Using Variational Calculus to study Pattern Formation in Plants

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1. Introduction

The aim of the project is to understand which mechanisms are responsible for patterns that occur in the placement of leaves and other organs in plants (phyllotaxis). Leaves are usually placed at regular intervals on the stem, with a leaf emerging at sites where the plant hormone auxin accumulates at the meristem (the growing tip of the plant). Our goal is thus to figure out how this regular spacing of leaves is regulated.

Figure 1: Arabidposis leaves: http://commons.wikimedia.org/wiki/File:Arabidopsis_thal_background.JPG

Auxin can move from and to neighbouring cells. One explanation for this is diffusion. Diffusion alone, however, is not enough to describe the full dynamical behaviour of auxin. There are also biological mechanisms at work. The main suspect is a PIN protein.

PIN is mainly located on the cell membrane and functions as an auxin efflux carrier, transporting auxin out of a cell. The flow of auxin due to these pumps depends on things such as the amount of auxin inside the cell and the number of PIN proteins on the cell-membranes.

Several mechanisms have been proposed on how PINs localise to membranes [1]. Here we propose a novel analytic method to explore the patterning capabilities of auxin-PIN dynamical models.
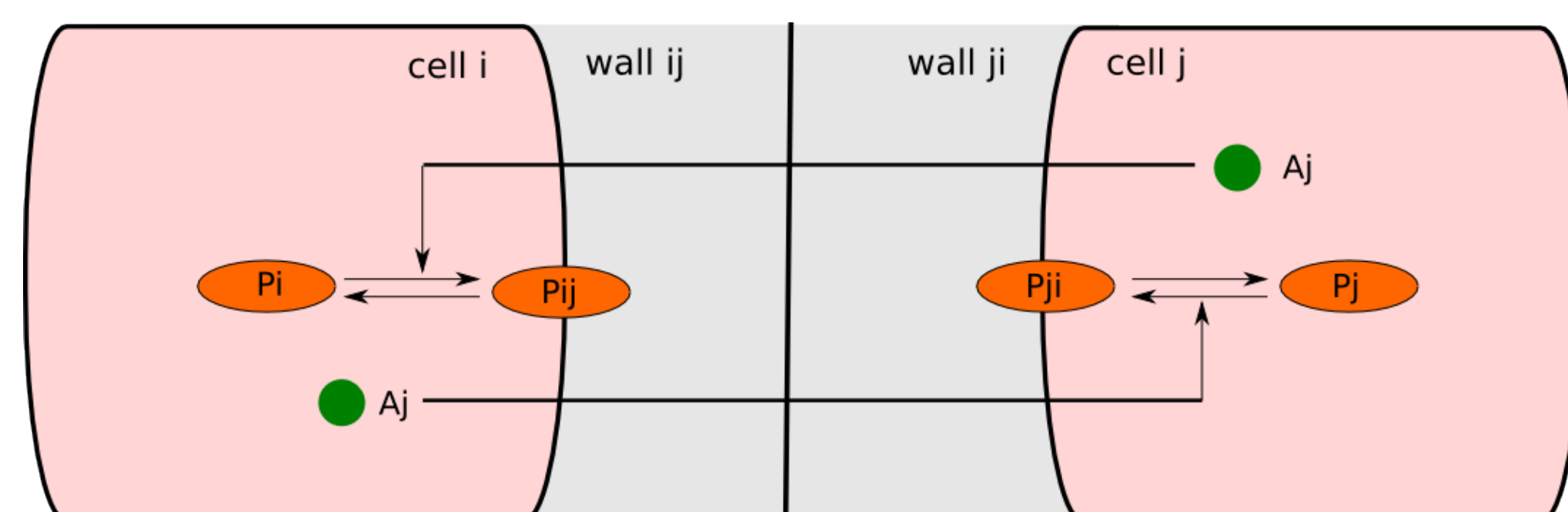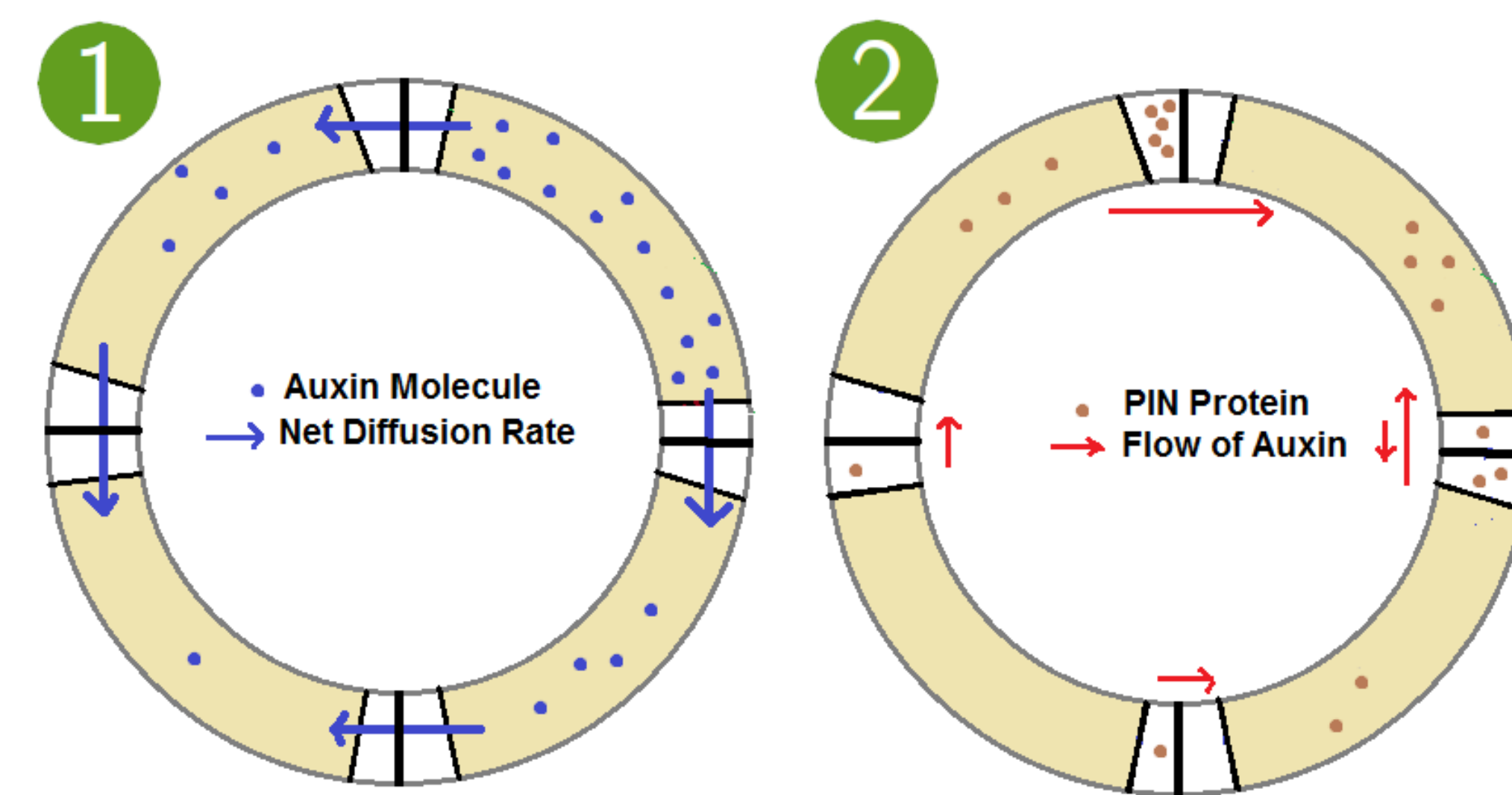

Figure 2: PIN polarisation mechanism: a high auxin concentration in a neighbouring cell enhances the amount of PIN on the membrane [2].

2. Setup

For simplicity we consider a ring of cells. Each cell has on both sides a cell wall and we study the flow of auxin to neighbouring cells, and PIN from the cell to the cell walls and back.

❶ Flow of auxin by diffusion,
❷ Auxin is pumped to neighbouring cells by PIN proteins.

