Numerical analysis of pattern formation in auxin transport models

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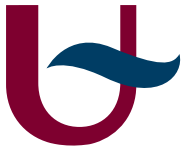
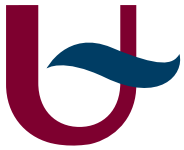


Outline

- Introduction and motivation
- Concentration-based transport models
- Pattern formation in an unbounded tissue
- Pattern formation in a bounded tissue
- Pattern formation in a growing tissue
- Conclusions and outlook



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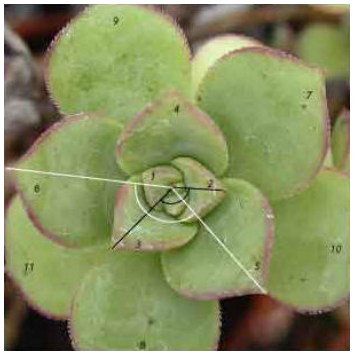
Introduction and motivation

Pattern formation

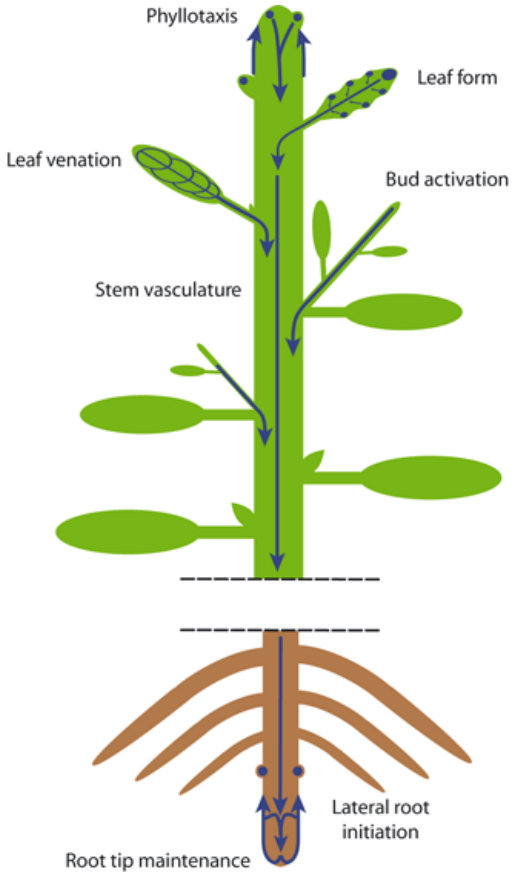
Regularity and mathematical properties



Introduction and motivation

IAA

- Indole-3-acetic acid
- Plant hormone
- Member of the auxin family



Transport of IAA

- Leads to accumulation points of IAA
- Plays a central role in pattern formation

Examples

P.Prusinkiewicz and A.Runions.
Computational models of plant development and form.

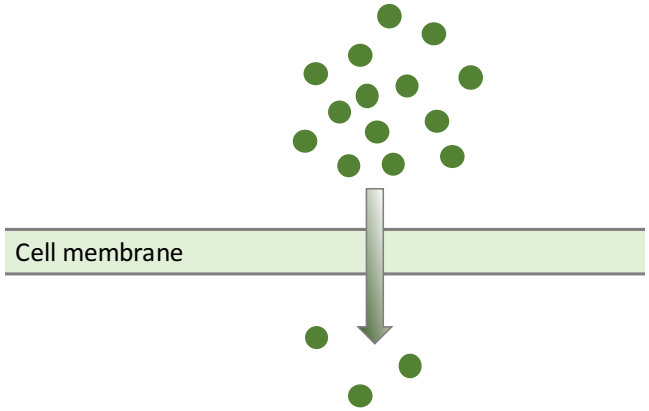
New Phytologist, 193(3):549-569,2012.

How is auxin (IAA) transported throughout a plant and how do auxin peaks arise?

IAA transport

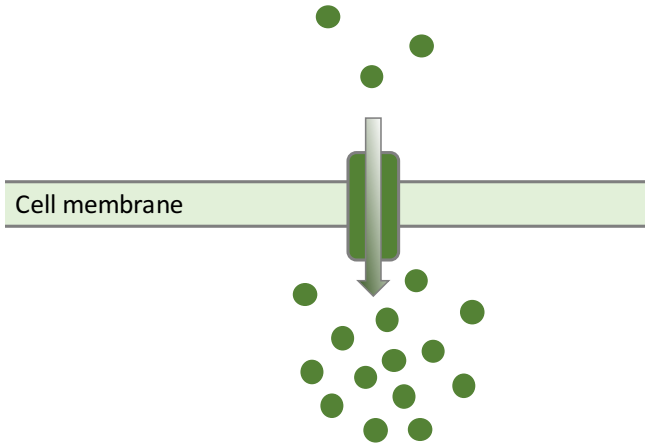
Passive transport

- Diffusion
- From high to low concentration
- Requires no energy

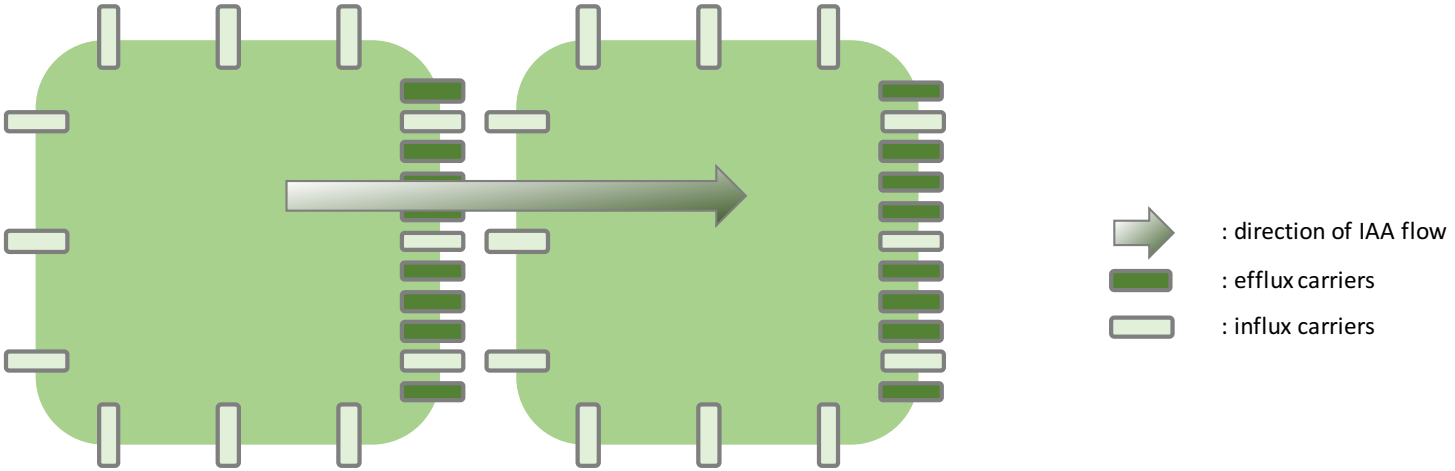


Active transport

- Most IAA is polarly charged
- From low to high concentration
- Requires auxin carriers



Active auxin transport

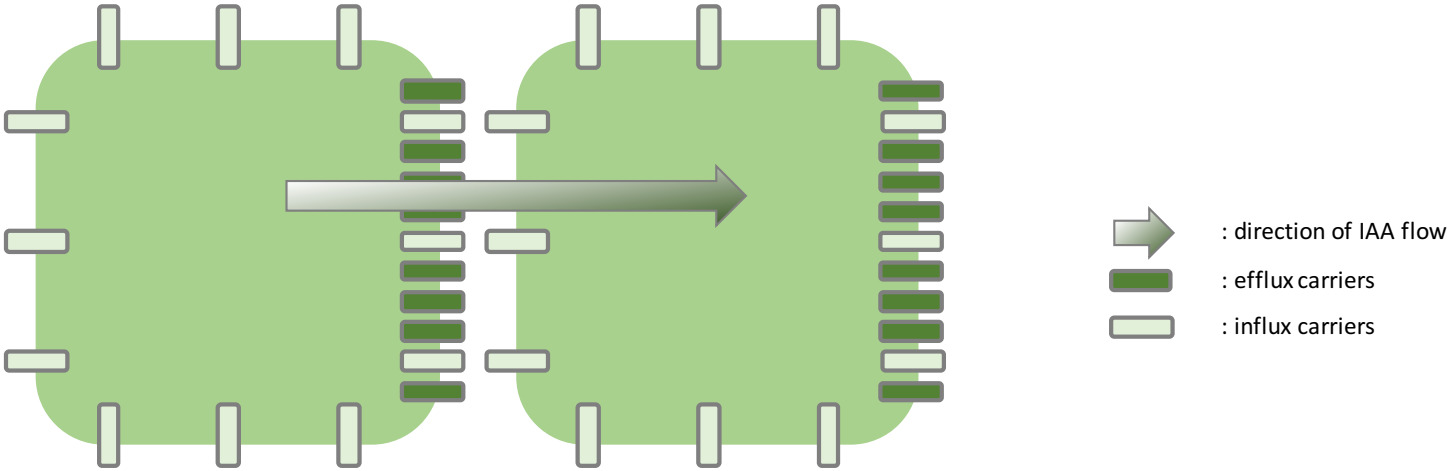


Auxin exporter PIN1

- Protein
- Member of the PIN family
- Main auxin efflux carrier
- Polar localization
  - Influenced by IAA

