

Engineering and physical challenges to engineered crops

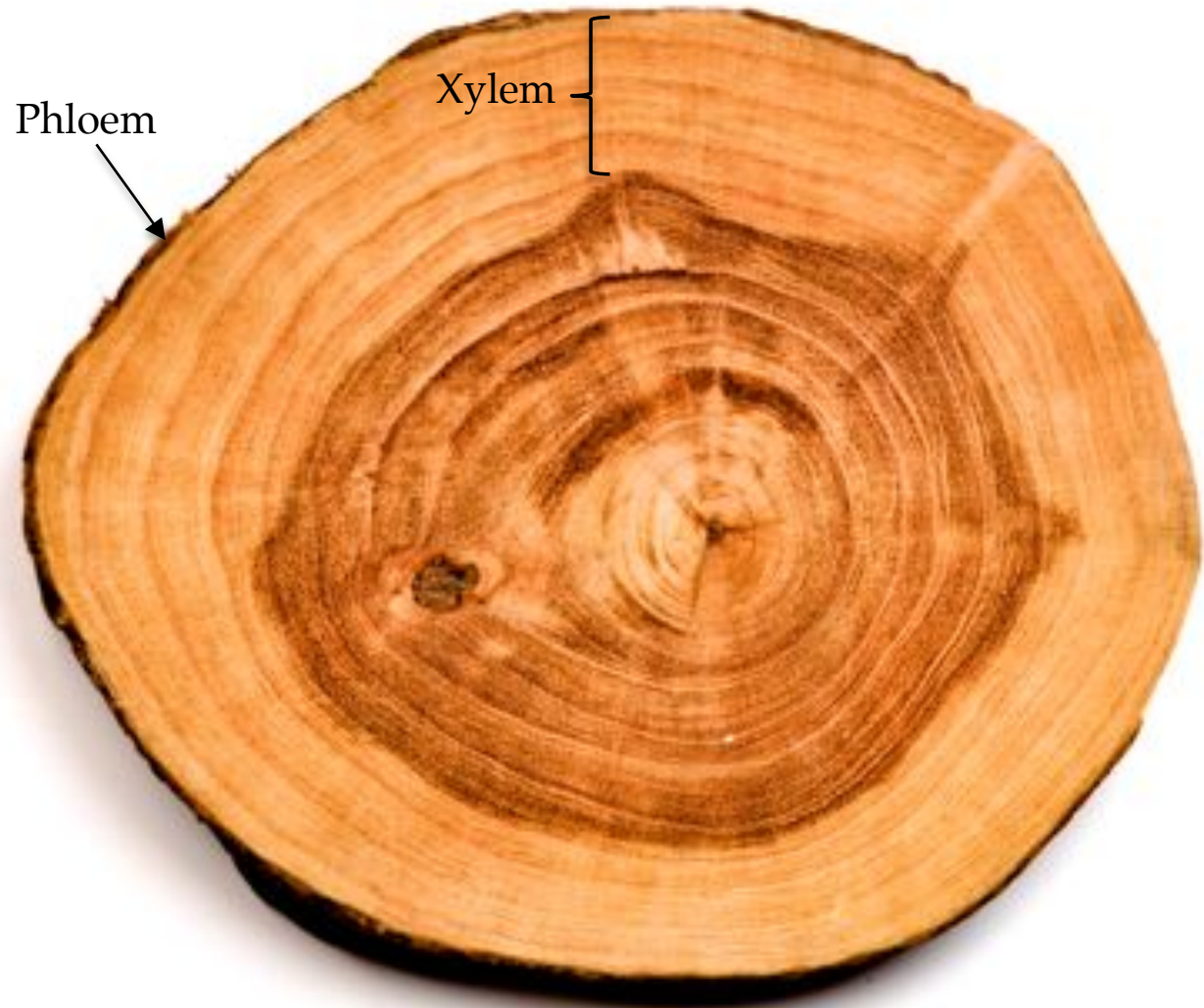
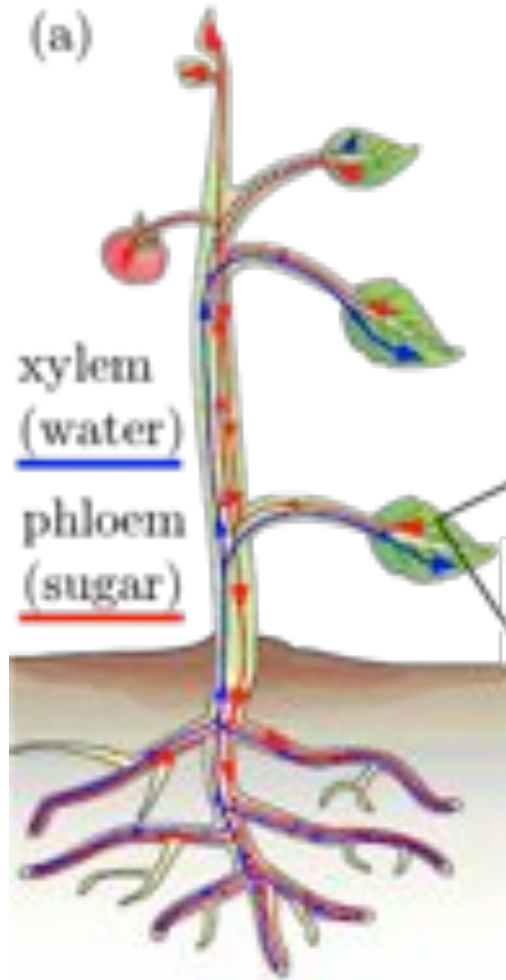
