Self-organization and pattern formation in auxin flow

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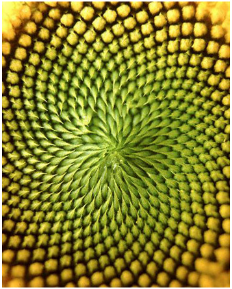
Motivation

Phyllotaxis = Observation of regular pattern in the arrangement of leaves on a stem.

(a) Aeonium

(b) Cone



(c) Sunflower

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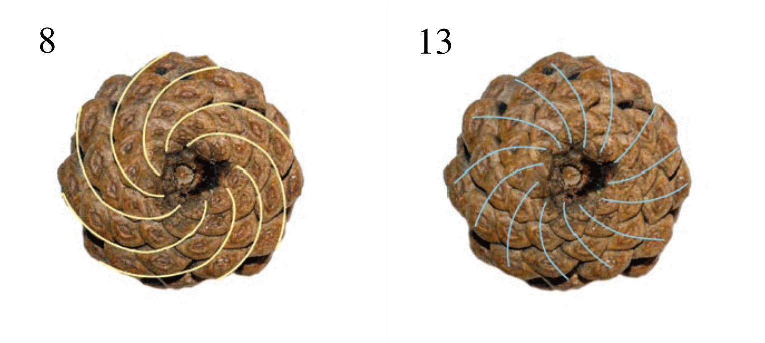
Fibonacci numbers and plants



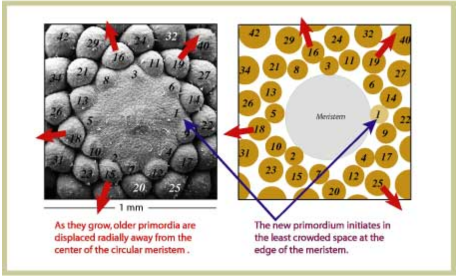
8 and 13 are also two consecutive Fibonacci numbers.

Golden angle and plants

Figure: The angle between two consecutive leaves is $\pm$ constant: this is the **divergence angle**, which is well approximated by $\phi \approx 137.5$ deg.

The principle of Hofmeister

- Hofmeister (1868) observed that the new primordia formed at the least crowded spot.



- Turing A. M. (1952) developed reaction-diffusion models to explain patterns. These models are used in morphogenesis and in phyllotaxis (Turing,Thornley (1975)).

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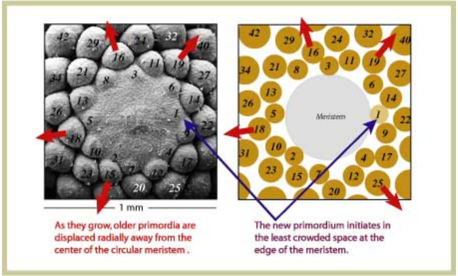

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Mathematical models based on the idea of repulsion

- Adler I. (1974) used the idea of repulsion in a static model.
- Levitov L. (1991) vortex model, using repulsive potentials. Theory based on hyperbolic geometry, and numerical simulations which show the emergence of Fibonacci numbers and of the Golden Angle.
- Douady S. and Couder Y. (1992) proposed an experiment for the Levitov's model. Magnetized ferrofluid droplets fall into a pool of silicone oil. The droplets are attracted to the edge of the pool and repel one another. Emergence of spirals.
- Kunz M. (1995). Rigorous mathematical study of these experiments using statistical mechanics. Relations with number theory.
- Atela P., Golé C. and Hotton S. (2002) Rigorous mathematical study of a dynamical system, in the spirit of Levitov and Kunz. Strong use of hyperbolic geometry and number theory.

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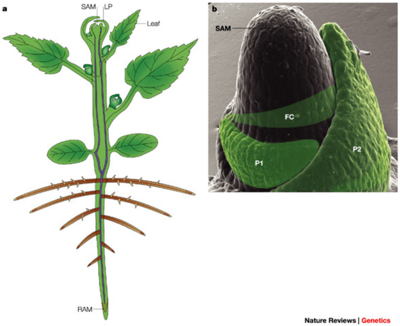
The plant hormone auxin is the main actor of growth



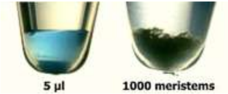


Figure: from M. Tsiantis and A. Hay, Nature Reviews Genetics 4, 2003

- Organ of a plant = leaves, flowers
- Initiation of the organ on the top of the stem (meristem).

