An auxin transport model for regulation of plant organ initiation

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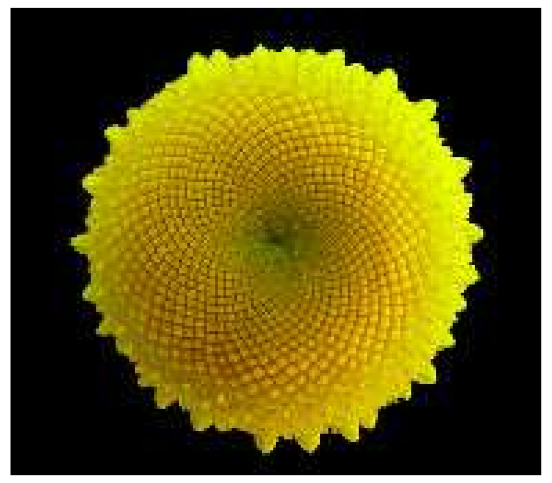
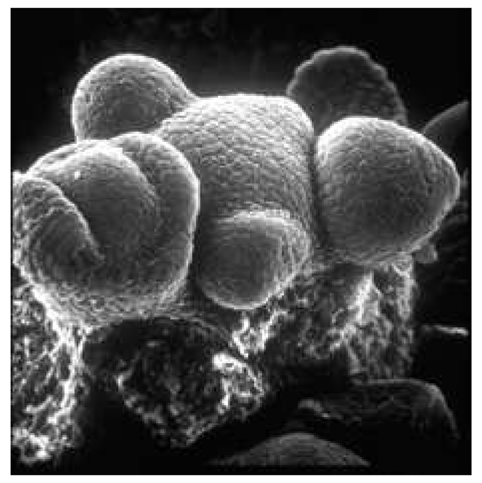
Plant organs, such as leaves and flowers, are initiated at the shoot apex resulting in regular patterns called phyllotaxis. These patterns have long inspired scientists due to their high symmetry and their connections to classical mathematics. Recently, ever more detailed molecular experiments have revealed that auxin and its polarly located efflux mediator protein PIN1 are at the heart of the pattern forming mechanism. We present a computational model, based on feedback between auxin and PIN1 localization, which bridges the gap between modeling and molecular experiments.

Plant phyllotaxis

Plant organs are initiated in a very regular fashion leading to symmetric phyllotactic patterns. Typical patterns are spiral, pairwise, opposite, and whorled. We primarly study the model plant *Arabidopsis*, where new leaf and flower primordia form at the flank of the shoot apical meristem (SAM) in a spiral pattern.





It has been shown that spiral patterns naturally occur given three mechanisms. First a mechanism leading to a **minimal spacial distance** between primordia. Second, a radially symmetric **initiation zone** as the peripheral zone in the SAM. Last, **tissue growth** such that older primordia moves away from the apex.

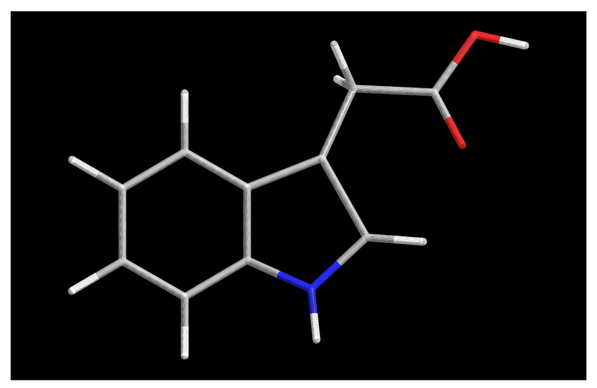
Mathematical symmetry

- **Golden ratio** The angle between consecutive primordia is often close to 137.5°, which corresponds to the division of the circumferece according to the golden ratio.
- **Fibonacci sequence** The number of visible spirals (parastichies) in opposite directions are often two consecutive numbers in the Fibonacci sequence (1, 1, 2, 3, 5, 8, 13, ...)

Molecules involved

The model is based on polarized auxin transport mediated by PIN1, together with unpolarized transport including both passive membrane transport as well as transport mediated by AUX1.