KAARE H. JENSEN
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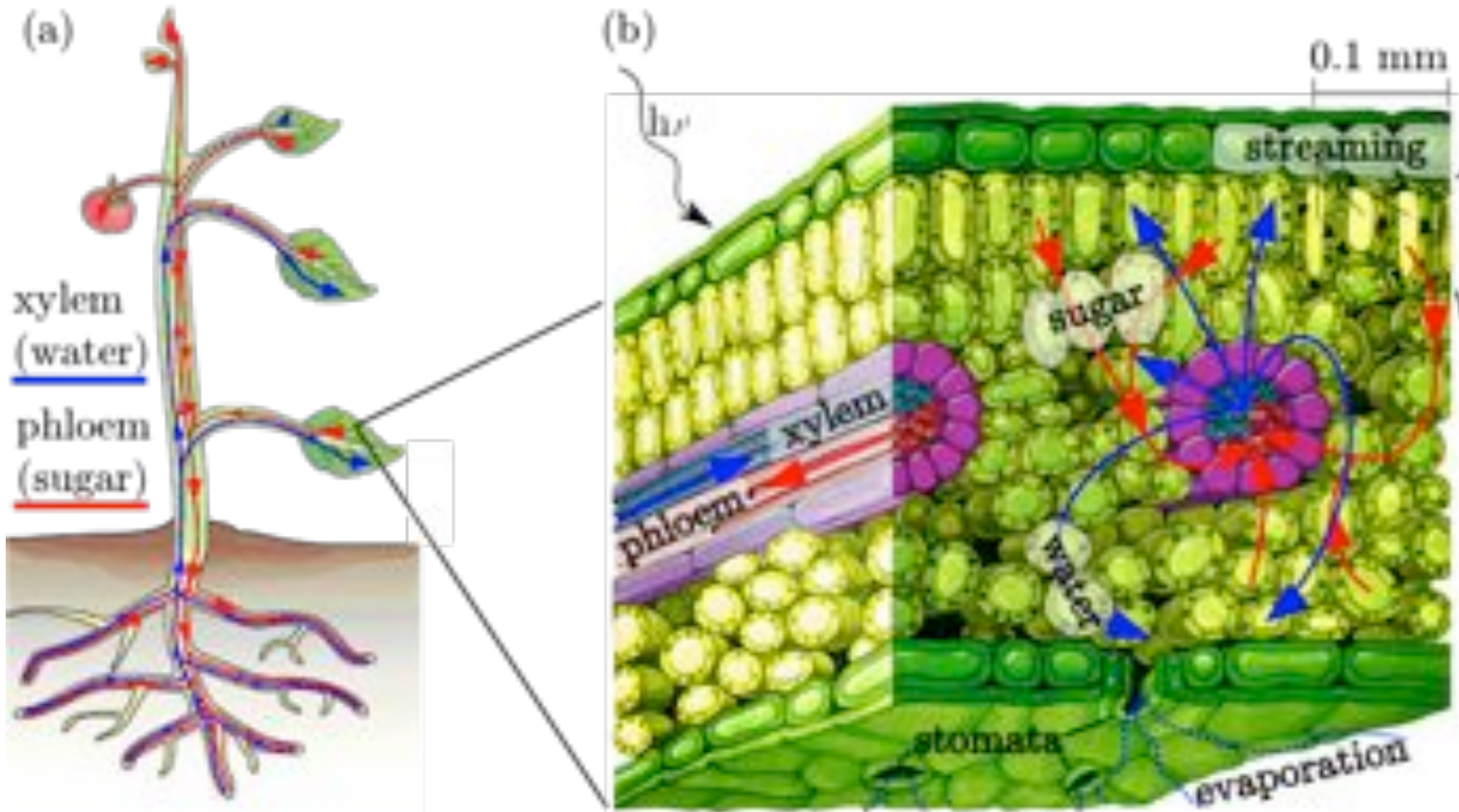
Why study sugar transport in plants?