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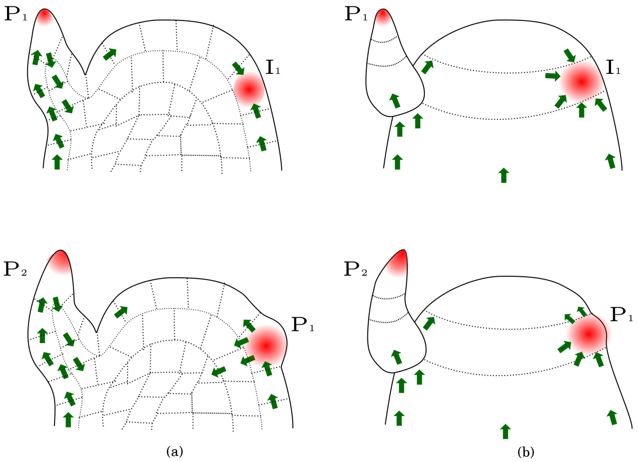
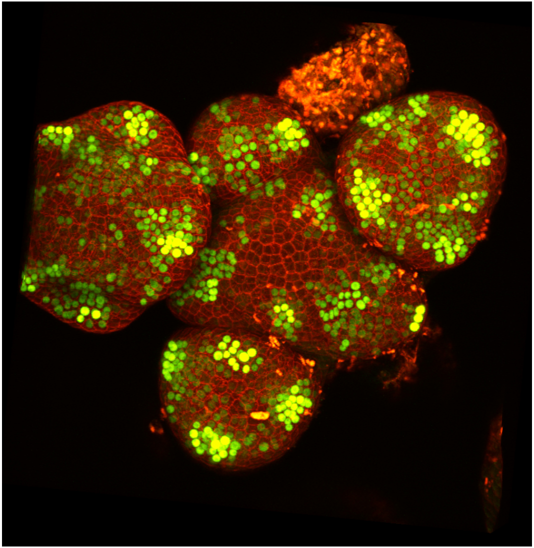


(a) Transversal section. PIN polarization soon after incipient primordium formation. (b) External view.

Auxin accumulates in some cells, creating local hot spots of high auxin density, which can be seen as pre-patterns



Models based on meristem elasticity and on auxin flow

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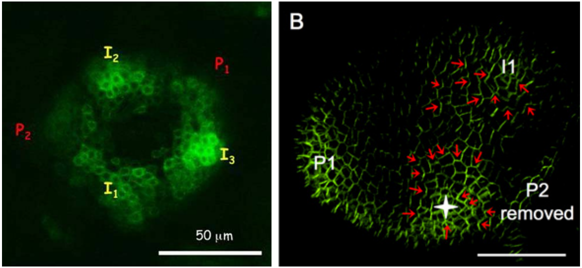
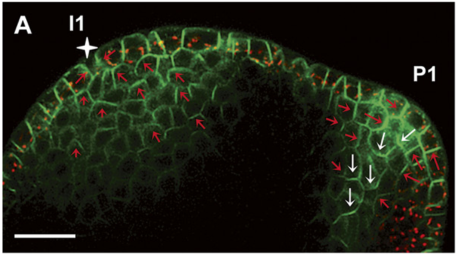
I:Polarization of the auxin flow toward primordia



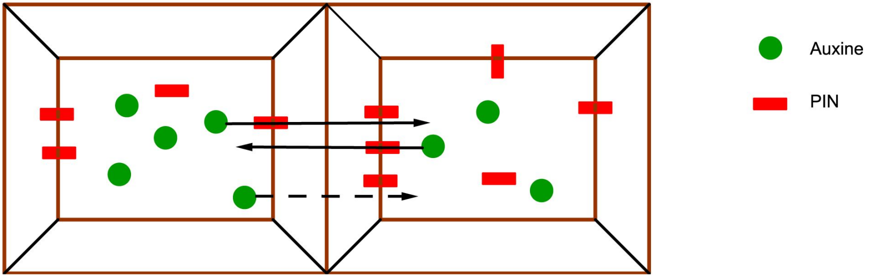
II: Self-organization of the vascular system

In a second step, the primordia must evacuate auxin by initiating the formation of midveins.