! complete feedback loop between IAA and PIN1

Active auxin transport



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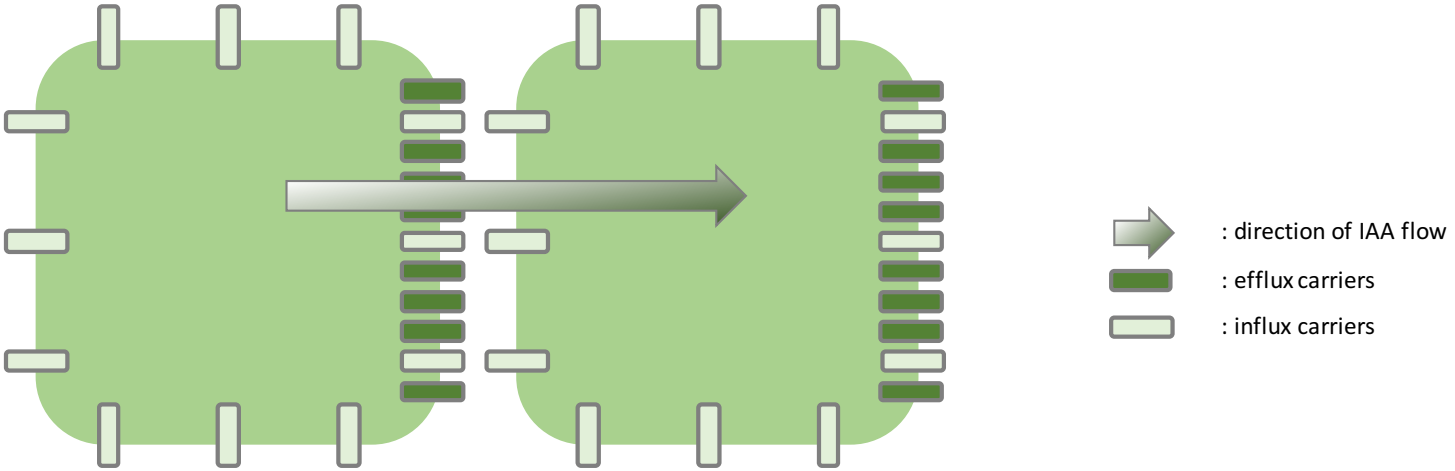
Different hypotheses

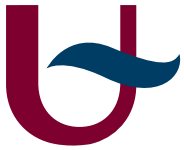
! complete feedback loop between IAA and PIN1

Active auxin transport



Auxin importer AUX/LAX

- Protein
- Limited role in comparison with PIN1
- Uniformly distributed on cell membrane



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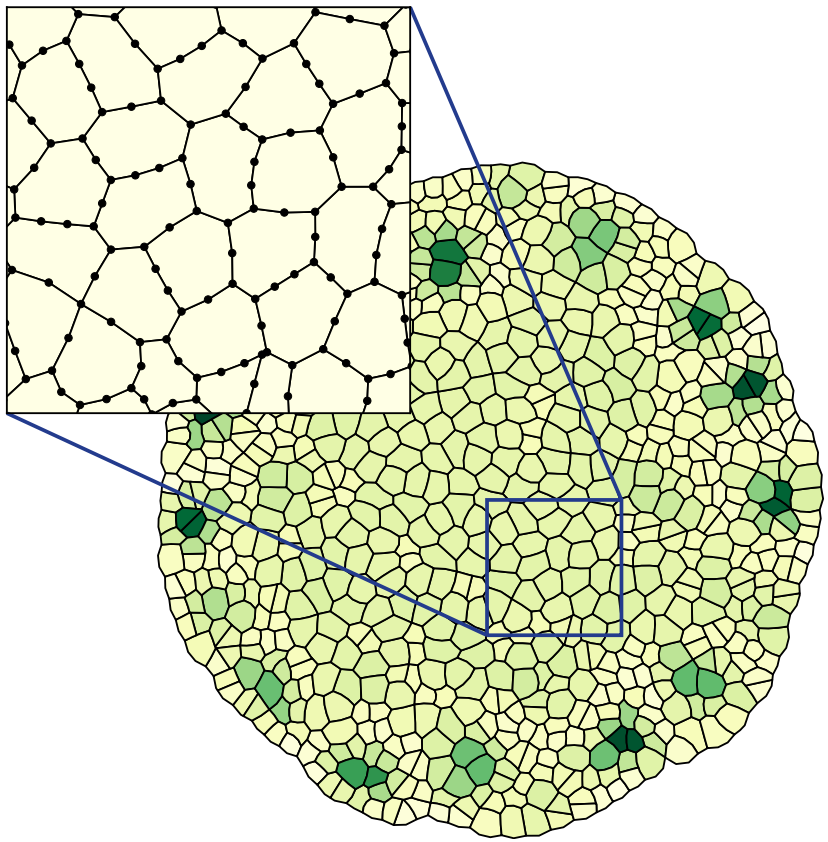
Geometric representation of tissue

A graph H:

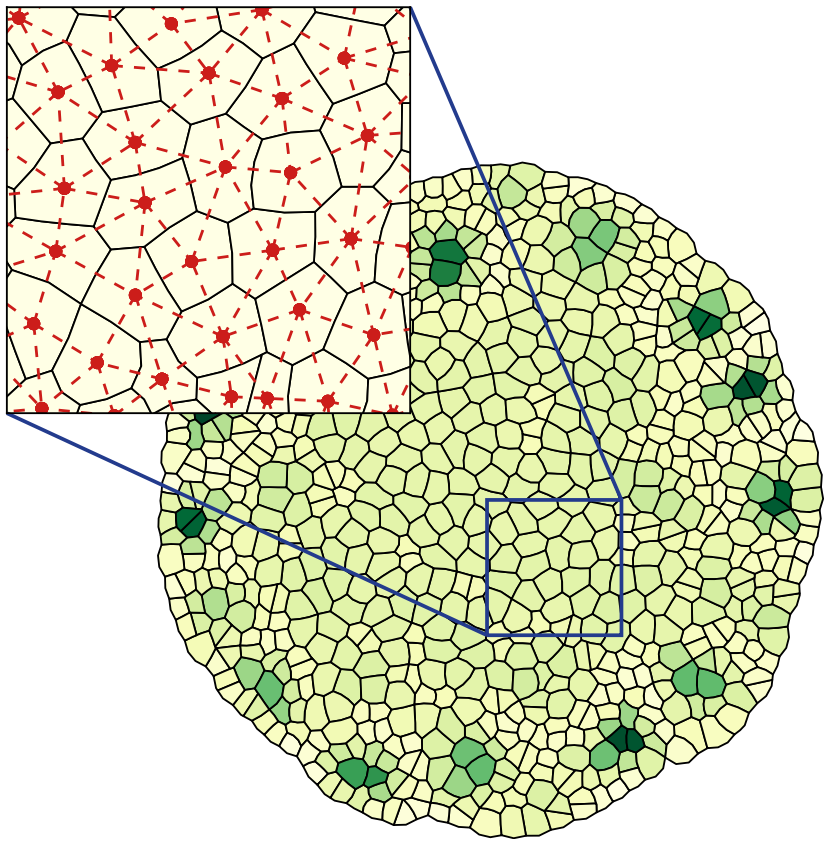
- Cell walls are represented by the edges e
- Cell vertices are the vertices v
- Cells are represented as polygons, the faces of the graph
- Neighboring cells have common edges



Topological representation of tissue

A graph H^*:

- Dual graph of H
- Cells $i \in \{1, \ldots, n\}$: vertices
- Connection between neighboring cells: edges
- $\mathcal{N}_i$: cells up to distance 1 from cell i
- Weighted graph: labelling each edge with relevant information
- State variables per cell (m)



General transport model

Definition (concentration-based model)

A concentration-based model is a set of $m \times n$ ODEs of the form

$$\begin{aligned}\dot{\mathbf{y}}_i &= \pi(\mathbf{y}_i) - \delta(\mathbf{y}_i) + \frac{\boldsymbol{D}}{V_i}\sum_{j\in\mathcal{N}_i} l_{ij}(\mathbf{y}_j - \mathbf{y}_i) \\ &\quad + \frac{\boldsymbol{T}}{V_i}\sum_{j\in\mathcal{N}_i} \boldsymbol{\nu}_{ji}(\mathbf{y}_1,\ldots,\mathbf{y}_n|H^*) - \boldsymbol{\nu}_{ij}(\mathbf{y}_1,\ldots,\mathbf{y}_n|H^*)\end{aligned}$$

for $i = 1,\ldots,n$ and $\pi, \delta : \mathbb{R}_+^m \to \mathbb{R}_+^m$, the production and decay functions, $\boldsymbol{D} \in \mathbb{R}^{m\times m}$ is a diagonal diffusion matrix, $T \in \mathbb{R}_+$, is the active transport parameter, and $\boldsymbol{\nu}_{ij} : \mathbb{R}_+^m \times \cdots \times \mathbb{R}_+^m \to \mathbb{R}_+^m$ are the active transport functions.

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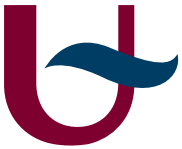
Example: model of Smith et al.