Liquid dynamics in plants



Liquid dynamics in plants



Liquid dynamics in plants

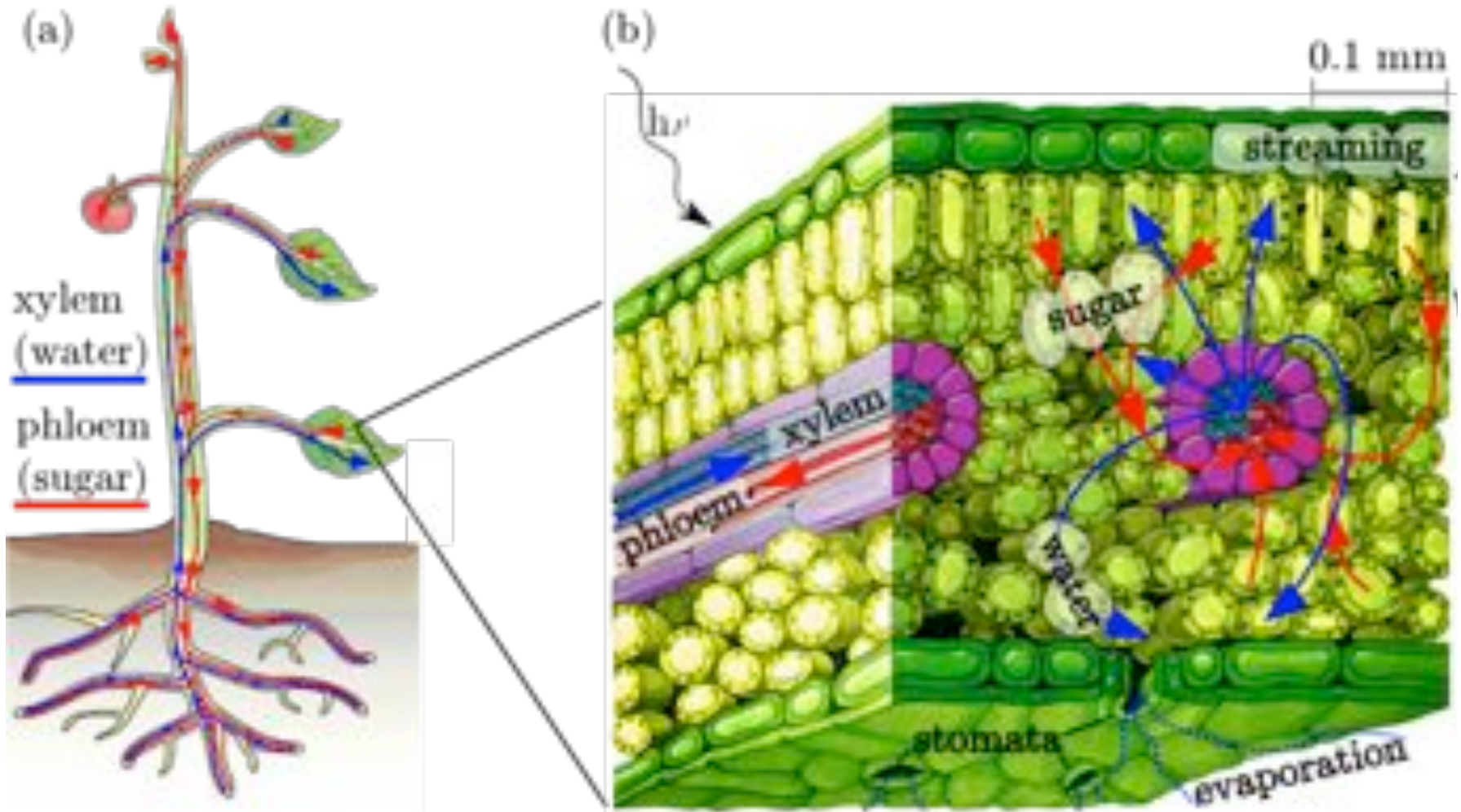
Phloem

- Sugar transport
 - Sugar: 1 kg/day
 - Water: 4 kg/day
- Cell diameter: 10 μm
- Flow velocity: 100 $\mu\text{m/s}$
- Reynolds number: 10^{-3}