Auxin molecules and PIN proteins

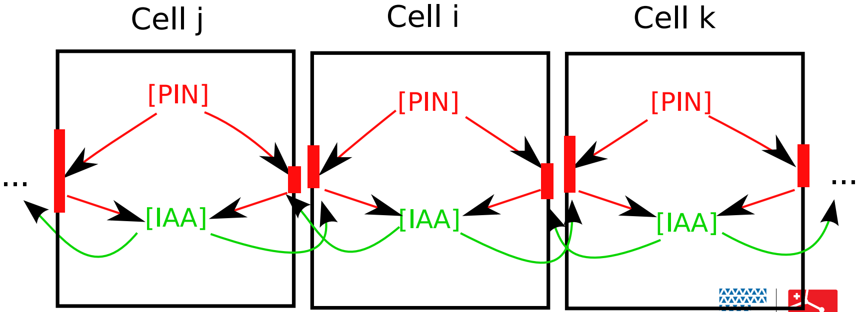
Polarization of the auxin flow and PIN proteins. 7 kinds of PIN proteins.
Graph of cells (arbitrary).



Localisation of auxin molecules and PIN proteins in two neighbouring cells

Concentration based model of the auxin flow

$$\begin{aligned} a_i &= \text{auxin concentration in cell } i \text{ in mol}/m^3 \\ p_i &= \text{PIN concentration in cell } i \\ p_{ij} &= \text{PIN concentration on the membrane of cell } i \text{ facing cell } j \end{aligned} \tag{1}$$



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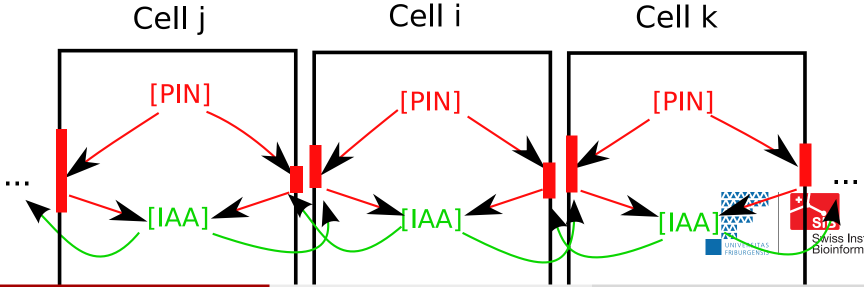
Concentrations based models of auxin active transport

Equations of Jönsson et al. and Smith et al. (2006):

$$\begin{aligned}\frac{da_i}{dt} &= \mu - \nu a_i + D\sum_{k\sim i}(a_k - a_i) + T\sum_{k\sim i}(a_k p_{ki} - a_i p_{ik})\\ \frac{dp_{ij}}{dt} &= \kappa_1 \mathbf{a_j}\, p_i - \kappa_2 p_{ij}\\ \frac{dp_i}{dt} &= \sum_{k\sim i}(\kappa_2 p_{ik} - \kappa_1 a_k p_i) \qquad (2)\end{aligned}$$



Simplified model, self-organization of the auxin flow

Taking adiabatic limit one obtains

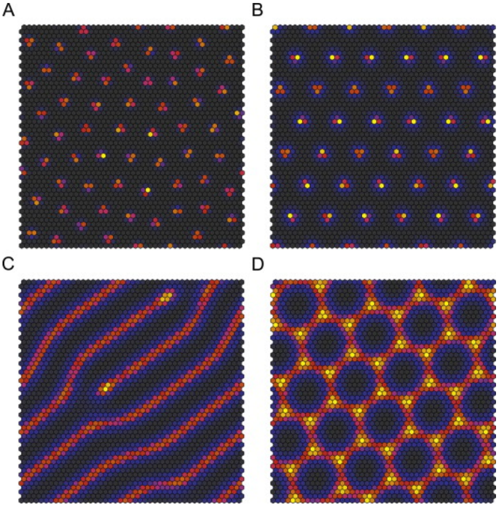
$$\frac{da_i}{dt} = D\sum_{k\sim i}(a_k - a_i) + T\sum_{k\sim i}(a_k P_{ki} - a_i P_{ik}) \tag{3}$$

