Growing into the Right Shape

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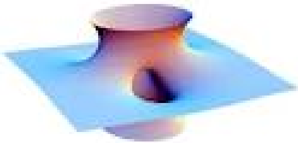
PDE models in continuum physics

Many geometric shapes found in Nature

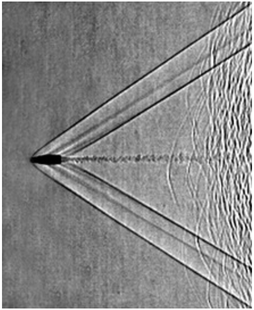
can be described in terms of PDEs

catenary



minimum surface

vortex rollup



shock waves

However, many other interesting shapes

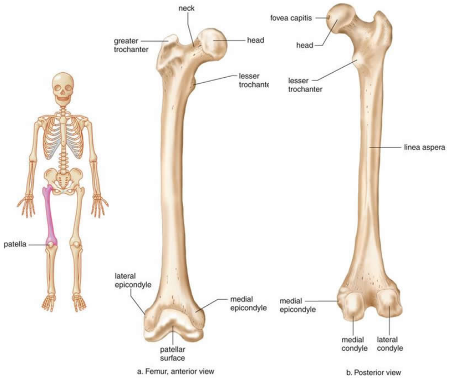
are not found in PDE books

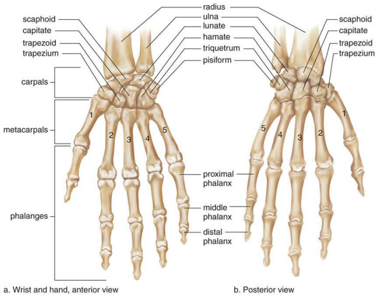
 

leaf shapes



flower shapes


neck
greater trochanter
head
lesser trochante
fovea capitis
head
lesser trochanter
linea aspera
patella
lateral epicondyle
medial epicondyle
medial epicondyle
patellar surface
medial condyle
lateral condyle
a. Femur, anterior view
b. Posterior view


radius
ulna
lunate
hamate
triquetrum
pisiform
scaphoid
capitate
trapezoid
trapezium
scaphoid
capitate
trapezoid
trapezium
carpals
metacarpals
phalanges
proximal phalanx
middle phalanx
distal phalanx
1
2
3
4
5
5
4
3
2
1
a. Wrist and hand, anterior view
b. Posterior view

bone shapes

Controlling the growth of living tissues

- For higher living forms (plants, animals), growing into the right shape is essential for survival
- How can Nature control growth, sometimes in an amazingly precise way?
- Can we write PDEs describing this feedback control mechanism?

What is the **simplest** system of PDEs generating the shapes found in nature?

"With four parameters I can fit an elephant, and with five I can make him wiggle his trunk" *(John von Neumann)*

Two main settings

- One-dimensional curves, growing in $\mathbb{R}^3$ (plant stems)
- Two-dimensional sets, growing in $\mathbb{R}^2$ (leaves)

numerical simulations (done)

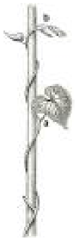
$+$

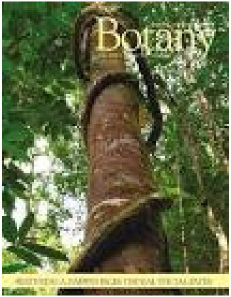
analytical proofs (in progress)

Stabilizing stem growth

what kind of stabilizing feedback is used here?

Growth in the presence of obstacles



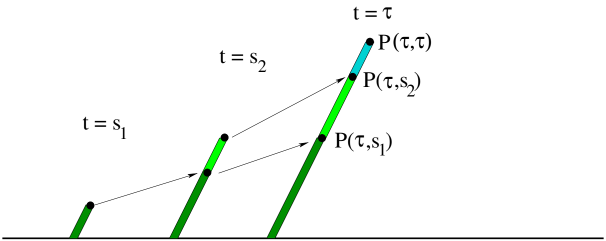


Are the growth equations still well posed, when an obstacle is present?

What additional feedback produces curling around other branches?