Xylem

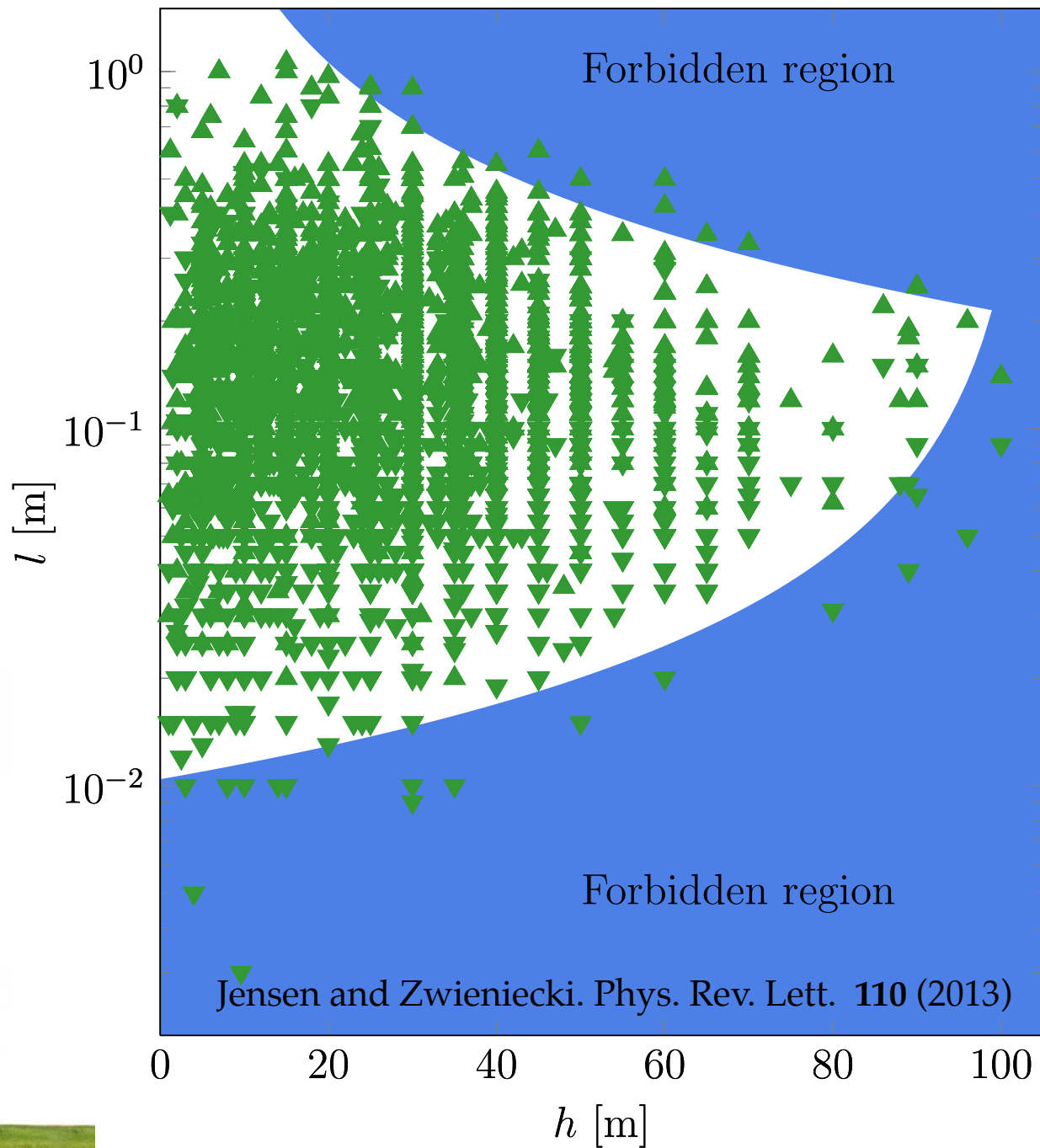
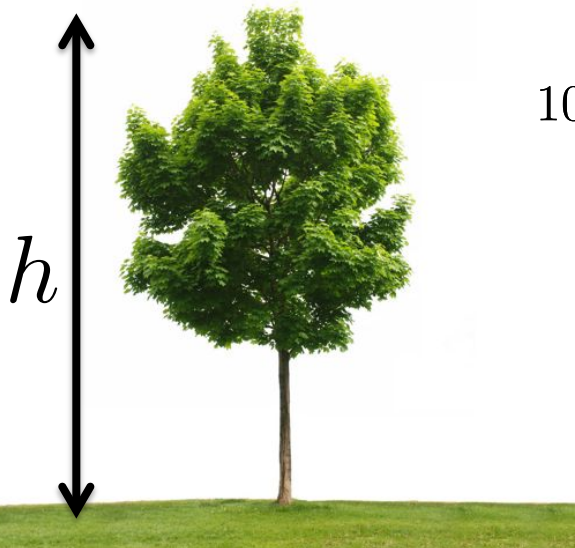
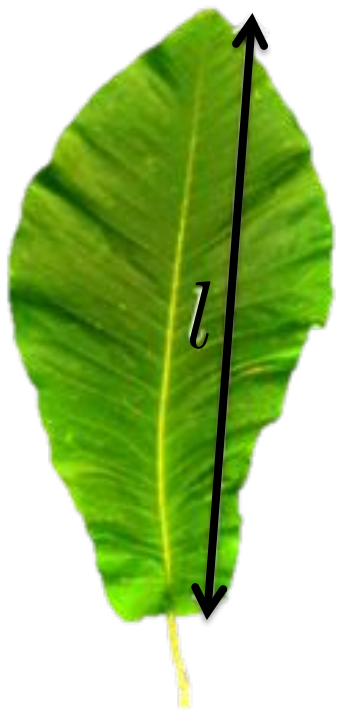
- Water transport
 - Water uptake: 100 kg/day
 - Evaporation: 95 kg/day
 - Photosynthesis: 1 kg/day
 - Phloem: 4 kg/day
- Cell diameter: 100 μm
- Flow velocity: 1 mm/s
- Reynolds number: 10^{-1}

