Getting to the root of the problem: using maths to feed the world

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with thanks to CPIB, University of Nottingham.

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A bit about me....

- 4 year undergraduate Masters in Maths.
- 4 year PhD in Applied Mathematics sponsored by the paper industry where I worked on an industrial fluid mechanics problem.
- 3.5 years as a Postdoc at the University of Nottingham working in a large interdisciplinary centre looking at plant root growth. Based in Biosciences rather than Maths.
- Lecturer at UoB for three years.

Some random things I've worked on:

- How do plant roots grow?
- How do you put a shiny coating onto paper?
- How should you go about designing a pregnancy testing kit?
- How do currents/waves in the sea affect the performance of towed arrays (long thin cables towed behind a boat for seismic surveying)?
- How do you get drugs into tumours?
- How do fluid flows in the eye affect retinal detachment?
- What's the best way to grow a new bit of tissue to implant into the body or experiment on in the lab?
- How do the anthers in flowers open?
- …

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Interesting mechanics problems with interesting applications! Focus on modelling.

How does a plant root grow?

Why do we care how a plant root grows?!

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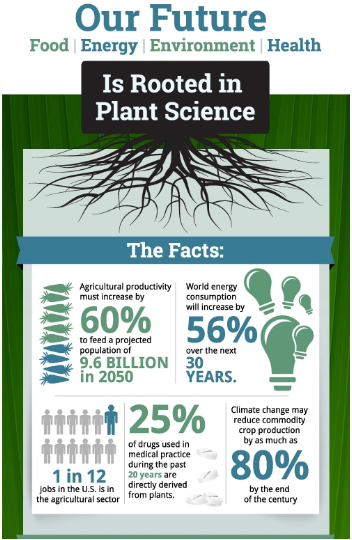
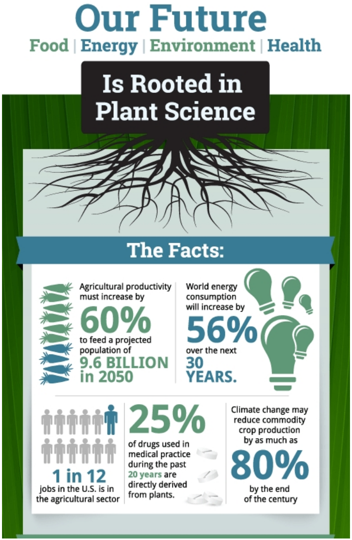


From ASPB blog.

Why do we care how a plant root grows?!



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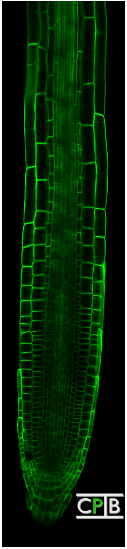
- Everything we eat ultimately comes from plants - food security.
- By understanding how a plant root grows we can make it grow “better” in difficult environments (e.g. drought).
- Healthy plant root = healthy plant.
- Plant roots are a good “model organ” - if we understand how these grow we can say things about other bits of the plant.

Plant root growth



- Takes a cell around 100 hours to move through the division zone undergoing division.
- Then takes 6 hours to pass through the elongation zone whilst the cell length increases 30 fold (but with minimal radial expansion).
- Video.

Simplified mechanics of plant root cell growth

- Tough cell wall containing oriented cellulose microfibrils embedded within a pectin ground matrix.
- Cell is subject to high internal turgor pressure which is regulated very quickly by the cell, and so may be approximated as constant.
- The turgor pressure exerts a tension in the cell wall; if this tension is above a yield stress the wall will extend and exhibit irreversible growth in length with minimal radial expansion.

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Aside:

A bit like blowing up a balloon - internal pressure stretches the wall making it expand.

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Cell case: Constant pressure with varying wall properties so cell expands.

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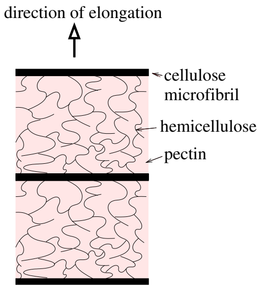
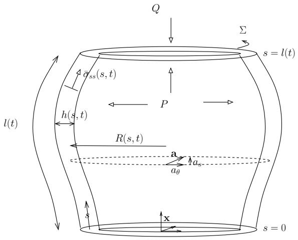
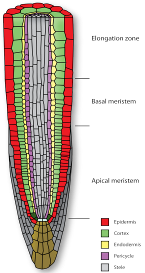
- Current models used by biologists are variations on the "Lockhart" model (1965)