A model of stem growth (F. Ancona, A.B., O. Glass)

- New cells are born at the tip of the stem
- Their length grows in time, at an exponentially decreasing rate



$P(t,s)$ = position at time t of the cell born at time s

$$d\ell \;=\; |\partial_s P(t,s)| \;=\; \big(1 - e^{-\alpha(t-s)}\big)\, ds$$

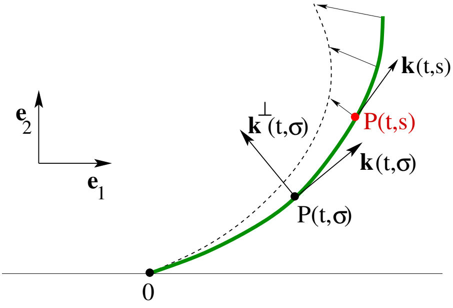
Unit tangent vector to the stem: $\mathbf{k}(t,s) = \dfrac{\partial_s P(t,s)}{|\partial_s P(t,s)|}$

Stabilizing growth in the vertical direction

stem not vertical $\Longrightarrow$ local change in curvature

$$e^{-\beta(t-s)} = \text{stiffness factor}, \qquad \mathbf{k} = (k_1, k_2), \quad \mathbf{k}^\perp = (-k_2, k_1)$$

$$\frac{\partial}{\partial t} P(t,s) = \int_0^s \alpha e^{-\alpha(t-\sigma)}\, \mathbf{k}(t,\sigma)\, d\sigma + \int_0^s \mu\, e^{-\beta(t-\sigma)}\, k_1(t,\sigma) \cdot \big(P(t,s) - P(t,\sigma)\big)^\perp \big(1 - e^{-\alpha(t-\sigma)}\big)\, d\sigma$$

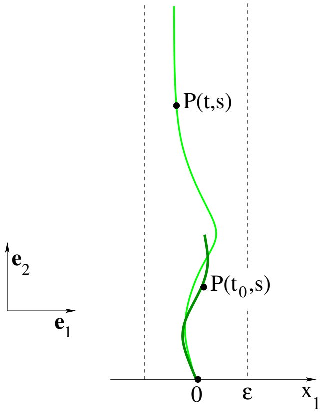


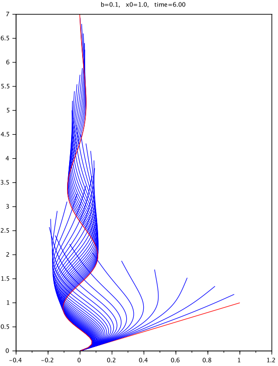
$$\begin{cases} P(t_0, s) = \overline{P}(s) & s \in [0, t_0] \\ P_{ss}(t,s)\Big|_{s=t} = 0 \end{cases}$$

We say that the growth equation is **stable in the vertical direction** if for any initial time $t_0 > 0$ and every $\varepsilon > 0$ there exists $\delta > 0$ such that

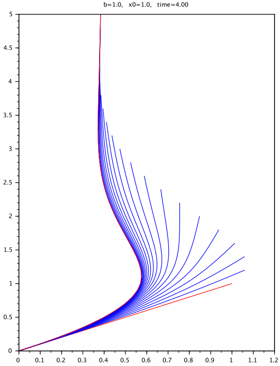
$$\left|\mathbf{e}_1 \cdot \frac{\partial}{\partial s} P(t_0, s)\right| \;\leq\; \delta \qquad \text{for all } s \in [0, t_0]$$

$$\text{implies} \qquad \left|\mathbf{e}_1 \cdot P(t, s)\right| \;\leq\; \varepsilon \qquad \text{for all } t > t_0, \quad s \in [0, t]$$

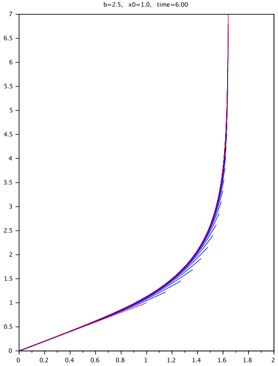




$\beta = 0.1$



$\beta = 1.0$



$\beta = 2.5$

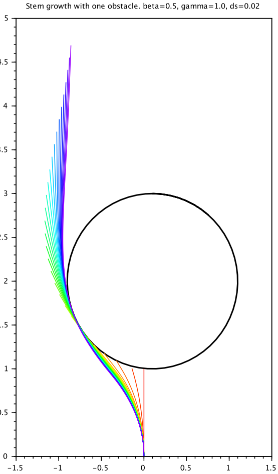
- stability is always achieved
- increasing the stiffness reduces oscillations

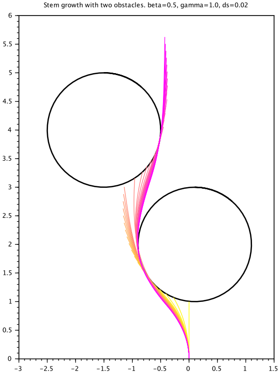
Analytical results (F. Ancona, A.B., O. Glass)

