Auxin regulated polarity in Populus and Arabidopsis

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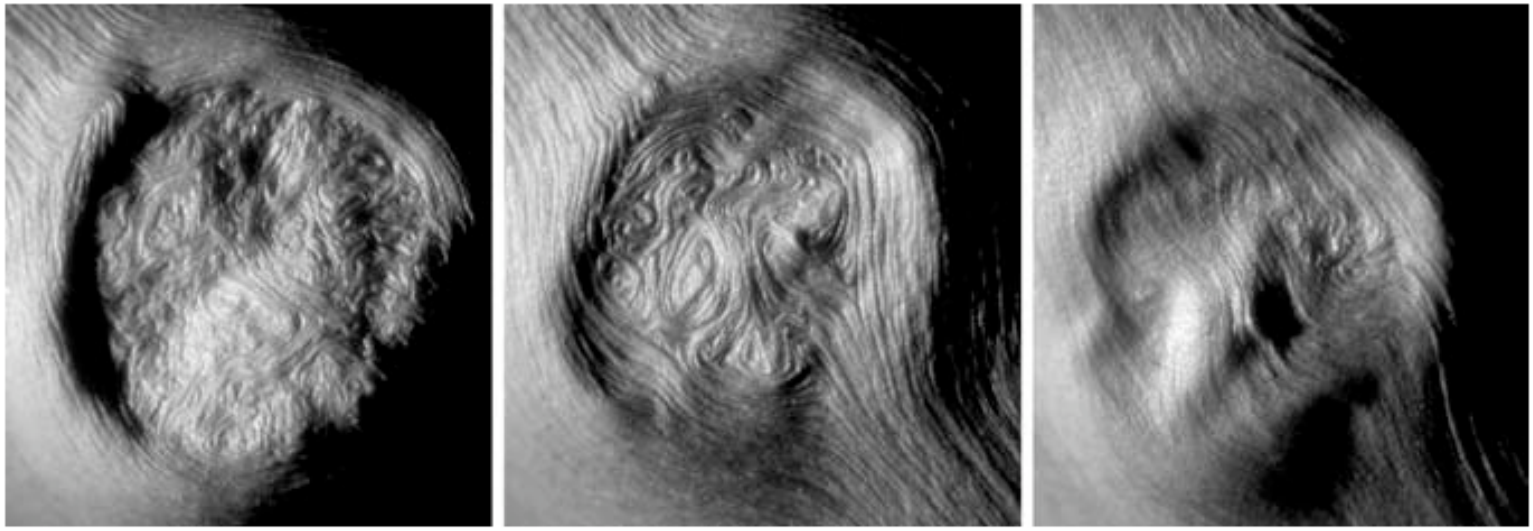
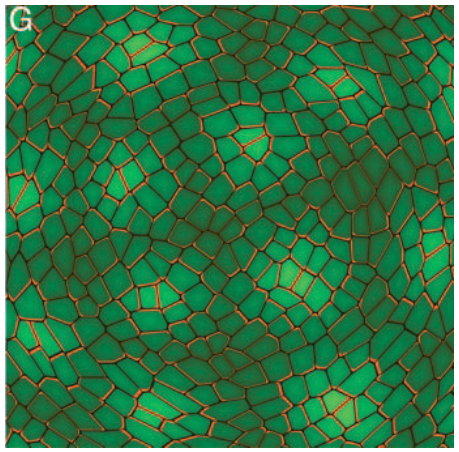
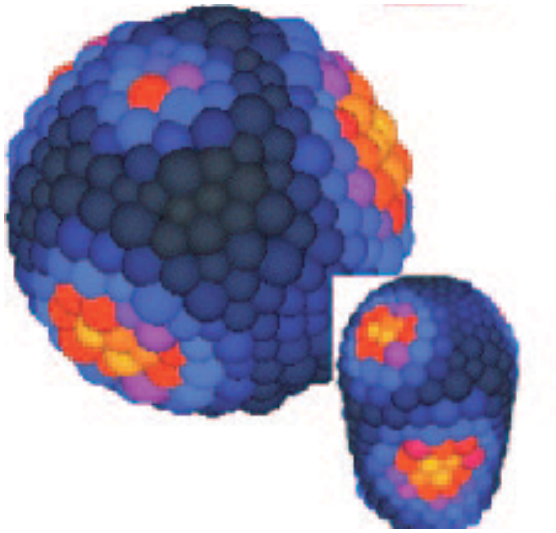