- **Auxin** The plant hormone auxin is involved in many aspects of plant development. At the shoot apical meristem, auxin is transported to the positions of new primordia.
- **PIN1** The family of PIN proteins mediates polarized auxin transport in different plant tissues, where PIN1 is most important for phyllotaxis as a knockout creates a pinformed plant.
- **AUX1** AUX1 is included in a family of proteins and has been shown to mediate auxin influx to the cells.

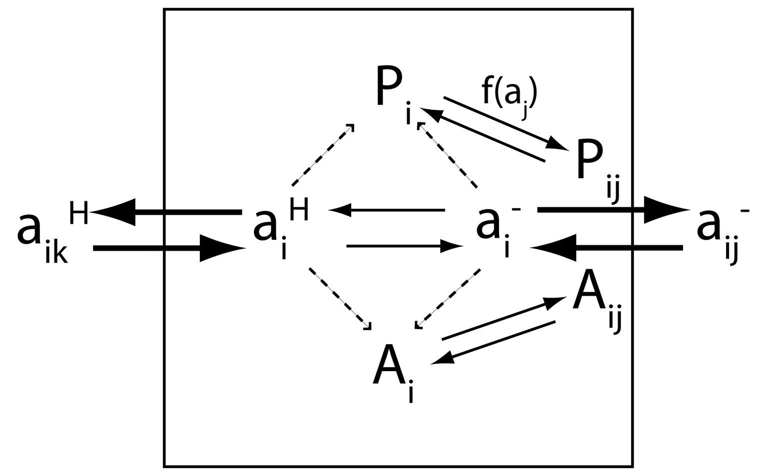


The model

A model environment is developed that allows for simulation of plant shoot development at a cellular resolution including cell growth and proliferation, mechanical interactions, gene regulatory networks, and molecular reactions and transport.

Auxin transport model

Central for phyllotaxis is an auxin pattern mechanism, where the new primordia appear at auxin peaks. Data indicates that PIN1 polarizes towards young primordia and positions where new primordia are about to form. Our main hypothesis is a feedback from auxin in neighboring cells to PIN1 cycling rates leading to a PIN1 polarization towards neighboring cells with higher auxin concentration. The model is based on the chemiosmotic transport theory, where auxin is passively transported through membranes while its anion transport is mediated by PIN1 and AUX1. Experimental estimates are used for most model parameters.



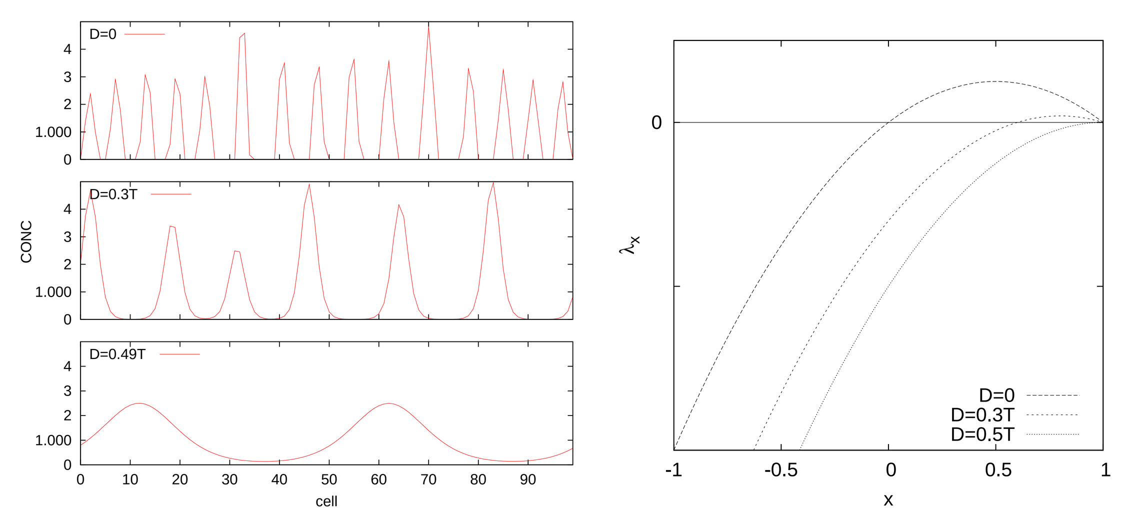
$a^H(a^-)$ - auxin (anion) concentrations
$P(A)$ - PIN1(AUX1) concentrations
Solid arrows denote auxin transport and protein cycling. Dashed arrows denote transcriptional regulation.