We will consider a simplified model where

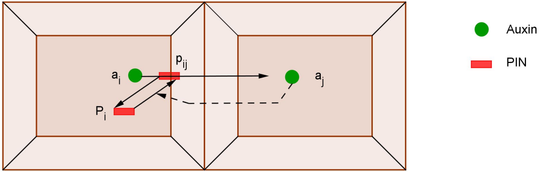
$$P_{ki} = P\frac{a_i}{\kappa + \sum_{j\sim k} a_j}$$

Auxin molecules present in cell *k* move to cells *i* having high auxin concentrations.

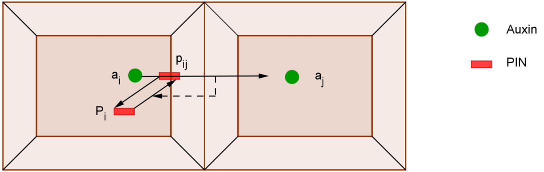
Simulation from Sahlin et al. (2009), hexagonal lattice with diffusion, production and degradation



The concentration-based and the flux models



(a)



(b)

Figure: From Feller and Mazza, PlosOne 2015

Flux-based model of auxin transport (canalization)

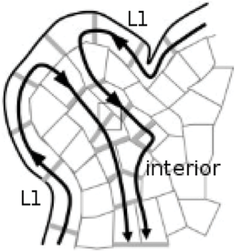


Figure: From Walker, Farcot, Traas and Godin, PlosOne 2013

The flux from i to j is

$$J_{i\to j} = \gamma_D(a_i - a_j) + \gamma_T(a_i p_{ij} - a_j p_{ji})$$

The flux model (simplified model)

$$\begin{aligned}
\frac{da_i}{dt} &= \alpha_a - \beta_a a_i - \frac{1}{V_i}\sum_{j\sim i} S_{i,j}\left(\gamma_D(a_i - a_j) + \gamma_A(a_i P_{i,j} - a_j P_{j,i})\right) \\
\frac{dP_{ij}}{dt} &= \Phi(J_{i\to j}) + \rho_0 - \mu P_{i,j} \\
\Phi(x) &= \mathrm{I}_{x>0}\, x^2 \text{ or } \mathrm{I}_{x>0}\,\frac{x^\eta}{K^\eta + x^\eta}
\end{aligned}$$

Φ **is the nonlinear response function**, which is increasing and non-negative. No PIN insertion ($\Phi(J_{i\to j}) = 0$) when the number of incoming auxin molecules $a_j p_{ji}$ is larger than the number of outgoing auxin molecules $a_i p_{ij}$.

Flux-based model of auxin transport (canalization)

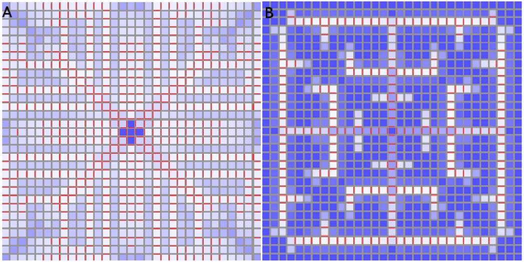


Figure: From Walker, Farcot, Traas and Godin, PlosOne 2013

- There is no consensus at present time for deciding between these two models
- Should be function of the local nature of PIN proteins.

Mathematical analysis

Pattern formation in auxin flux. Feller, C., Gabriel, J-P., Mazza, c. and Yerly F. *Journal of Mathematical Biology* **(68)**:879-909, 2014.