Examples

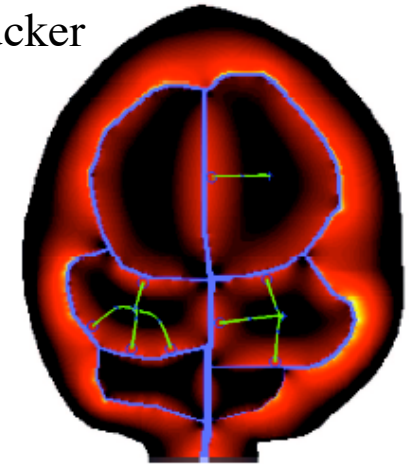
Smith et al. PNAS 2006



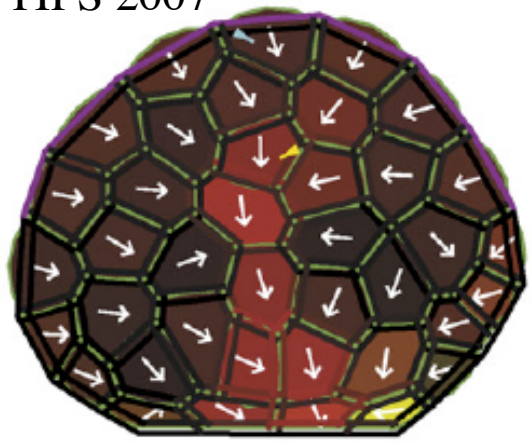
Jonsson et al. PNAS 2006



Dimitrov & Zucker
PNAS 2006

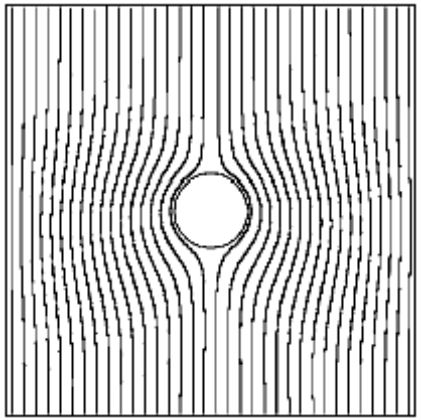


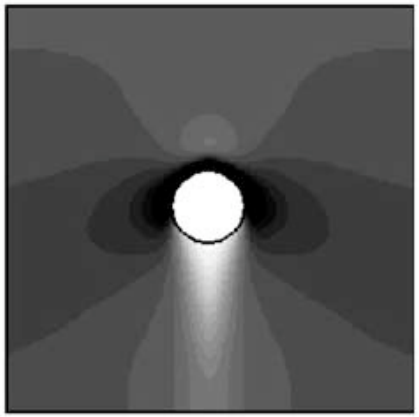
Merks et al. TIPS 2007

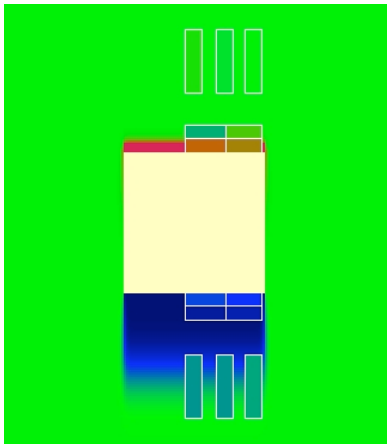


A talk in two parts

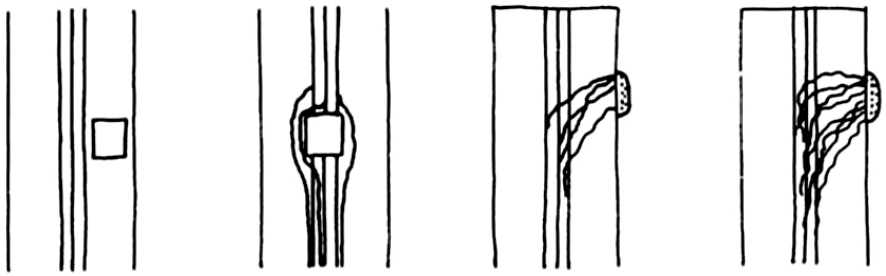
Wood grain patterning

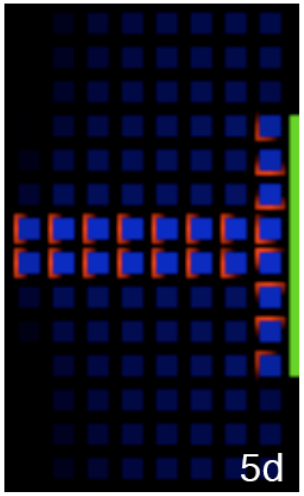




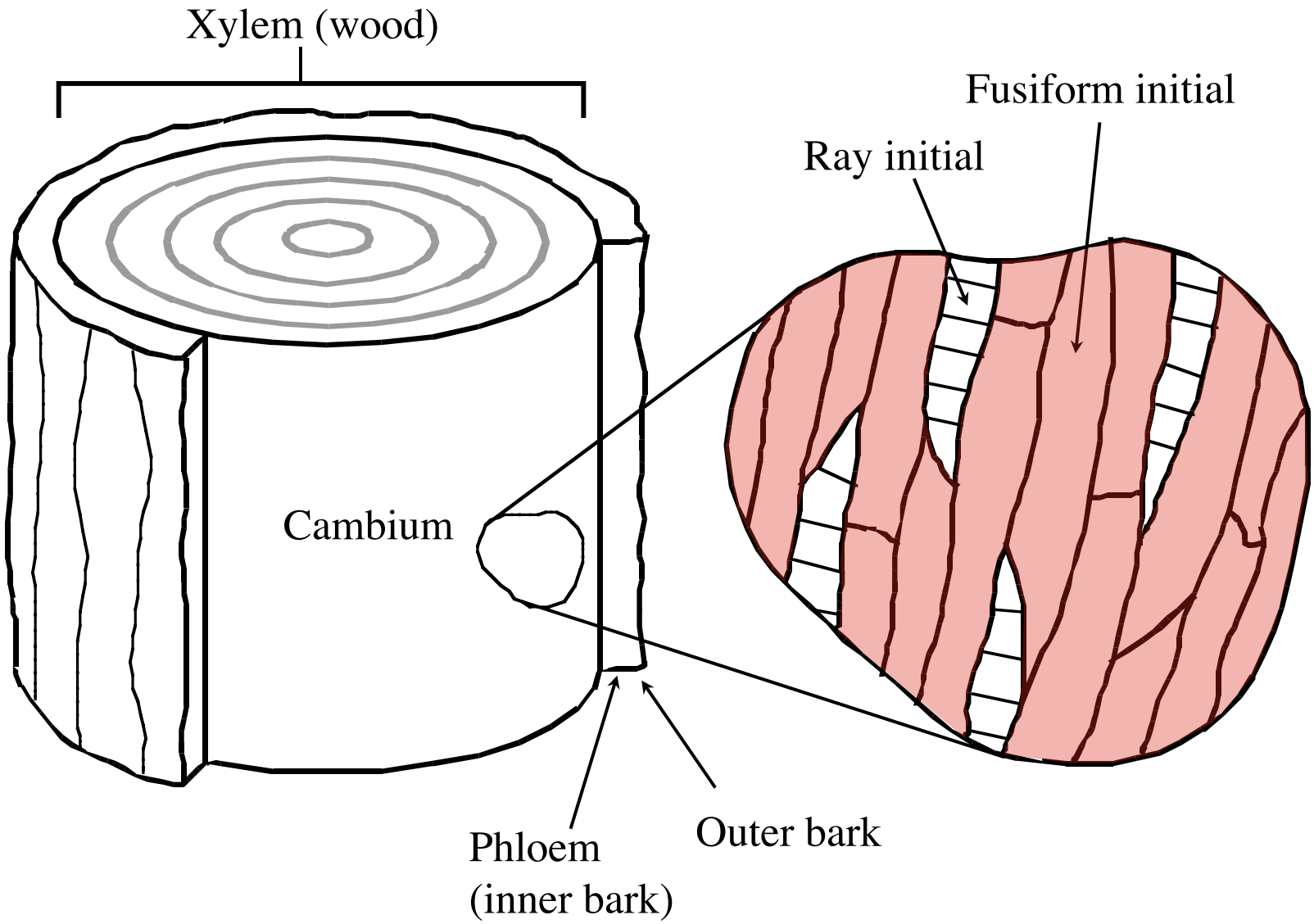


Vascular regeneration/auxin canalization

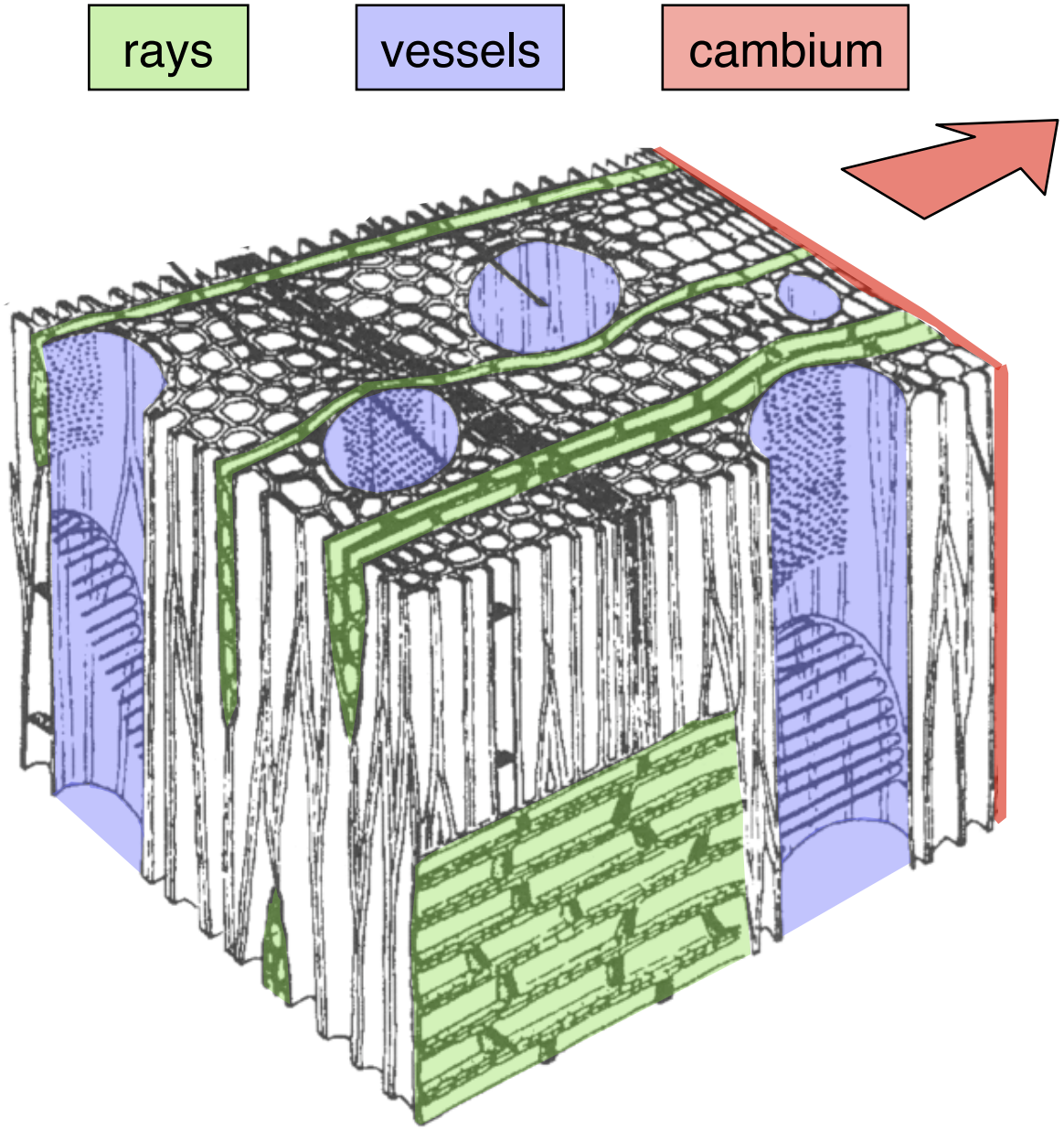




Stem anatomy

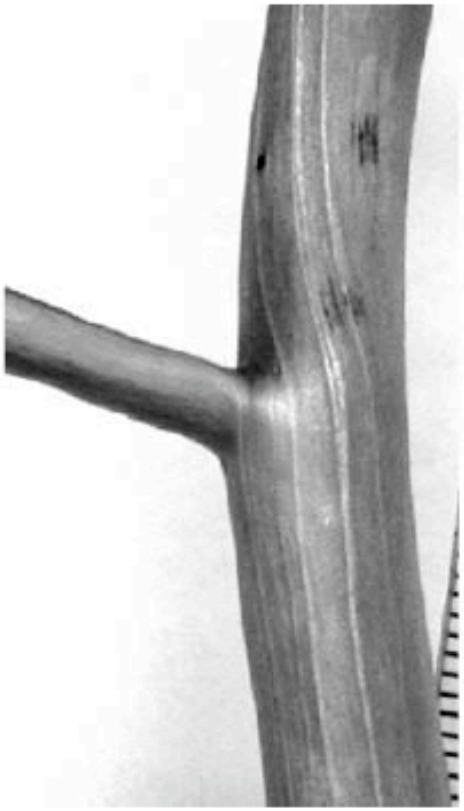


The xylem

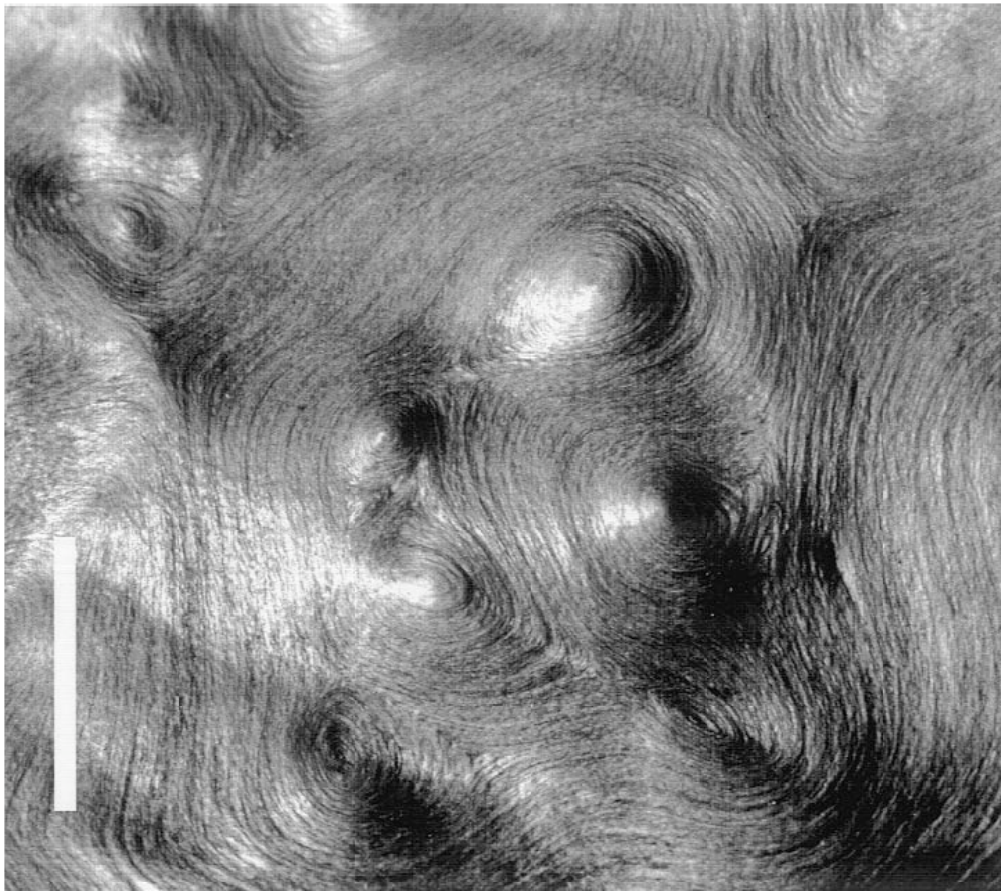


Wood grain at branch junctions

Pics of *Pinus strobus* (white pine) branch junctions
Source: Kramer & Borkowski 2004



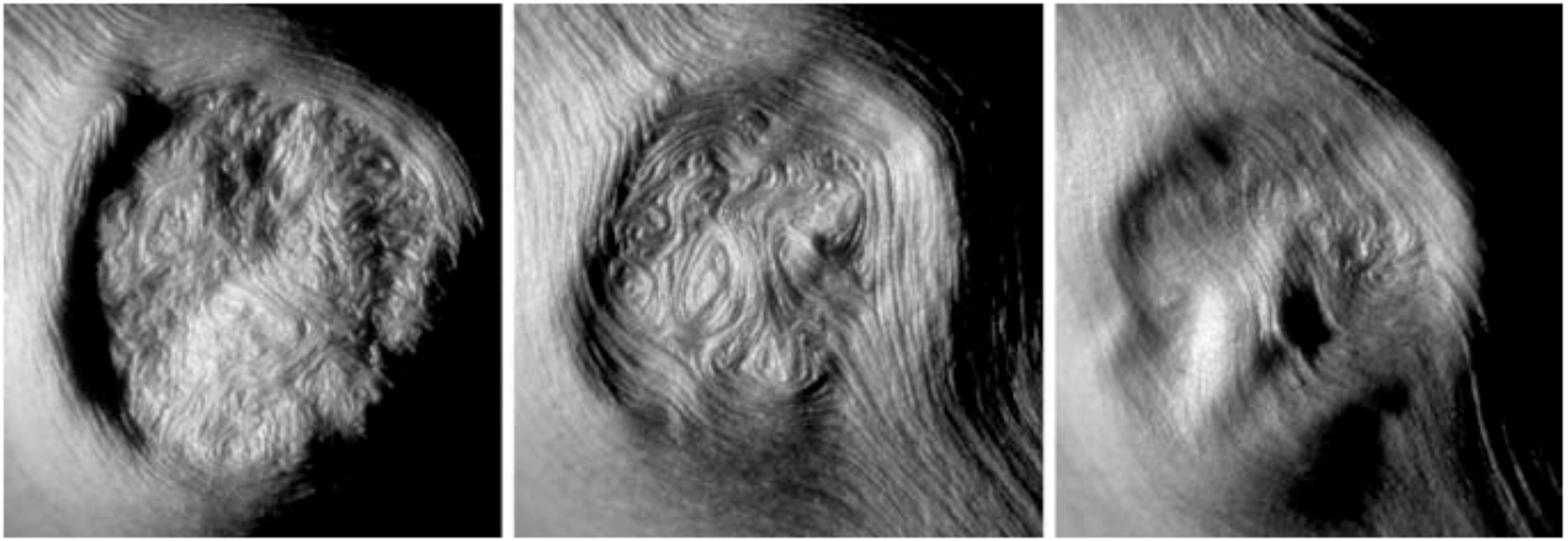
Whirled grain (*Populus deltoides*)



Bar = 6 mm

Whirled grain is dynamic

Branch abscission zones in cottonwood (*P. deltoides*). Changes take 1-3 yrs.

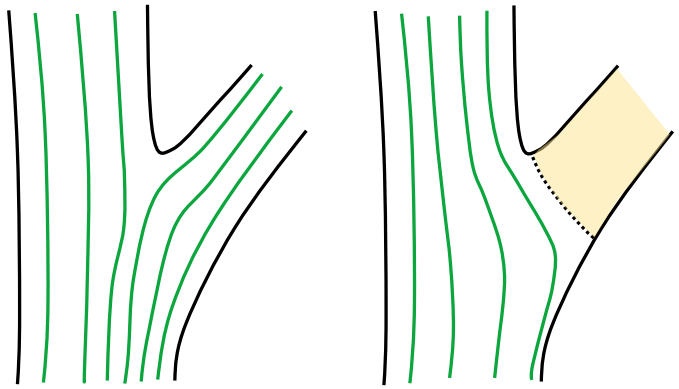


8 mm

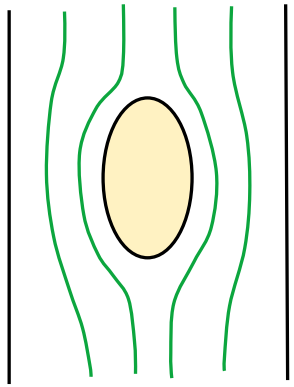
Kramer, JPGR 2006

*The grain reorients…

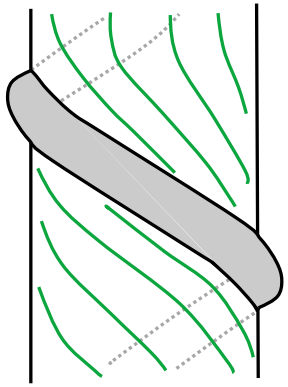
After branch death



After injury



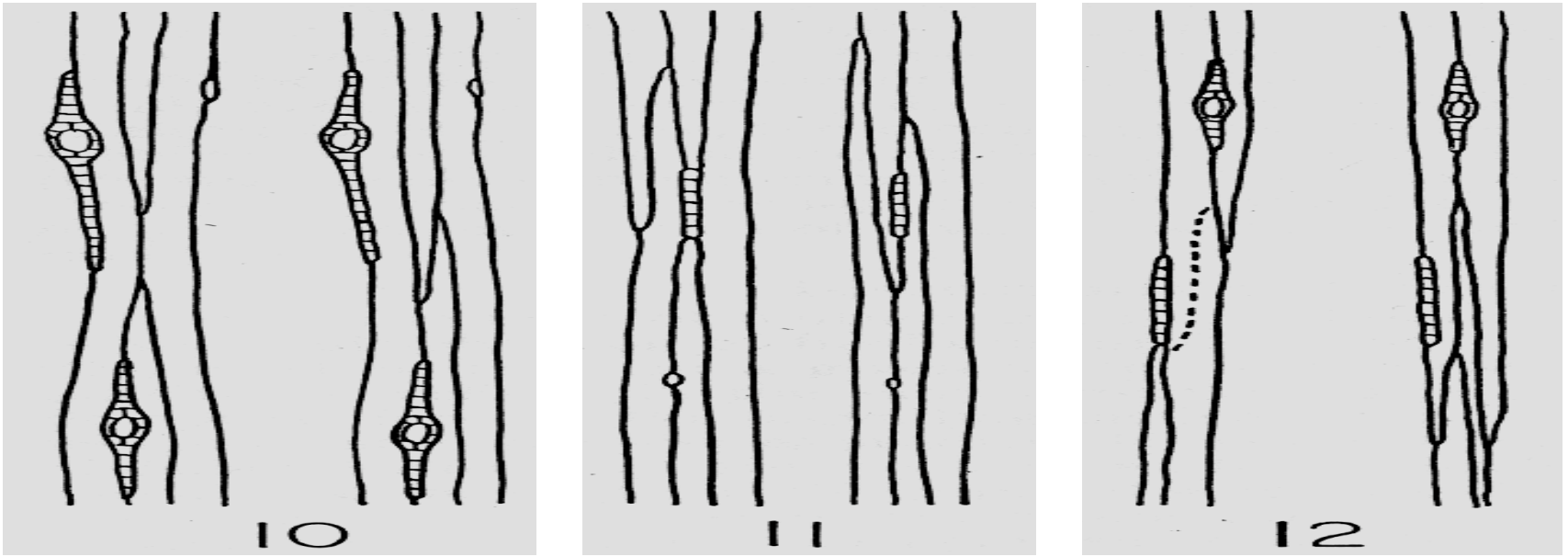
Near a winding vine



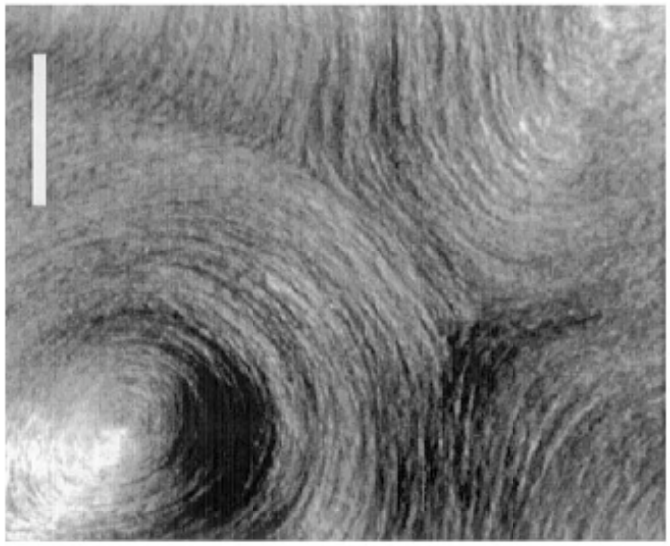
“But how can the grain direction change?”

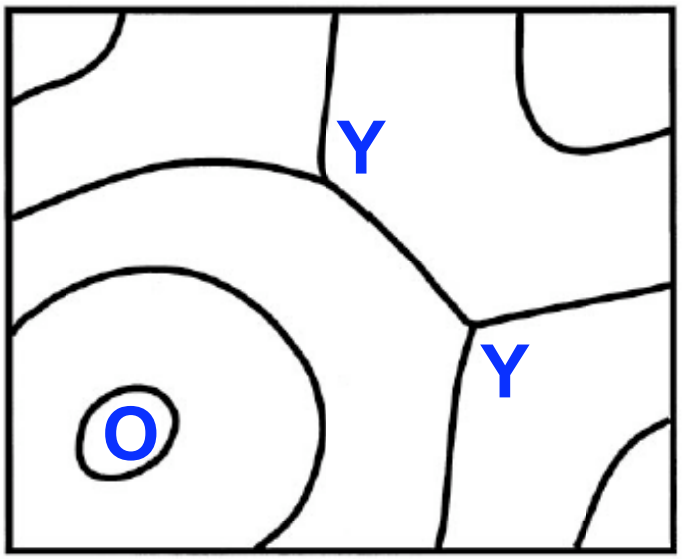
Image modified from: Bannan, Can. J. Bot. 1966
Sketches from micrographs of white spruce (*Picea glauca*).

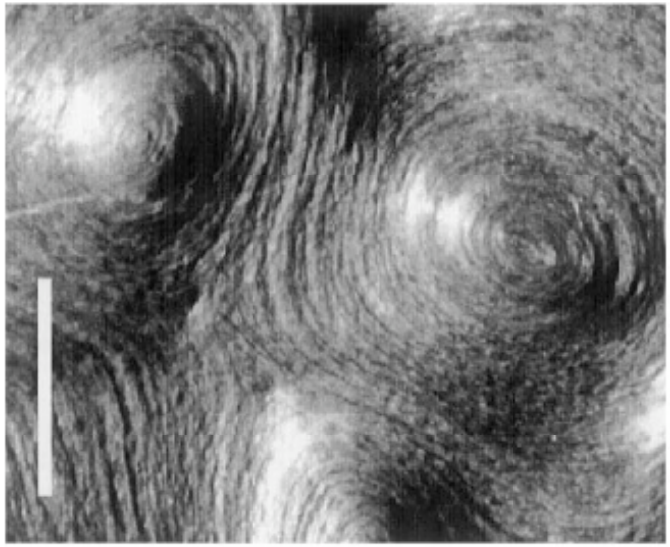
Serial transverse sections record a movie of cambial rearrangements.
Intrusive growth and pseudotransverse divisions.