> ### Why is it better?
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> The strength of the method really relies on the fact that in the continuum limit all noise vanishes. In a linear stability analysis we cannot make use of this property, since all the hard work has to be done before we can take a continuum limit.

4. How it should (can) be done

The idea is to consider a smooth distribution of auxin and to formulate the dynamical system in terms of a *Lagrangian* with potential V. This is usually not possible for systems that lose energy, such as ours. However, when we restrict the description to small regions around the fixed points, we can still extract all information of the system that is useful to us.

- Fixed points are found by setting $\delta V = 0$.
- Stability is determined by the sign of the second variation $\delta^2 V$.
- The frequency function for which $\delta^2 V$ attains its (global) negative minimum approximates the number of peaks of a non-trivial stable solution.

3. How it is usually done

These processes are modelled by a coupled system of differential equations of the form

$$\frac{dA_i}{dt} = f_i, \qquad \frac{dP_i}{dt} = g_i, \qquad \frac{dP_{ij}}{dt} = h_{ij}.$$

Here A and P_i stand for the auxin and PIN concentration in cell i respectively, and P_{ij} is the PIN concentration in the cell wall attached to cell i, pointing towards cell j.

- First, we look for fixed points. These are found by solving $f_i = g_i = h_{ij} = 0$.
- Then we do a linear stability analysis. The signs of the eigenvalues of the Jacobian tell us whether a solution is (un)stable.
- The frequency of a non-trivial auxin distribution is approximately given by the maximum positive eigenvalue of the Jacobian at the homogeneous solution.

5. Why does it work?

The method is very messy and there are many terms to consider. Since we are working in the continuum limit, however, a lot of these contributions can be ignored. In fact, we can show that only one term is really relevant and that all others act as small irrelevant perturbations. Figure 3 illustrates this.
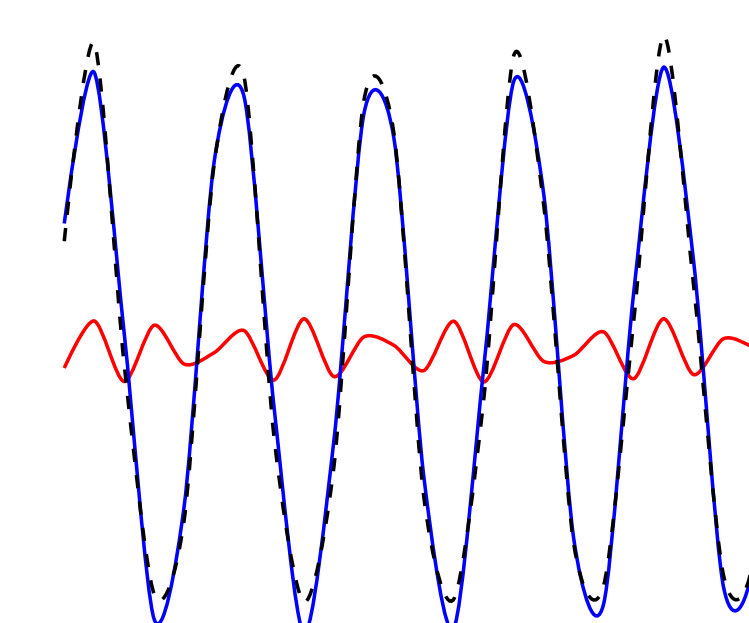

Figure 3: In the continuum limit all terms (the red line) but one (the blue line) can be ignored.

6. Results

We applied the new method to a model that was studied in [2] with a linear stability analysis. This leads us to the following conclusions.

> ### Conclusion
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> - The stability constraints agree.
> - The estimated number of auxin peaks is approximately the same.

We expect the method to prove particularly useful in multi-variable models.

References

[1] K. van Berkel et al. "Polar auxin transport: models and mechanisms." In: *Development* 140.11 (2013), pp. 2253–68.

[2] H. Jönsson et al. "An auxin-driven polarized transport model for phyllotaxis." In: *Proceedings of the National Academy of Sciences of the United States of America* 103.5 (Jan. 2006), pp. 1633–8.

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Acknowledgements