$$\frac{1}{l}\frac{dl}{dt} = \Phi\left(\Delta P - Y\right).$$

Multiscale process





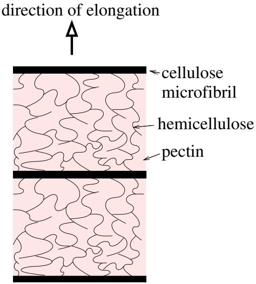


Cell wall

Single cell

Multicellular root

Multiscale process



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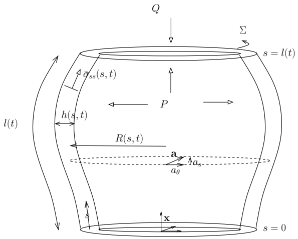
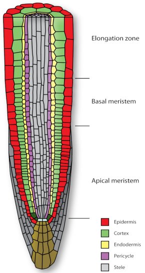


Single cell



Multicellular root

Modelling assumptions:

- Approximate cell as a pressurised hollow axisymmetric sheet with rigid end plates.
- Model cell wall as consisting of fibres embedded within a ground matrix - *i.e.* a fibre-reinforced material.
- We are interested in the long-timescale growth behaviour of the cell wall - therefore assume the wall is permanently yielded, so consider a viscous fluid.
- Exploit the geometry - the cell wall is much thinner than the radius of the cell so employ asymptotic analysis.

Modelling assumptions:

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Solution procedure

Following Van der Fliert, Howell and Ockendon (1995),

- conservation of mass with a source term representing deposition of new material,

$$\nabla \cdot \mathbf{U} = F(\mathbf{x}, t),$$

- conservation of momentum neglecting inertial effects

$$\nabla \cdot \boldsymbol{\sigma} = 0.$$

For a Newtonian fluid:

$$\sigma_{ij} = -p\delta_{ij} + 2\mu e_{ij}.$$

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For a fibre reinforced fluid:

$$\sigma_{ij} = -p\delta_{ij} + 2\mu e_{ij} + a_i a_j \left(\mu_1 + \mu_2 \zeta\right) + 2\mu_3 \left(a_i a_l e_{jl} + a_j a_m e_{mi}\right),$$

where

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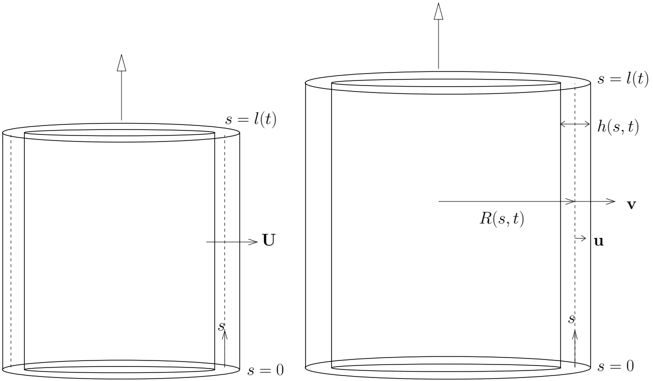
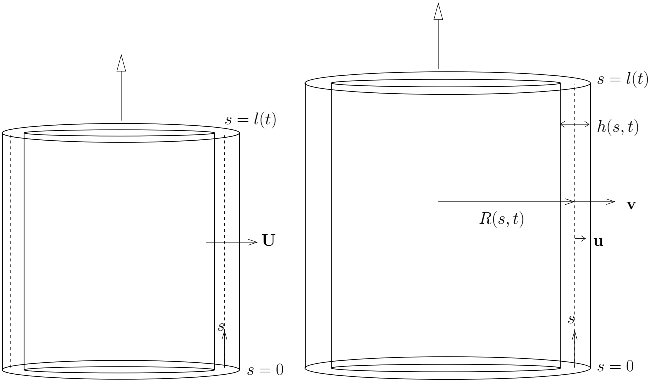
The fibre director field, **a**, evolves according to:

$$\frac{\partial \mathbf{a}}{\partial t} + \mathbf{U} \cdot \nabla \mathbf{a} + \zeta \mathbf{a} = \mathbf{a} \cdot \nabla \mathbf{U}.$$

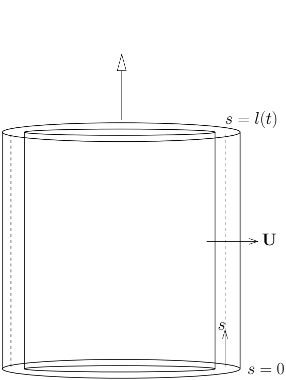
Write everything in terms of a moving curvilinear coordinate system, fixed within the moving sheet.