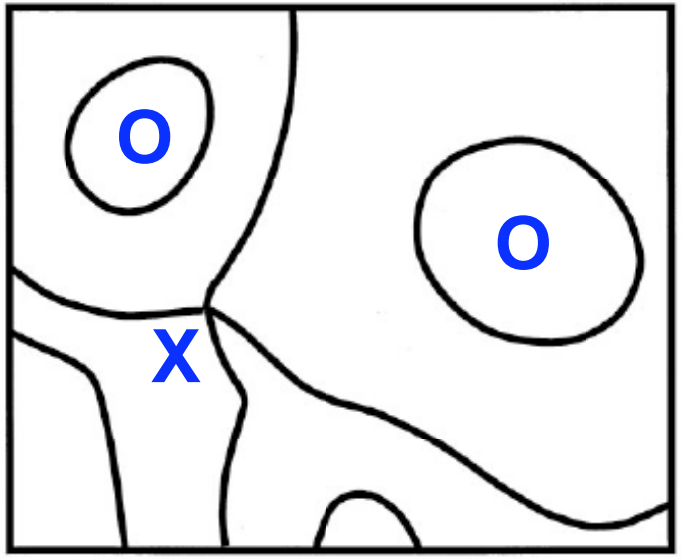


Topological defects…



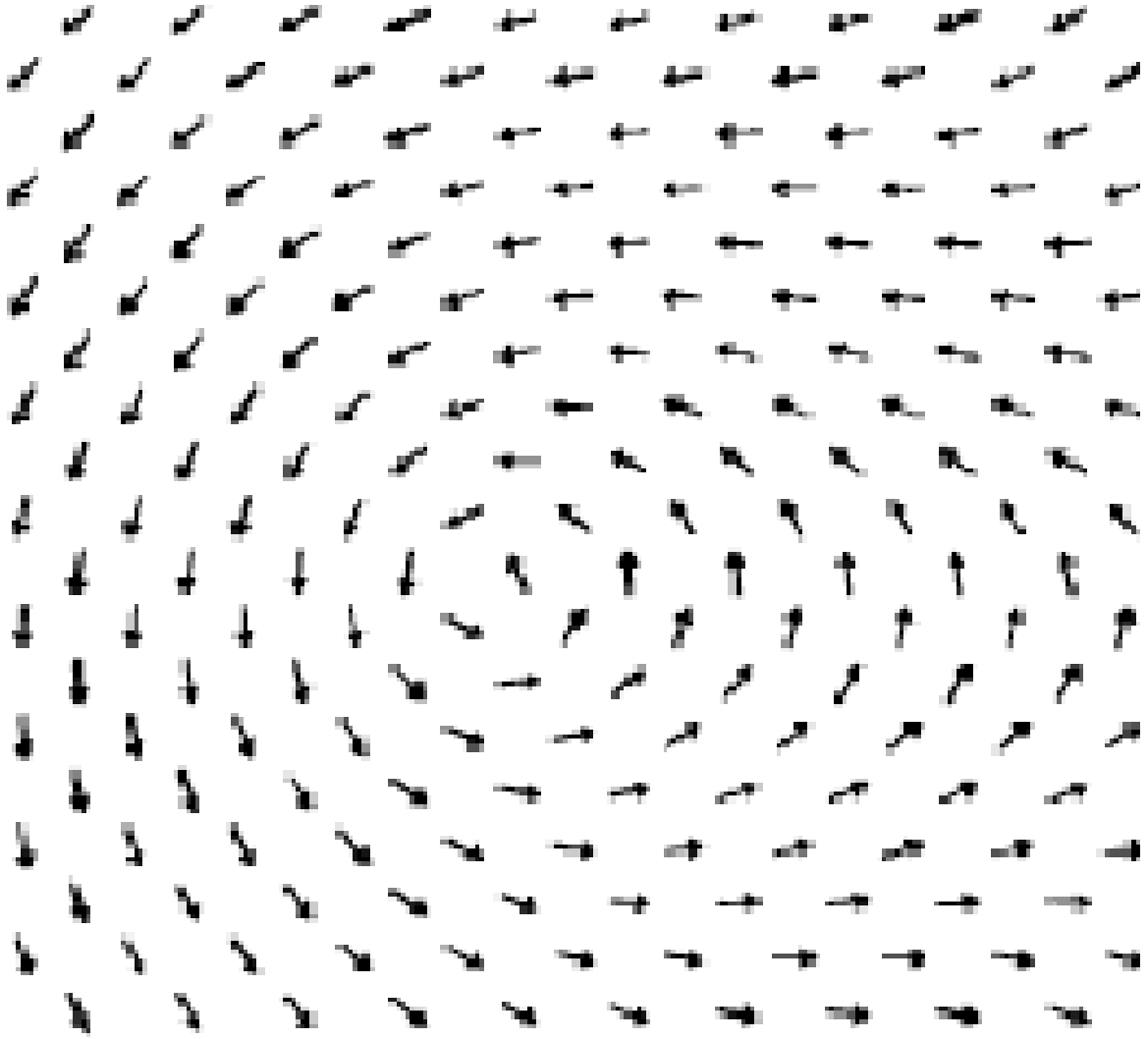




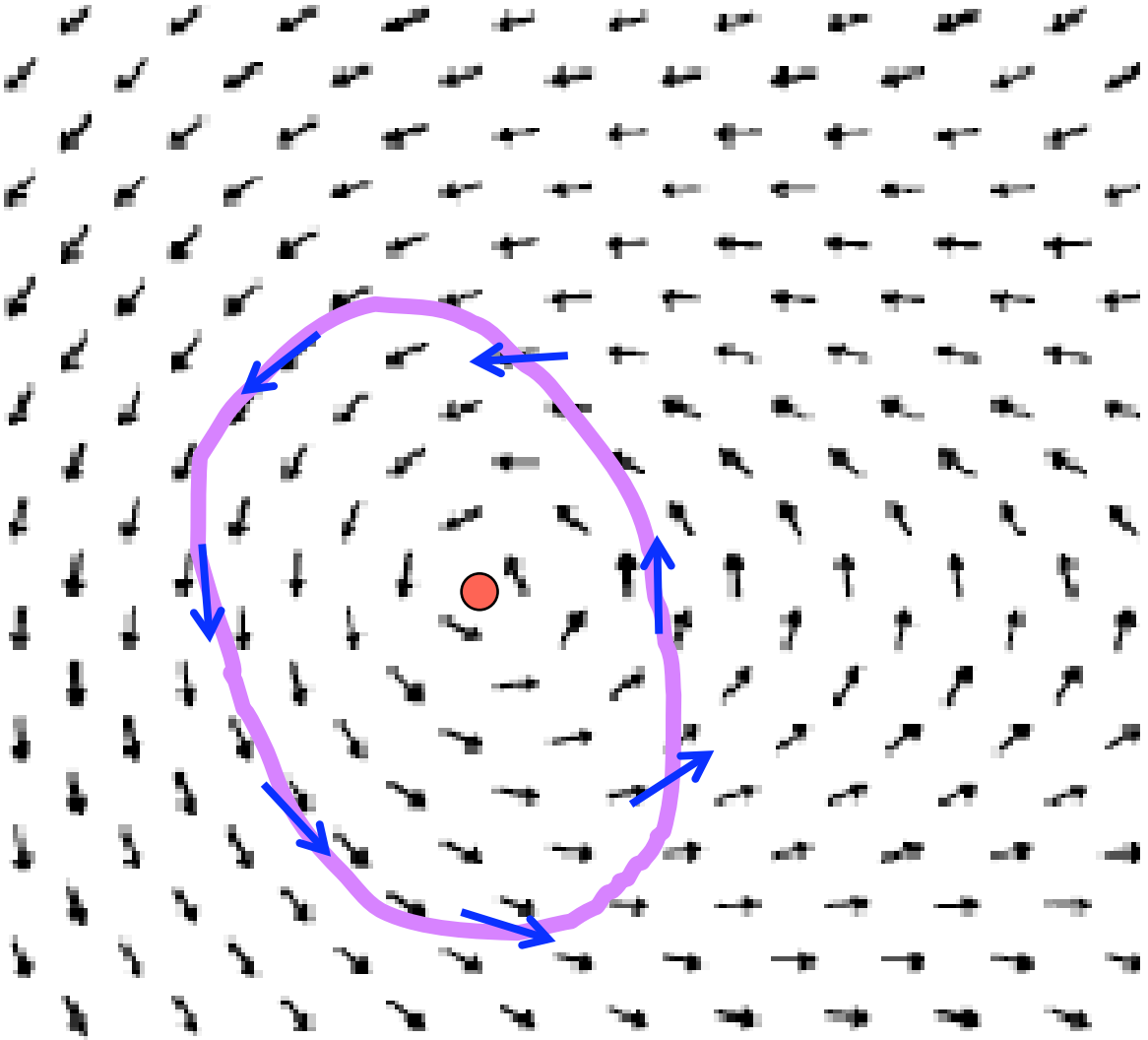


Bars =
3mm

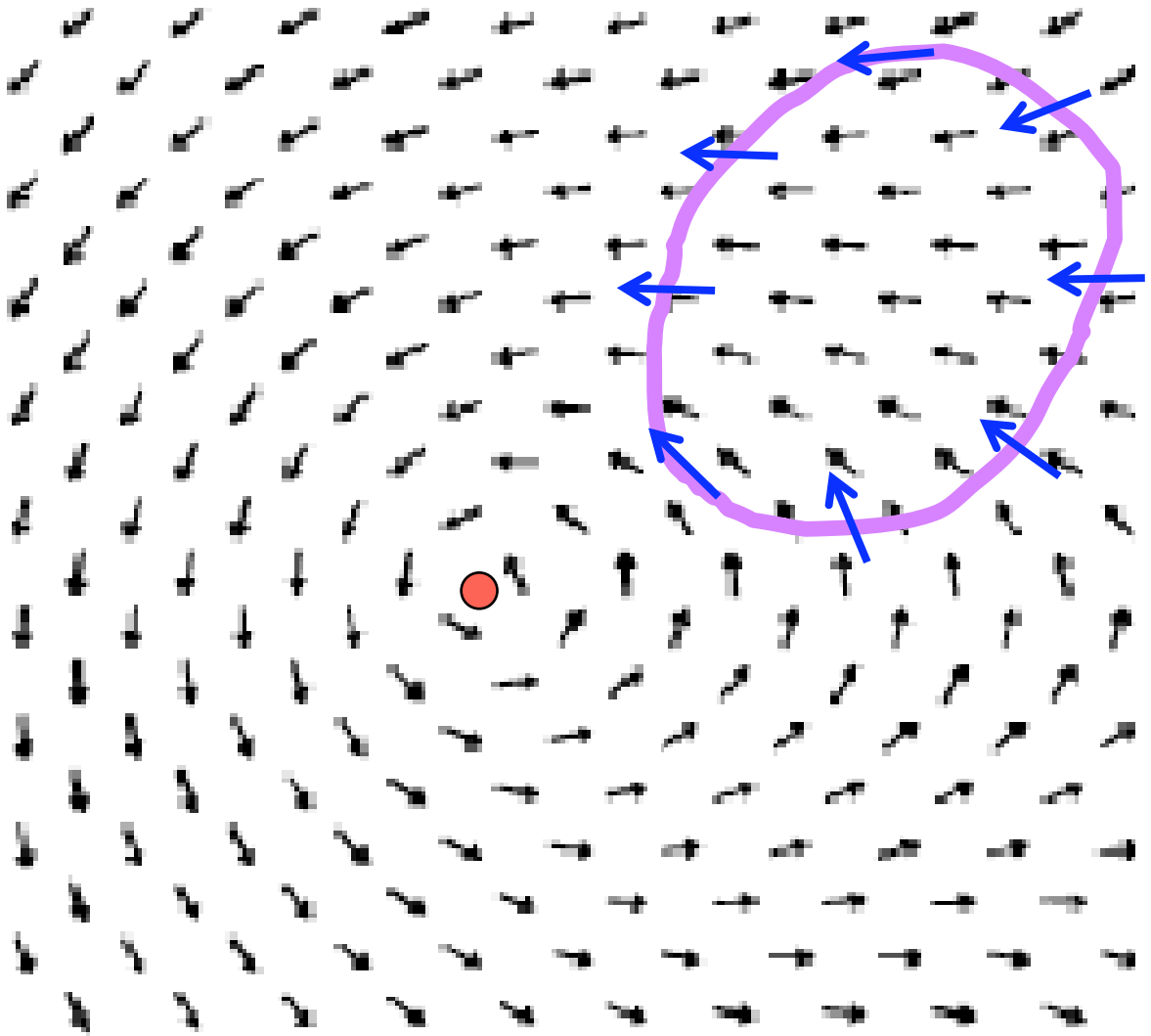
Some vocabulary



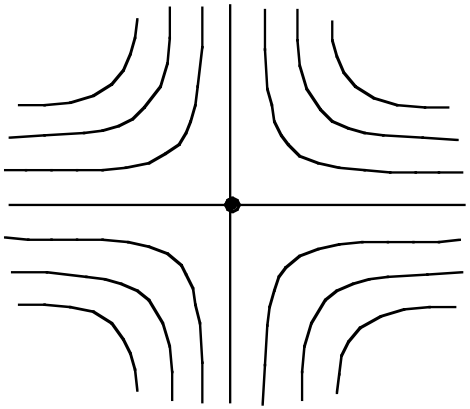
Winding number = +1



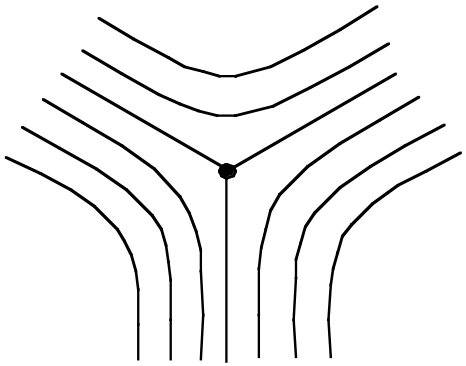
Winding number = 0



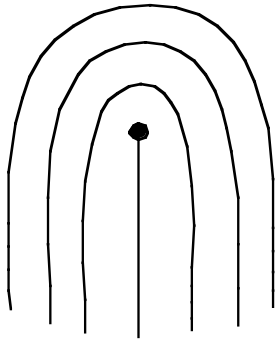
Some (hypothetical) defects



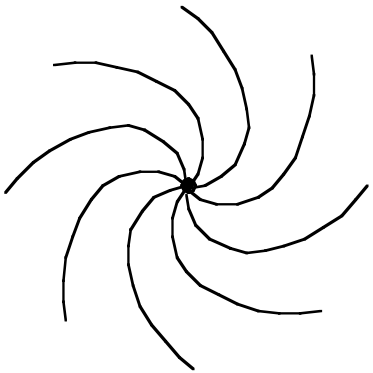
n = -1



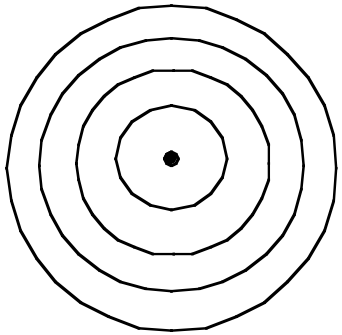
n = -1/2



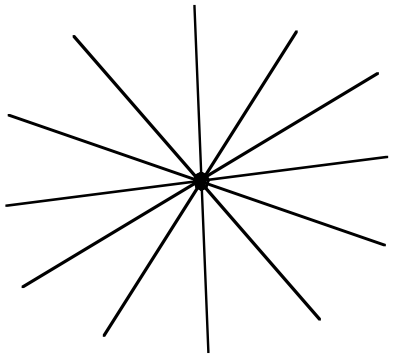
n = +1/2



n = +1

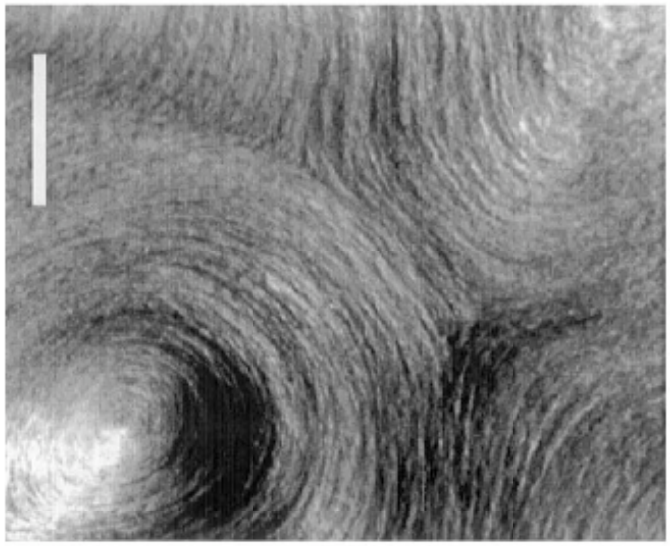


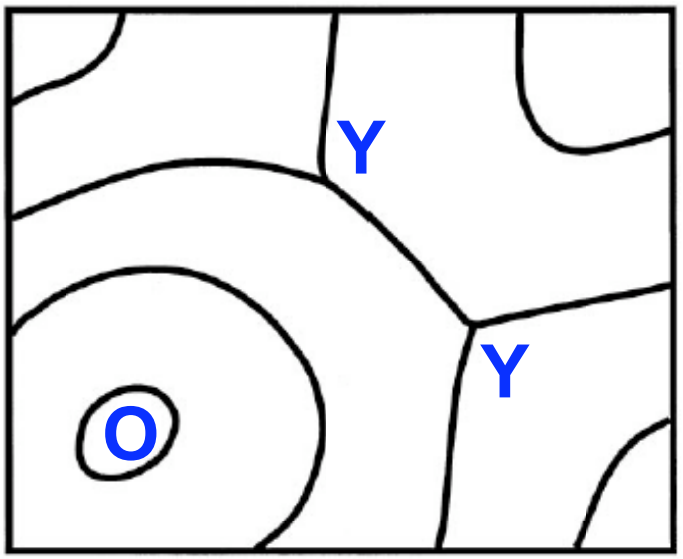
n = +1

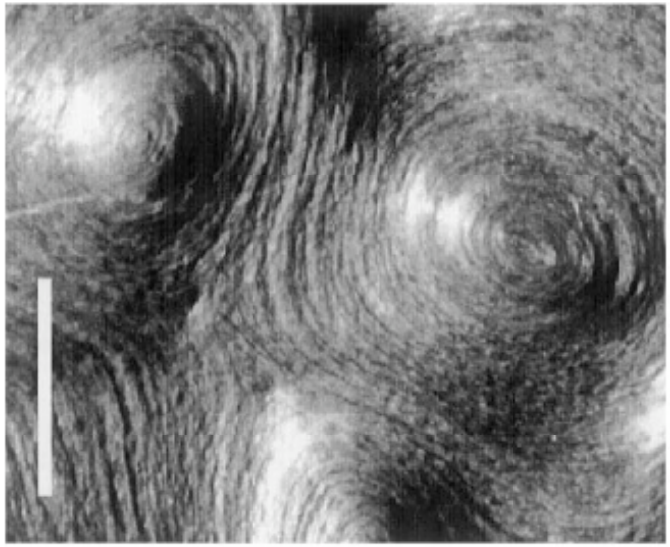


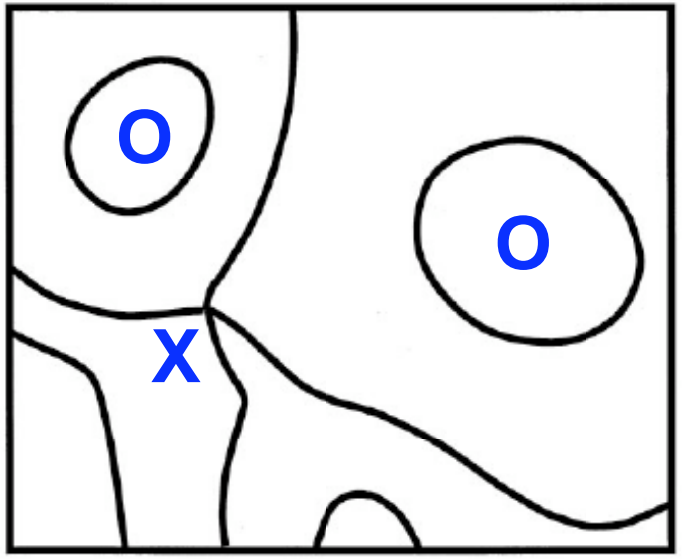
n = +1

Topological defects suggest vector order



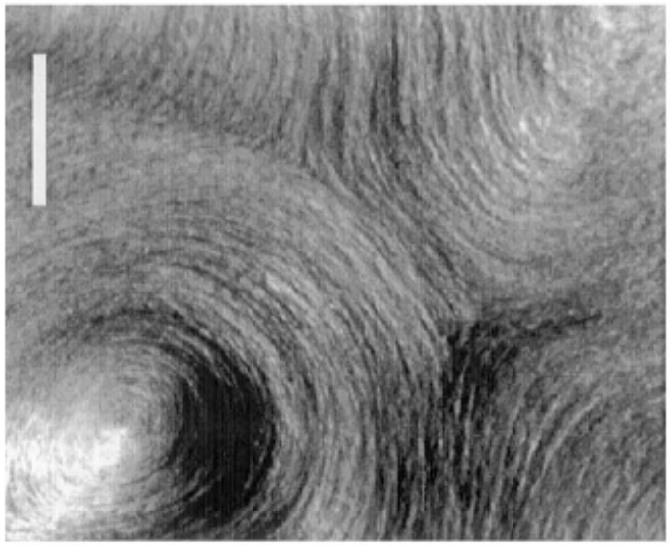


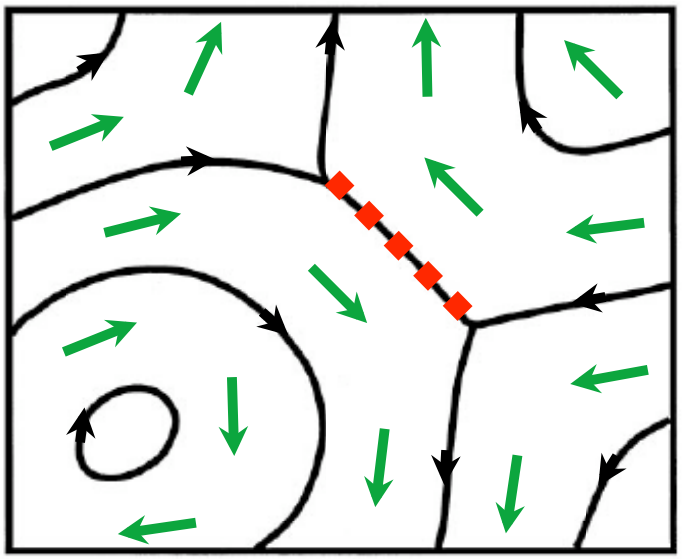


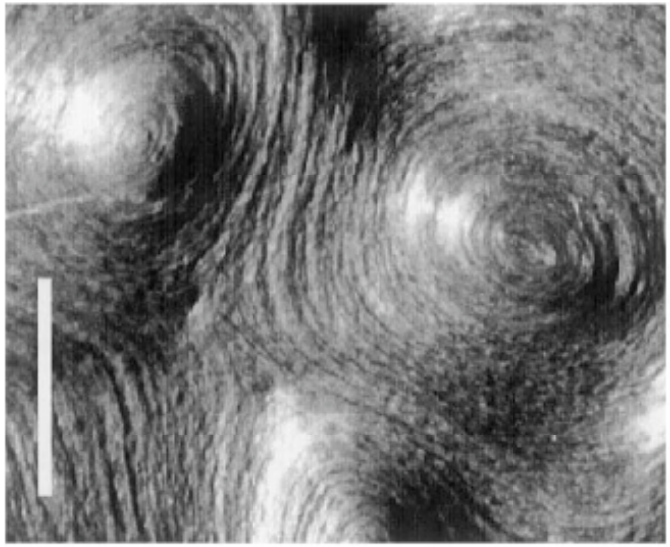


Bars = 3mm

Topological defects suggest vector order







Bars = 3mm

Defects rule out strictly mechanical theories