$\mathbf{y}_i = (a_i, p_i)'$: a_i: IAA concentration in cell i

p_i: PIN1 concentration in cell i



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Example: model of Smith et al.

$$\frac{da_i}{dt} = \pi(\mathbf{y}_i) \; - \; \delta(\mathbf{y}_i) \; + \; \frac{D}{V_i} \sum_{j \in \mathcal{N}_i} l_{ij}(\mathbf{y}_j - \mathbf{y}_i)$$

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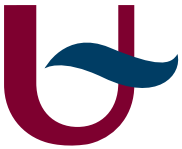

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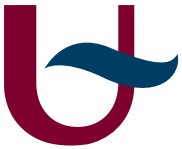

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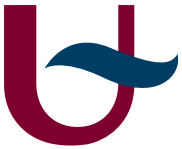

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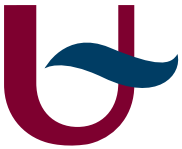

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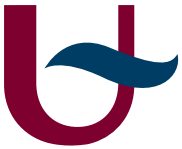

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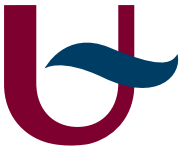

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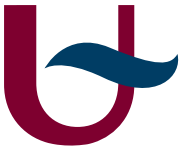

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$$+ \frac{T}{V_i}\sum_{j\in\mathcal{N}_i}\left[P_{ji}(\boldsymbol{a},\boldsymbol{p})\frac{a_j^2}{1+\kappa_T a_i^2} - P_{ij}(\boldsymbol{a},\boldsymbol{p})\frac{a_i^2}{1+\kappa_T a_j^2}\right]$$

$$\frac{dp_i}{dt} = \frac{\rho_{\mathrm{PIN}_0} + \rho_{\mathrm{PIN}} a_i}{1+\kappa_{\mathrm{PIN}} p_i} - \mu_{\mathrm{PIN}} p_i$$

with

$$P_{ij}(\boldsymbol{a},\boldsymbol{p}) = p_i \frac{l_{ij}\exp(c_1 a_j)}{\sum_{k\in\mathcal{N}_i} l_{ik}\exp(c_1 a_k)}$$

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Hypothesis (Active transport functions)

The active transport functions can be expressed as

$$(\boldsymbol{\nu}_{ij})_l = \psi_l(\mathbf{y}_i,\mathbf{y}_j|H^*)\frac{l_{ij}\varphi_l(\mathbf{y}_j)}{\sum_{k\in\mathcal{N}_i} l_{ik}\varphi_l(\mathbf{y}_k)}, \quad \textit{for } l = 1,\ldots,m$$

Model of Smith et al.

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So

$$\psi : \left(\begin{bmatrix} a_i \\ p_i \end{bmatrix}, \begin{bmatrix} a_j \\ p_j \end{bmatrix} \right) \mapsto p_i \frac{a_i^2}{1 + \kappa_T a_j^2}, \qquad \varphi : \begin{bmatrix} a_i \\ p_i \end{bmatrix} \mapsto \exp(c_1 a_i)$$

Type of solutions

System

- Dynamical system

$$\dot{\mathbf{y}} = F(\mathbf{y}, \lambda)$$

- Fixed geometry

Steady state solutions

- Motivation
  - Transport and diffusion measured in seconds
  - One cell cycle: 24 hours
- $\dot{\mathbf{y}} = F(\mathbf{y}, \lambda) = 0$

- Dynamical systems approach
  - Find steady state solution space in function of the parameters
  - Use continuation methods and bifurcation analysis

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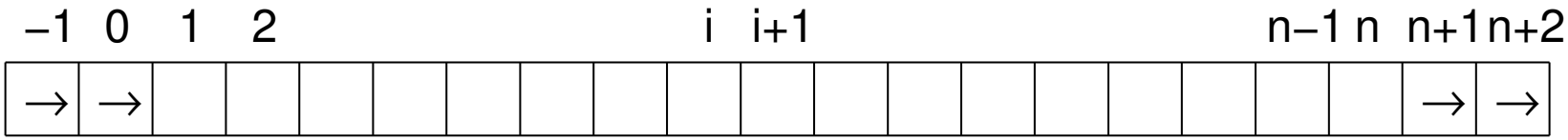
Pattern formation in an unbounded tissue

Unbounded regular domain



- $V_i = V^* \quad \forall i$
- $I_{ij} = I^* \quad \forall i$ and $j \in \mathcal{N}_i$
- Unbounded: $|\mathcal{N}_i| = |\mathcal{N}_j| \quad \forall i, j$

Homogeneous solution

- $\mathbf{y}^* = \mathbf{y}_i$
- Steady state problem: $0 = \pi(\mathbf{y}^*) - \delta(\mathbf{y}^*)$

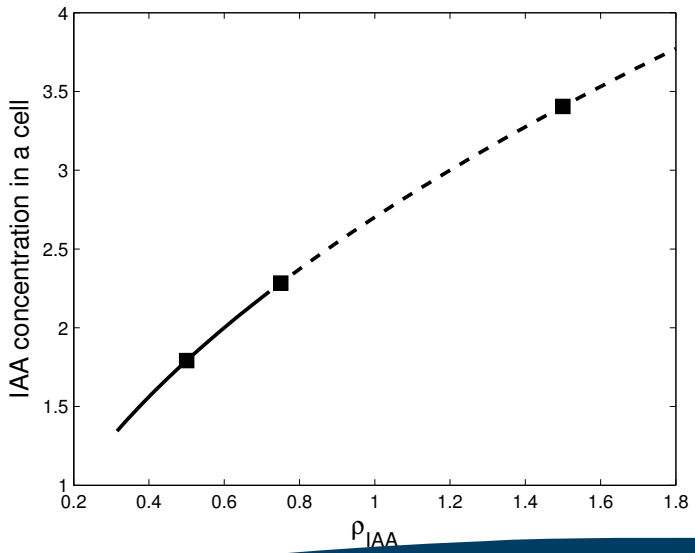
Homogeneous steady state

Example: model of Smith et al.

- Unbounded regular domain
- $$a^* = \frac{-1 + \sqrt{1 + 4\kappa_{\mathrm{IAA}}\rho_{\mathrm{IAA}}/\mu_{\mathrm{IAA}}}}{2\kappa_{\mathrm{IAA}}}$$

  $$p^* = \frac{-1 + \sqrt{1 + 4\kappa_{\mathrm{PIN}}\left(\rho_{\mathrm{PIN}_0} + \rho^*_{\mathrm{PIN}}\right)/\mu_{\mathrm{PIN}}}}{2\kappa_{\mathrm{PIN}}}$$

- Example:
  - File of 20 regular cells
  - Zero Neumann BC



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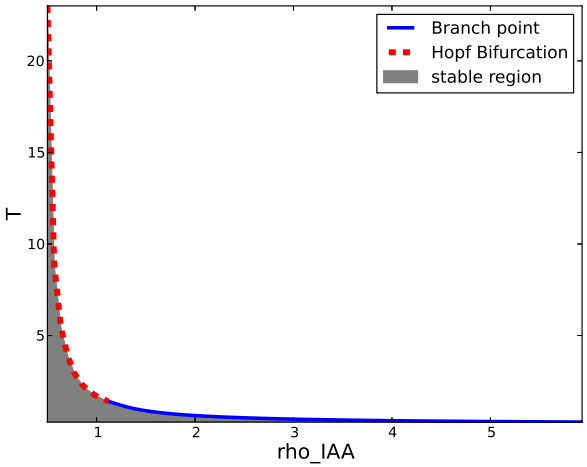
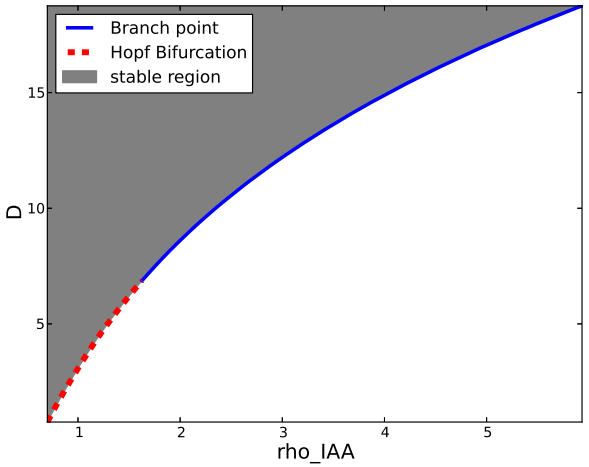
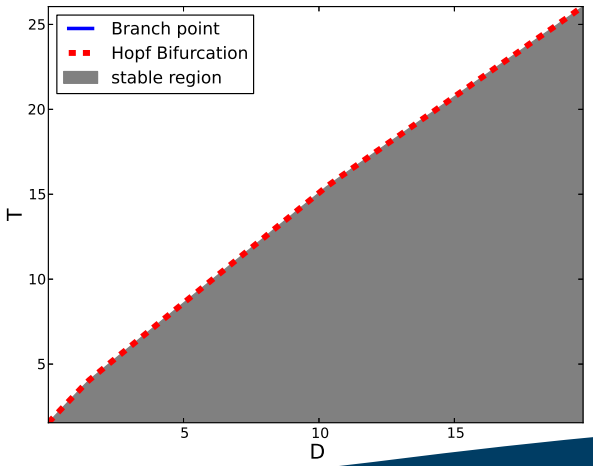
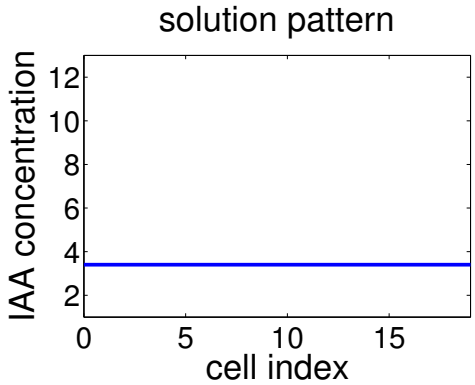




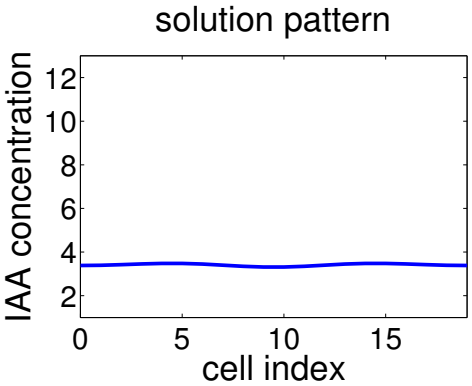


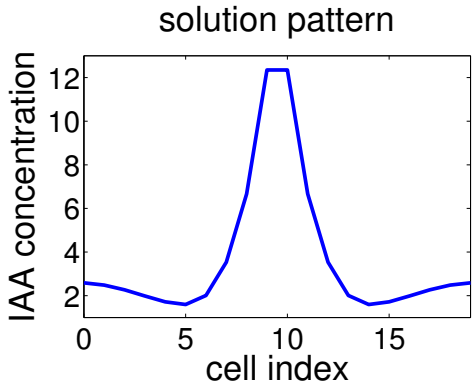
Pattern formation in an unbounded tissue