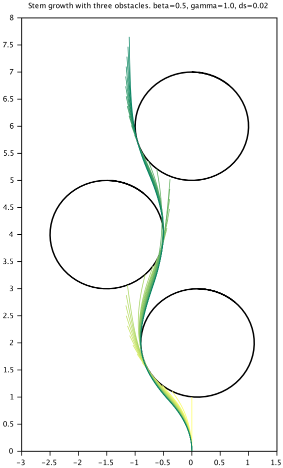
$\beta =$ stiffening constant, $\mu = 1$ (strength of response)

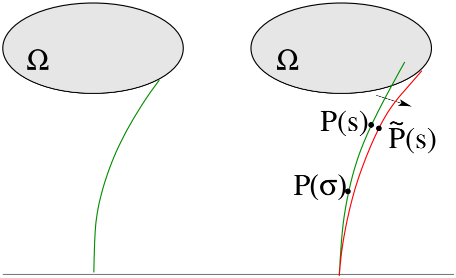
- If $\beta^4 - \beta^3 - 4 \geq 0$, then the growth is stable in the vertical direction (non-oscillatory regime: $\beta \geq \beta^* \approx 1.7485$)
- If $\beta \geq \beta_0$ for a suitable $\beta_0 < 1$, growth is still stable in the vertical direction (oscillatory regime)
- Stability apparently holds for all $\beta > 0$ (??)

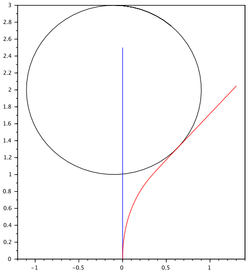
Growth with obstacles











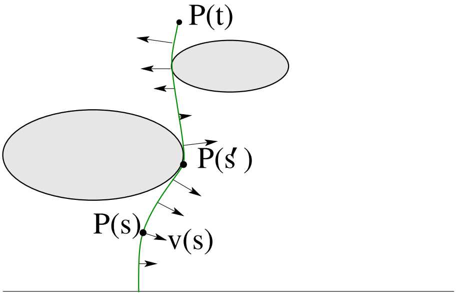
$\omega(\sigma)$ = additional bending of the stem caused the obstacle, at the point $P(\sigma)$

$$\widetilde{P}(s) - P(s) \;=\; \int_0^s \omega(\sigma) \times (P(s) - P(\sigma))d\sigma \qquad\qquad s \in [0, t]$$

Among all infinitesimal deformations that push the stem outside the obstacle,

$$\text{minimize the elastic energy: } \mathcal{E} \;=\; \frac{1}{2}\int_0^t e^{\beta(t-\sigma)}|\omega(\sigma)|^2\, d\sigma$$

A cone of admissible reactions



$$\chi(t) \doteq \{s' \in [0,t]\,;\quad P(s') \in \partial\Omega\} \qquad \text{(contact set)}$$

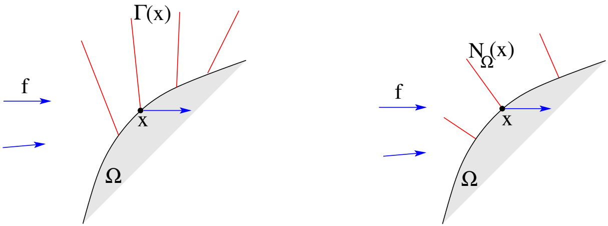
$$\Gamma \doteq \Bigg\{ \mathbf{v} : [0,t] \mapsto \mathbb{R}^3\,; \quad \text{there exists a positive measure } \mu \text{ supported on } \chi(t) \text{ such that}$$

$$\mathbf{v}(s) = \int \left(\int_0^s e^{-\beta(t-\sigma)} \Big(\mathbf{n}(t,s') \times \big(P(t,s') - P(t,\sigma)\big)\Big) \times \big(P(t,s) - P(t,\sigma)\big)\,d\sigma \right) d\mu(s') \Bigg\}$$

Motion in the presence of an obstacle

$$\dot{x} \;=\; f(x), \qquad x(t) \notin \overline{\Omega}$$

f Lipschitz, $\quad \Omega \subset \mathbb{R}^n$ open, with smooth boundary



differential inclusion:
$$\begin{cases} \dot{x} \;=\; f(x) & \text{if} \quad x \notin \overline{\Omega} \\ \dot{x} \;\in f(x) + \Gamma(x) & \text{if} \quad x \in \partial\Omega \end{cases}$$

upper semicontinuity + convexity $\Longrightarrow$ existence

Well posedness (also with a moving obstacle)

J. J. Moreau, Evolution problems associated with a moving convex set in a Hilbert space, *J. Differential Equat.* **26** (1977), 347–374.