Originally, the idea that spiral grain is due to torsions exerted by wind on asymmetric trees crowns.

Expanded on by Mattheck et al. to the idea that wood fibers tend to lie parallel to the direction of "force flow" in the tree.

However, the stress field is a tensor and inconsistent with vector order. The defects would be different!

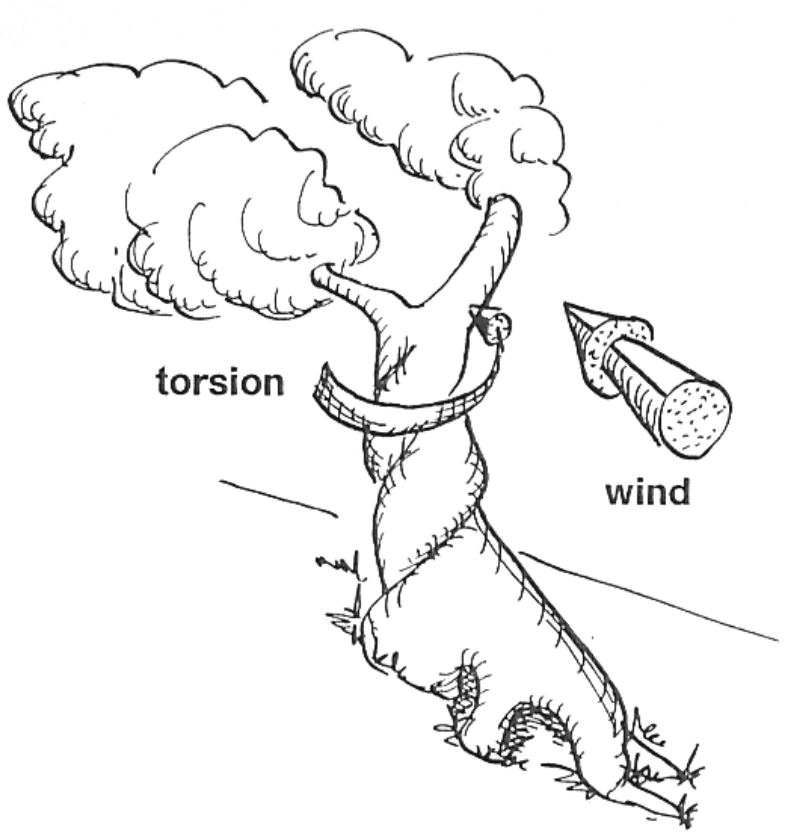
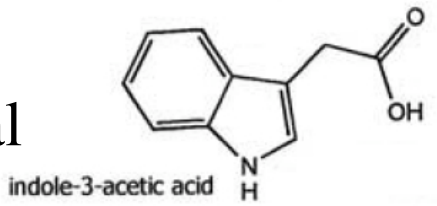


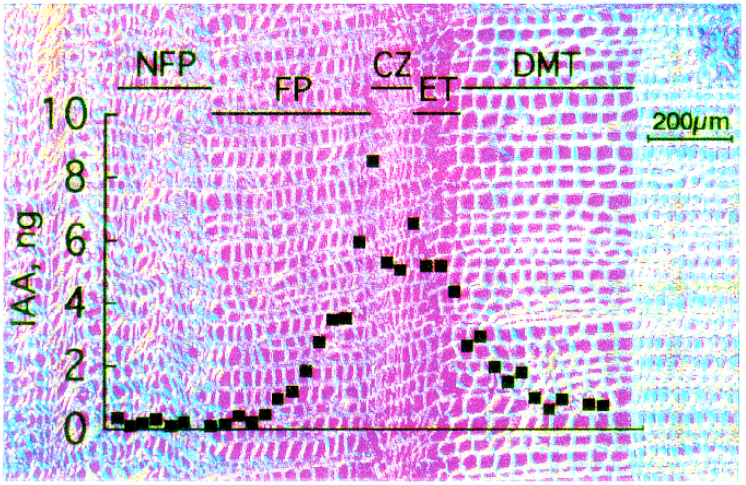
Image from: Mattheck, *Wood - the internal optimization of trees* (Springer, 1995)

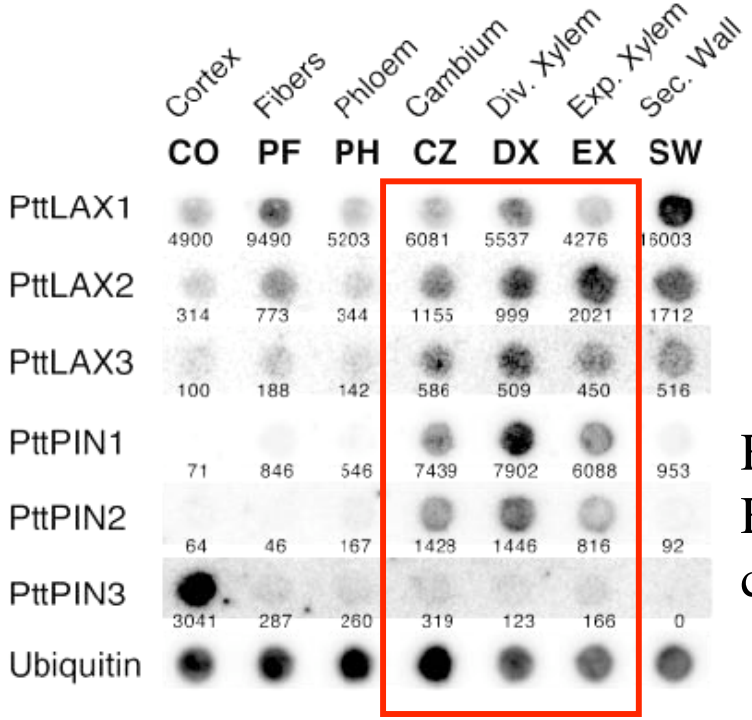
Auxin is a plausible signal



indole-3-acetic acid

From Uggla et al. PNAS 1996
Concentration of auxin across cambial zone.

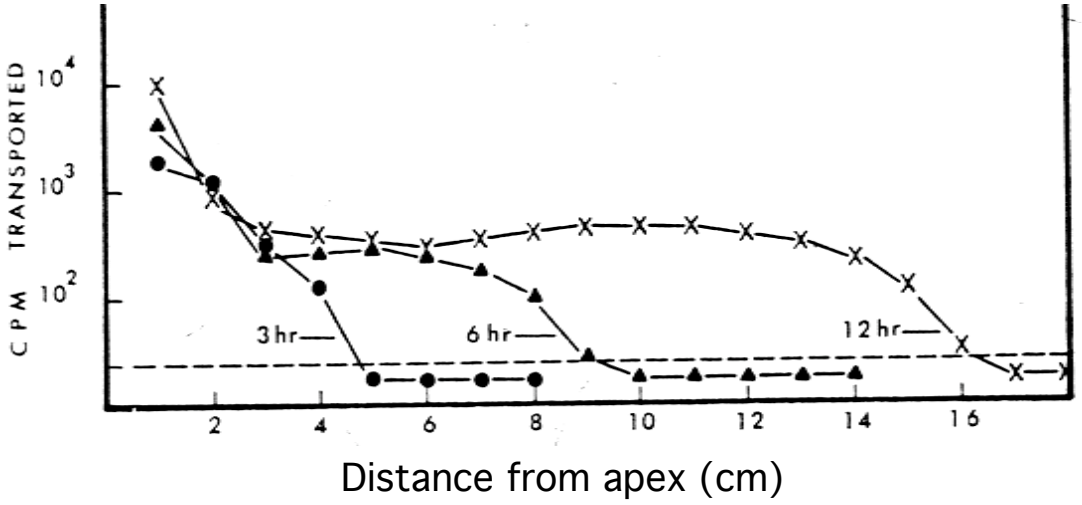


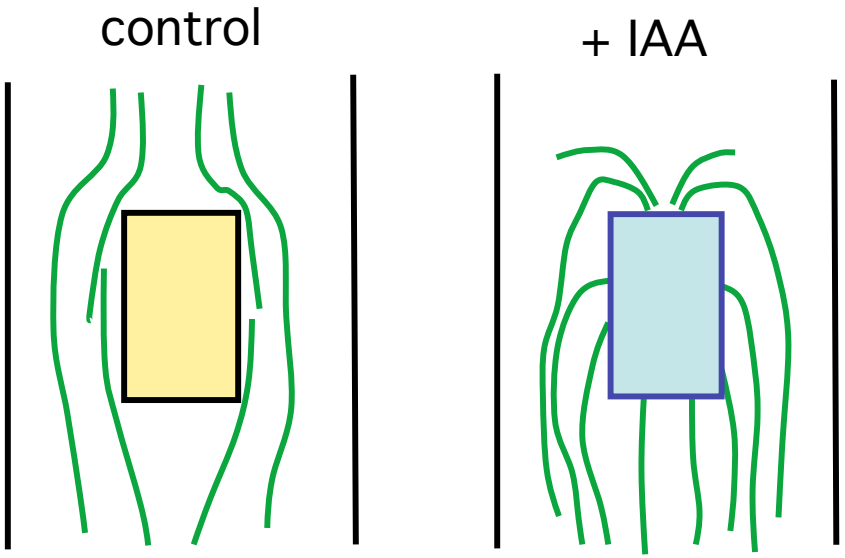


From Schrader et al. PNAS 2003
Expression of carriers across cambial zone in hybrid aspen.

Auxin is a plausible signal

From Hollis & Tepper, 1971
Auxin transport.

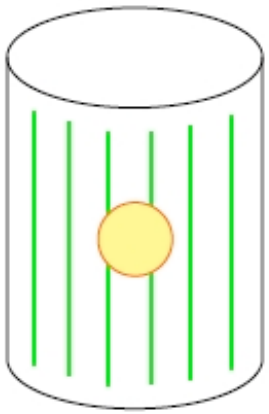




After Fayle and Farrar, 1965
Exogenous auxin changes vessel polarity.