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Simplified model

$$\frac{da_i}{dt} = D \sum_{k \sim i} (a_k - a_i) + T \sum_{k \sim i} (a_k P_{ki} - a_i P_{ik}) \tag{4}$$

where

$$P_{ki} = P \frac{a_i}{\kappa + \sum_{j \sim k} a_j}.$$

This system is conservative, that is,

$$\frac{\mathrm{d} \sum_i a_i(t)}{\mathrm{d}t} \equiv 0.$$

Equilibria when $D = 0$ (no diffusion)

The o.d.e. of interest is of the form

$$\frac{\mathrm{d}\boldsymbol{a}}{\mathrm{dt}} = f(\boldsymbol{a}),$$

with

$$f_i(\boldsymbol{a}) = \sum_{k\sim i}\left(a_k \underbrace{\frac{a_i}{\kappa + \sum_{j\sim k} a_j}}_{=q_{ki}(\boldsymbol{a})} - a_i \underbrace{\frac{a_k}{\kappa + \sum_{j\sim i} a_j}}_{=q_{ik}(\boldsymbol{a})}\right)$$

The related equilibria solve the equation $f(\boldsymbol{a}) = 0$, which can be rewritten as

$$0 = \boldsymbol{a}Q(\boldsymbol{a}),$$

where $Q(\boldsymbol{a})$ is the **Laplace operator associated with a Markov chain**

$$Q(\boldsymbol{a})_{ki} = q_{ki} \text{ and } Q(\boldsymbol{a})_{kk} = -\sum_{i\neq k} q_{ki}.$$

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The equation $\boldsymbol{a}Q(\boldsymbol{a})$ is in fact stating that

$$\boldsymbol{a} = \pi(\boldsymbol{a}),$$

where $\pi(\boldsymbol{a})$ is the invariant measure of the the generator $Q(\boldsymbol{a})$. Similar problems in the theory of reinforced random walks (Pemantle(1992) and various works of Benaïm).

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Lemma: When the graph is connected, the Markov chain is reversible and irreducible, with

$$\pi(a) = \left(\frac{a_i N_i}{Z(a)}\right),$$

where

$$N_i(a) = \kappa + \sum_{k \sim i} a_k,$$

and

$$Z(a) = \sum_i a_i N_i(a).$$

$$a = \pi(a) \quad \Leftrightarrow \quad a_i \equiv \frac{a_i N_i}{Z(a)}$$

$$\Leftrightarrow \quad N_i \text{ does not depend of } i.$$

Let Γ be the adjacency matrix of the graph. Then

$$N_i \text{ independent of } i \Leftrightarrow \Gamma a = c(1, \cdots, 1)^*,$$

for some positive constant c.

General equilibria

$$a_i = 0,\ i \in I,\ \ a_i > 0,\ i \in I^c,\ I \subset \{1, \cdots, L\}$$

induces a sub-graph of connected components g_k. For each such component, let Γ_k be the related adjacency matrix. Then we look for a such that

$$\Gamma_k a\big|_{g_k} = c_k \mathbf{1}\big|_\gamma.$$

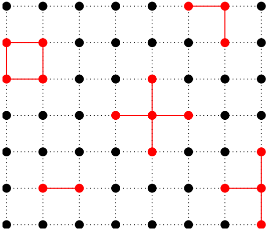
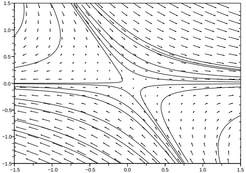
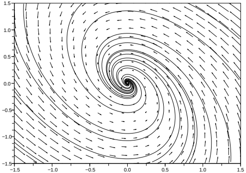


Figure: Black dots correspond to cells i for which $a_i^* = 0$. In red: the various components g_k

Stability





One must check that the eigenvalues of the Jacobian matrix $Df(a^*)$ have negative real parts, where DF is the matrix with entries given by

$$\frac{\partial f_i}{\partial a_j}.$$

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Stability of the equilibria

For any equilibria $a > 0$, the Jacobian matrix is

$$\mathrm{d}f(a) = \frac{1}{N^2}\mathrm{diag}(a)\Gamma(c\mathrm{id} - \mathrm{diag}(a)\Gamma).$$

a is stable when

$$\Re(\lambda) \leq 0 \ \forall\lambda \in \mathrm{Spec}(\mathrm{d}f(a)).$$

Let V_i be the neighbourhood of i. Using spectral estimates for the spectral gap of discrete Laplace operators and Dirichlet forms, we have proven the

Proposition: Assume that the graph is connected, of adjacency matrix Γ, and let a be such that