G. Colombo and V. Goncharov, The sweeping processes without convexity. *Set-Valued Anal.* **7** (1999), 357–374.

G. Colombo and M. Monteiro Marques, Sweeping by a continuous prox-regular set. *J. Differential Equat.* **187** (2003), 46–62.

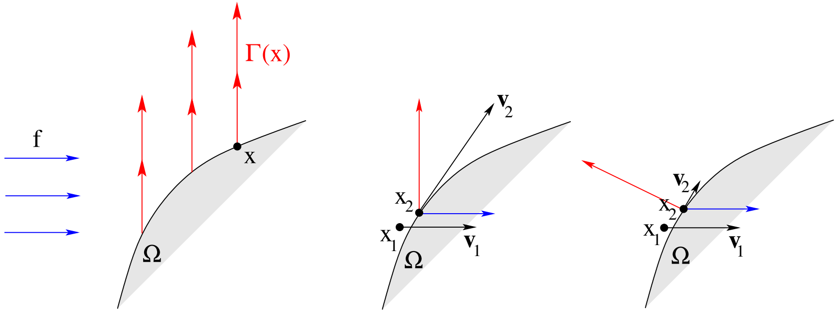
R. Rossi and U. Stefanelli, An order approach to a class of quasivariational sweeping processes. *Adv. Differential Equat.* **10** (2005), 527–552.

Continuous dependence

If $\Gamma(x) = N_\Omega(x)$ = normal cone, then

$$\frac{d}{dt}|x_1(t) - x_2(t)| \;\leq\; C|x_1(t) - x_2(t)|$$

$\Longrightarrow$ uniqueness, continuous dependence

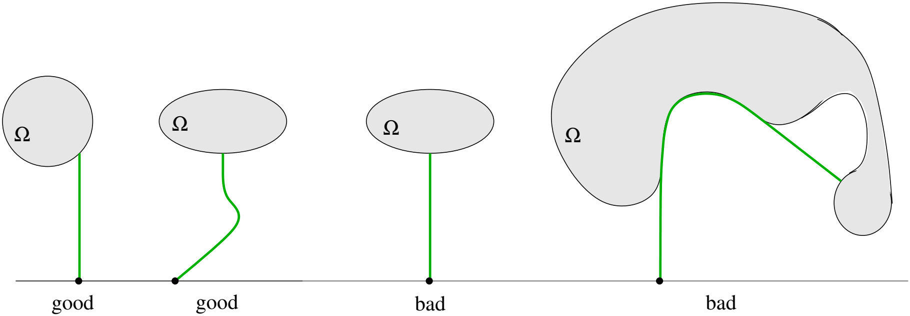


Possible approach when $\Gamma(x) \neq N_\Omega(x)$: introduce a Riemann metric on the Hilbert space $(= \mathbb{R}^n$ or $H^2(\mathbb{R})$) which renders each $\Gamma(x)$ a normal cone

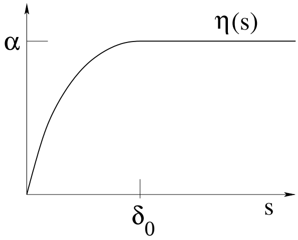
Well-posedness of the stem growth model with obstacle

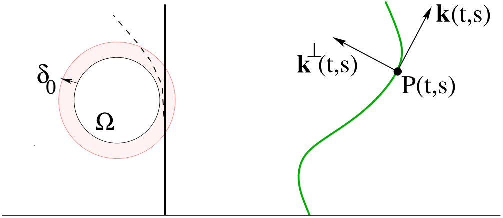
(A.B. - M.Palladino, work in progress)

Solutions exist and are unique except if a (highly non-generic) breakdown configuration occurs



- add a term which bends the stem toward the obstacle, at points which are sufficiently close (i.e., at a distance $< \delta_0$ from the obstacle)