The wood grain (cell polarity) model

Kramer JTB 2002, Kramer JPGR 2006



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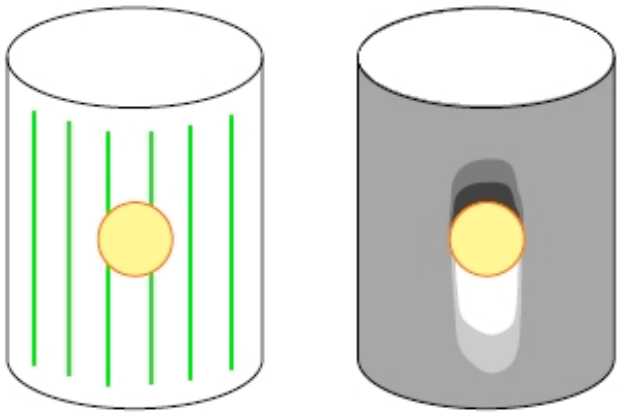
Kramer JTB 2002, Kramer JPGR 2006



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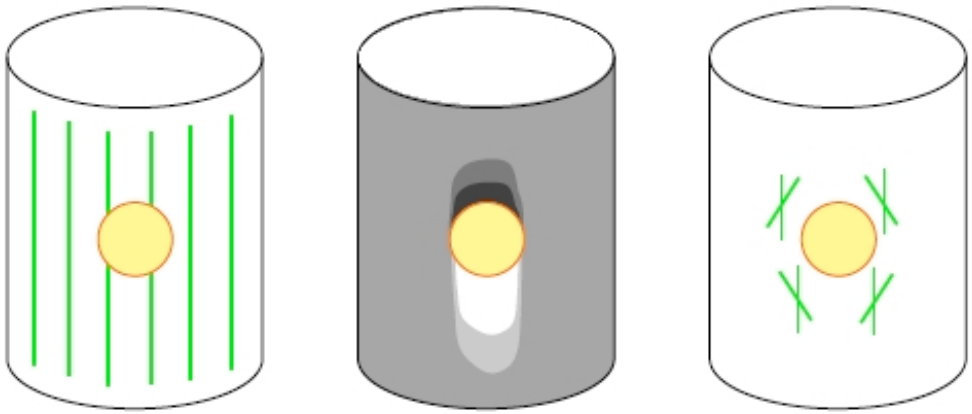

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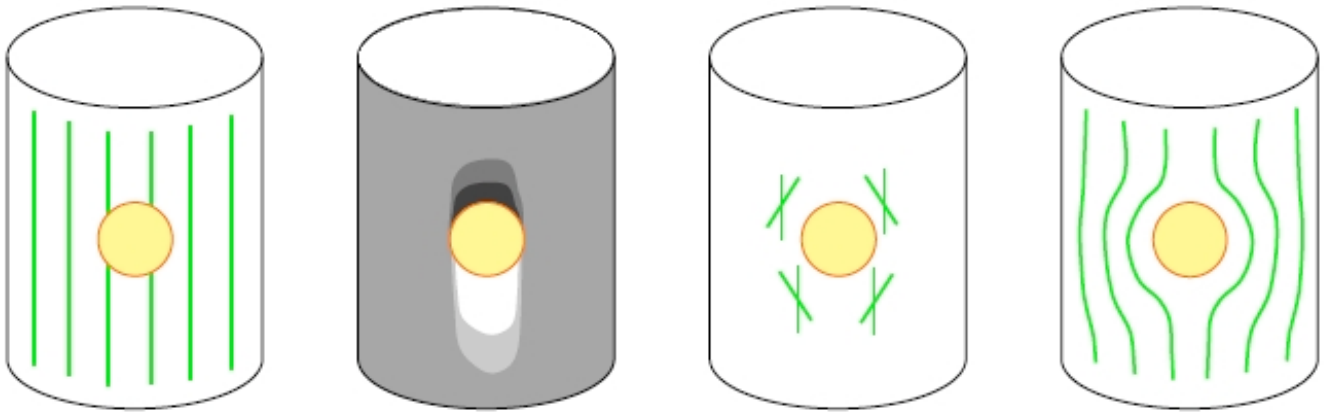
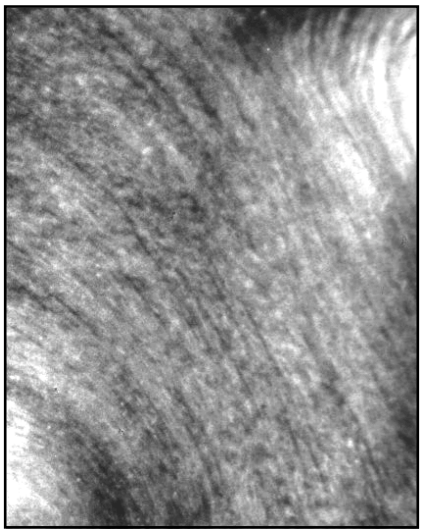


Modeling wood grain patterning

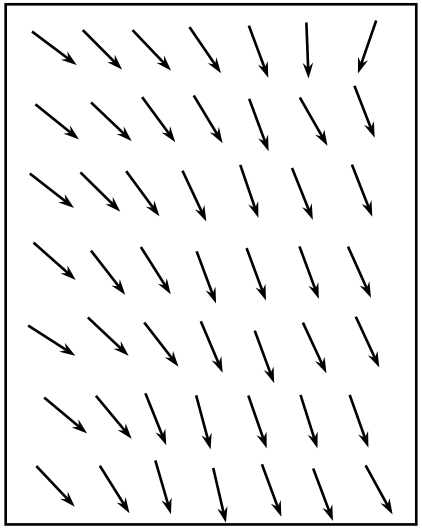
Two supracellular, 2-dimensional fields:

(1) The grain direction, **u**(x,y,t) (unitless)

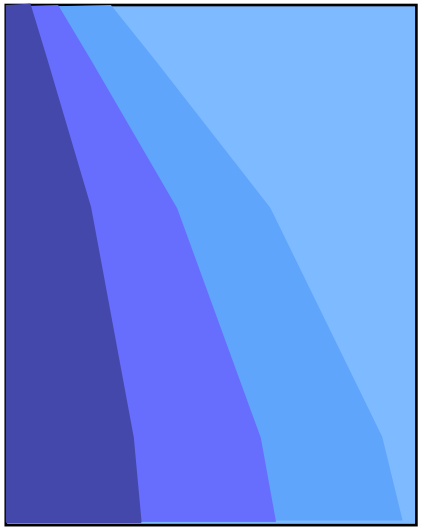
(2) The auxin concentration, m(x,y,t) (ng/cm^2)



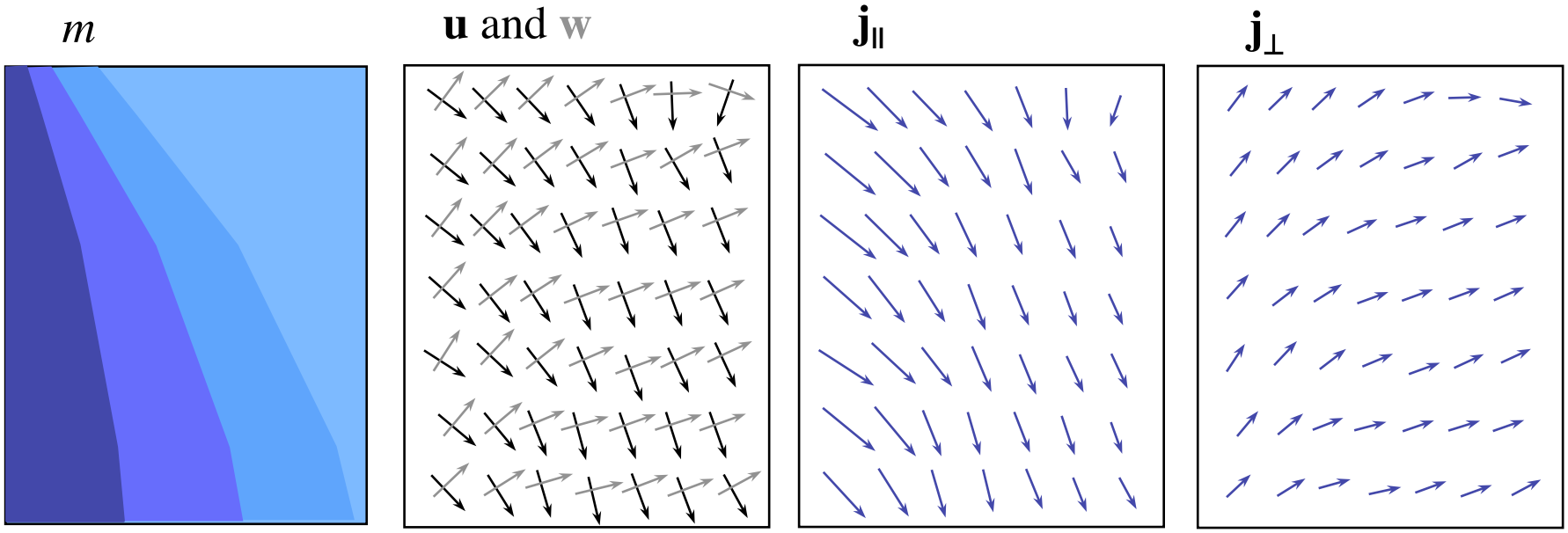
u



m



The flux equation



$$\mathbf{j} = \left(-D_{\parallel}\nabla_{\parallel} m + v\, m\right)\mathbf{u} + \left(-D_{\perp}\nabla_{\perp} m\right)\mathbf{w}$$

j is the flux of IAA (ng/cm/hr)

Transport speed $v = 0.5$ cm/h

Diffusion coefficients = ??

The continuity equation

Few published studies of IAA metabolization/synthesis in the cambium.

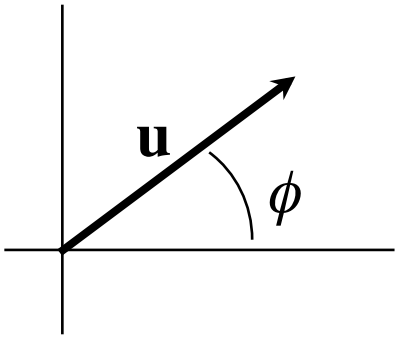
Sundberg & Uggla, Physiol. Plant. (1998) found that the majority of radiolabelled IAA survived 10 cm of transport through current-year shoots of *Pinus sylvestris*.

Levels of conjugated IAA are typically < 20% of net IAA.

$$\frac{\partial m}{\partial t} = -\nabla \cdot \mathbf{j} = -\frac{\partial j_x}{\partial x} - \frac{\partial j_y}{\partial y}$$

The grain orientation equation

Kramer, JTB 2002



$$\frac{\partial \phi}{\partial t} = K \nabla^2 \phi - \mu \nabla_{\perp} m$$

$K \sim 0.005$ cm^2/y the grain "stiffness", penalty for curved cells.

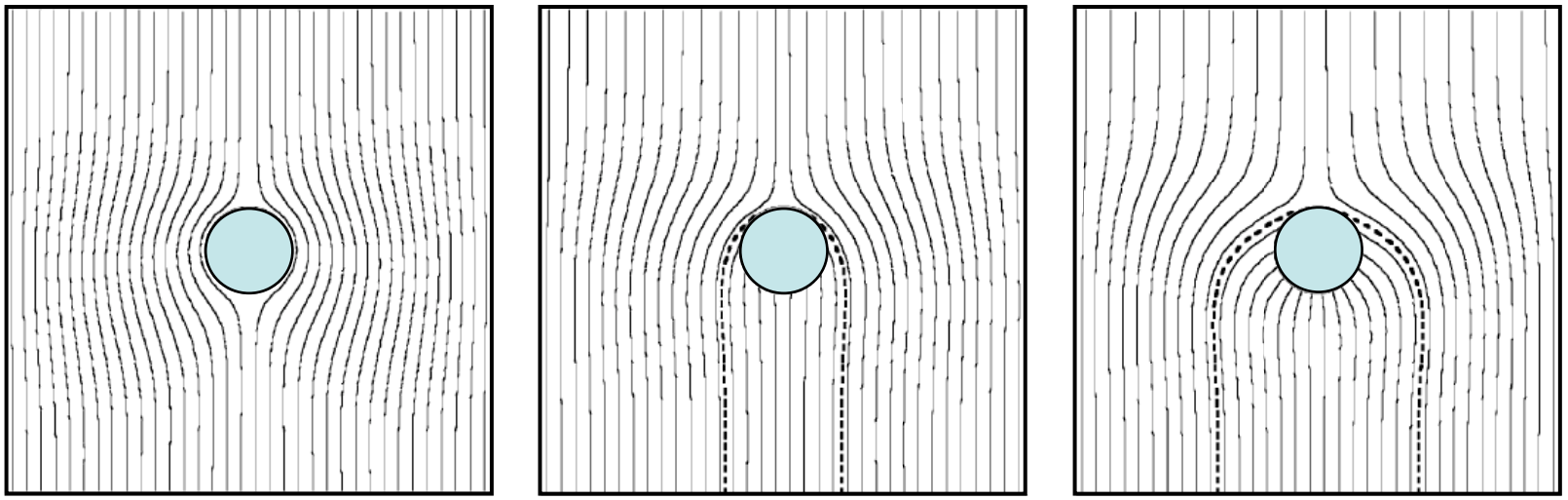
$\mu \sim 0.1$ cm/ng/y characterizes the chemotropic tendency of cambial cells to point towards an auxin maximum.

Note units of *years*.

Model branch junctions

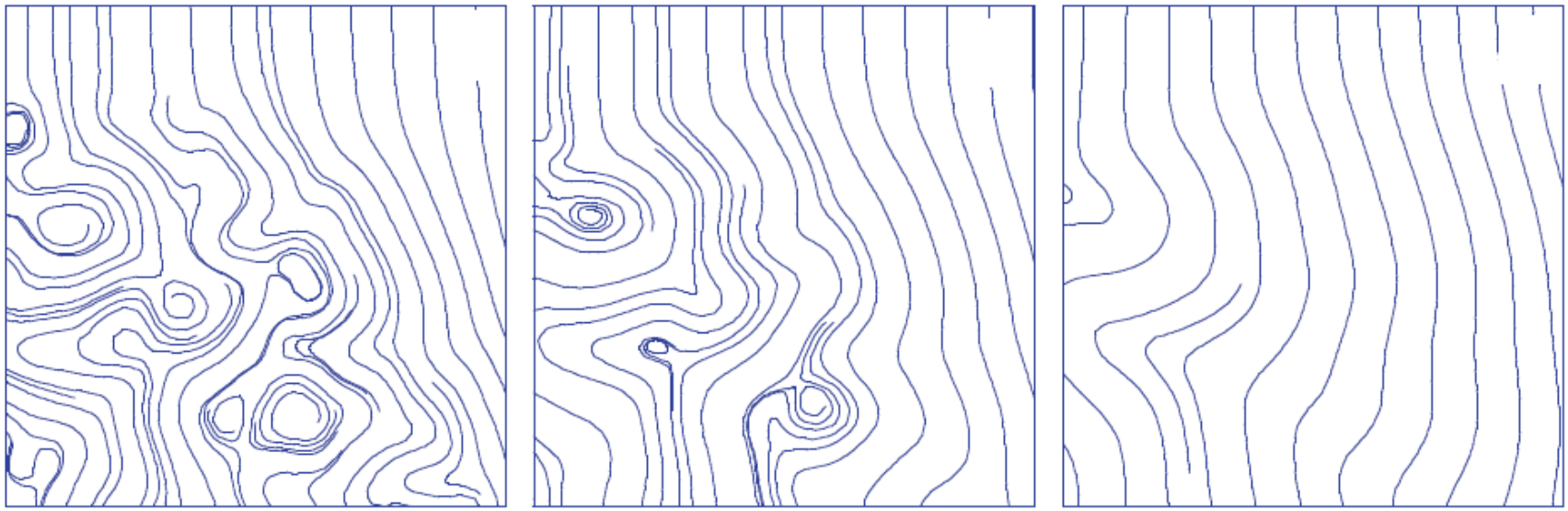
Kramer & Borkowski 2004

Grain runs into branches that export auxin.
Grain avoids branches that don’t export auxin.