Pattern formation

This polarized transport network is capable of spontaneously creating peaks and troughs in auxin concentration. The distance between auxin peaks is determined by model parameters (Figure below). A simplified model is described by

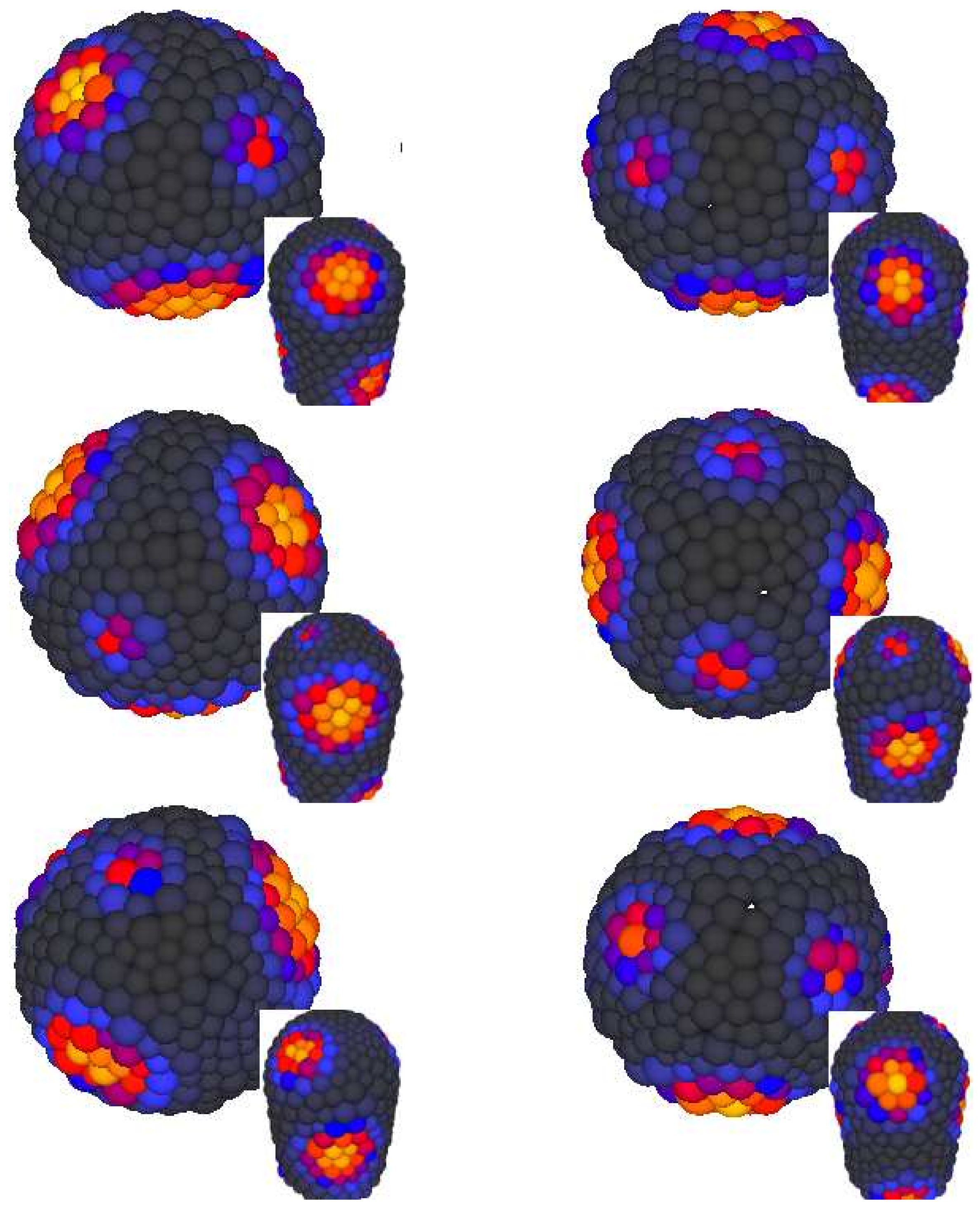
$$\frac{da_i}{dt} = D\sum_{k\in\mathcal{N}_i}(a_k - a_i) + T\sum_{k\in\mathcal{N}_i}(P^*_{ji}\frac{a_j}{K_a + a_j} - P^*_{ij}\frac{a_i}{K_a + a_i})$$

$$P^*_{ij} = \frac{k_1 a_j P_i^{tot}}{k_2 + \frac{k_1}{|\mathcal{N}_i|}\sum_{k\in\mathcal{N}_i} a_k}$$