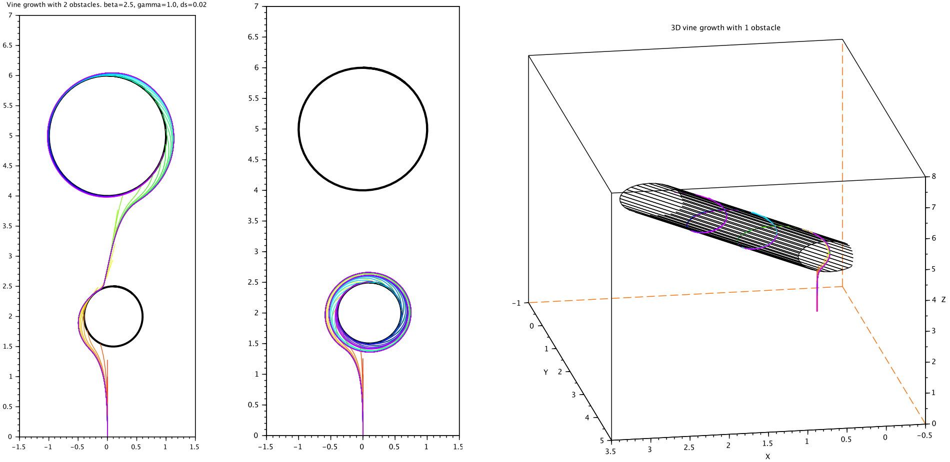


$$\psi(x) \doteq \eta\big(d(x,\Omega)\big)$$

In the case of a vine that clings to a branch of another tree, the evolution equation contains an additional term ($\Longrightarrow$ bending toward the obstacle)

$$\frac{\partial}{\partial t}\mathbf{k}(t,s) = \cdots + \left(\int_0^s e^{-\beta(t-\sigma)}\Big\langle \nabla\psi(P(t,\sigma)),\, \mathbf{k}^\perp(t,\sigma)\Big\rangle d\sigma\right)\mathbf{k}^\perp(t,s)$$

Numerical simulations (Wen Shen)



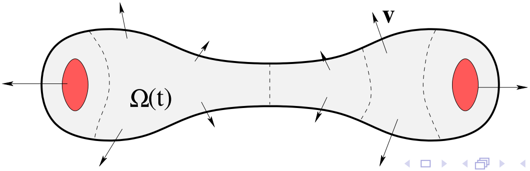
A system of PDEs modeling controlled growth in $\mathbb{R}^n$

- To grow into a specific shape, different portions of the living tissue must expand at different rates. This can be achieved by a **chemical gradient**.

The system of PDEs should include:

(1) One or more diffusion equations, describing the density of growth-inducing nutrients/morphogens inside the living tissue

(2) A dynamic equation, describing how particles on the tissue move, as a result of bulk growth



A linear diffusion-adsorption equation

$\Omega(t)$ = region occupied by living tissue at time t

$w(t,x)$ density of (morphogen-producing) signaling cells, at time t, at point $x \in \Omega(t)$

$$\begin{cases} u_\tau \;=\; w + \Delta u - u & x \in \Omega(t) \\[2mm] \nabla u \cdot \mathbf{n} \;=\; 0 & x \in \partial\Omega(t) \end{cases}$$

u = density of growth-inducing chemical. Determined by

production + diffusion + adsorption

Diffusion of chemicals within the living tissue is much faster than the growth of the tissue itself

By separation of time scales, it is appropriate to consider the steady state

$$\begin{cases} u - \Delta u \;=\; w & x \in \Omega(t) \\[2mm] \nabla u \cdot \mathbf{n} \;=\; 0 & x \in \partial\Omega(t) \end{cases}$$

The growth equations

$\mathbf{v}(t,x)$ = velocity determined by bulk growth

Uniquely determined (up to a rigid motion) by the variational problem

$$\begin{cases} \text{minimize:} & E(\mathbf{v}) \doteq \dfrac{1}{2}\displaystyle\int_{\Omega(t)} |\mathrm{sym}\,\nabla\mathbf{v}|^2\,dx \\ \text{subject to:} & \mathrm{div}\,\mathbf{v} = u \end{cases}$$

$E(\mathbf{v})$ = elastic energy of the infinitesimal deformation

$$\mathrm{sym}\,A \doteq \frac{A+A^T}{2}, \qquad \mathrm{skew}\,A \doteq \frac{A-A^T}{2}, \qquad |A|^2 \doteq \sum_{ij} A_{ij}^2$$