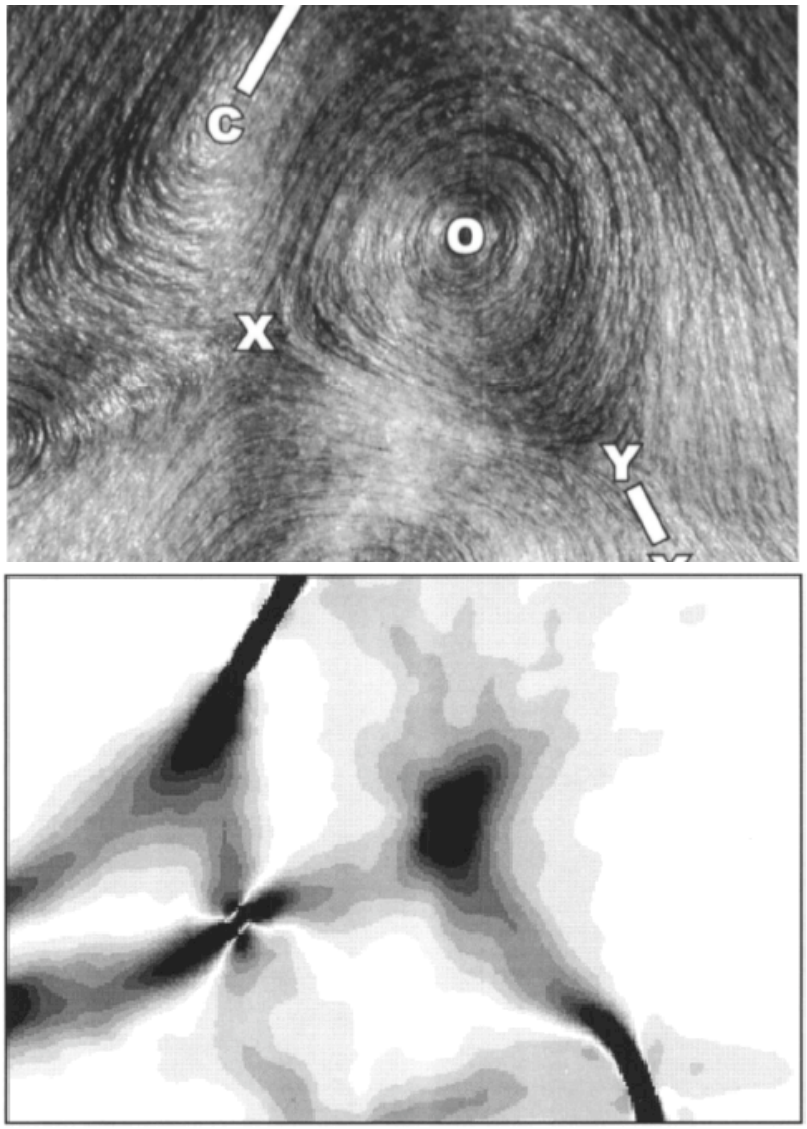


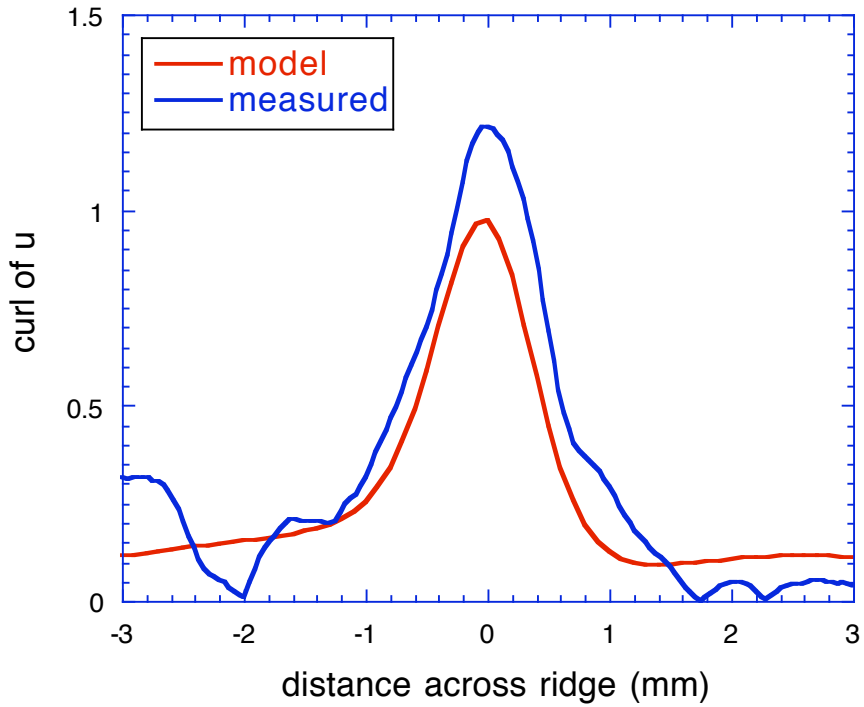
Model: whirled grain coarsens

Kramer 2006
Wood grain model of an abscission zone
After 25, 50, and 100 days of active growth.

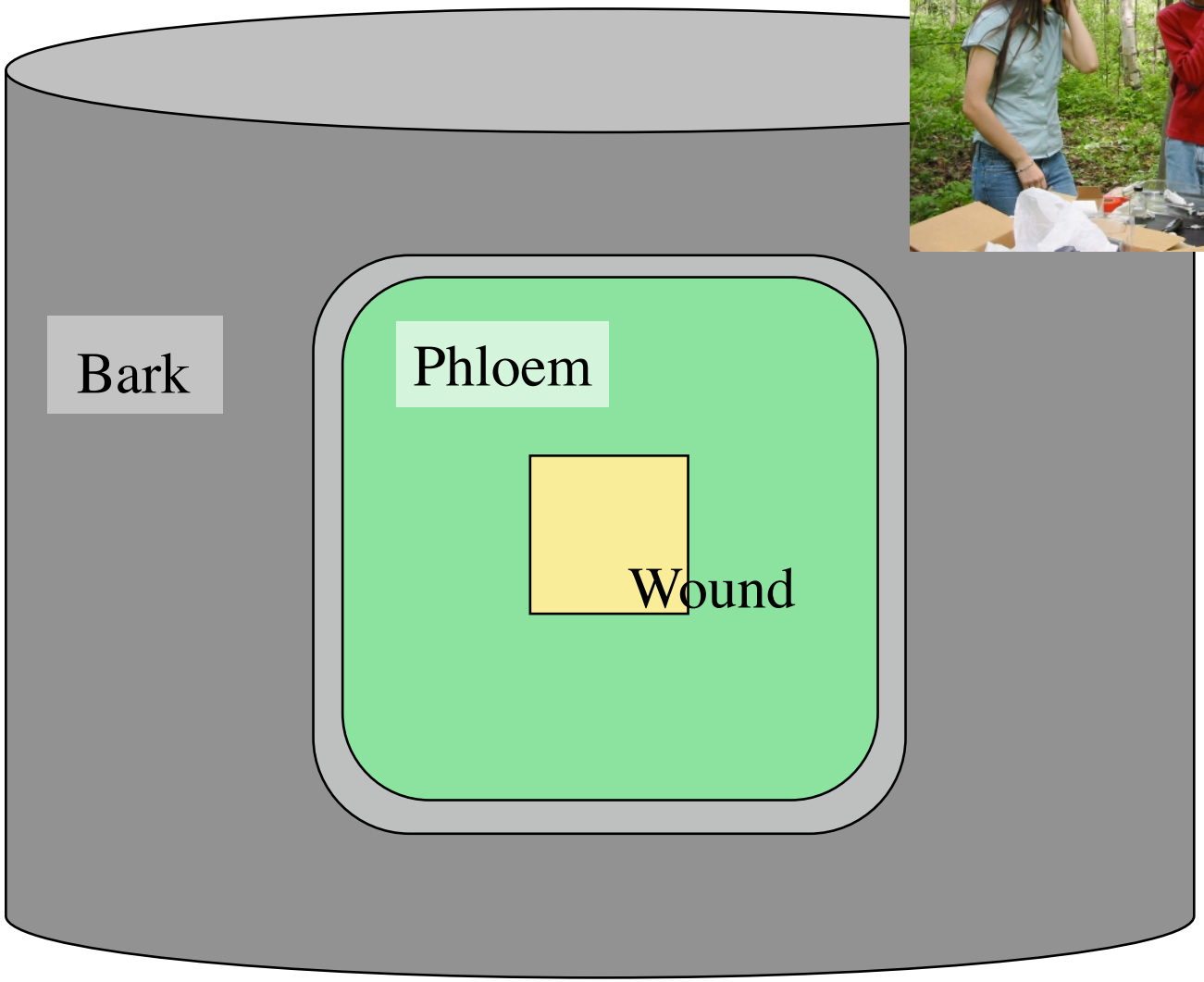


Determining the ratio K/μ

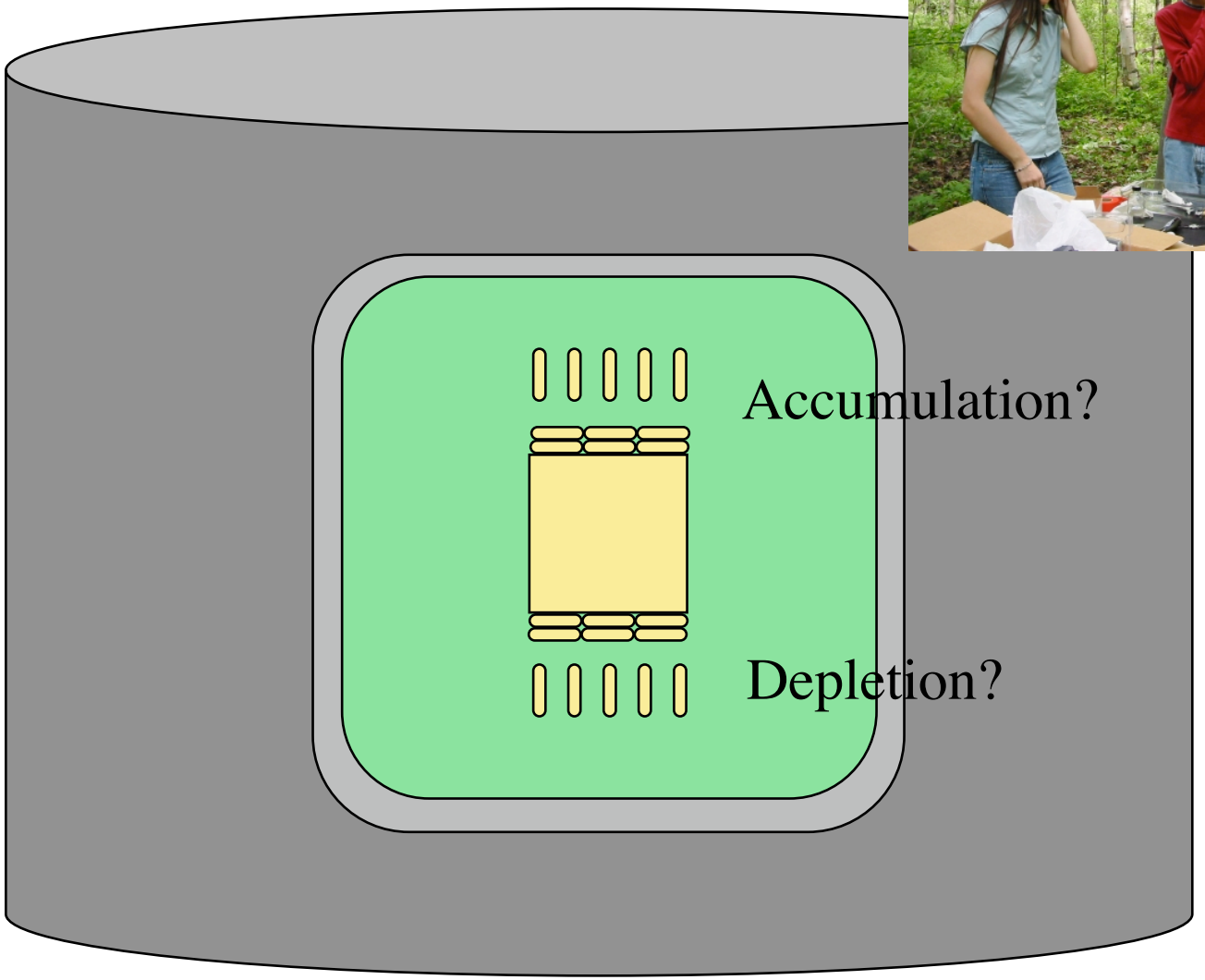




Measuring auxin redistribution



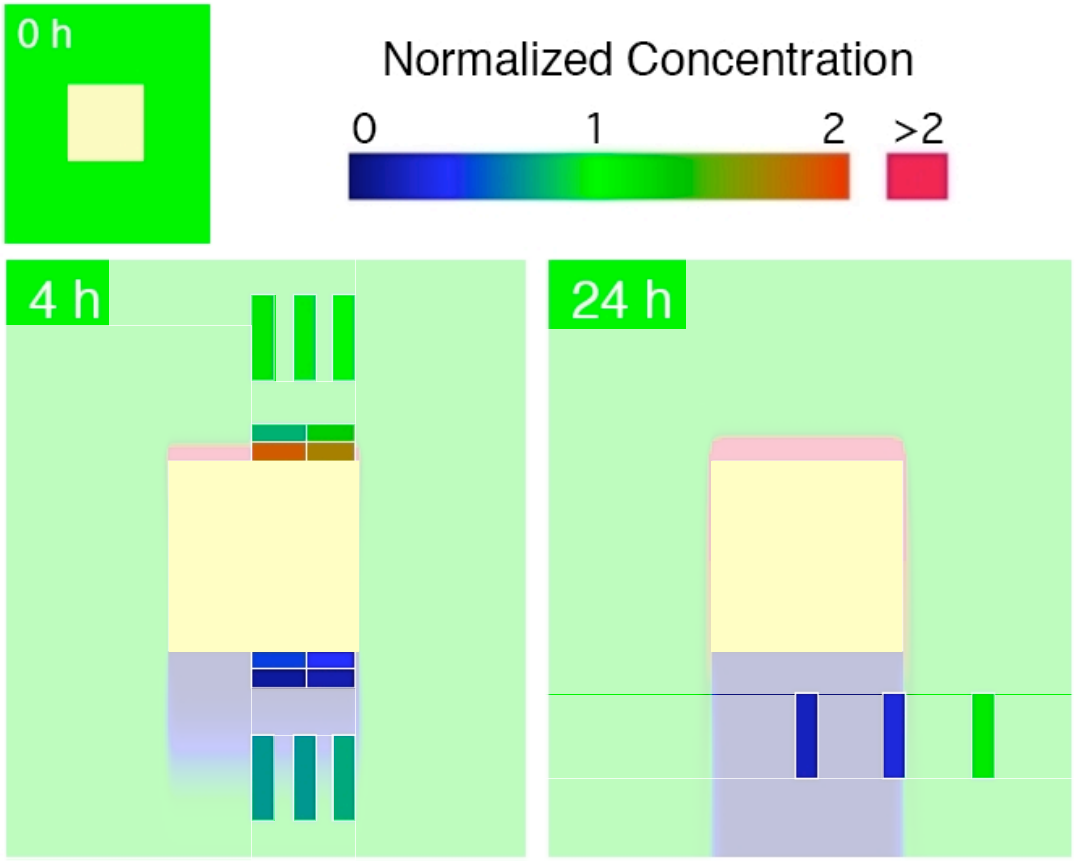
Measuring auxin redistribution



Auxin gradients in the cambium

Kramer et al. Science 2008

Populus cambium: GC-MS endogenous auxin concentrations in cambium.