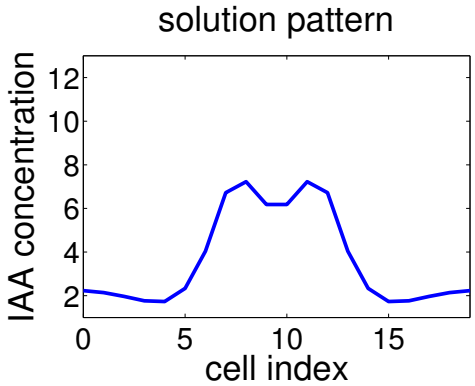
Homogeneous solution exists



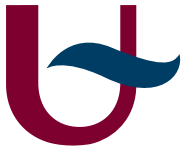
Solutions with IAA peaks exist







$\longrightarrow$ Peaks form with a Turing instability



Outline

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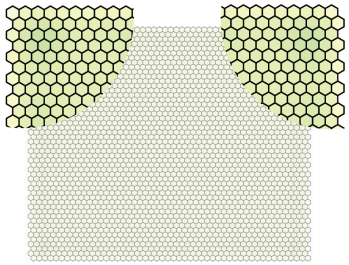
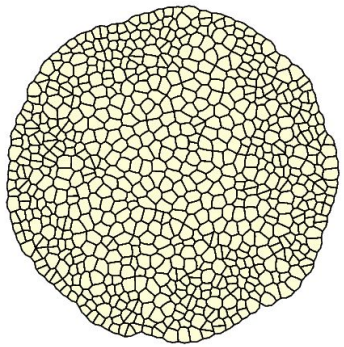
- Pattern formation in an unbounded tissue
- **Pattern formation in a bounded tissue**
- Pattern formation in a growing tissue
- Conclusions and outlook

Pattern formation in a bounded tissue

Bounded domain





Main results

- Homogeneous steady state
- Origin of IAA peaks
- Formation of stable IAA spots

Homogeneous steady state

Steady state problem

$$
\begin{aligned}
0 \;=\; & \pi(\mathbf{y}^*) - \delta(\mathbf{y}^*) + \frac{\boldsymbol{D}}{V_i} \sum_{j \in \mathcal{N}_i} l_{ij}(\mathbf{y}^* - \mathbf{y}^*) \\
& + \frac{\boldsymbol{T}}{V_i} \sum_{j \in \mathcal{N}_i} \Bigg(\psi(\mathbf{y}^*, \mathbf{y}^* | H^*) \odot l_{ij} \varphi(\mathbf{y}^*) \oslash \sum_{k \in \mathcal{N}_j} l_{jk} \varphi(\mathbf{y}^*) \\
& \qquad - \; \psi(\mathbf{y}^*, \mathbf{y}^* | H^*) \odot l_{ij} \varphi(\mathbf{y}^*) \oslash \sum_{k \in \mathcal{N}_i} l_{ik} \varphi(\mathbf{y}^*) \Bigg)
\end{aligned}
$$

Homogeneous solution

- $T = 0 : \forall i : \quad \mathbf{y}_i = \mathbf{y}^*$ is steady state solution
- $T \neq 0$: Homogeneous distribution is NOT always a steady state solution
  - $\rightarrow$ Peaks do not form with a Turing bifurcation

Steady state problem, zero diffusion

$$0 = \boldsymbol{\pi}(\mathbf{y}_i) - \boldsymbol{\delta}(\mathbf{y}_i) + \frac{\boldsymbol{T}}{V_i} \sum_{j \in \mathcal{N}_i} \left(\psi(\mathbf{y}_j, \mathbf{y}_i) \odot l_{ij} \varphi(\mathbf{y}_i) \oslash \sum_{k \in \mathcal{N}_j} l_{jk} \varphi(\mathbf{y}_k) - \psi(\mathbf{y}_i, \mathbf{y}_j) \odot l_{ij} \varphi(\mathbf{y}_j) \oslash \sum_{k \in \mathcal{N}_i} l_{ik} \varphi(\mathbf{y}_k) \right)$$

Steady state solution for $0 < T \ll 1\,\mu m^3/s$

Steady state problem, zero diffusion

$$0 = \boldsymbol{\pi}(\mathbf{y}_i) - \boldsymbol{\delta}(\mathbf{y}_i) + \frac{\boldsymbol{T}}{V_i} \sum_{j \in \mathcal{N}_i} \left(\psi(\mathbf{y}_j, \mathbf{y}_i) \odot l_{ij} \varphi(\mathbf{y}_i) \oslash \sum_{k \in \mathcal{N}_j} l_{jk} \varphi(\mathbf{y}_k) - \psi(\mathbf{y}_i, \mathbf{y}_j) \odot l_{ij} \varphi(\mathbf{y}_j) \oslash \sum_{k \in \mathcal{N}_i} l_{ik} \varphi(\mathbf{y}_k) \right)$$

Steady state solution for $0 < T \ll 1\,\mu\mathrm{m}^3/\mathrm{s}$

- $\mathbf{y}_i = \mathbf{y}^* + T\boldsymbol{\eta}_i + \mathcal{O}(T^2)$ for $i = 1, \ldots, n$ and $(\boldsymbol{\eta}_i)_j = \mathcal{O}(1)$
- Taylor expansion around $(\mathbf{y}^*, \ldots, \mathbf{y}^*)^T \in \mathbb{R}^{nm}$

Irregular domains

$$\forall i: \ \mathbf{y}_i = \mathbf{y}^* + \xi_i T \left(\boldsymbol{\pi}'(\mathbf{y}^*) - \boldsymbol{\delta}'(\mathbf{y}^*)\right)^{-1} \psi(\mathbf{y}^*, \mathbf{y}^*)$$

$$\xi_i = \frac{1}{V_i}\left(1 - \sum_{j \in \mathcal{N}_i} \frac{l_{ij}}{\sum_{k \in \mathcal{N}_j} l_{jk}}\right)$$

$\longrightarrow$ Purely geometric mechanism

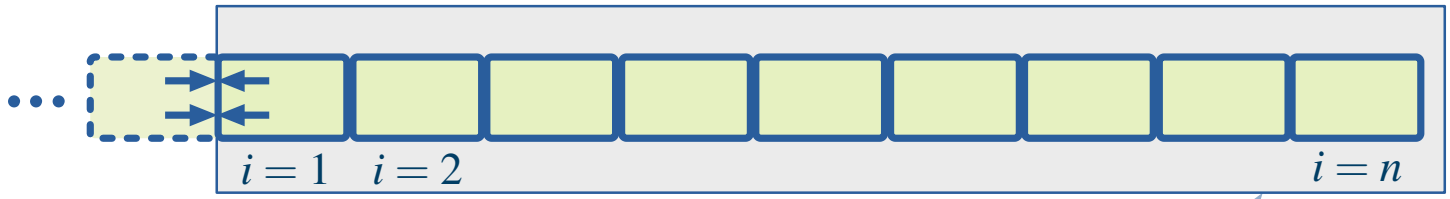
Regular domains

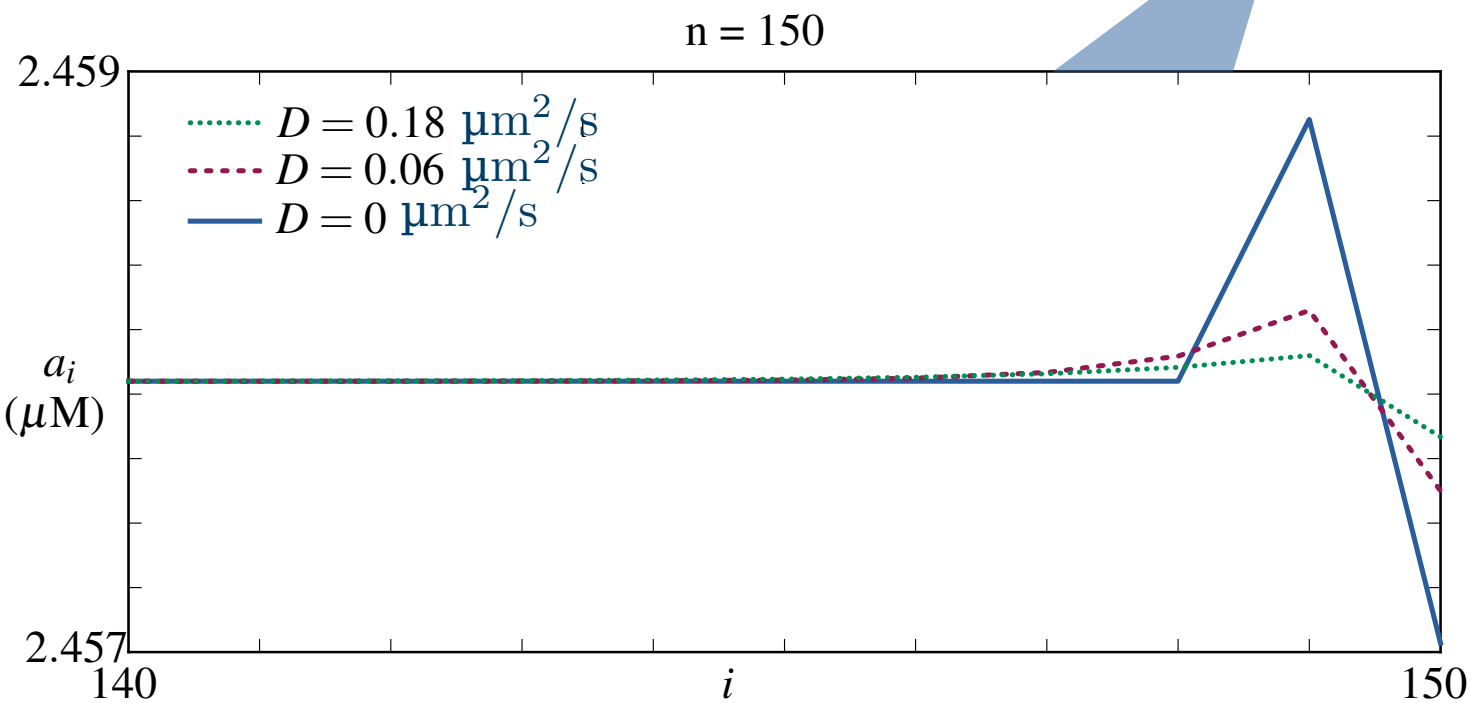
- $V_i = V^*, \ l_{ij} = l^*$
- Peaks form at the boundary

$$\xi_i = \frac{1}{V^*}\left(1 - \sum_{j \in \mathcal{N}_i} \frac{1}{|\mathcal{N}_j|}\right)$$