Physical challenges

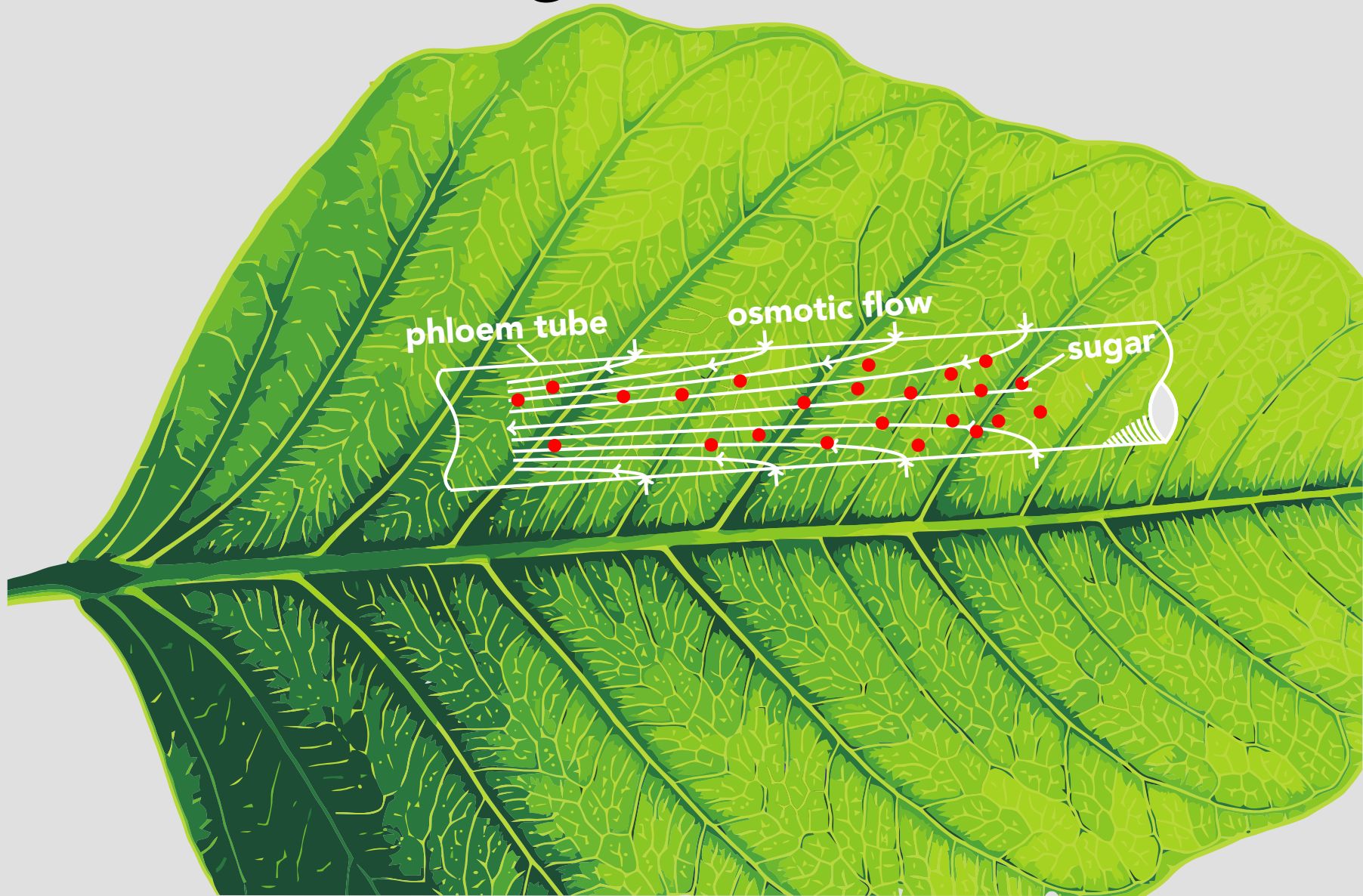


Leaf size

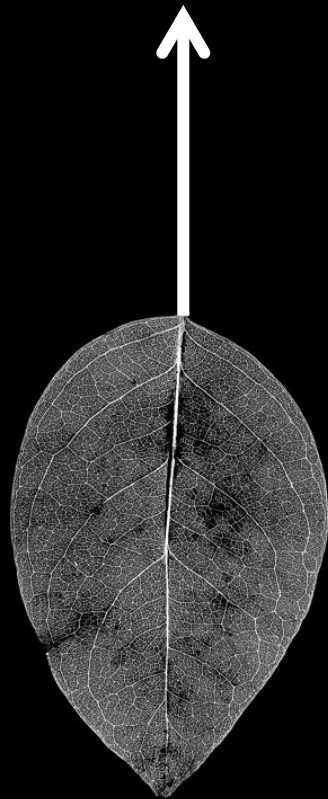




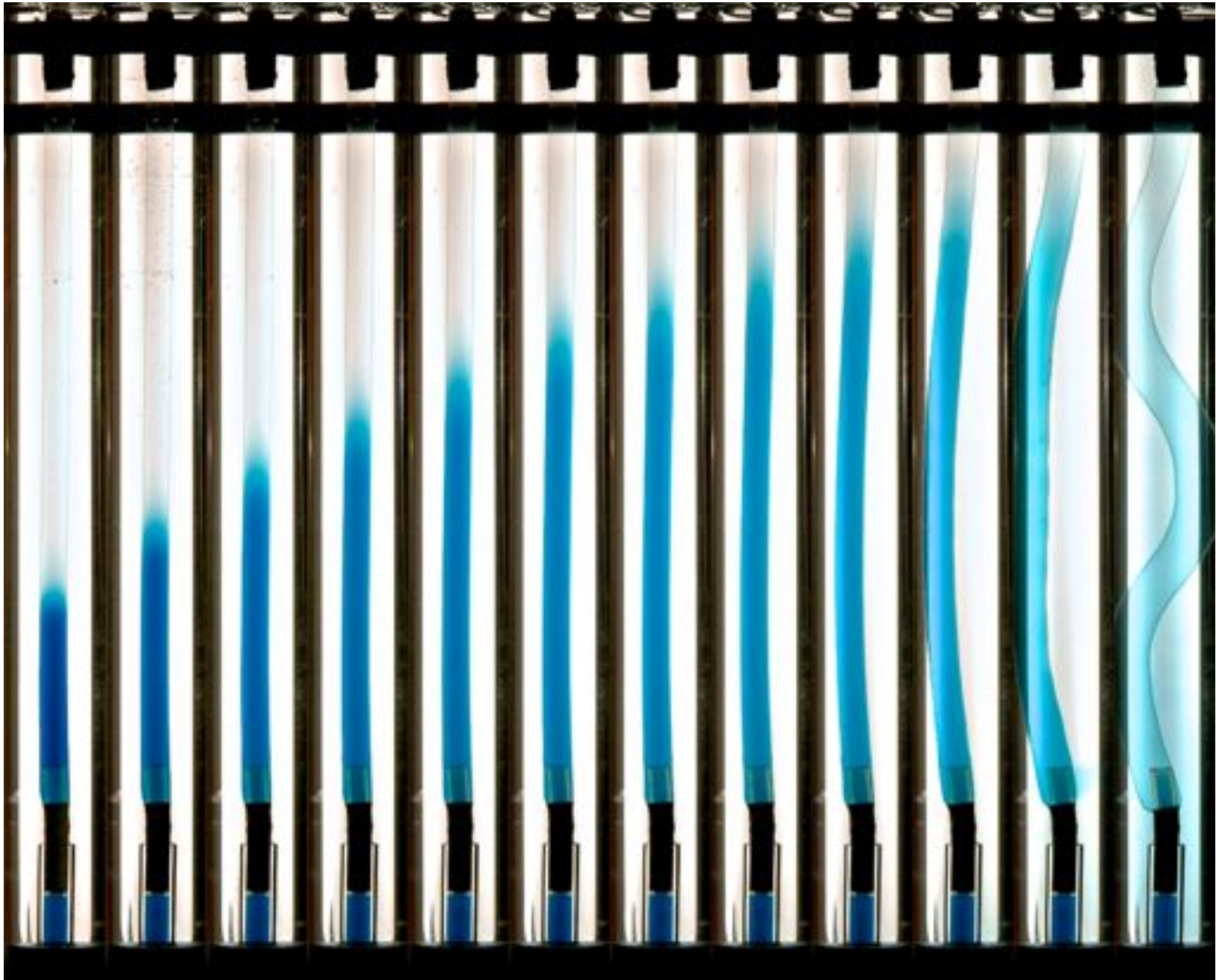
Sugar flow



The leaf, an osmotic pump



1 cm, 5 frames/hour

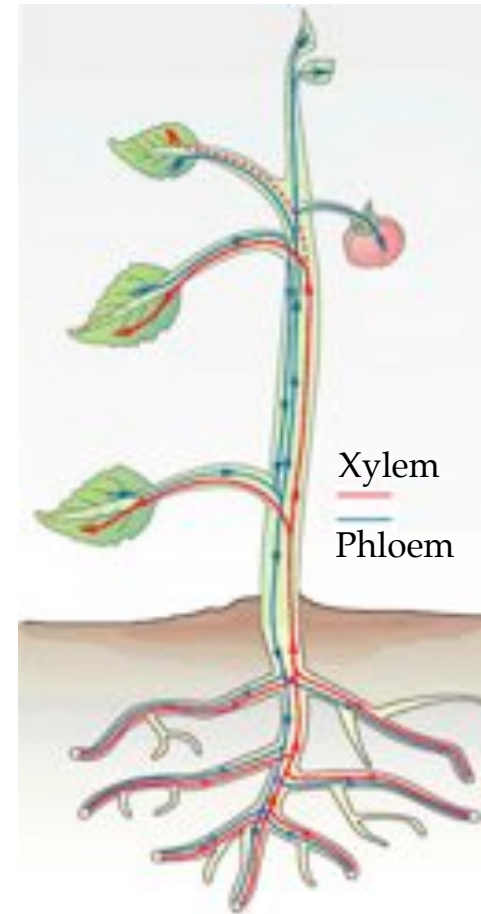


Sugar speed – scaling analysis

- Leaf dominant $R_l = \frac{1}{2\pi r l L_p}$
 $u = \frac{2L_p l}{r} \Delta p$

- Stem dominant $R_s = \frac{8\eta h}{\pi r^4}$
 $u = \frac{r^2}{8\eta h} \Delta p$

- Münch number $M\ddot{u} = \frac{\text{STEM}}{\text{LEAF}} = \frac{16L_p \eta l h}{r^3}$