The position of the centre-surface, $R(s,t)$, and thickness of the sheet, $h(s,t)$, form part of the solution.

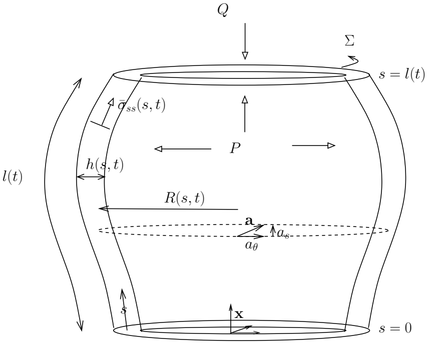


Decompose total fluid velocity, $\mathbf{U}$, into velocity of the centre-surface, $\mathbf{v}$, and the fluid velocity relative to the moving centre-surface, $\mathbf{u}$, so that $\mathbf{U} = \mathbf{v} + \mathbf{u}$.



- Assume the wall is thin compared to the length/radius of the cylinder. Find
  - no variations across the thickness of the wall - plug flow.
  - any normal movement is due to the whole sheet moving.
- Assume axisymmetry so no dependence on angle round cylinder.
- Assume centre-line of cylinder is straight.
- Everything is a function of the length along the cylinder, s, and time, t, only.

Model



$$\frac{\partial}{\partial t}(Rh) + \frac{\partial}{\partial s}(u_s Rh) = F(s,t), \qquad \kappa_s \bar{\sigma}_{ss} + \kappa_\theta \bar{\sigma}_{\theta\theta} = P,$$

$$\frac{\partial}{\partial s}\left(R^2 \kappa_\theta \bar{\sigma}_{ss}\right) = PR\frac{\partial R}{\partial s}, \qquad \frac{\partial}{\partial s}\left(R^2 \bar{\sigma}_{s\theta}\right) = 0,$$

where $\bar{\sigma}$ are the integrated stress components (so $\bar{\sigma}_{ss}$ gives the axial tension etc.), κ are the curvatures.

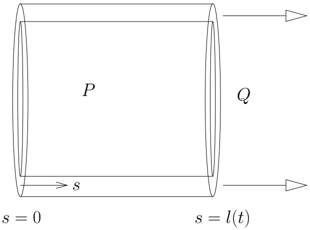
If we assume there is no normal component of the fibre director field, take $\mathbf{a} = \cos\phi \mathbf{e}_\theta + \sin\phi \mathbf{e}_s$, we find

$$\begin{aligned} \frac{\partial \phi}{\partial t} + (u_s + v_s)\frac{\partial \phi}{\partial s} &= -\sin^2\phi \left(\frac{\partial u_\theta}{\partial s} - \frac{u_\theta}{R}\frac{\partial R}{\partial s} \right) \\ &\quad + \sin\phi\cos\phi \left(\frac{\partial u_s}{\partial s} - \frac{1}{R}\frac{DR}{Dt} \right). \end{aligned}$$

$$
\begin{aligned}
\bar{\sigma}_{ss} &= \frac{2h}{R}\mu\left(2R\frac{\partial u_s}{\partial s}+\frac{DR}{Dt}\right)+ha_s^2\left(\mu_1+\mu_2\zeta\right)\\
&+ 4h\mu_3\left(a_s^2\frac{\partial u_s}{\partial s}+\frac{a_s a_\theta}{2}\left(\frac{\partial u_\theta}{\partial s}-\frac{u_\theta}{R}\frac{\partial R}{\partial s}\right)\right),\\
\bar{\sigma}_{s\theta} &= h\mu\left(\frac{\partial u_\theta}{\partial s}-\frac{u_\theta}{R}\frac{\partial R}{\partial s}\right)+ha_s a_\theta\left(\mu_1+\mu_2\zeta\right)\\
&+ 2h\mu_3\left(\frac{1}{2}\left(\frac{\partial u_\theta}{\partial s}-\frac{u_\theta}{R}\frac{\partial R}{\partial s}\right)+\frac{a_s a_\theta}{R}\left(\frac{DR}{Dt}+R\frac{\partial u_s}{\partial s}\right)\right),\\
\bar{\sigma}_{\theta\theta} &= \frac{2h}{R}\mu\left(R\frac{\partial u_s}{\partial s}+2\frac{DR}{Dt}\right)+ha_\theta^2\left(\mu_1+\mu_2\zeta\right)\\
&+ 4h\mu_3\left(\frac{a_\theta^2}{R}\frac{DR}{Dt}+\frac{a_s a_\theta}{2}\left(\frac{\partial u_\theta}{\partial s}-\frac{u_\theta}{R}\frac{\partial R}{\partial s}\right)\right),
\end{aligned}
$$

$$
\zeta = \left(\frac{a_\theta^2}{R}\frac{DR}{Dt}+a_\theta a_s\left(\frac{\partial u_\theta}{\partial s}-\frac{u_\theta}{R}\frac{\partial R}{\partial s}\right)+a_s^2\frac{\partial u_s}{\partial s}\right).
$$

