

# Control of the kinematics of wood formation by a morphogenetic gradient

**Félix Hartmann<sup>1,2</sup>**, Cyrille Rathgeber<sup>1</sup>, Meriem Fournier<sup>1</sup>,  
Bruno Moulia<sup>3</sup>

<sup>1</sup>Institute for Plant Sciences, University of Bern

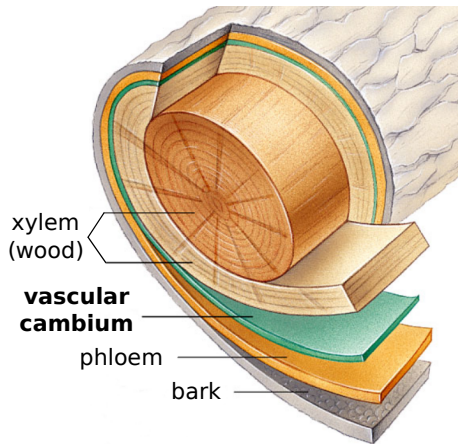
<sup>2</sup>LERFoB, AgroParisTech / INRA Nancy

<sup>3</sup>PIAF, Université Blaise Pascal / INRA Clermont-Ferrand

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# The vascular cambium, a meristem responsible for wood formation



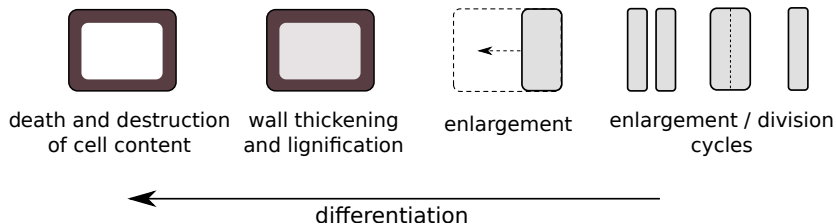
The vascular cambium produces two tissues:

- phloem, which conducts ascending sap
- xylem, which conducts descending sap

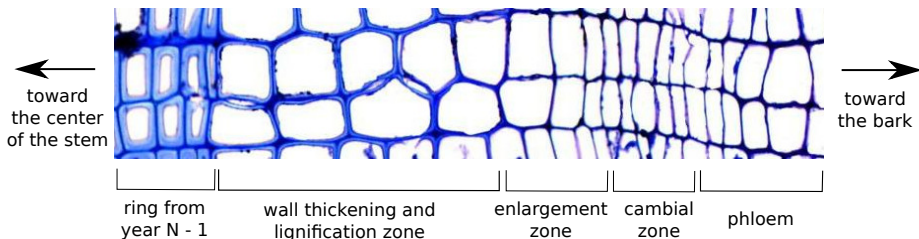
The seasonal formation of xylem results in a succession of tree-rings.

# Differentiation of cambial cells into tracheids

Several phases of differentiation:



Zonation in the developing xylem:



# The cell flow and its coordination

## Continuum mechanics point of view

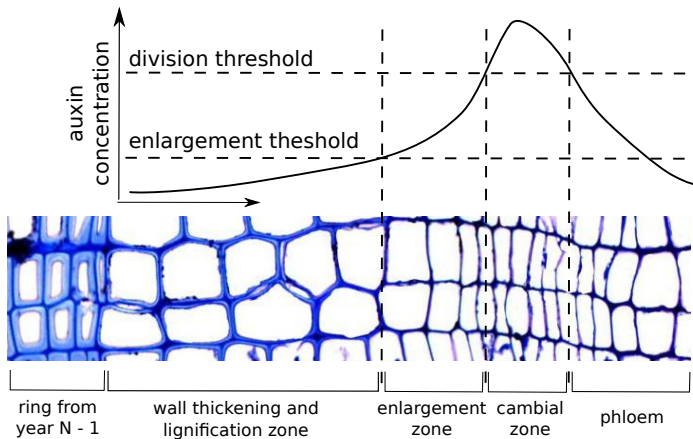
Cell enlargement causes movements in the developing tissue, with a complex kinematics.

## Major issue

The cell flow has to be coordinated at the tissue scale in order to regulate the growth and produce the anatomical structure of the tree-ring.

# Coordination via biochemical signals

A graded concentration profile of auxin has been measured in wood-forming tissue. It has been hypothesized that this gradient provides a positional information to the cells:



From Bhalerao and Fischer (2014).