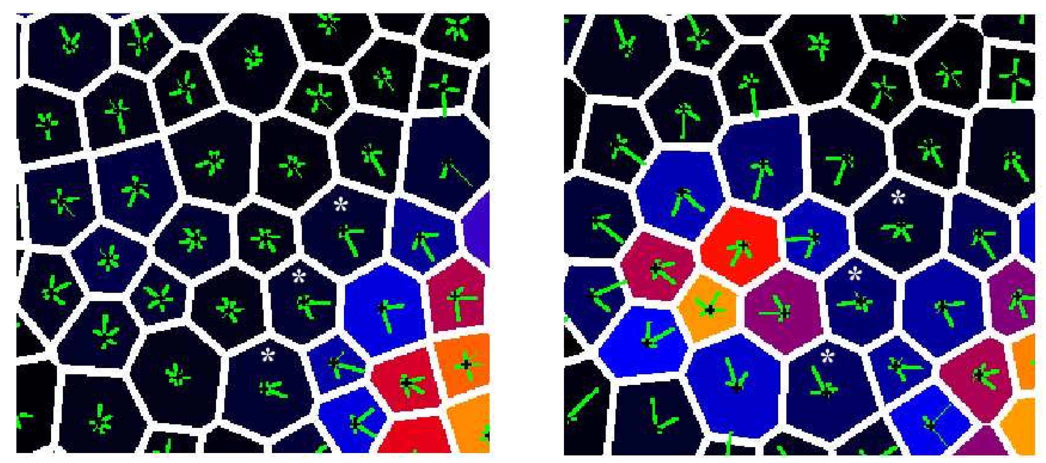
Phyllotaxis simulations

A simple cell growth/division and mechanical model is included with the molecular model to produce a phyllotaxis model capable of producing spiral and other patterns on a growing epidermal tissue.



PIN1 reversal

An important experimental finding is that the PIN1 polarity in individual cells reverses its direction as new primordia are formed. This behavior is mimicked in the simulations.