Boundary conditions on $s = l\,(t)$



applied torque:

$$\bar{\sigma}_{s\theta}(l,t) = \Sigma$$

prescribed end radius:

$$R(l,t) = R_0(l_0)$$

Pressure acting on end plate is balanced by the tension in walls and external compressive force:

$$\bar{\sigma}_{ss} = \frac{(P-Q)R}{2\left(1-\left(\frac{\partial R}{\partial s}\right)^2\right)^{1/2}}$$

fluid velocity = elongation rate:

$$u_s\,(l,t) = \frac{dl}{dt}$$

Do the simplest case first...

- Fibres are horizontal – $\phi = 0$ satisfies the evolution equation identically, so they stay horizontal, azimuthal components decouple.
- Assume there is **exactly** enough deposition (*i.e.* we pick $F(s,t)$ appropriately in the conservation of mass equation) to make the thickness of the wall constant $h \equiv h_0$.
- If we take the material to be really hard to stretch in the fibre direction ($\mu_2 + 4\mu_3$ to be big), we find a solution in which the radius is approximately constant (*i.e.* R_0).
- Leaves us to solve

$$\frac{\partial \bar{\sigma}_{ss}}{\partial s} = 0, \qquad \bar{\sigma}_{ss} = 4\mu\left(s,t\right) h_0 \frac{\partial u_s}{\partial s}.$$

If we assume $\mu = \mu(t)$ this reduces to

$$\frac{1}{l}\frac{dl}{dt} = \frac{R_0}{8\mu\left(t\right)h_0}\left(P - Q - 0\right).$$

If we compare this to the Lockhart model

$$\frac{1}{l}\frac{dl}{dt} = \Phi\left(\Delta P - Y\right),$$

we now have the extensibility Φ in terms of the physical parameters R_0, h_0 and μ.

We have

$$\Phi = \frac{R_0}{8\mu(t)\,h_0},$$

for horizontal fibres. But what about the non-zero fibre angle?

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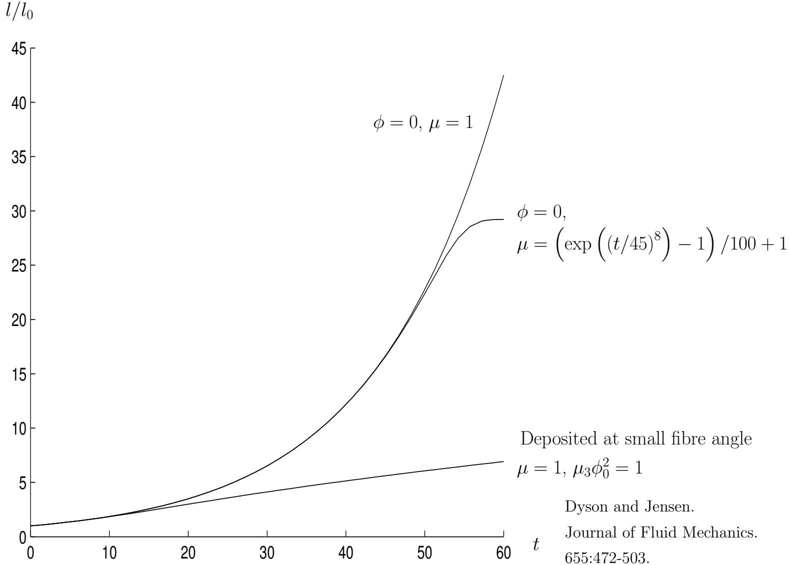
for horizontal fibres. But what about the non-zero fibre angle?

Much harder to solve!

Small fibre angle

- Continual deposition of new fibres at a constant (non-zero but small) angle onto inner wall.
- Fibre angle increases as fibres are carried through the elongating wall.

$$\frac{1}{l}\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{R_0(P-Q)}{8h_0\left(\mu+\mu_3\phi_0^2\left(2l/l_0-1-(1+\log(l/l_0))^2\right)\right)},$$

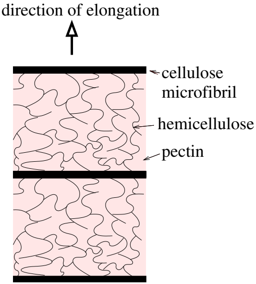


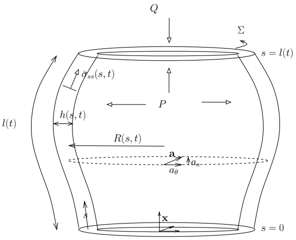
Dyson and Jensen.
Journal of Fluid Mechanics.
655:472-503.

