\dot{\epsilon}$ is coupled to external stresses on the organ σ, as described by the Lockhart model:

$$\dot{\epsilon} \propto (P - Y - \sigma)\Theta(P - Y - \sigma) \tag{29}$$

where P is the plant's Turgur pressure, Y is the cell wall's yield stress, and Θ is the Heavyside function. We therefore see that growth can stop if the external stresses σ are high enough.
To implement this coupling in our model, I suggest to project this relation to the local tangent direction. Then, the local growth rate would be written by:

$$\dot{E}(s,t) = \dot{E}_0(s,t) \cdot \left(1 - \frac{\sigma_3}{\sigma_{\max}}\right) \tag{30}$$

where σ_3 is the stretch along $\hat{T}$ (or $\hat{\mathcal{D}}_3$), and $\dot{E}_0(s,t)$ is the predefined growth rate without stresses on the segment.

Aging effects

To insert aging effects, one must give a time dependence to both the bending modulus of the organ $B = B(s,t)$, and to the radius, as radial growth is possible in long times. At first, we ignore these effects completely.

Growth model - intrinsic curvature and actual curvature

By definition, active growth processes affect the shape of the organ by changing its intrinsic curvature and torsion. Then, an elastic relaxation of the form of the organ will give its actual form. However, signals' directions should be related to the actual form of the organ, as the organs' sensors are assumed to respond to the local stimuli (neglecting memory phenomena). If we mark the intrinsic curvature by κ_0, the actual curvature by κ, and the intrinsic torsion as $\tau_0 = \partial\phi_0/\partial s$, our growth dynamics can be written as:

$$\frac{1}{\dot{E}}\frac{D(R\kappa_0)}{Dt} = \vec{\Delta} \cdot \hat{N} = \vec{\lambda} \cdot \hat{N} - \gamma\kappa_0 \tag{31}$$

$$\frac{\kappa_0}{\dot{E}}\frac{D(R\phi_0)}{Dt} = \vec{\Delta} \cdot \hat{B} = \vec{\lambda} \cdot \hat{B} \tag{32}$$

where $\vec{\lambda}$ is the local sensitivity vector, parallel to the direction of a certain stimulus, and γ is the proprioception coefficient. In contrast, in Chelakkot2017 a simpler formalism was assumed for the curvature's dynamics (as they delt only with 2-d organs):

$$\frac{1}{\dot{E}}\frac{D(R\kappa_0)}{Dt} = \vec{\lambda} \cdot \hat{N} - \gamma\kappa \tag{33}$$

One can see that here the proprioception term is written using the actual curvature. Since the microscopic biological details of proprioception are unknown, both models are possible.

This form does not include relaxation of the intrinsic curvature and torsion to the actual curvature and torsion. However, plants do relax internal strains using growth (see Goldstein and Goriely, Phys. Rev. E 74, 010901(R), 2006). This relaxation can either arise from a process related to the axial growth, in which case it should be implemented in our model, or from a radial growth processes, which is yet to be implemented. Assuming a strain relaxation process does takes place in the axial direction, the growth model may take the form:

$$\frac{1}{\dot{E}}\frac{D(R\kappa_0)}{Dt} = \vec{\lambda} \cdot \hat{N} + \gamma(\kappa - \kappa_0) \tag{34}$$

$$\frac{D\tau_0}{Dt} = \frac{\partial}{\partial s}\left(\frac{\dot{E}}{R\kappa_0}\vec{\lambda}\cdot\hat{B}\right) + \gamma\frac{\dot{E}}{R}(\tau - \tau_0) \tag{35}$$

We note that we replaced the proprioception term with the strain relaxation process. We now turn to try and compare the three growth models presented.

2-D calculation

To check which model for proprioception should be used, we here try to analytically solve the spatio-temporal shape of an organ that responds to gravity. We assume that an organ has two interactions with gravity: it actively grows against it, and gravity acts on it as an external force. We note that in a certain limit, the real shape should fit the experiments done on 11 different angiosperms (by Renaud), that is, the stable state found should reproduce a decaying exponential, as validated experimentally. This limit should *probably* arise in the weightless regime. To find out where this regime is in our parameter space, we use unit analysis: the bending modulus of rods B and the local gravity force ρg gives a length scale to the elastic response to gravity:

$$L_e = \left(\frac{B}{\rho g}\right)^{\frac{1}{3}} \tag{36}$$

and a unitless number that compares this response to the length of the growth zone (as was done in Chelakkot 2017):

$$\mathcal{E} = \frac{L_{gz}}{L_e} \tag{37}$$

the weightless regime is therefore $\mathcal{E} \ll 1$.
To simplify the calculations, we assume the intrinsic growth approximation ($D/Dt \to \partial/\partial t$), and turn to write the governing equations. Since this is a 2-D quasi-static dynamics, the elastic equations are the force balance and the torque balance. The force balance can be written as:

$$\frac{\partial\vec{n}}{\partial s} + \vec{f} = 0 \tag{38}$$

where $\vec{n}$ marks contact forces and $\vec{f}$ marks body forces. For gravity alone, we can write: $\vec{f} = -\rho g\hat{y}$. We can hence integrate Eq. **??** and use the free rod boundary condition $\vec{n}(s = L) = 0$ to obtain:

$$\vec{n}(s) = -\rho g(L - s)\hat{y} \tag{39}$$

The second elastic equation is the torque balance:

$$B\frac{\partial}{\partial s}(\kappa - \kappa_0)\hat{B} + \hat{T}\times\vec{n} = 0 \tag{40}$$

Where B is the bending modulus, and the difference of curvatures is the local strain. Marking θ as the local angle with respect to the $\hat{y}$ direction, we can write: $\partial\theta/\partial s = \kappa \equiv \theta'$ and $\partial\theta_0/\partial s = \kappa_0 \equiv \theta_0'$. Inserting these notation and Eq. **??** into Eq. **??** gives:

$$B(\theta'' - \theta_0'') - \sin(\theta)\rho g(L - s) = 0 \tag{41}$$

The active growth dynamics in 2-D with intrinsic growth in the proprioception term is governed by Eq. **??** and the intrinsic growth approximation:

$$\dot{\theta}_0' = -\lambda\sin(\theta) - \gamma\theta_0' \tag{42}$$

The active growth dynamics in 2-D with the actual growth in the proprioception term is governed by Eq. **??** and the intrinsic growth approximation:

$$\dot{\theta}_0' = -\lambda\sin(\theta) - \gamma\theta' \tag{43}$$

And lastly Eq. ?? with strain relaxation instead of proprioception gives:

$$\dot{\theta}_0' = -\lambda \sin(\theta) + \gamma(\theta' - \theta_0') \tag{44}$$

We thus have two coupled equations for θ and θ_0: Eq. ?? and Eq. ?? for proprioception with intrinsic curvature, Eq. ?? and Eq. ?? for proprioception with actual curvature, and Eq. ?? and Eq. ?? for strain relaxation. All of these sets of equations can be solved numerically and compared to experiments. Here we take the small angle limit ($\sin(\theta) \approx \theta$) and find the stable state solution.

Proprioception with intrinsic curvature: Starting from Eq. ?? and assuming a stable state and small angels, we obtain:

$$\theta_0' = -\frac{\lambda}{\gamma}\theta \tag{45}$$

Inserting this into Eq. ?? and taking once again the small angles limit gives:

$$\theta'' - \frac{\lambda}{\gamma}\theta' - \theta\frac{\rho g}{B}(L - s) = 0 \tag{46}$$

One can see that in the weightless regime $\rho g L^3 \ll B$ we obtain a decaying exponential with the characteristic length γ/λ as in the original solution.

Proprioception with actual curvature: Starting from Eq. ?? and assuming a stable state and small angels, we obtain:

$$\theta' = -\frac{\lambda}{\gamma}\theta \tag{47}$$

we thus obtain a decaying exponential with the characteristic length γ/λ as in the original solution.

Strain relaxation stable state: Starting from Eq. ?? and assuming a stable state and small angels, we obtain:

$$\theta_0' = \theta' - \frac{\lambda}{\gamma}\theta \tag{48}$$

Inserting this into Eq. ?? and taking once again the small angles limit gives:

$$\frac{\lambda}{\gamma}\theta' - \theta\frac{\rho g}{B}(L - s) = 0 \tag{49}$$

This gives:

$$\theta(s) = \theta(0)\exp\left(\frac{\gamma\rho g}{\lambda B}(Ls - \frac{s^2}{2})\right) \tag{50}$$

An increasing exponential. This contradicts the known exponential decay, even in the very stiff limit ($\rho g \ll B$). We can therefore say that proprioception acts in the axial growth regardless of strains, and that the strain relaxation probably happens in a different axial process or a radial growing process (for radial growth and how it affect intrinsic curvature see Goriely).

To sum up, we note that we cannot deduce from this simple calculation which model of proprioception to use, as both lead to a decaying exponential in the weightless limit. One should simulate both models and see for which values of $\mathcal{E}$ a significant difference in shapes will arise, in order to see if one of the models can be disqualified with an experiment, or if the difference between models is negligible. Since these simulations involve a mechanical relaxation to gravity, it'll be simpler to wait for the new 3d code to be functional than to write a 2-d model from scratch.