## Central hypothesis

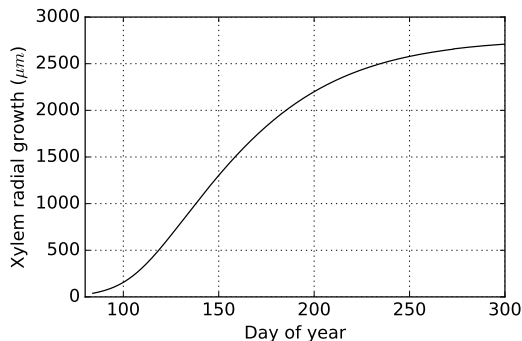
A concentration gradient of some biochemical signal provides enough information to guide the development of the tissue and produce the final anatomical structure observed.

Several candidate signals:

- auxin (the most often mentioned);
- peptides (e.g. TDIF);
- cytokinins;
- ...

# Observable 1: Seasonal dynamics of xylem radial growth

According to data from Michelot et al. (2012):



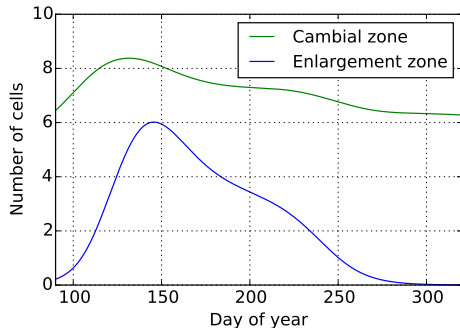
After an initial phase of exponential growth, the radius increase becomes linear, then slows down until final arrest.

## Question 1

Can a morphogenetic gradient control the radial growth and curb the exponential divergence?

## Observable 2: Number of cells in each developmental zone

Using core samples, it is possible to obtain the average trend in cell number in each zone.



Rapid increase in cell numbers at the beginning of the growing season, then progressive decrease.

From Cuny et al. (2013).

### Question 2

Can a morphogenetic gradient control zonation and its trend through the growing season?



## Observable 3: Anatomical structure of a tree-ring formed

Fully-formed tree-rings have a characteristic anatomical structure:

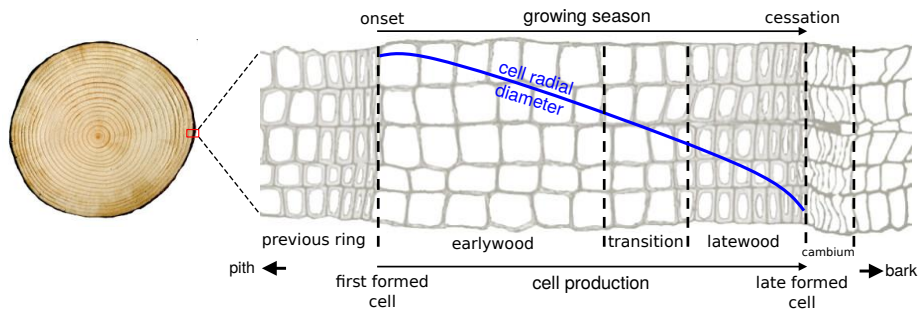


Illustration adapted from Cuny et al. (2014).

⇒ large cells in earlywood / narrow cells in latewood

### Question 3

Can a morphogenetic gradient account for the tree-ring structure?

# CoXyS (*Conifer Xylogenesis Simulator*)

## Objectives and core principles

### Objectives

- Assessing the morphogenetic-gradient hypothesis.
- More broadly, unveiling the kinematics of wood formation.

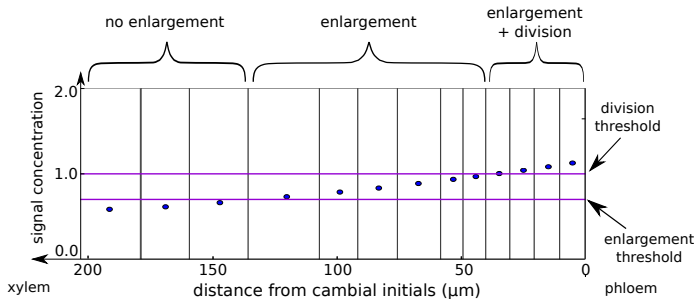
### Core of the CoXyS models

- basic unit = cell
- a single radial file of cells is considered
- the signal enters the file from the phloem side

Two possible kinds of signal transport:

- diffusion in the cell walls (e.g. TDIF peptide)
- polar active transport (e.g. auxin)

# CoXyS core: cell identity and enlargement



Signal concentration in a cell (blue dots) defines its identity:

- if concentration  $>$  division threshold, the cell can enlarge and divide;
- between the two thresholds, the cell enlarges without dividing;
- below the enlargement threshold, the cell does not enlarge.