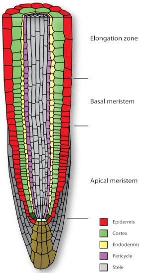
Conclusion part 1:

- Lockhart works pretty well, and now we can identify the factors which appear in the "extensibility".
- Modified Lockhart equation which takes into account fibre reorientation.
- In the simplest case, everything collapsed to considering a flat sheet of fluid.

Multiscale process





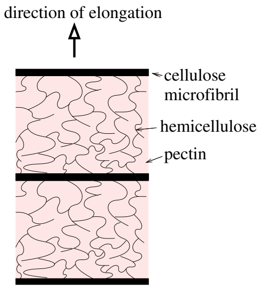


Cell wall

Single cell

Multicellular root

Multiscale process



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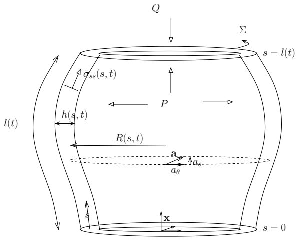

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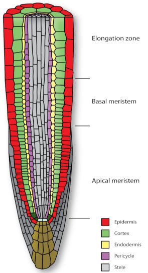
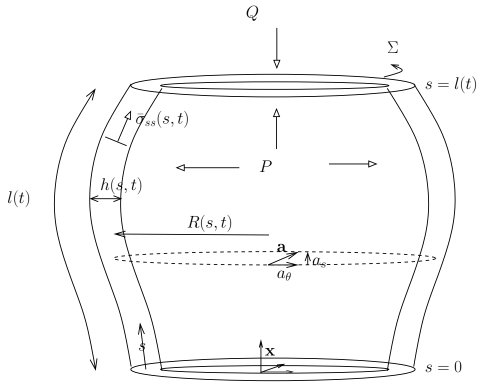
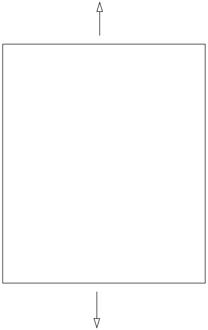


Multicellular root

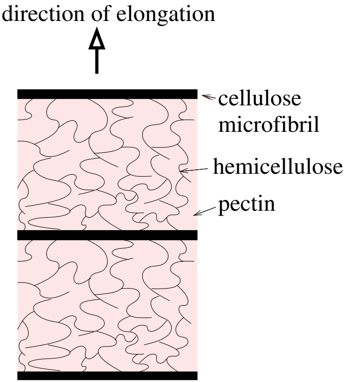


Q
Σ
$s = l(t)$
$\bar{\sigma}_{ss}(s,t)$
P
$l(t)$
$h(s,t)$
$R(s,t)$
$\mathbf{a}$
a_s
a_θ
s
$\mathbf{x}$
$s = 0$

Single cell

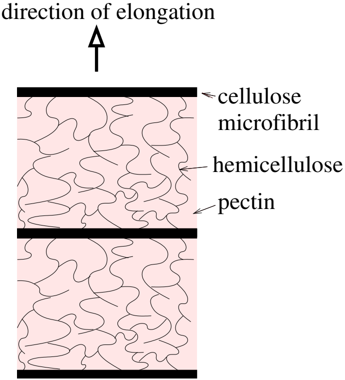


Sheet of fluid



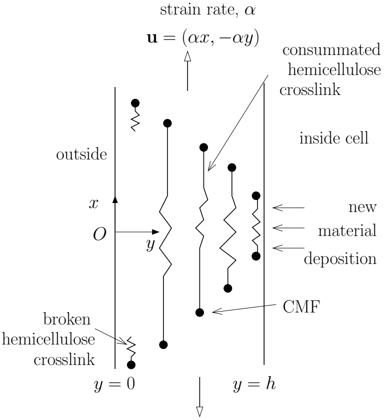
Sheet of wall material

Wall properties are controlled by hormones via enzyme action



- Cell wall is a complex structure.
- Enzymes act on
  - pectin (altering viscosity)
  - hemicellulose network (breaking or lengthening bonds).
- Mechanical effects can be considered separately - focus on hemicellulose network.