Origin of IAA peaks in regular domains

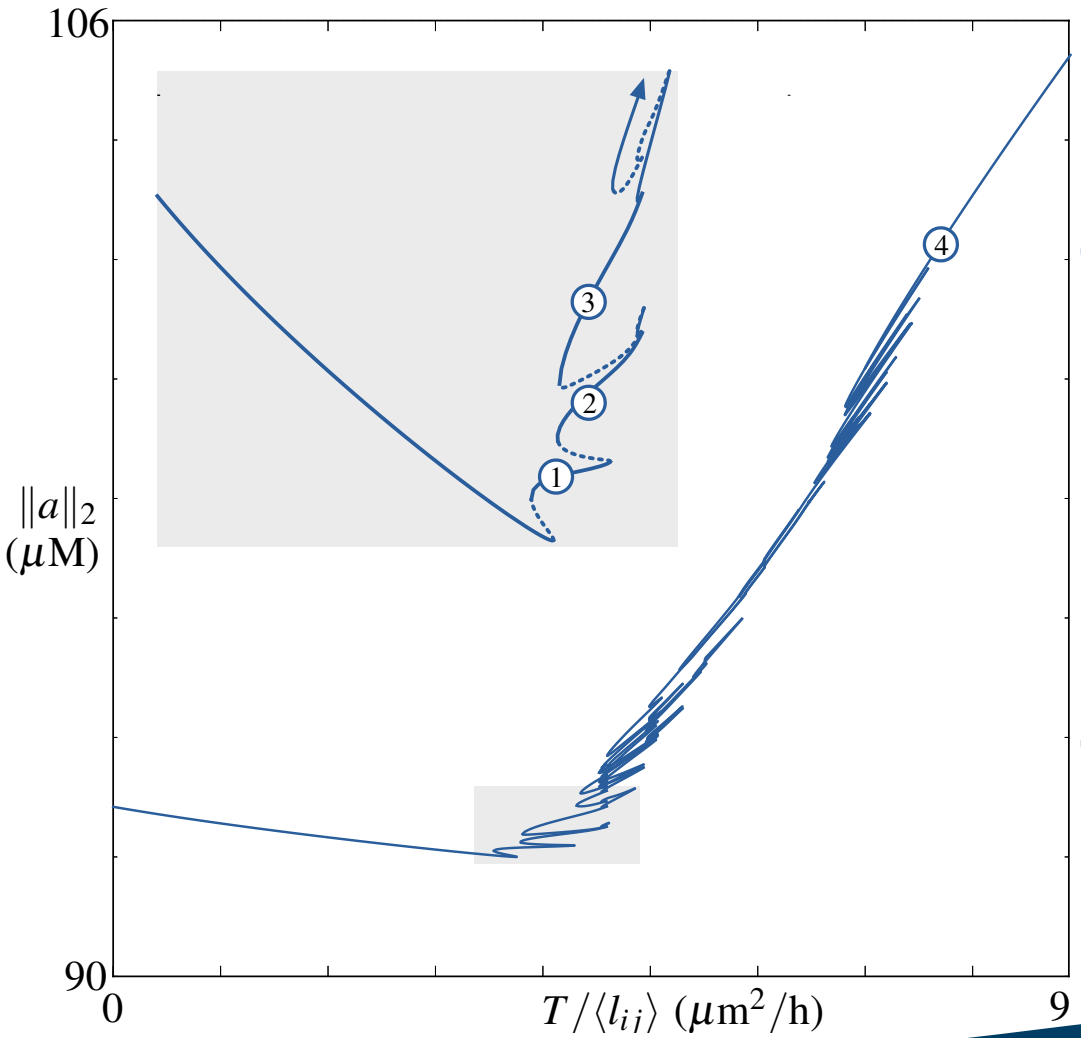
1D regular

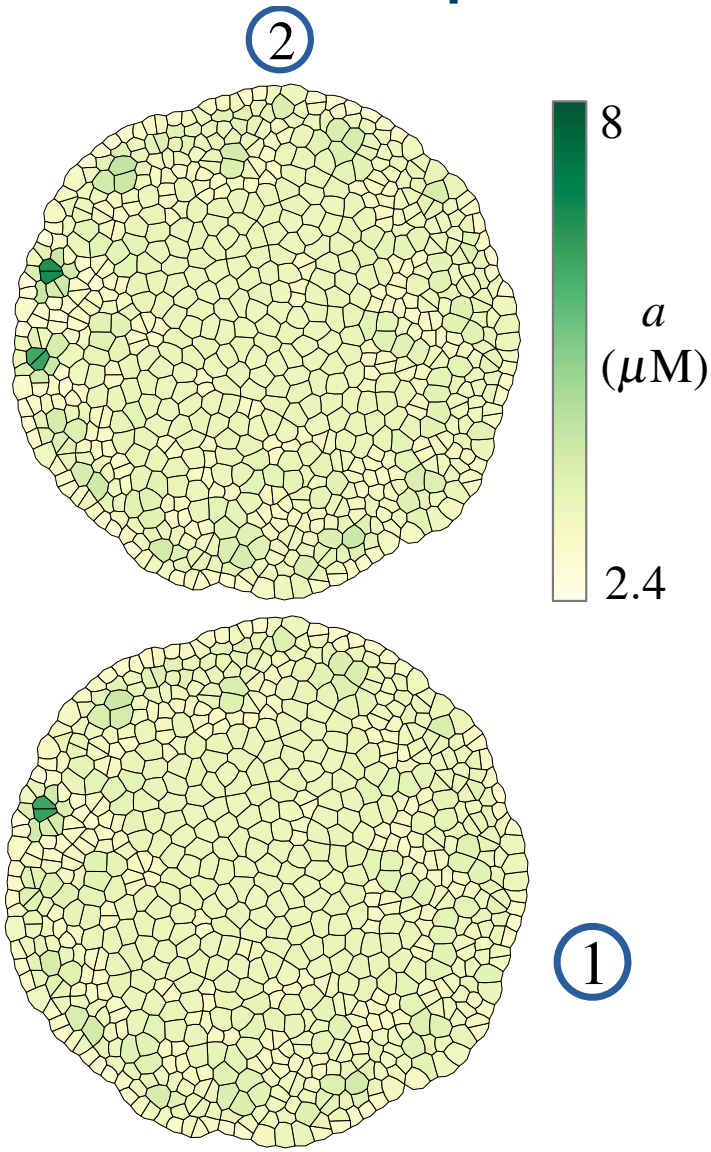




Formation of stable IAA spots

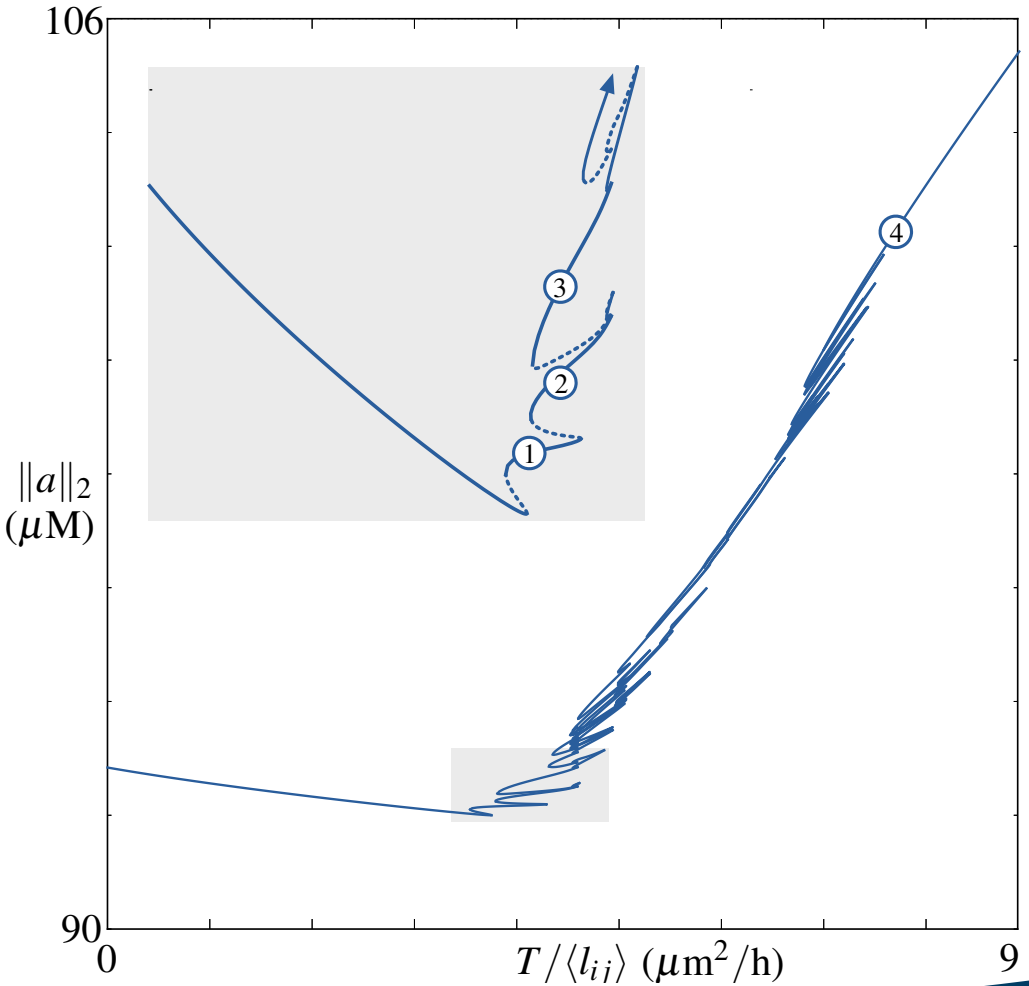
2D irregular

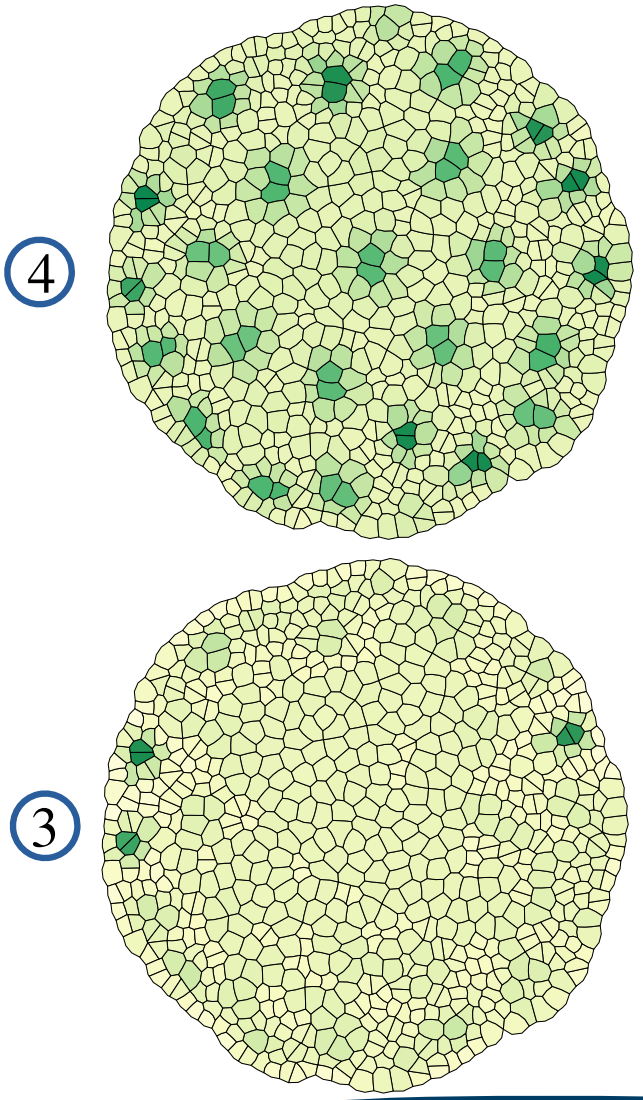


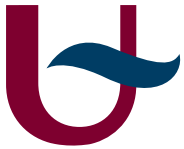


Formation of stable IAA spots

2D irregular







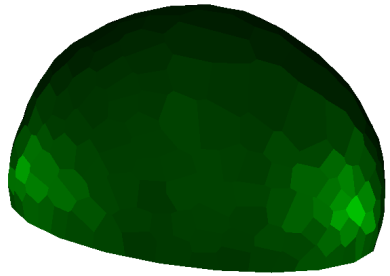
Outline

- Introduction and motivation
- Concentration-based transport models
- Pattern formation in an unbounded tissue
- Pattern formation in a bounded tissue
- **Pattern formation in a growing tissue**
- Conclusions and outlook

Pattern formation in a growing tissue

Assumptions

- Consider only external layer
  - Layer of irregular cells curved in 3D space
- Assume sequential order of processes



Model

- Physically based Mass Spring System
- Auxin transport models
- Material to a cell wall is added when wall is under tension

Pattern formation in a growing tissue

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  - Layer of irregular cells curved in 3D space