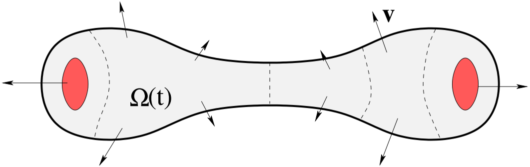
The growth equations

Finally, we assume that morphogen-producing cells are passively transported within the tissue, so that

$$w_t + \mathrm{div}\,(w\mathbf{v}) \;=\; 0 \qquad\qquad x \in \Omega(t)$$

This has to be supplemented by assigning an initial domain and an initial distribution of morphogen-producing cells:

$$\Omega(0) \;=\; \Omega_0, \qquad\qquad w(0,\cdot) \;=\; w_0$$



Summary of the equations

- Density of morphogen

$$u \;=\; \text{argmin} \int_\Omega \left(\frac{|\nabla u|^2}{2} + \frac{u^2}{2} - wu\right) dx \qquad \Longleftrightarrow \qquad \begin{cases} u - \Delta u &= w \qquad x \in \Omega \\ \nabla u \cdot \mathbf{n} &= 0 \qquad x \in \partial\Omega \end{cases}$$

- Velocity field determined by bulk growth

$$\begin{aligned} \mathbf{v} \;&=\; \text{argmin} \textstyle\int_\Omega |\text{sym}\, \nabla \mathbf{v}|^2\, dx \\ \text{subject to:} &\qquad \text{div}\, \mathbf{v} \;=\; u \end{aligned} \qquad \Longleftrightarrow \qquad \begin{cases} -\Delta \mathbf{v} + 2\nabla p &= \nabla u \qquad x \in \Omega \\ \text{div}\, \mathbf{v} &= u \qquad x \in \Omega \\ (\text{sym}\, \nabla \mathbf{v} - p\mathbf{I})\mathbf{n} &= 0 \qquad x \in \partial\Omega \end{cases}$$

- Density of morphogen-producing cells

$$w_t + \text{div}\, (\mathbf{v}\, w) \;=\; 0$$

Construction of solutions *(A.B. - Marta Lewicka, work in progress)*

- Initial domain: $\Omega(0) \;=\; \Omega_0$, with boundary $\partial\Omega_0 \in \mathcal{C}^{2,\alpha}$
- Initial density of signalling cells: $w_0 \in \mathcal{C}^{\alpha}(\Omega_0)$.

A solution is constructed locally in time, with

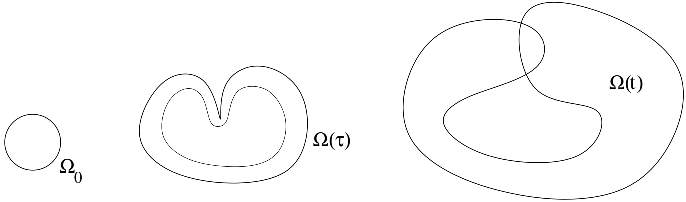
$$\begin{cases} \partial\Omega(t) & \in \; \mathcal{C}^{2,\alpha} \\ w(t,\cdot) & \in \; \mathcal{C}^{\alpha}(\Omega(t)) \end{cases} \qquad\qquad \begin{cases} u(t,\cdot) & \in \; \mathcal{C}^{2,\alpha}(\Omega(t)) \\ \mathbf{v}(t,\cdot) & \in \; \mathcal{C}^{2,\alpha}(\Omega(t)) \end{cases}$$

- Discretize time
- Korn inequality $\Longrightarrow$ existence of a velocity field $\mathbf{v}$ minimizing the instantaneous deformation energy (unique up to rigid motions)
- Schauder-type estimates by *Agmon-Douglis-Nirenberg (1964)* $\Longrightarrow$ regularity of approximate solutions

$\Longrightarrow$

- local existence of solutions

- uniqueness, up to rigid motions



Shapes

The shape of a set is its equivalence class modulo

- rotations and translations: $x \mapsto Rx + \mathbf{a}$
- homothetic rescalings: $x \mapsto \lambda x, \quad \lambda > 0$

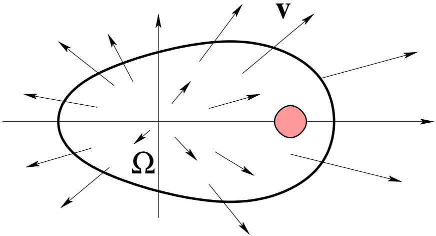
What kind of shapes can be produced by these controlled growth equations ?