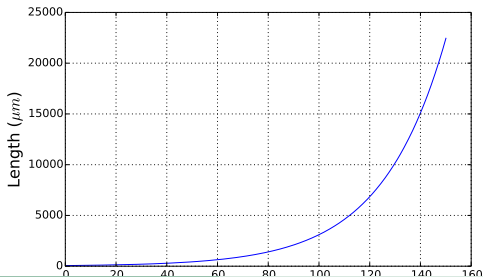
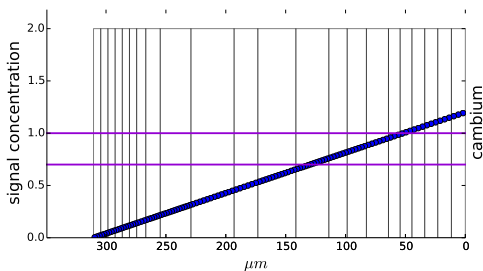
The enlargement rate of a cell is proportional to its concentration of signal. If a cell has an identity that allows division, it divides when it reaches twice its initial diameter.

# Diffusible signal which is not absorbed nor diluted

We assume that the signal

- is not absorbed by the tissue
- diffuses fast enough so that dilution due to growth is negligible

Concentration is held fixed at both endpoints. The profile remains linear, but becomes flatter and flatter as the file is growing. This leads to an exponential growth (positive feedback).

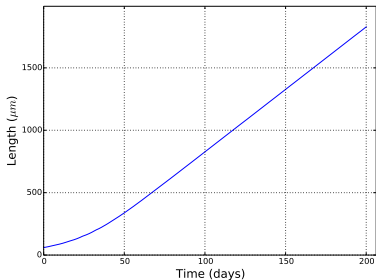
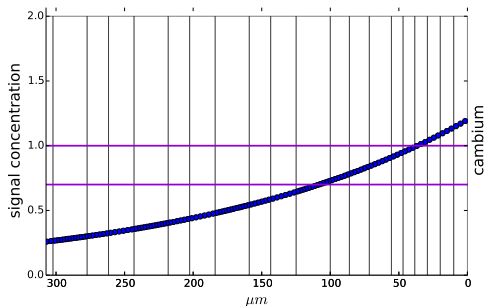


# Diffusible signal which is absorbed, but not diluted

- dilution is still neglected
- the signal is absorbed by the tissue

The concentration profile reaches a steady state, with an exponential shape.

After an initial exponential phase, the growth of the file reaches a constant speed.

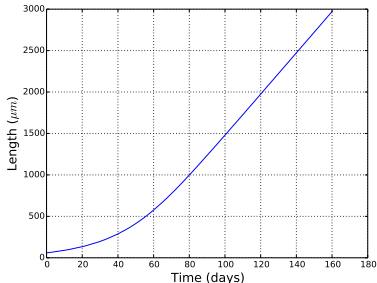
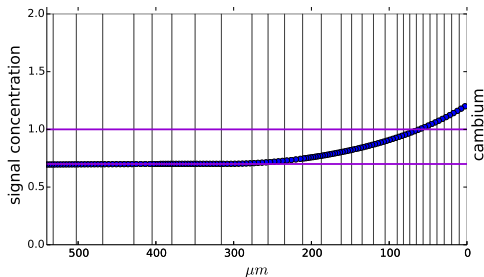


# Diffusible signal which is not absorbed, but diluted

- dilution is no longer neglected
- the signal is not absorbed by the tissue

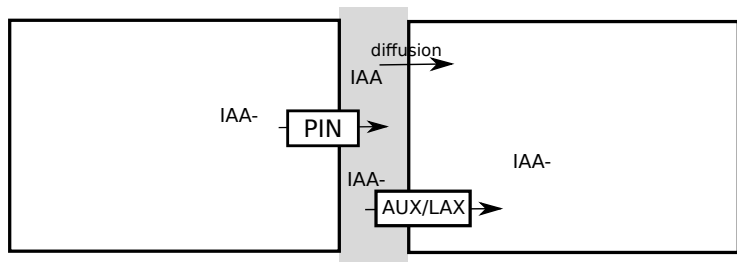
Where cells are enlarging, the concentration profile reaches a steady state, with an approximate exponential shape.

