Growth of Form in Thin Elastic Structures

Salem Al Mosleh[1], Ajay Gopinathan[2],* and Christian Santangelo[1†]
Department of Physics, University of Massachusetts Amherst, Amherst, MA 01003, USA[1] *and*
Department of Physics, University of California Merced, Merced, CA 95343, USA[2]

Heterogeneous growth plays an important role in the shape and pattern formation of thin elastic structures ranging from the petals of blooming lilies to the cell walls of growing bacteria. Here we address the stability and regulation of such growth, which we modeled as a quasi-static time evolution of a metric, with fast elastic relaxation of the shape. We consider regulation via coupling of the growth law, defined by the time derivative of the target metric, to purely local properties of the shape, such as the local curvature and stress. For cylindrical shells, motivated by rod-like E. *coli*, we show that coupling to curvature alone is generically linearly unstable and that additionally coupling to stress can lead to stably elongating structures. Our approach can readily be extended to gain insights into the general classes of stable growth laws for different target geometries.

APPENDIX A: MICROSCOPIC TOY MODELS

In this section we will consider various toy (or semi-realistic!) models of growth processes. This will give us valuable insight into how the various terms in the growth law might appear and the order of magnitude of their coefficients.

The first model is inspired by the process of swelling polymers films [7, 8]. When polymer films are exposed to a solvent, the solvent molecules will diffuse through the pores in the film and cause swelling of the material. The local rate of swelling can be controlled by different external stimuli such as light and chemical gradients. In the present model we will consider the heterogeneous swelling caused by the curvature of the shells, assuming that only the inner surface is exposed to the solvent.

Since only one side of the shells is exposed then the rate of solvent absorption will depend on the average pore area in the exposed surface. In order to understand the effect of curvature on the exposed pore area, we express the exposed surface $\mathbf{X}_{\rm exp}$ in terms of the mid-surface of the shell in a manner consistent with the Kirchhoff-Love assumptions. Specifically,

$$\mathbf{X}_{\rm exp} = \mathbf{X} - \frac{\tau}{2}\,\hat{\mathbf{N}}. \tag{A1}$$

We can use this relation to relate the area element in the exposed surface $dA_{\rm exp}$ to the area element in the mid-surface dA using the relation $dA_{\rm exp} \equiv \sqrt{g_{\rm exp}}\; du^1 du^2$. Using Eq. (A1), we can relate the two metrics using the formula

$$g^{\rm exp}_{ij} = g_{ij} + \tau\; b_{ij} + \frac{\tau^2}{4} b^{\ell}_{i}\; b_{\ell j}. \tag{A2}$$

Then, using this relation and the identity $\det(M) = \exp[Tr\{\log(M)\}]$, we can find the relation between the two area elements as

$$\frac{dA_{\rm exp}}{dA} = 1 + \tau H + \frac{\tau^2}{4} K. \tag{A3}$$

Finally, allowing for the possibility of strain ϵ_{ij}, we can relate the target and actual mid-surface area elements as

$$dA = \left(1 + \frac{\epsilon}{2} + O\left(\epsilon^2\right)\right)\, d\bar{A}, \text{ where } \epsilon = \bar{g}^{ij}\,\epsilon_{ij} \tag{A4}$$

In these systems the growth process is isotropic, meaning that only terms of the form $F_1(H, K, \epsilon)\; g_{ij}$ will contribute. Since curvature and strain change the area element of the inner surface by the given geometric factor, we conclude that the average exposed pore area will be affected by the same factor. Finally, assuming that the absorption rate in the absence of curvature and strain is given by α_1, we can write the growth law as $\partial_t(d\bar{A})/dA_{\rm exp} = \alpha_1$.

Putting all of this together we get in the curved case that

$$F_1(H, K) = \alpha_1 \left(1 + \tau H + \frac{\tau^2}{4} K\right)\, \left(1 + \frac{\epsilon}{2}\right). \tag{A5}$$

Note that the term H^2 does not appear in this formula due to cancellations in the calculation of the determinant. In addition, the Ricci flow term is suppressed by an additional power of the thickness. Interestingly, the strain coupling term $\epsilon\; g_{ij}$ in the growth law will have a coefficient $\sigma_2 = \alpha_1/2$.