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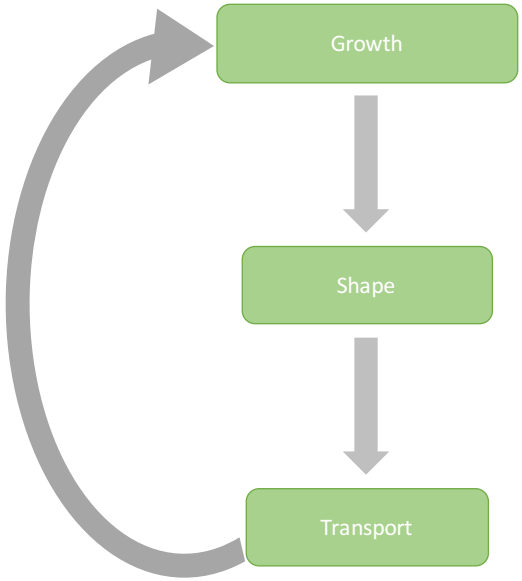

Model

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Pattern formation in a growing tissue

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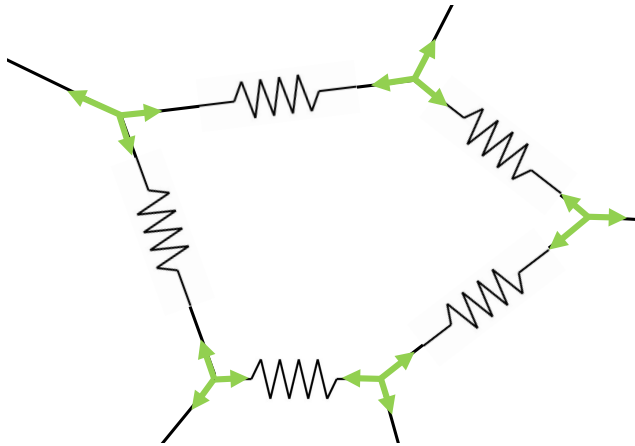


Model

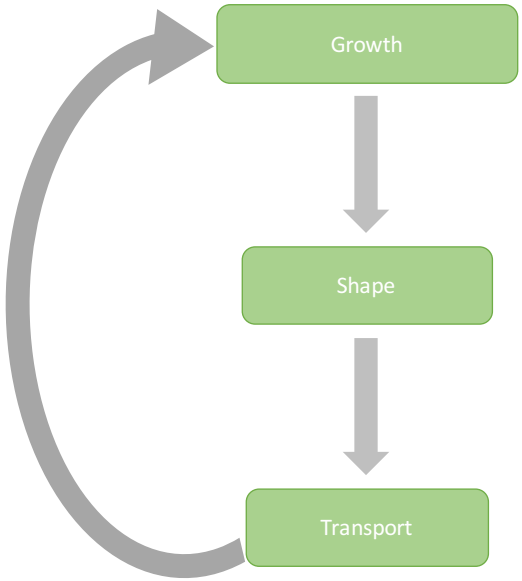
- Physically based Mass Spring System
  - Tissue is a damped elastic system
  - Each edge *e* is associated with a spring
  - Each vertex *v* is attached with a mass

  Relate forces acting on the springs with displacement of vertices
- Auxin transport models
- Material to a cell wall is added when wall is under tension

Pattern formation in a growing tissue

Assumptions

- Consider only external layer
- Assume sequential order of processes

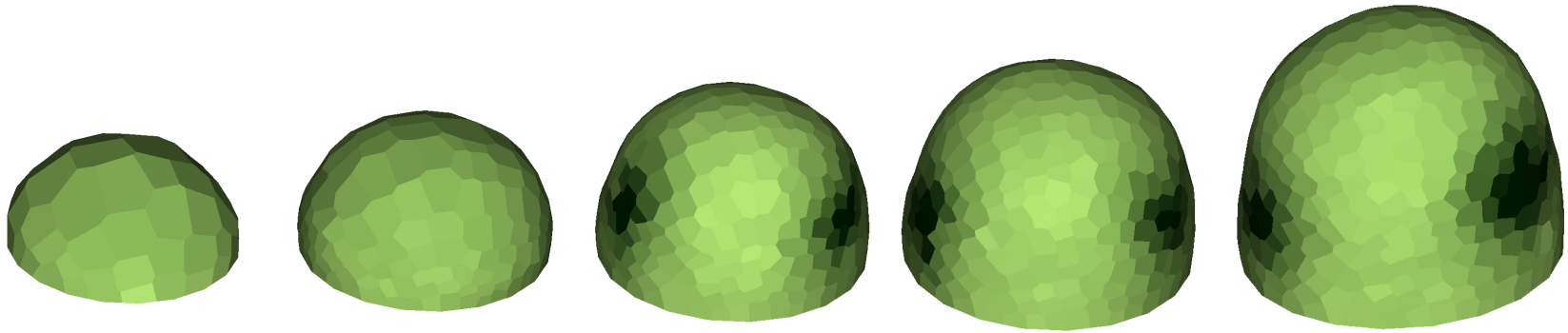


Model

- Physically based Mass Spring System
- Auxin transport models
- Material to a cell wall is added when wall is under tension
  - Relate with changing restlength over time
  - Dependent on IAA concentration