Studying the limit of $\Omega(t)$ as $t \to +\infty$ is NOT meaningful

Problem: Find $\lambda > 0$, a domain Ω and a density $w : \Omega \mapsto R_+$ such that the corresponding growth velocity $\mathbf{v}$ satisfies

$$\mathbf{v}(x) - \lambda x \;=\; 0 \qquad x \in \Omega$$

$$\frac{d}{dt}\,[\text{shape}] \;=\; 0$$



more generally:
$$\begin{cases} \operatorname{div}\,\big((\mathbf{v} - \lambda x)\,w\big) \;=\; 0 & x \in \Omega \\ (\mathbf{v} - \lambda x)\cdot \mathbf{n} \;=\; 0 & x \in \partial\Omega \end{cases}$$

(eigenvalue-eigenfunction problem, in a set-valued framework)

Does this framework generate a rich variety of shapes?

General **Ulysses S. Grant**:

"I my whole life I could only learn to play two songs on the piano. One was *Yankee Doodle* and the other wasn't."

$$\text{Two shapes:} \qquad \begin{cases} \text{radially symmetric} \\ \text{not radially symmetric} \end{cases}$$

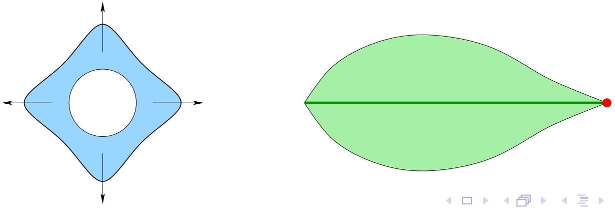
How to break away from radial symmetry?

Turing instability

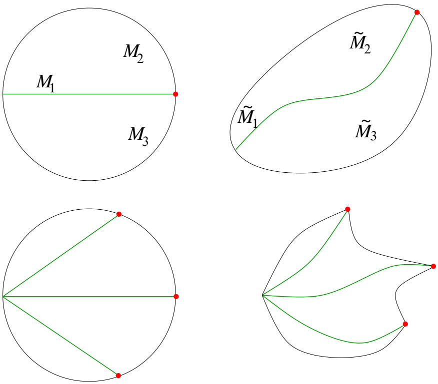
- requires at least two components (u_1, u_2), diffusing at different rates
- produces periodic patterns

Stratified domains

- the growing domain $\mathcal{M} = \mathcal{M}_1 \cup \cdots \cup \mathcal{M}_n$ is the union of manifolds of different dimensions
- Different topologies should give raise to different morpho-stationary configurations



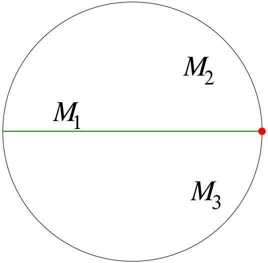
Does each (topological) equivalence class of stratified domains yield a finite-parameter family of morpho-stationary configurations?



To construct a morpho-stationary configuration:

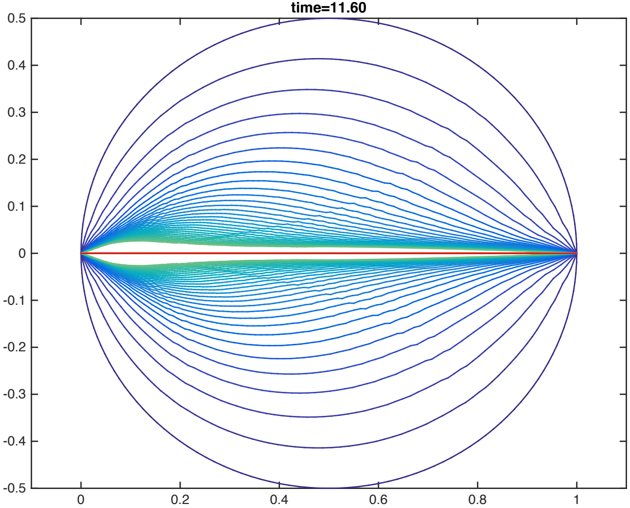
- solve the dynamic evolution equation, adding a rescaling term that keeps the diameter of the domain constant
- let $t \to +\infty$, prove that a nonsingular limit is achieved

