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# Understanding phyllotaxis by building a quantitative atlas of SAM development

A parametric active 4D model for the automatic construction of developmental atlases from confocal images of shoot apical meristems

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## Phyllotaxis as self-organized patterning of organs at the shoot apical meristem: the Inhibitory Field theory

Shoot apical meristem  
Stem cell niche producing lateral organs

**The inhibitory field model of phyllotaxis** (Douady & Couder, 1996)

- Radially moving organs generate an inhibition that sums into a spatial field
- New organ primordia emerge on a central circle, at local minima of inhibition

Center/Organ size ratio controls the type of phyllotaxis

## Quantifying auxin dynamics in the SAM to understand patterning

**Auxin (hormonal signal)**  
Natural candidate for biological inhibition

- Needed to trigger organogenesis
- Depleted by transport around organs

17 SAM sequences (0h – 4h – 8h)

Time-lapse confocal imaging of ratiometric negative auxin reporter **r2DII** (Weijers, 2014)  
Automatic reconstruction of 2D continuous maps of epidermal auxin signal from images

Reference channel

Signal channel

Detected nuclei

Quantified L1 signal

L1 auxin map

## Automatic 3D nuclei detection and signal quantification pipeline

3D confocal microscopy image stacks (0.5x0.5x1µm voxels)  
Cell nuclei detected as spherical blobs of typical size

- Local maxima in 3D Gaussian scale-space ( $\sigma$  from 0.8 to 1.4µm)

**Method evaluated on expertized SAM images**

- **Precision > 0.98, Recall > 0.95**

Estimate signal intensity on nuclei points

- Gaussian-weighted average of image intensity
- Ratiometric quantification Signal/Reference

Automatic labelling of L1 nuclei

- Epidermis (implicit) surface mesh reconstruction
- Distance-based selection of detected nuclei

## How to aggregate all the information from different time sequences into a single developmental atlas?

**A 3D cylindrical referential for the SAM**

Dome as the tip of a long ellipsoid

- Position of the apex + main vertical axis

Organs as spheres arranged in spiral

- Radial axis: direction of the last organ
- Angular axis: orientation of the spiral

Project data into this common frame  
( $r, \theta, Z$ ) coordinates of all points

**Spatio-temporal registration method: fitting a 4D parametric SAM shape model**

**Regular patterning**  
Natural common shape

**Spiral phyllotaxis**  
Spatio-temporal periodicity

Phyllotaxis-based meristem shape model with few parameters

- **6 parameters** for the dome, **2 parameters** for the organ referential
- **1 developmental time parameter** controls organ parameters ( $r, \theta, Z, R$ )
- Assuming regular "golden" divergence angle:  $\theta_{i+1} = \theta_i + \phi \cdot \psi$
- **Time periodicity of 1 plastochron** (gap between consecutive organs)
- Manual measures on images to fit phyllotactic laws of development

$r(\tau) = r_0 e^{\omega \tau}$

$Z(r) = Z_p + \zeta(r - \rho)^2$

$R(r) = R_0 e^{\alpha r}$

Deformable shape that defines a cylindrical referential and is indexed by (developmental) time

## Parametric active model optimization: energy minimization by gradient descent in the parameter space

Optimize the shape model on the whole registered sequence point cloud

Energy functional with a classical formulation: **external + internal terms**

$$E(\mathcal{M}, \mathcal{P}) = \omega_{ext} E_{ext}(\mathcal{M}, \mathcal{P}) + \omega_{int} E_{int}(\mathcal{M})$$

Evaluated on a voxel grid

- External energy measures the fit to points: maximize the total density inside the model
- Internal energy constrains the model shape: minimize the deviation from a vertical axis

Energy minimization by **iterative variation** of the model parameter values

- Compute the energy variation associated with moving each parameter in both directions
- Amplitude of variations and change probability controlled by a cycling temperature
- Orientation is set manually but could be optimized (separately from other parameters)

Possible **local optimization** of organ parameters afterwards (same energy)

**Directly transform nuclei points into the 3D SAM referential & index the sequence by developmental time**

**Evaluation of SAM model**

Expertized meristem organs  
Inexact young organ distance  
High angular precision  
**Uncertain center positioning**

## Aligned SAM maps of L1 auxin

## Average dynamics of auxin in primordium development: formation of an "inhibitory field" in the peripheral zone only

**Formation of an auxin maximum from the center**

- Constrained by older organs (depletion zone)

**Appearance of a very focused auxin minimum**

- Acting in the peripheral zone during 2-3 plastochrons

**Directional inhibition (central ring) not isotropic**

**Perspectives of improvement & further developments**

- Measure local spatio-temporal correlations of auxin & growth
- More accurate dome center location using CZ marker (**CLV3**)
- Better estimation of developmental time using auxin itself?