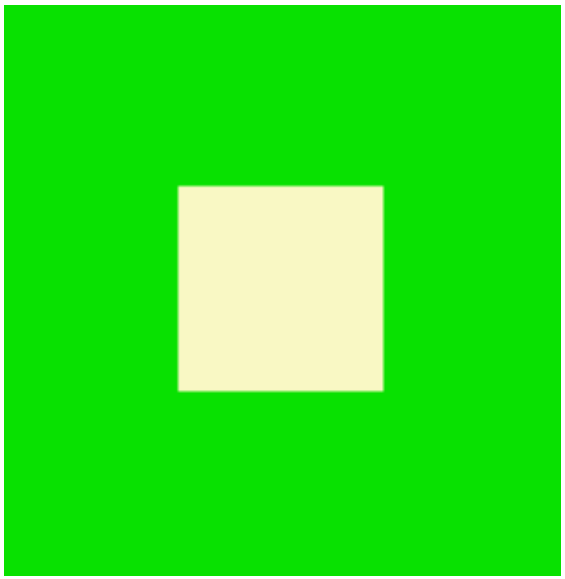


Best fit transport model

Transport speed $v = 0.41$ cm/h (0.35 - 0.46)

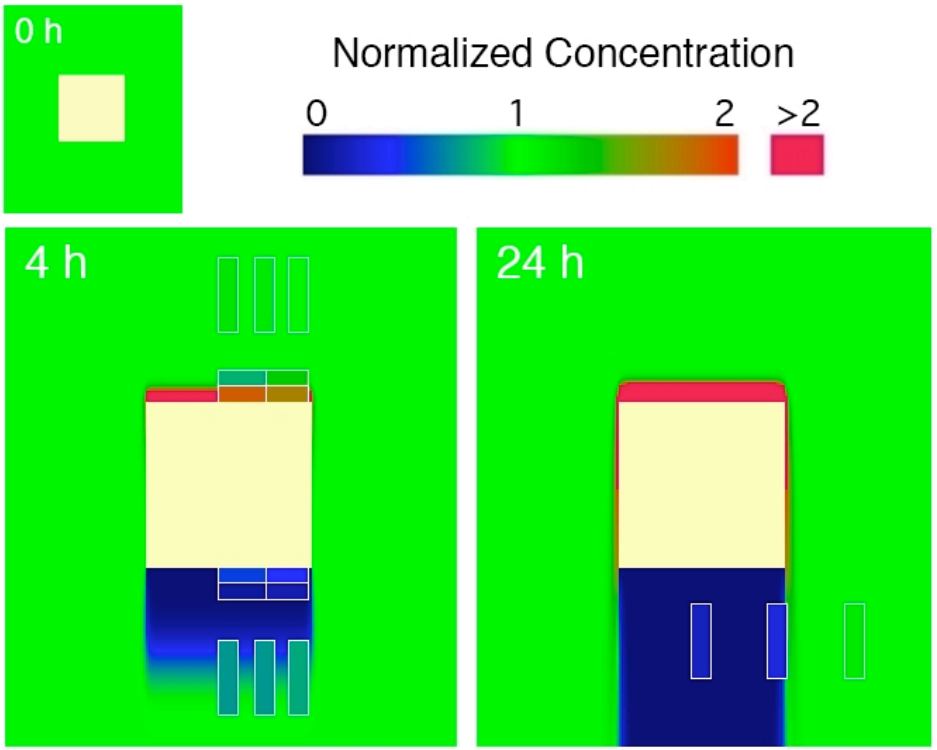
diffusion coefficients $D_{\parallel} = 0.018$ cm^2/h (0.008 - 0.035)

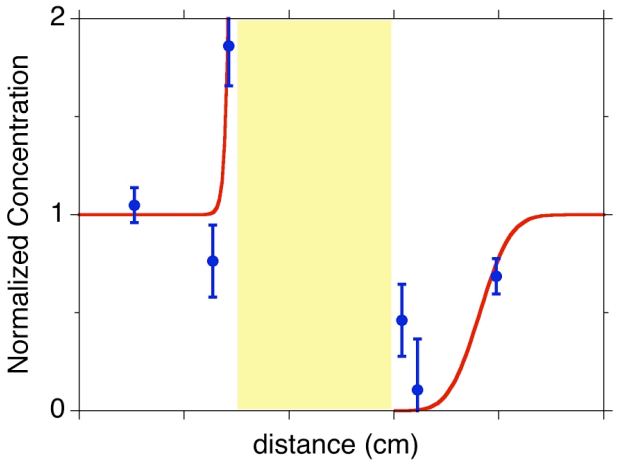
$D_{\perp} = 0.0005$ cm^2/h (0 - 0.046)



Auxin gradients in the cambium

Kramer et al. Science 2008
Populus cambium: comparison of GC-MS conc and model.





*The next steps…

The fundamentals:

Localize auxin carriers (PINs, AUX/LAX, PGPs)

Auxin reporters

Molecular/cell biology of polarity changes?

Applications:

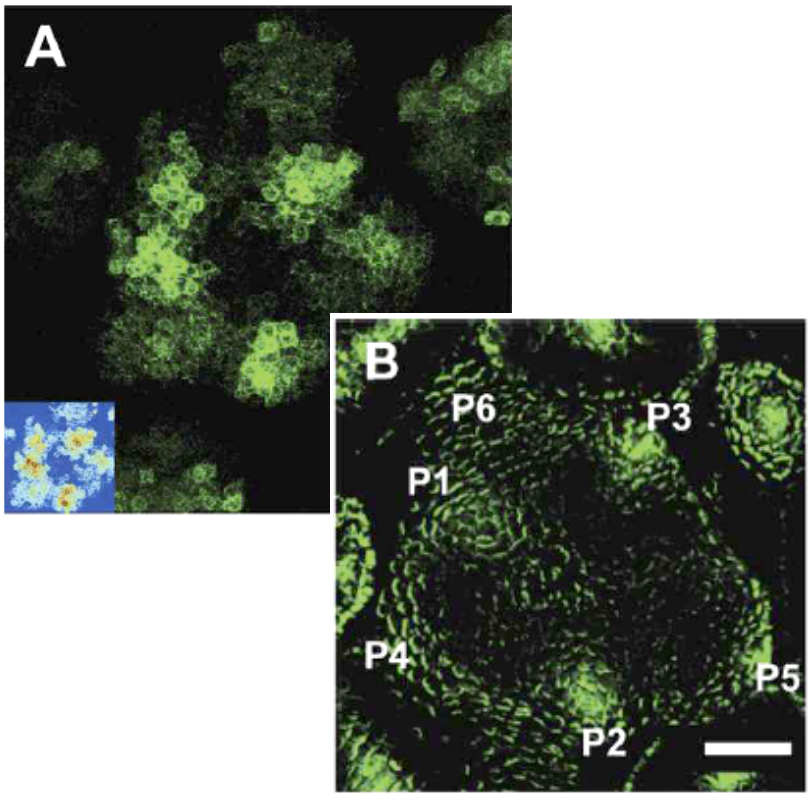
Can we manipulate grain patterns?

Long term: Designer wood grain, stronger lumber, and drought resistance.

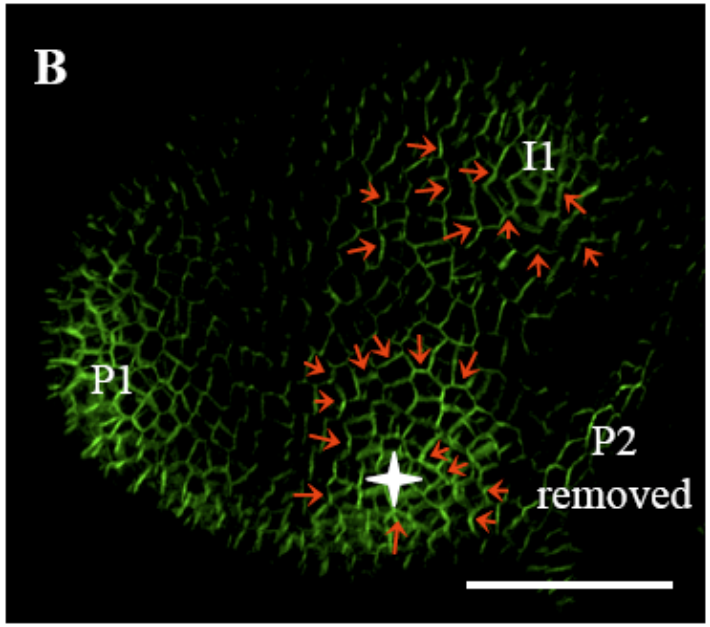
Part 2: Arabidopsis
(and everything else that isn’t a tree)

Other polar events: phyllotaxis

Bainbridge et al. 2008
DR5 and PIN1 in the SAM

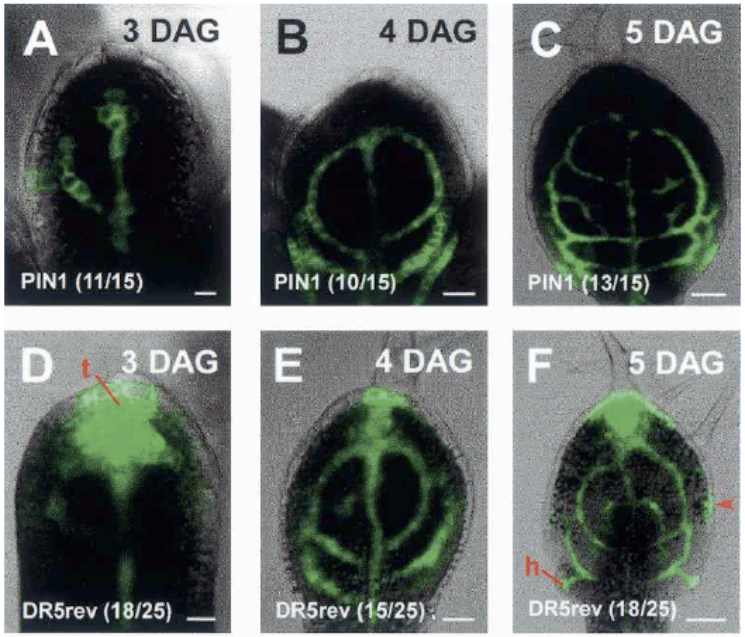


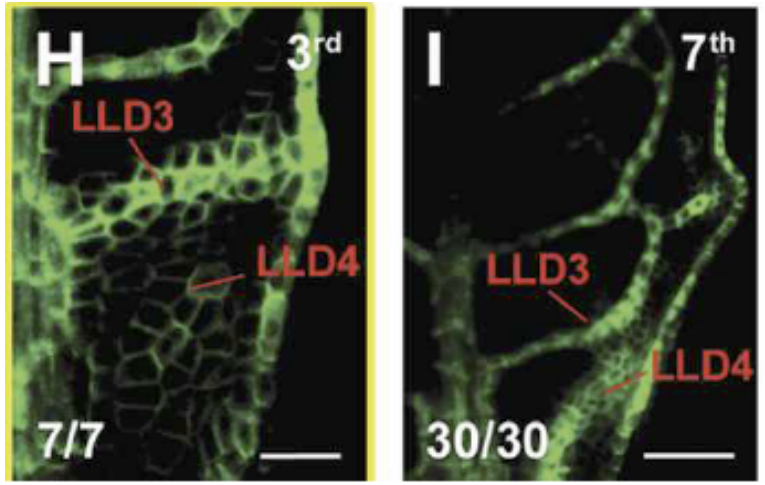
Beyer et al. 2009
PIN1 reorients to point towards
Site of auxin application.

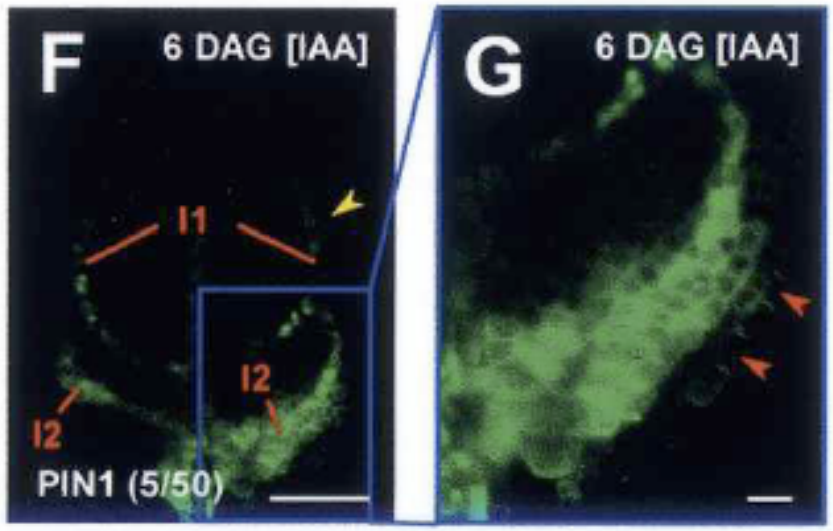


Other polar events: leaf vein development

Scarpella et al. 2006
DR5 and PIN1 in At leaves (bottom)
PIN1 canalization (right)
Auxin application (right, bottom)

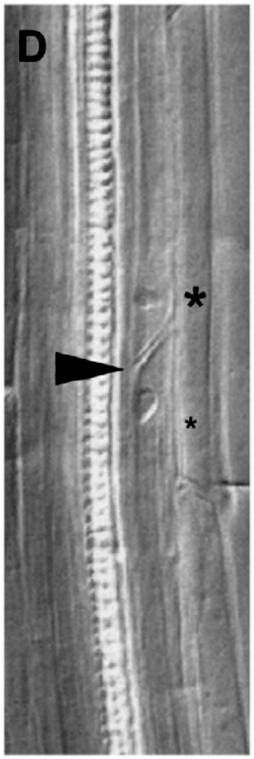




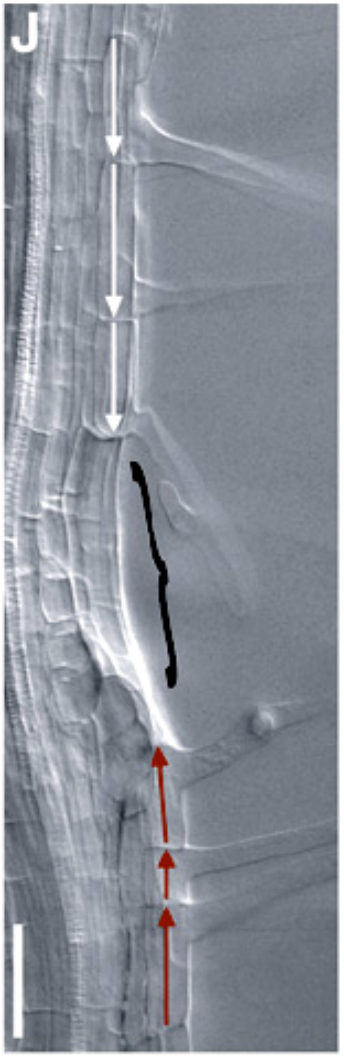


Other polar events…

Pericycle nuclear migration in
LRP founder cells.
De Smet 2007



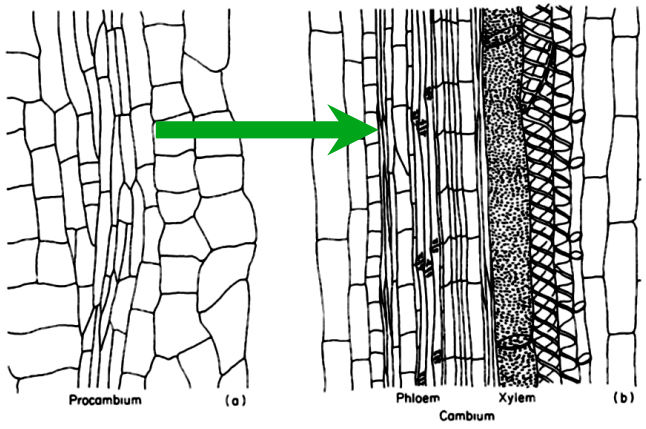
Root hair polarity
Fischer et al. 2006

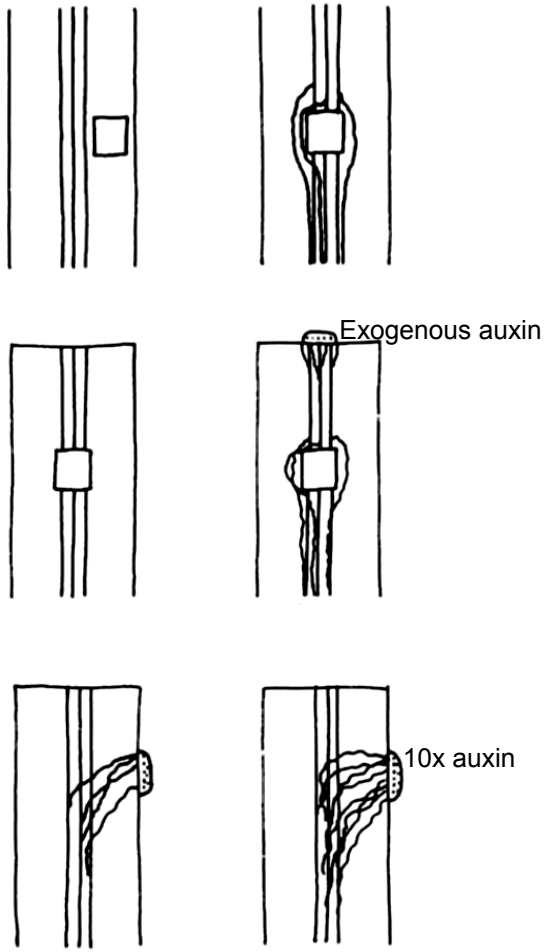


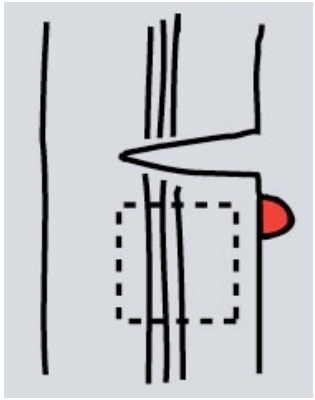
Canalization, histology

Sachs 1981
Vascular differentiation experiments in pea stems.