Engineering challenge #1: Measuring phloem flow speed

- Radioactive tracers

Minchin and Troughton
Ann. Rev. Plant Physiol. 31 (1980)

- Nuclear magnetic resonance imaging (NMR)

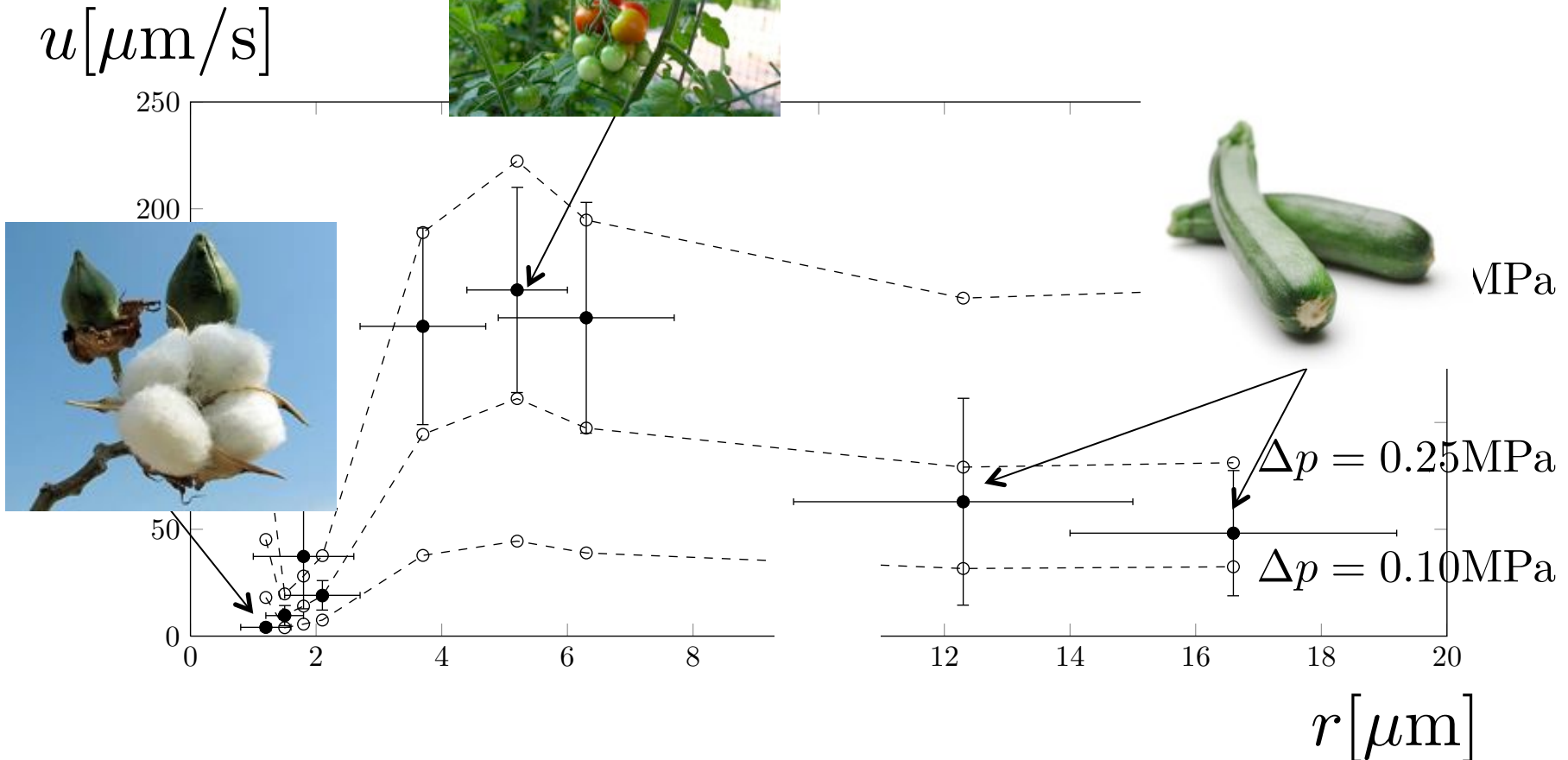
- Fluorescent dye