The terms proportional to the tensors b_{ij} and ϵ_{ij} are not generated if the growth is isotropic.

Next, we describe toy models where the growth rate of a shell depends on the local concentration of some particle on the surface. This is similar to E. *coli* where the local concentration of the protein MreB affects the growth rate of the cell wall [12]. Here we will describe a simple model of passively diffusing particles on the surface. The heterogeneity results from the dependence of the adhesion energy on the local curvature [22, 23]. Another method for achieving heterogeneity would be active particles moving inside or on the surface of the shell [24]

Fig. (B1) shows a simple diffusing particle composed of two identical orthogonal filaments each with a natural curvature $\bar{\kappa}$ and length $\bar{\ell}$. Assuming that the particles adheres strongly to the surface we can take the realized curvatures of the filaments $(\kappa_{R1}, \kappa_{R2})$ to be determined

*e-mail: agopinathan@ucmerced.edu
†e-mail: csantang@physics.umass.edu

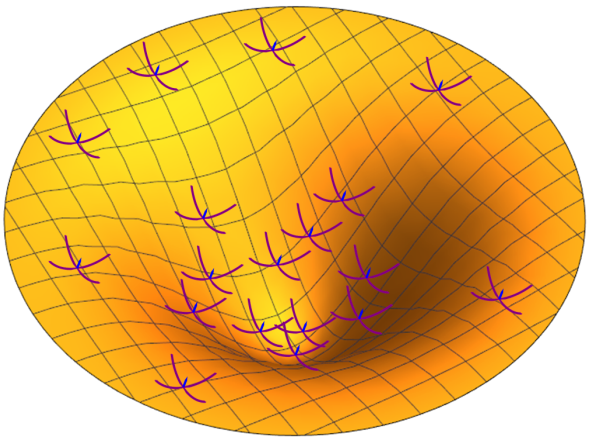

FIG. B1: Shows a "molecule" composed of two perpendicular filaments each with natural curvature $\bar{\kappa}$ and length $\bar{\ell}$ diffusing passively on the surface. The vector shown points to the inside of the closed surface when the filament is attached. The difference in density along the surface is due to biased diffusion based on curvature dependence of adhesion energy

by the principle curvatures of the surface and the angle θ between the filaments and the principle directions. Explicitly,

$$\kappa_{R1} = \cos(\theta)^2\ \kappa_1 + \sin(\theta)^2\ \kappa_2, \tag{A6}$$

where $\kappa_{1,2}$ are the principle curvatures of the surface. κR_2 follows a similar expression with $\theta \to \pi/2 - \theta$. If we take the bending energy of each filament to be $E_{bi} = Kb\ \bar{\ell}\ (\kappa_{Ri} - \bar{\kappa})^2$, then the total energy in terms of the Gaussian and mean curvatures will be

$$E_b = Kb\ \bar{\ell}\ \bar{\kappa}^2\ \times \left(2 - 4\frac{H}{\bar{\kappa}} + \frac{3H^2 - K}{\bar{\kappa}^2} + \frac{H^2 - K}{\bar{\kappa}^2}\cos(4\theta)\right). \tag{A7}$$

We can easily see that this energy is minimized when $\theta = \pi/4$. The steady state concentration of randomly diffusing particles will be given by a Boltzmann factor $\rho \propto \exp(-\beta\ E_b)$. We also assume, as we have throughout the paper, that the curvatures of the surface are small compared to the natural curvature of the filament $H << \bar{\kappa}$. Assuming a growth rate proportional to concentration $\partial_t(dA)/dA = C\ \rho$, we get finally that

$$\partial_t \bar{g}_{ij} = \left(\alpha_1 + \beta_1\ a_0 H + \delta_1\ \frac{H^2}{\bar{\kappa}^2} + O\left(\frac{H}{\bar{\kappa}}\right)^3\right)\ g_{ij}, \tag{A8}$$

were $\alpha_1 \equiv C\ \rho_0$ with ρ_0 being the concentration of the particles when the surface is flat and C being a constant relating the growth rate to the concentration. We also defined

$$\beta_1 \equiv \frac{4\ \beta\ K_b\ \bar{\ell}\ \bar{\kappa}\ \alpha_1}{a_0} \approx 1.3\ \alpha_1, \tag{A9}$$

$$\delta_1 \equiv \frac{\beta_1\ (\bar{\kappa}\ a_0\ \beta_1 - \alpha_1)}{\bar{\kappa}\ a_0\ \alpha_1}, \tag{A10}$$

where the parameter β_1 was estimated at room temperature, for an MreB-like filament with 10 monomers ($\bar{\ell} \approx 50$nm) and following Ref. [25], $K_b\bar{\kappa}^2 \approx 8.2 \times 10^{-13}$. Finally, we assumed that $a_0\bar{\kappa} = 0.1$.