Hypothesized that auxin reinforces its own flux through positive feedback.

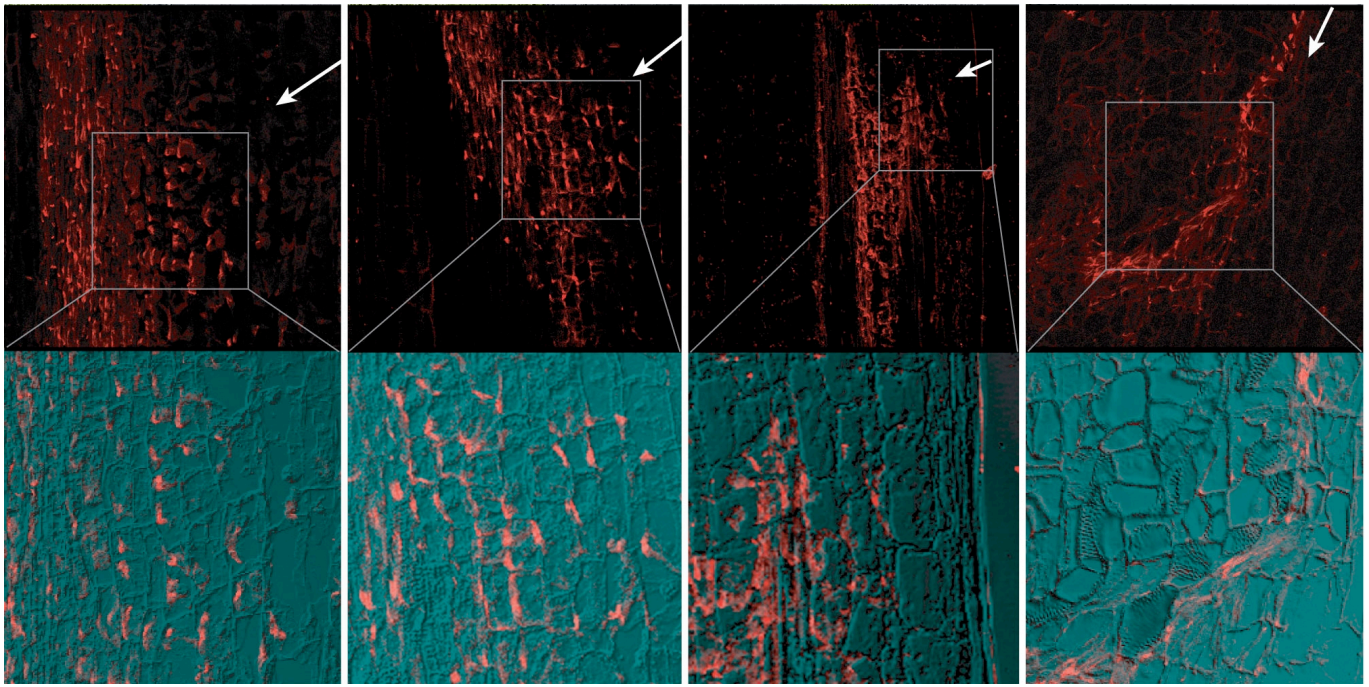






Canalization & PINs

Sauer et al. 2006
Immunolocalization of putative PsPIN1 using AtPIN1 antibodies in pea.

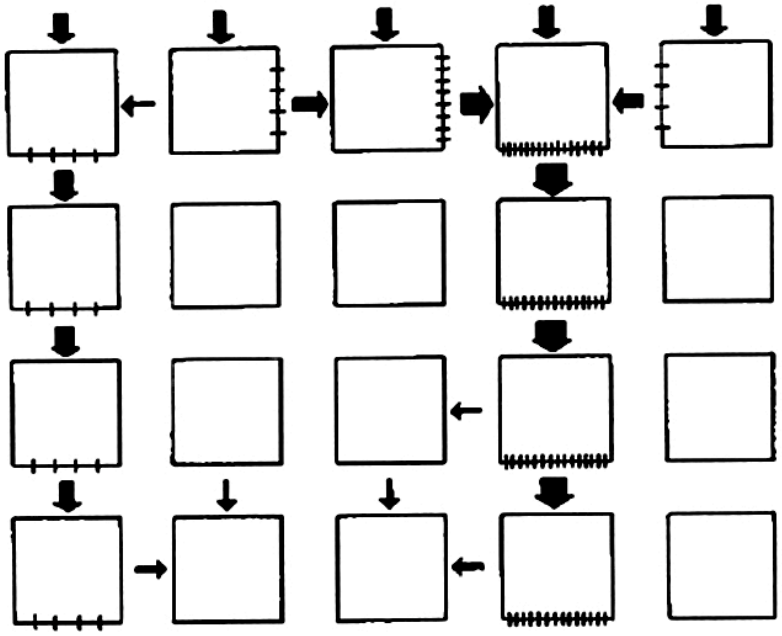


Canalization model

Mitchison 1981

Auxin efflux carriers are recruited to the cell membrane in proportion to the amount of flux through the membrane.
i.e. a positive feedback mechanism.

First computer model of vein formation.

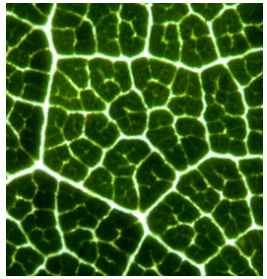


Problems with Canalization Models

Problems with Mitchison's canalization model:

1. Low auxin concentration in canal.

2. In leaves, gives branched vein networks instead of closed mesh.



3. Requires a membrane-bound auxin flux sensor.

4. May only work in simplified models that don't include the apoplast (??).

Problems with Canalization Models

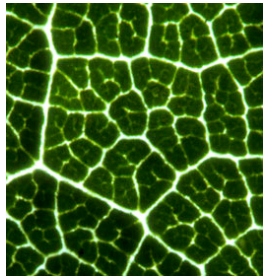
Problems with Mitchison's canalization model:

1. Low auxin concentration in canal.

   Easy to fix: include influx carriers or change the regulation of efflux carriers.

2. In leaves, gives branched vein networks instead of closed mesh.

   Requires additional levels of regulation: moving auxin sources, second signals, or mechanical stress/strain sensors?



3. Requires a membrane-bound auxin flux sensor.

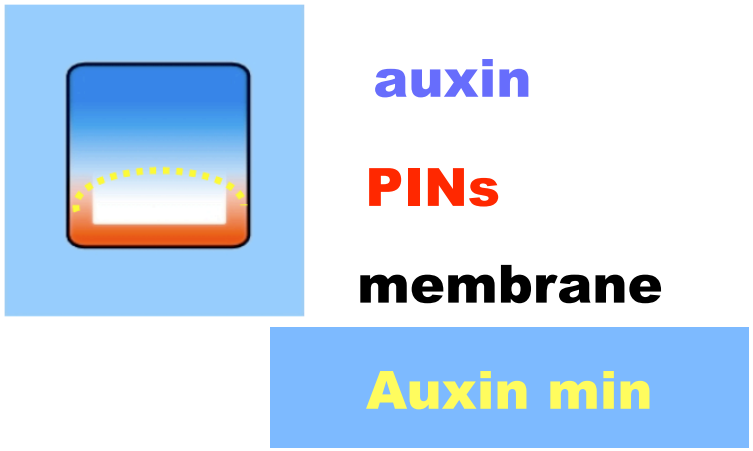
   May not exist. TIR1/AFB acts in nucleus. ABP1 ??

4. May only work in simplified models that don't include the apoplast (??).

   A new hypothesis, based on an analogy with eukaryotic chemical gradient sensing, does work.

A new hypothesis:
Canalization via the cytoplasmic auxin gradient

Kramer 2009



A new hypothesis:
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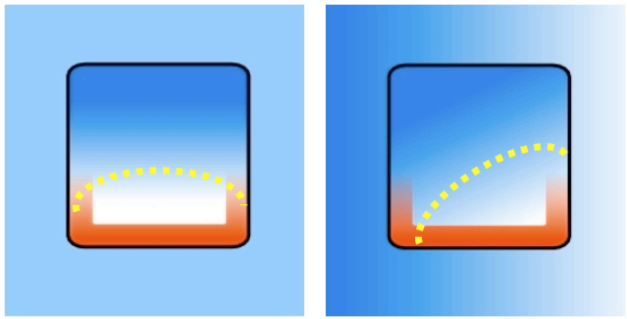
Kramer 2009



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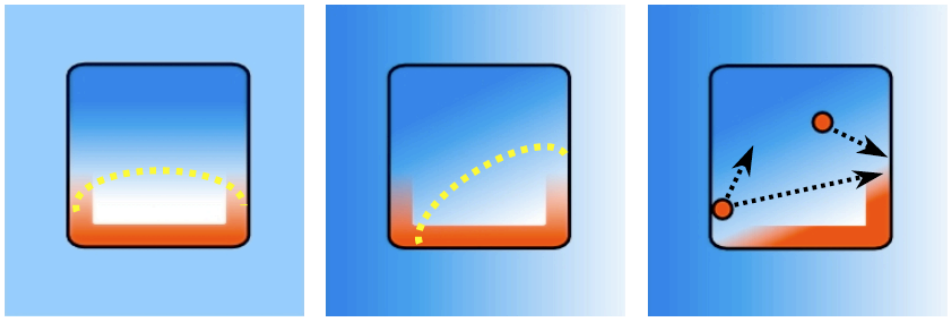
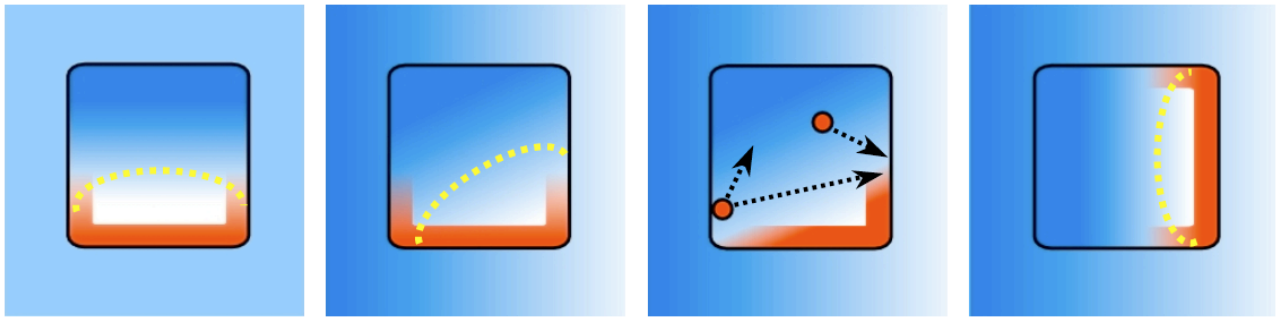


A new hypothesis:
Canalization via the cytoplasmic auxin gradient

Kramer TIPS 2009



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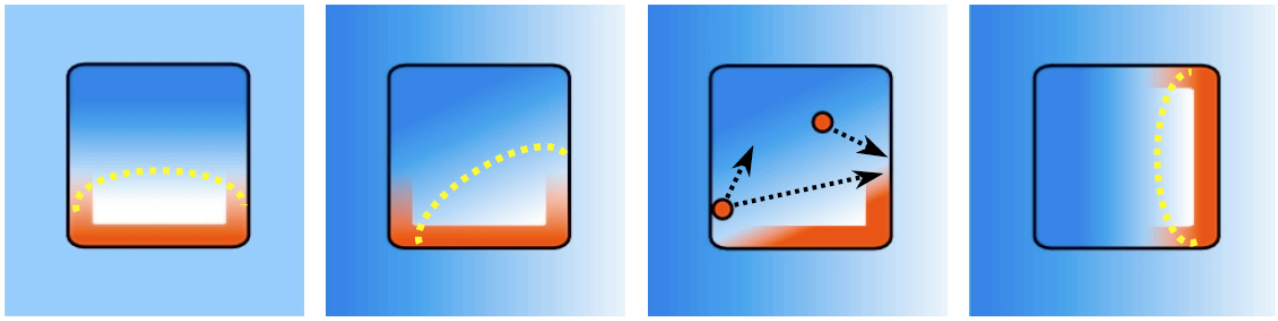
Kramer TIPS 2009



The full canalization model:

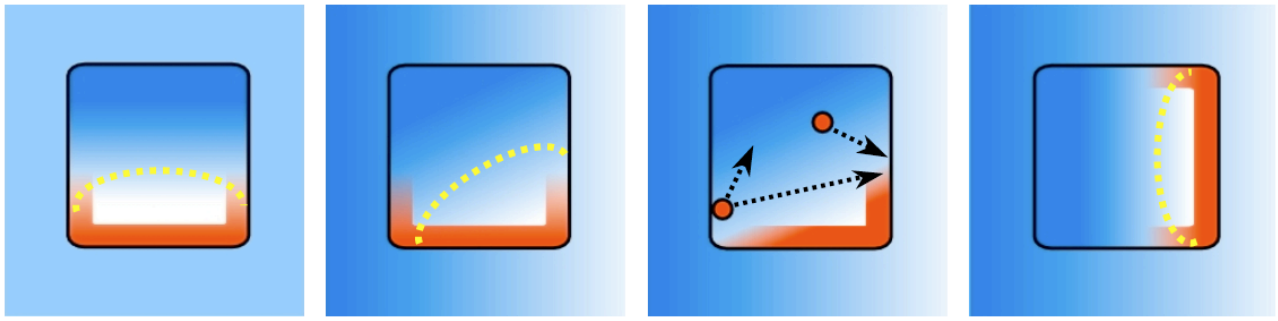
1. If cyt gradient < 1%, cell inactive. No PIN delivered to membrane.

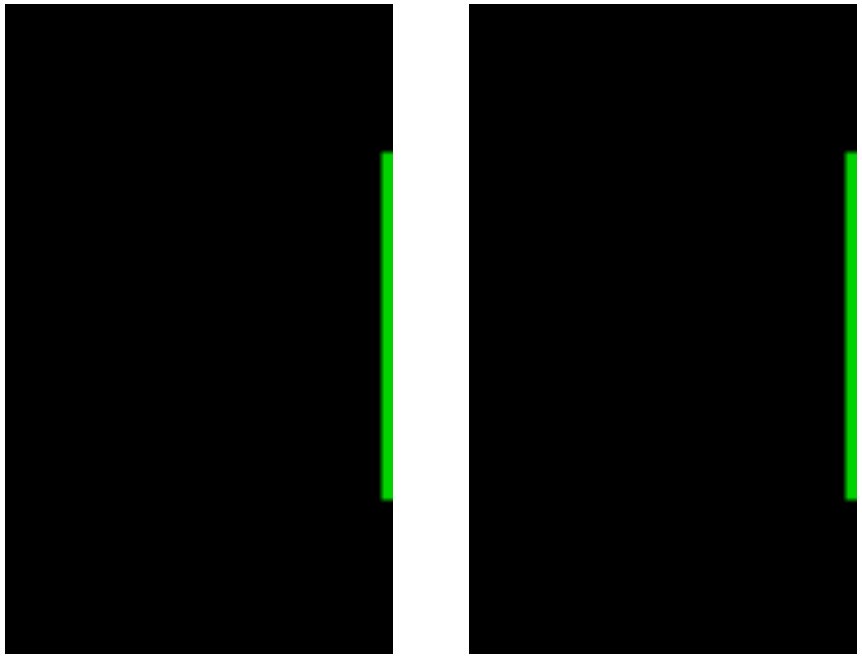
2. If cyt gradient >1%, cell active. PIN produced and delivered to bottom of gradient. Influx carrier (AUX1/LAX) delivered to all membranes.

3. Constitutive PIN endocytosis.

A new hypothesis:
Canalization via the cytoplasmic auxin gradient

Kramer 2009





Conclusions

(1) In arabidopsis, models of auxin transport are beginning to illuminate gene function. A new subdiscipline has started.

(2) In Populus, model of auxin transport in the cambium and wood grain pattern formation works well.

(3) Just one example of an auxin-mediated polar regulatory network in plants.

(4) The receptor and signaling pathways for the polar system remain unknown.

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