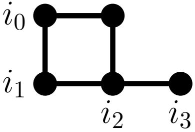
$$\Gamma a = c\mathbf{1},$$

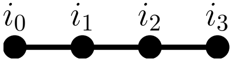
be an equilibrium. a is unstable when there is a path

$$i_0 \to i_1 \to i_2 \to i_3,$$

such both i_2 and i_3 avoid i_0 and its neighbourhood, that is

$$i_k \notin \{i_0\} \cup V_{i_0}, \quad k = 2, 3.$$





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Stable equilibrium configurations

On a rectangular grid, **the stable equilibrium configurations are formed of basic building blocks isolated in a background of auxin depleted cells.** These basic configurations are given by

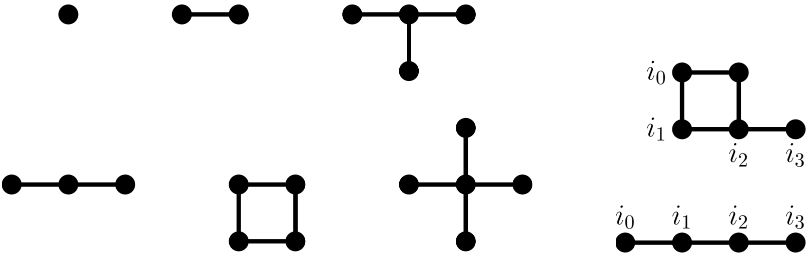


Figure: (a) All possible subgraphs γ of the two-dimensional grid that can potentially yield l-stable configurations. (b) Any configuration $\boldsymbol{a} > 0$ will be unstable on these two subgraphs of the two-dimensional grid

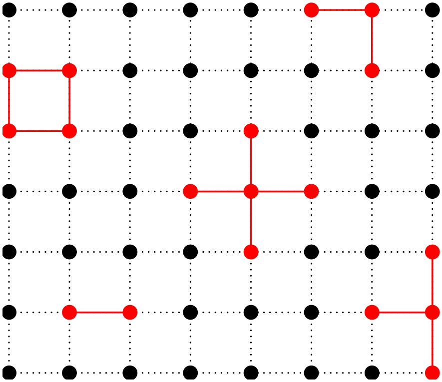


Figure: A potentially stable configuration, with some components g_k (in red) Such stable equilibria do not form geometrically regular patterns.

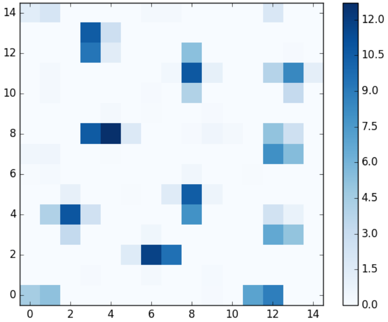
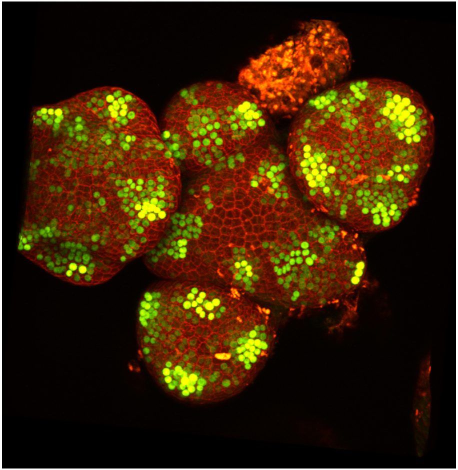


Figure: Simulation of the pure transport process.

Real auxin patterns on a meristem



Stable configurations for small production and degradation

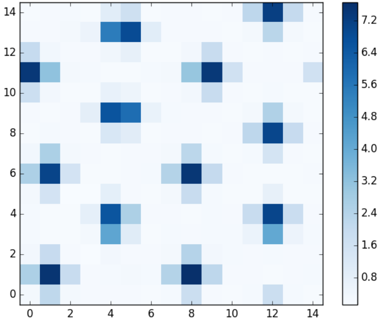


Figure: Stable configurations for small production and degradation rates

Conclusion

- The stable equilibria are composed of basic building blocks that are isolated in a background of auxin depleted cells. For pure transport processes, the stable equilibria do not exhibit geometrical regularities in general.
- Geometrically regular patterns might be obtained by developing mathematical models that include auxin flow and meristem elasticity.

Thank you for your attention !

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Plant Growth in a Changing Environment