It is intriguing – keep in mind that the estimate could be wrong by a couple of orders of magnitude in either direction – that this number came out to be of order 1. Although we don't consider strain coupling in this model, we expect it to also behave as $\sigma/\alpha_1 \sim O(1)$, just as it did in the absorption model above. The fact that σ is on the same order as α_1 was a natural consequence of the growth. On the other hand, $\beta_1 \sim \alpha_1$ depends on the actual value of temperature and rigidity of MreB.

As mentioned in appendix (**??**), the term $H\ g_{ij}$ is dependent on the definition of the normal to the surface. It appears in Eq. (A8) because we assumed the filament attaches to the inner surface with the arrow pointing opposite to $\hat{N}$. If we relax this assumption or consider an energy like $E_b \sim (\kappa_R^2 - \bar{\kappa}^2)^2$, this term disappears and the leading order terms will be $H^2 g_{ij}$ and $K g_{ij}$.

APPENDIX B: SCALING BEHAVIOR FOR SMALL WAVELENGTHS

In this section, we will study more closely the growth of modes with small wavelengths, namely $q_P \to \infty$. We will gain insight by contrasting the finite and zero thickness cases, starting with the latter.

As can be seen from the zero thickness growth rate derived in the main text, small wavelength modes, $q_P \to \infty$, can be stabilized by requiring $\Gamma_2 > 0$. This term ultimately comes from the growth terms Hg_{ij}, Hb_{ij} and Kg_{ij} in the growth law. Furthermore, we can easily show that as $q_P \to \infty$, these terms scale as

$$H\ g_{zz} \sim H\ b_{zz} \sim K\ g_{zz} \sim q_P^2\ \rho_{mq}. \tag{B1}$$

We can also easily see, from the isometric solutions given in the main text, that $\rho_{mq} \sim G_{\phi\phi}$. This, together with Eq. (B1) leads to the stabilizing term $q_P^2\ \Gamma_2$ in the expression for the growth rate.

Now we can understand qualitatively how finite thickness would change this result. Bending energy suppresses deformations that have wavelengths comparable to thickness, specifically, we get $\rho_{mq} \sim G_{\phi\phi}/q_P^4$. Therefore the stabilizing term proportional to Γ_2 would disappear as $q_P \to \infty$. Next, we examine this case a little more concretely.

First, we minimize the energy with a given metric deformation G_{ij}, and solve for the displacements ρ_{mq}, h_{mq} and ψ_{mq}. we get, for example, that

$$\rho_{mq} \sim O\left(\frac{G_{\phi\phi}}{q_P^4}\right) + O\left(\frac{G_{z\phi}}{q_P^5}\right) + O\left(\frac{G_{zz}}{q_P^6}\right). \tag{B2}$$

We then plug these solutions back into the growth law and get, for example, that $\partial_t G_{\phi\phi} \propto -\Gamma_2\ G_{\phi\phi}/q_P^2$. Thus we see that $G_{\phi\phi}$ can still be stabilized if $\Gamma_2 > 0$ and in

what follows, we set $G_{\phi\phi} \to 0$. The other two equations give

$$\partial_t G_{zz} \sim 2\, R_0\, G_{zz} \quad \text{and} \quad \partial_t G_{z\phi} \sim 2\, R\, \frac{G_{zz}}{q_P}. \tag{B3}$$

Finally, combining Eqs. (B3) and (B1) we discover that

$$\frac{\partial_t \rho_{mq}}{\rho_{mq}} = 4R_0 + O\left(\frac{1}{q_P}\right), \tag{B4}$$

which validates the result obtained in the main text.

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