Again, the growth of the file reaches a constant speed. The growth curbs itself through dilution (negative feedback).



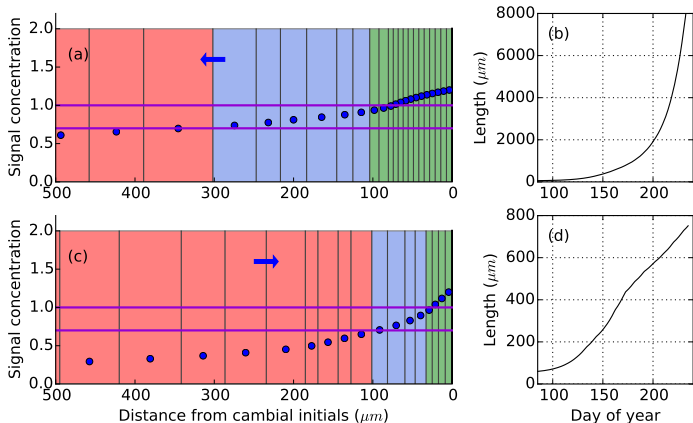
## Polar transport of auxin

Auxin transport from one cell to another relies on special carriers (PIN and AUX/LAX).



The non-uniform distribution of PIN proteins on the membrane makes auxin transport polar.

# What if polar transport is involved?

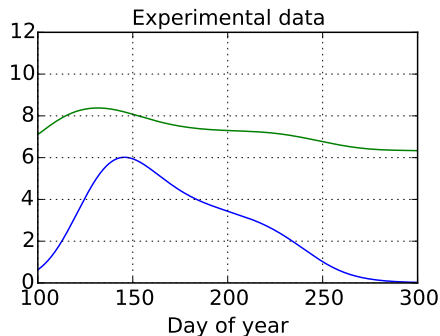
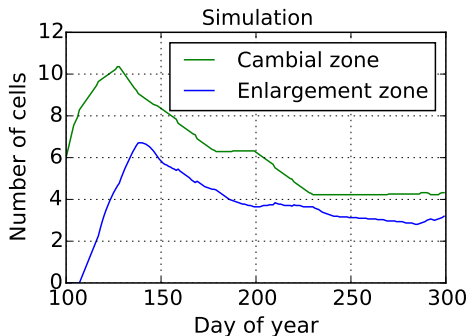


- Carriers oriented toward the xylem (a): the signal accumulates and the growth is exponential.
- Carriers oriented toward the cambium (c): the concentration profile reaches a steady state and the growth is under control.



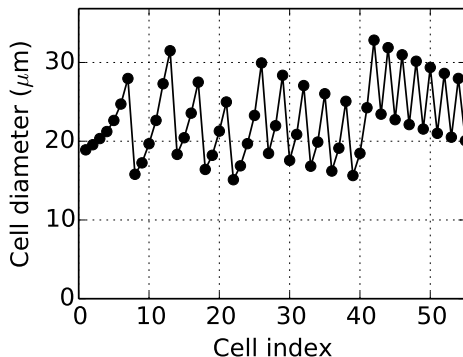
# Simulating the variations in cell numbers through a season

By tuning the absorption rate through a whole season, we could reproduce most of the trends observed:



# Simulated cell sizes

Cell sizes of a tree-ring obtained from a simulation with a realistic zonation:



- no difference between earlywood and latewood
- cell size oscillations

## Back to the morphogenetic-gradient hypothesis

- 1 Control of growth dynamics: **yes** (except for the progressive arrest at the end of the growing season).
- 2 Control of the zonation: **yes**.
- 3 Control of the anatomical structure: **no**.

## Next move

Going beyond the morphogenetic-gradient hypothesis, but still with a kinematic approach.

Thank you for your attention!



Max Ernst, *They have slept in the forest too long*

# References

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