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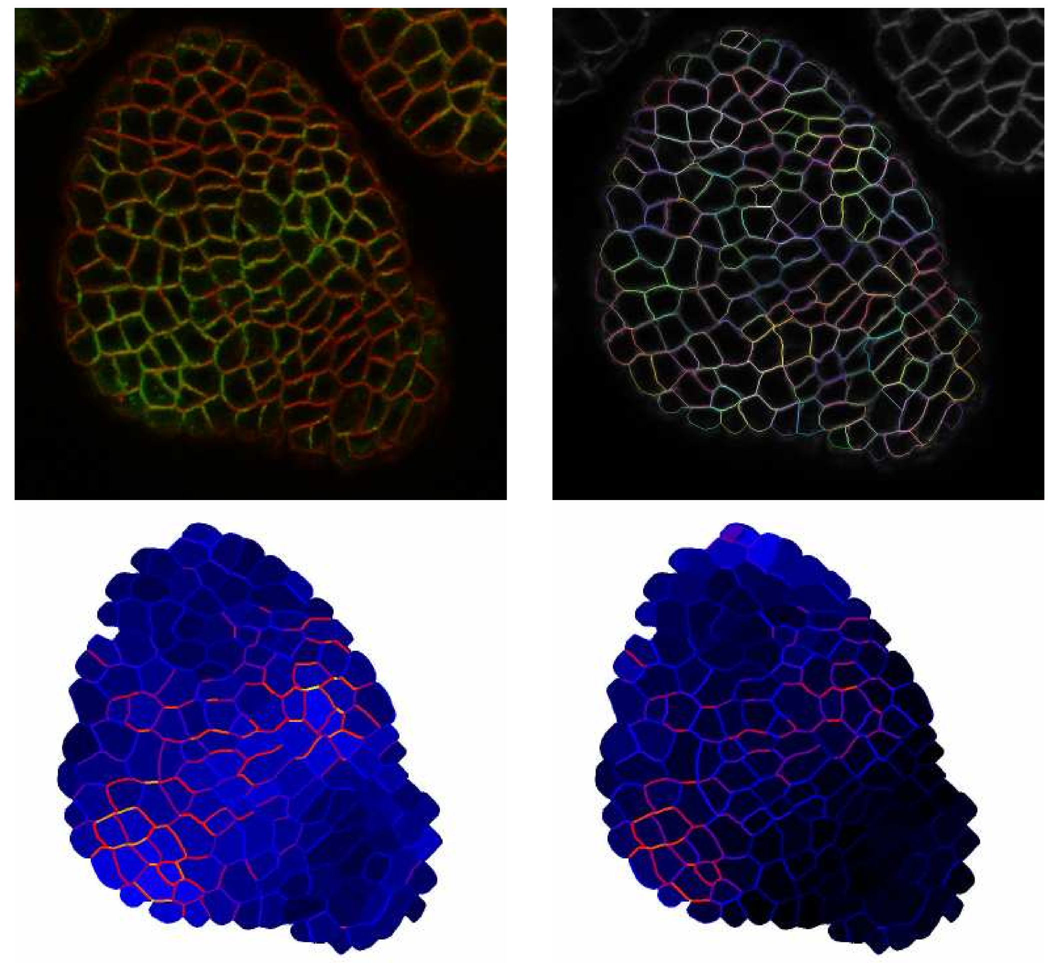
GFP data from living plants

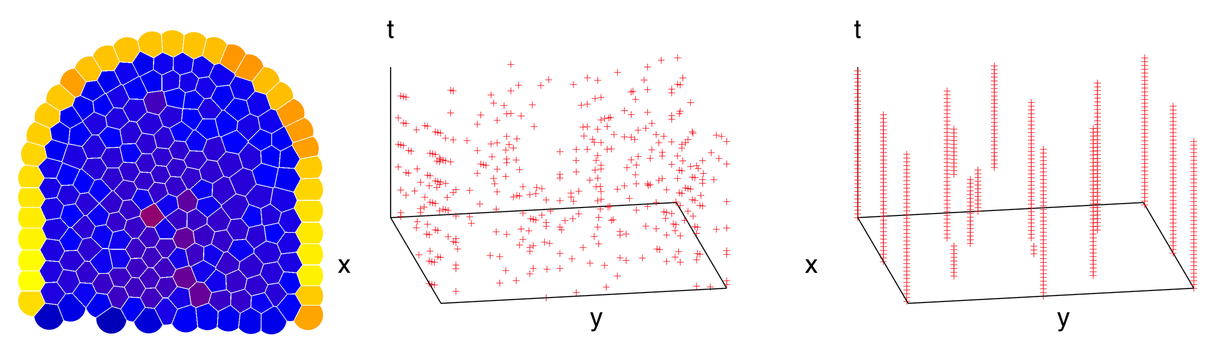
PIN1 localization is extracted from an experimental template of confocal images.



Top left shows pPIN1::PIN1-GFP data. Top right shows extracted walls. Bottom left shows extracted PIN1 intensities in cells and membranes. Bottom right shows equilibrium auxin concentrations from model simulation using extracted PIN1 as input.

AUX1 and auxin-induced transport mediators

Simulations show that AUX1 is important for keeping the auxin in the epidermal cell layer (left) as well as for pattern robustness when the known mechanism of auxin-induced transport mediators is included in the model (right).



Conclusions

- A morphogen model based on polarized transport and a local cell-neighbor feedback leads to a global patterning mechanism. The model agrees with current molecular data for auxin and PIN1.
- Together with a growth and mechanical model, simulations lead to phyllotactic patterns.
- The inclusion of the influx carrier is important for keeping the auxin in the epidermal layer and can act as a stabilizing factor.

References

Jönsson, H, Heisler, MG, Shapiro, BE, Meyerowitz, EM, and Mjolsness, E. (2006) *PNAS* **103**:1633-1638.