Basic parameters

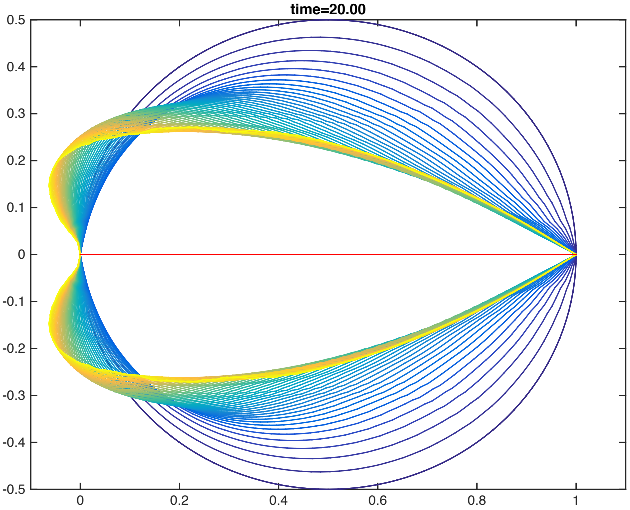


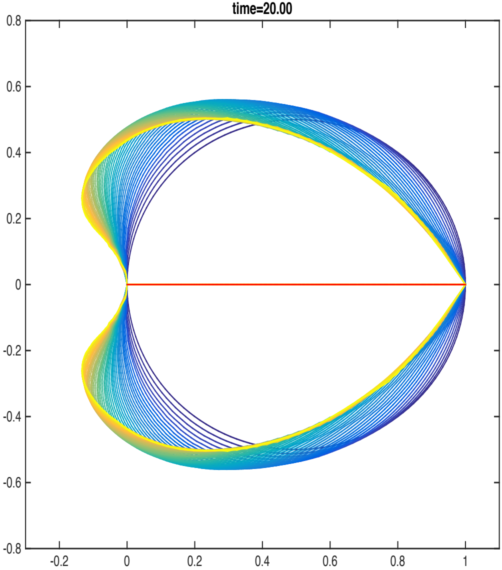
- diffusion, adsorption coefficients on the 1-D manifold $\mathcal{M}_1$
- diffusion, adsorption coefficients on the 2-D manifolds $\mathcal{M}_2, \mathcal{M}_3$
- elongation rate on $\mathcal{M}_1$
- area growth rate on $\mathcal{M}_2, \mathcal{M}_3$

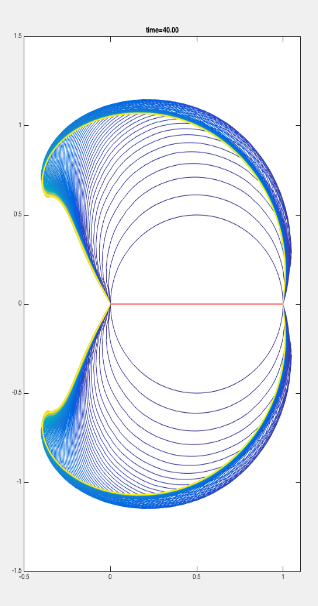
Numerical simulations (Wen Shen)



area growth rate $<<$ elongation rate


time=20.00
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
0
0.2
0.4
0.6
0.8
1


time=20.00
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-0.2
0
0.2
0.4
0.6
0.8
1

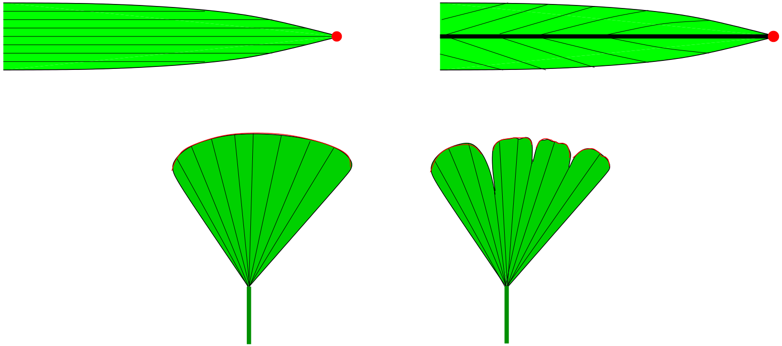


area growth rate $\gg$ elongation rate

Further issues . . .

- **Anisotropic diffusion and stress-strain response**

$\Longrightarrow$ additional ways to produce non radially symmetric shapes



- **Growth of curved surfaces in $\mathbb{R}^3$**

Growth of Stem + Branches

Introduce rules for

- initiation of new branches
- growth and bending of branches

Is there a feedback "stabilizing" the growth of trunk + branches toward a particular tree shape?

Conclusions . . .

- Interesting shapes can be obtained from **eigenvalue-eigenfunction problems in a set-valued framework** (morpho-stationary configurations on stratified domains)

- **Control & Stabilization of Growth Equations** will provide a rich source of mathematical problems