Wall properties



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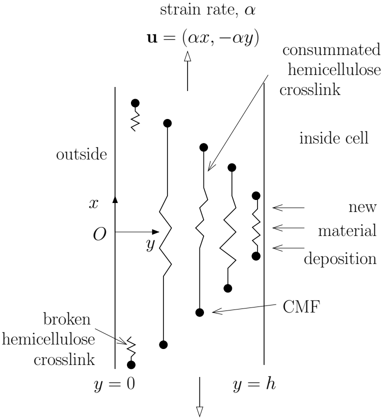


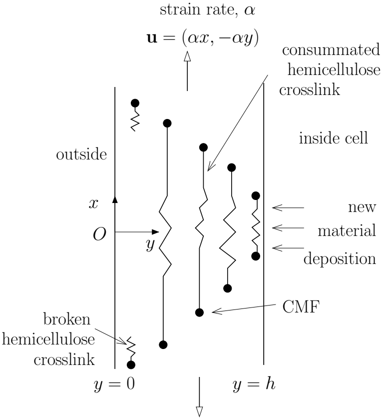
$$\frac{\partial n(y,t)}{\partial t} + u_y \frac{\partial n(y,t)}{\partial y} = -k_{\text{off}}\, n(y,t),$$

$$k_{\text{off}} = k_0 \exp\left(\frac{\kappa\,(L - L_0)^2}{2 k_b T} \right),$$

$$L = L_0 h / y,$$

$$n|_{y=h} = n_0,$$

Wall properties



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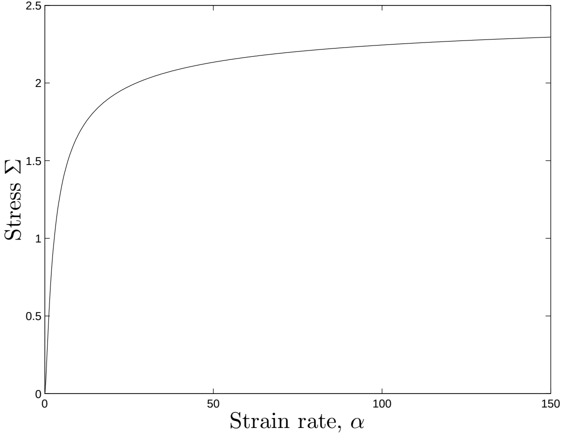
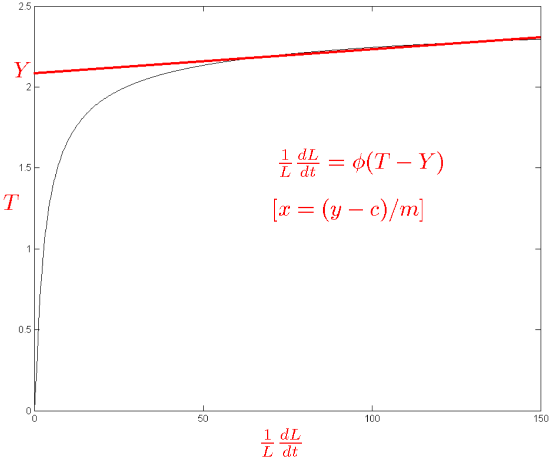
$$\Sigma = \int_0^h n(y,t)\kappa\,(L - L_0)\ \mathrm{d}y.$$

Mechanical behaviour

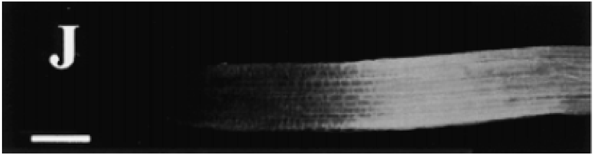


Mechanical behaviour

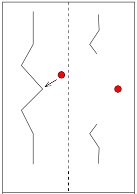


Dyson, Band and Jensen, 2012

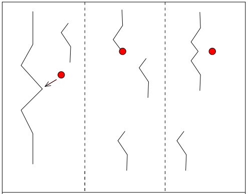
- Vissenberg *et al.* (The Plant Cell, 2000) show that XTH (enzyme) levels are high in the elongation zone:



Enzyme action



XEH action



XET action

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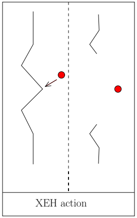
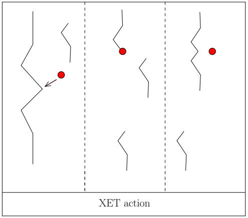




$$\frac{\partial n(y,t)}{\partial t} + u_y \frac{\partial n(y,t)}{\partial y} = -k_{\text{off}}\, n(y,t),$$