Pattern formation in a growing tissue

Domains

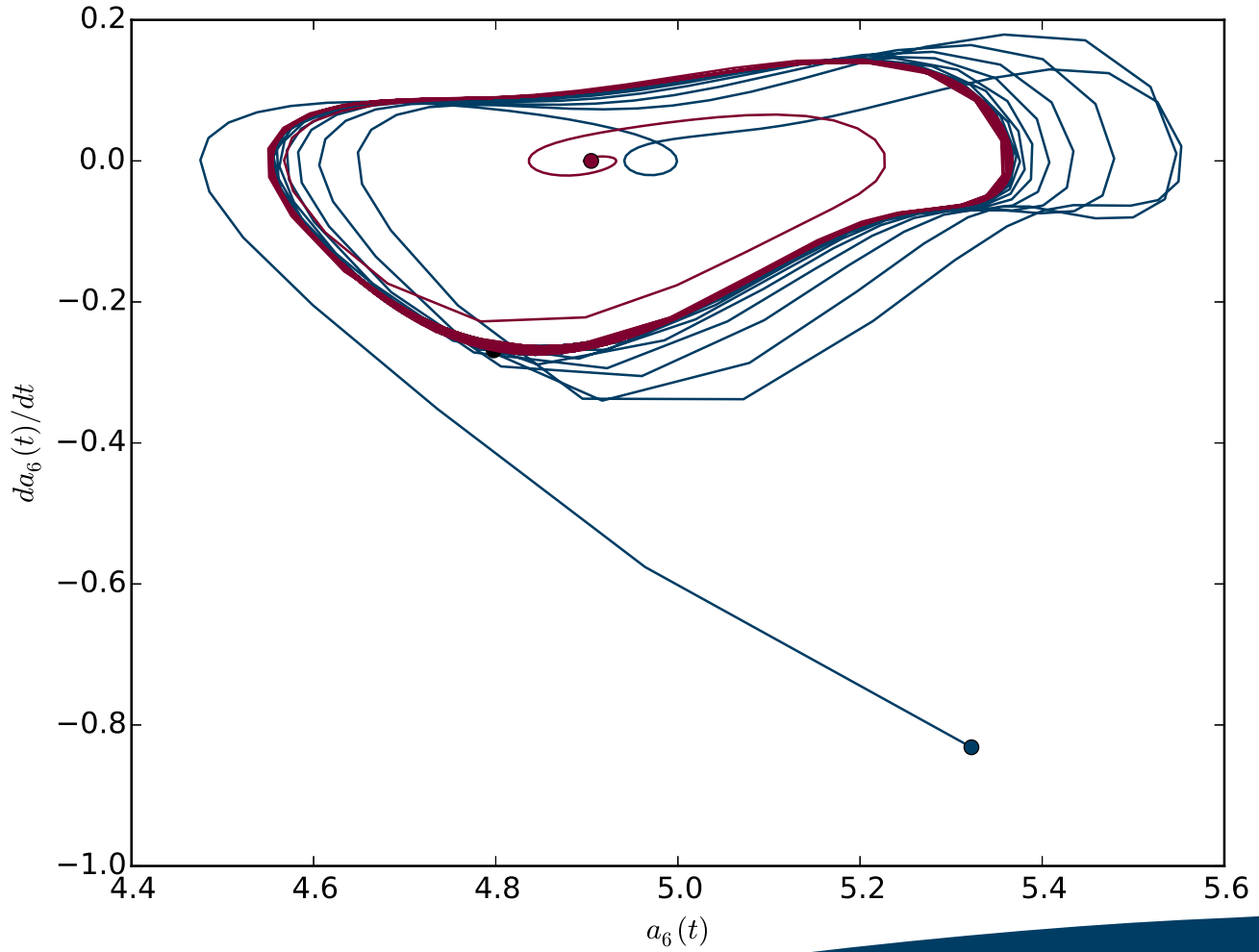


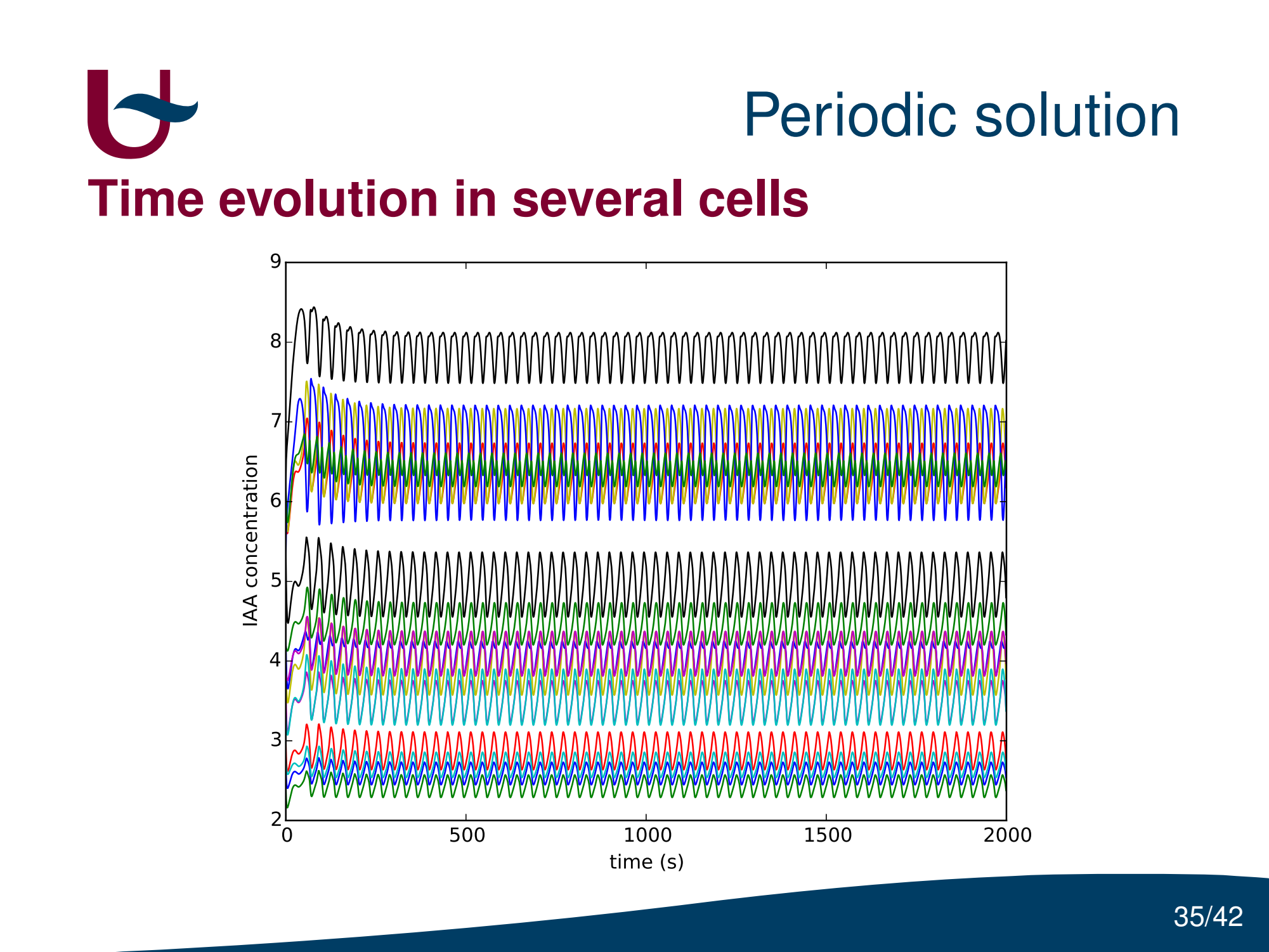
Main results

- Timeframe till steady state
- Periodic or quasi periodic solutions

Timeframe till steady state

Trajectory



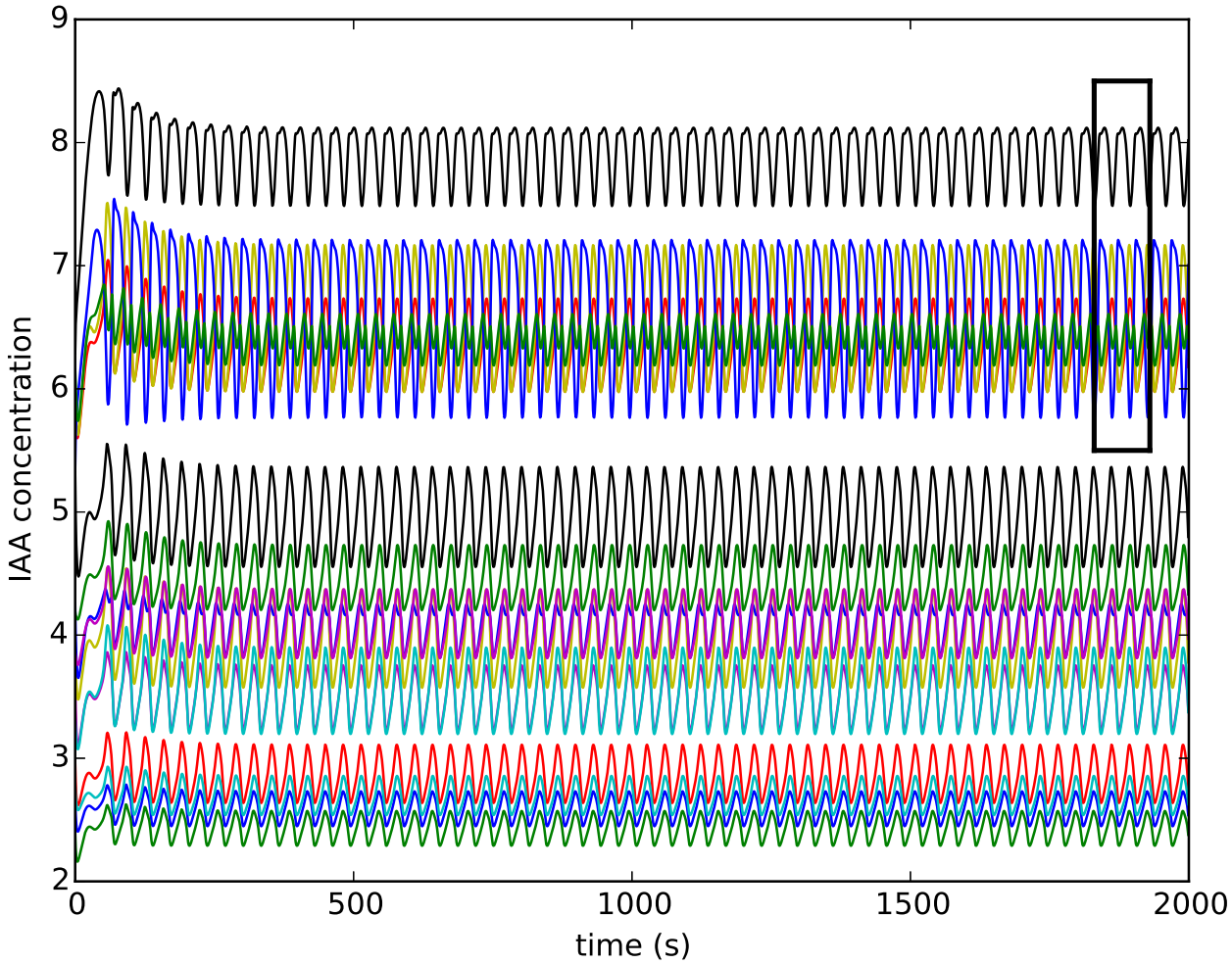


Periodic solution

Time evolution in several cells

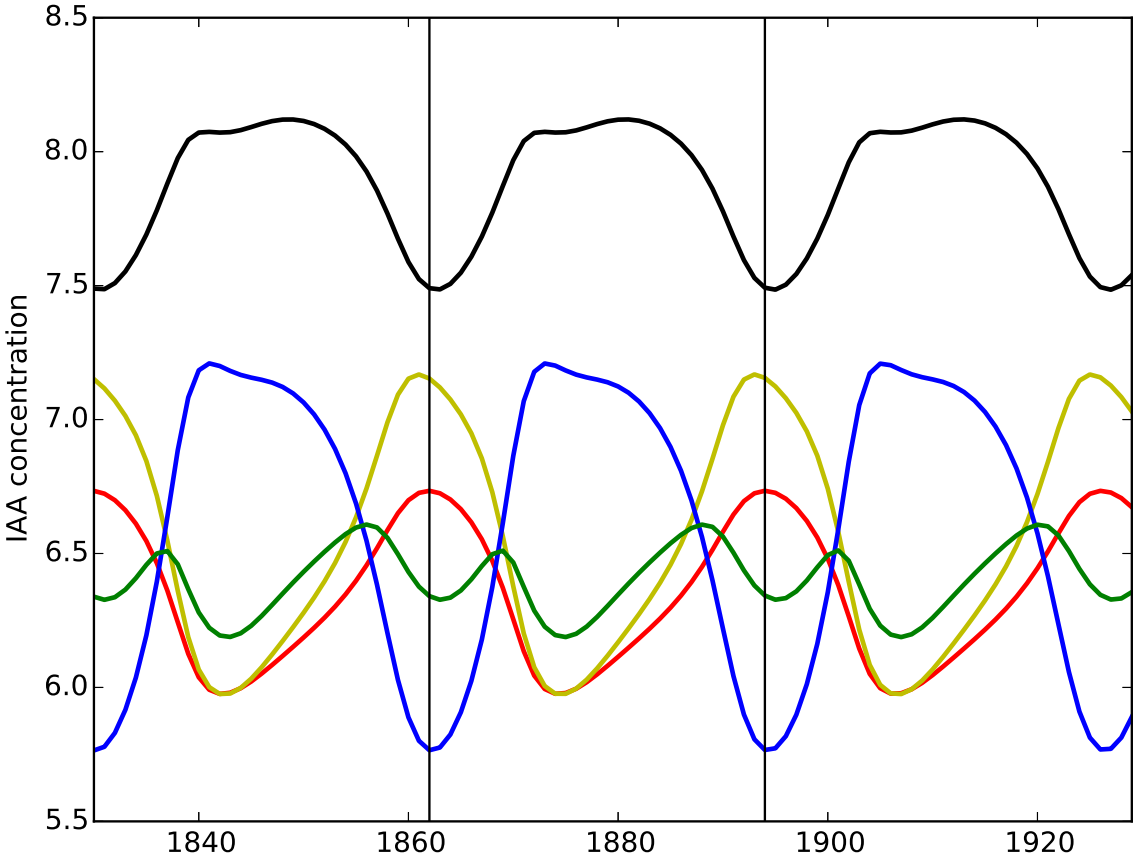
Periodic solution

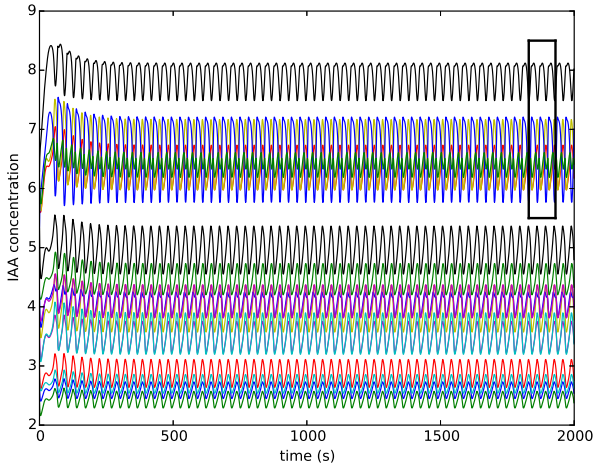
Time evolution in several cells



Periodic solution

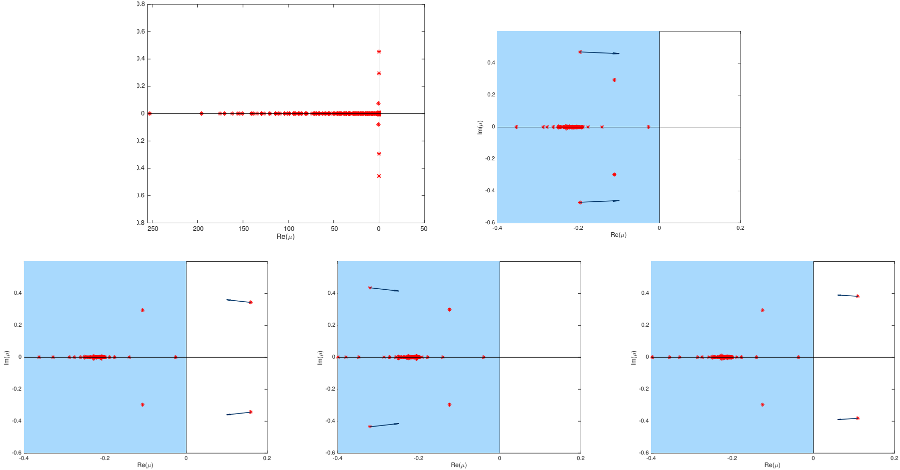
Time evolution in several cells

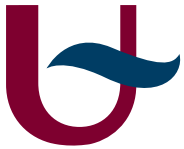




Periodic solution

Spectrum





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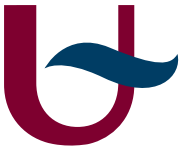
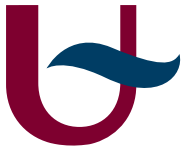


Conclusions and Outlook

Conclusions

- Formulated a mathematical description of auxin transport models
  - Introduced a general definition and hypothesis
  - Studied auxin transport models as dynamical systems
- Developed PyNCT
  - Numerical Continuation Toolbox in Python
  - Based on sparse linear algebra
- Examined steady state solutions as a function of model parameters
  - Calculated a homogeneous solution
  - Proved the formation of IAA peaks
  - Revealed a snaking bifurcation scenario
- Studied a growth model with a complete feedback loop between growth and IAA



Conclusions and Outlook