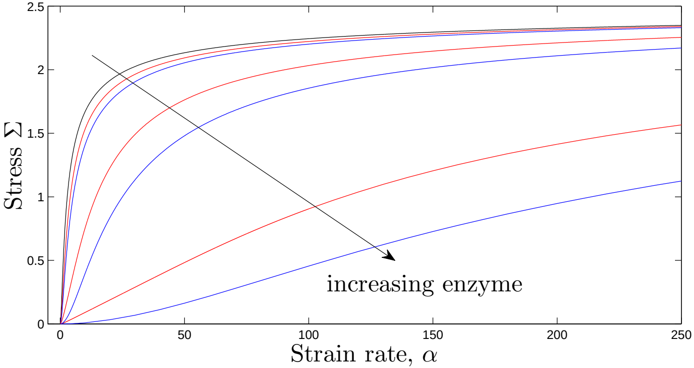
$$k_{\text{off}} = k_0 \left(\exp\left(\frac{\kappa\,(L-L_0)^2}{2k_bT} \right) + g_{XET} + g_{XEH} \right),$$

$$n|_{y=h} = n_0$$

$$+ \int_0^h \frac{k_0 g_{XET}}{\alpha} \exp\left(\frac{\kappa\,(L-L_0)^2}{2k_bT} \right) n \,\mathrm{d}y,$$

$$\Sigma = \int_0^h n(y,t)\kappa\,(L-L_0)\,\mathrm{d}y.$$

Mechanical behaviour with enzyme effects



- XEH action only blue lines.
- XET action only red lines.

Conclusion part 2:

- Lockhart works pretty well, and now we can identify the factors which appear in the “extensibility”.

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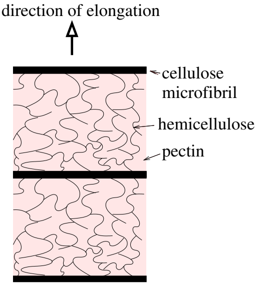
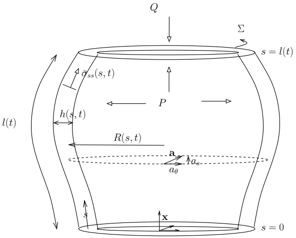
- Lockhart works pretty well, and now we can identify what governs the yield stress and link enzyme action with changes to mechanical properties.