Outlook

- Compare and improve auxin transport models
  - Classify existing and new auxin transport models
  - Transform models to models with dimensionless parameters
  - Calculate the complete solution space in function of parameters
    - Extend functionalities PyNCT
    - Study automatically the behaviour of new and existing models when parameters are changed
- Improve growth model
  - Study the influence of IAA on growth
  - Investigate cell division mechanism
  - Eliminate separation of time-scales
  - Create interface between PyNCT and existing software to model growth

Selected publications

[P1] Draelants D., Vanroose W., Broeckhove J., Beemster G.T.S.: *Influence of an exogeneous model parameter on the steady states in an auxin transport model*, Proceedings PMA, 2012.

[A1] Draelants D., Broeckhove J., Beemster G.T.S., Vanroose W.: *Pattern formation in a cell based auxin transport model with numerical bifurcation analysis*, J Math Biol, 2013.

[A1] Draelants D.[1], Avitabile D.[1], Vanroose W.: *Localized auxin peaks in concentration-based transport models of the shoot apical meristem*, J. R. Soc. Interface, 2015.

[P1] Draelants D., Kłosiewicz P., Broeckhove J., Vanroose W.: *Solving general auxin transport models with a numerical continuation toolbox in Python: PyNCT*, LNCS, 2015.

[1] These authors contributed equally and should be considered as joint first authors.