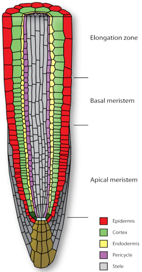
Multiscale process



Cell wall

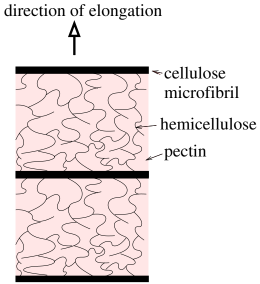


Single cell

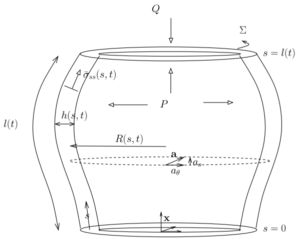


Multicellular root

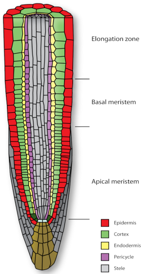
Multiscale process



Cell wall

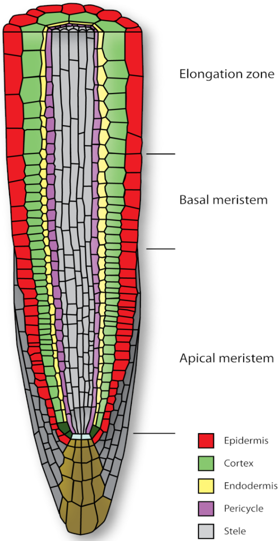


Single cell



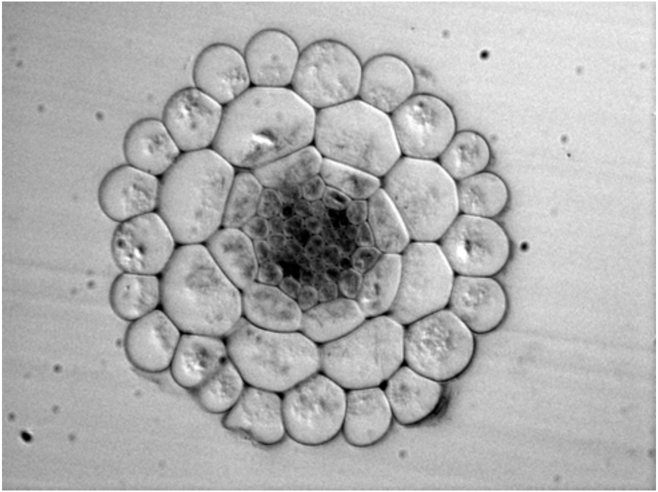
Multicellular root

Multicellular root

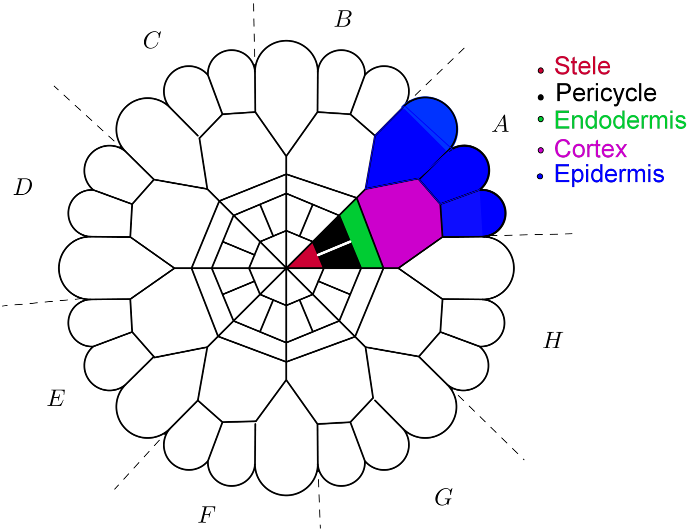


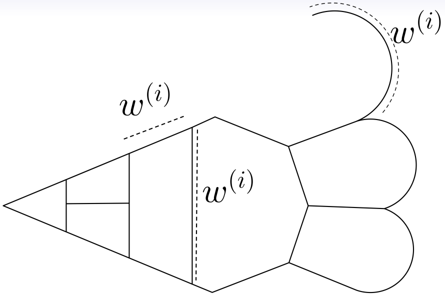
- Multiple different cell files.
- Each cell file's properties can vary independently.
- Cells are tightly stuck together.
- But all the cells in a given cross section grow at the same rate.
- Which cell file has the biggest effect on the growth?

Actual root structure



Approximation of root structure





Each bit of wall grows according to:

$$\frac{1}{L}\frac{dL}{dt} = \phi_i \left(T_i - \bar{Y}_i\right).$$

where

$$\bar{Y}_i = \int_0^{h_i} Y \, \mathrm{d}y,$$

$$\phi_i = 1/\int_0^{h_i} 4\mu_i(y) \, \mathrm{d}y$$

Then force balance on top plate gives:

$$PA = \sum T_i w^{(i)},$$

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Hence whole slice grows according to

$$\frac{1}{L}\frac{dL}{dt} = \phi_{\mathrm{eff}}\left(PA - Y_{\mathrm{eff}}\right),$$

$$\frac{1}{\phi_{\mathrm{eff}}} = \sum \frac{w^{(i)}}{\phi_i},$$

$$Y_{\mathrm{eff}} = \sum w^{(i)} \bar{Y}_i.$$

Then force balance on top plate gives:

$$PA = \sum T_i w^{(i)},$$

Hence whole slice grows according to

$$\frac{1}{L}\frac{dL}{dt} = \phi_{\text{eff}} \left(PA - Y_{\text{eff}}\right),$$

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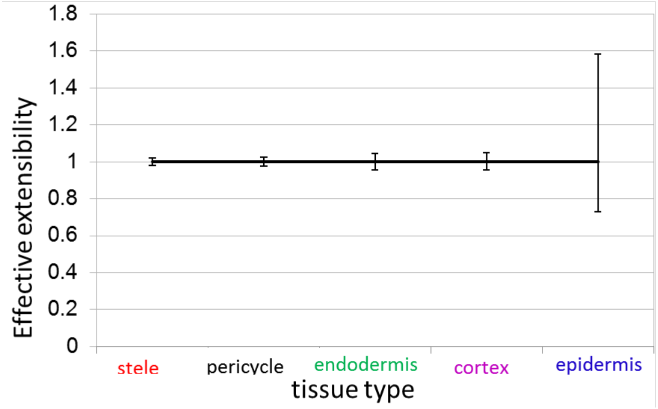
Effective extensibilities



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Final conclusions

- Lockhart works pretty well!
- Identified the geometric and mechanical factors which govern the mechanical growth of a plant root, exploiting mathematical models at different spatial scales.
- We can link molecular level changes in plant cells (via enzyme levels) to changes in the plant phenotype (i.e. what the whole root looks like). Make predictions without doing costly experiments.