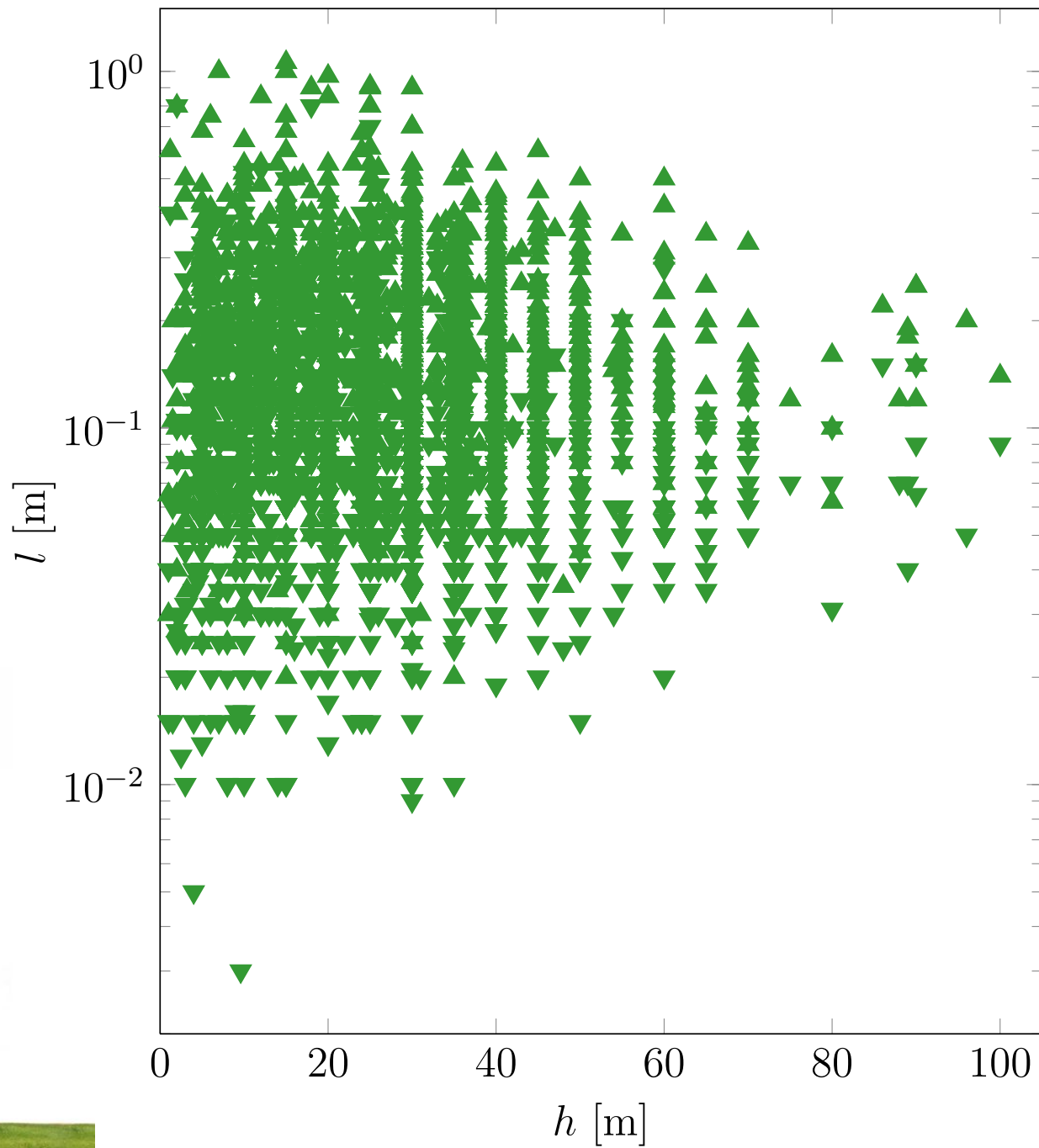
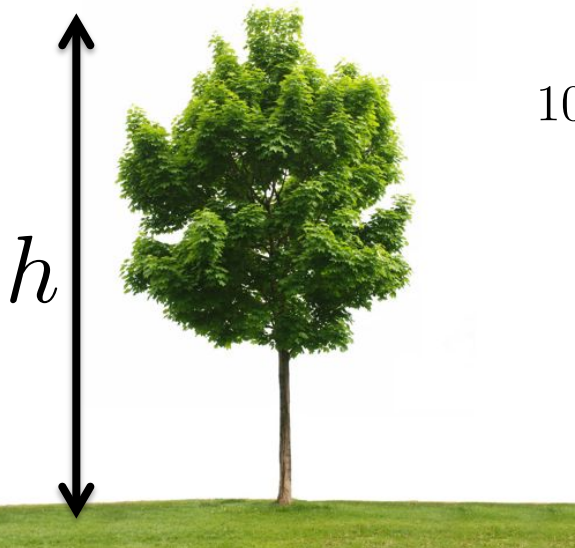
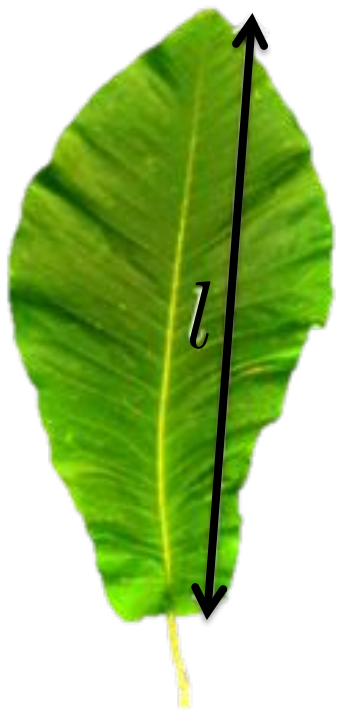
Savage, Zwieniecki, Holbrook
Plant Physiology 163 (2013)

Windt *et al.* Plant, Cell & Environment 29 (2006)

Sugar speed – scaling analysis

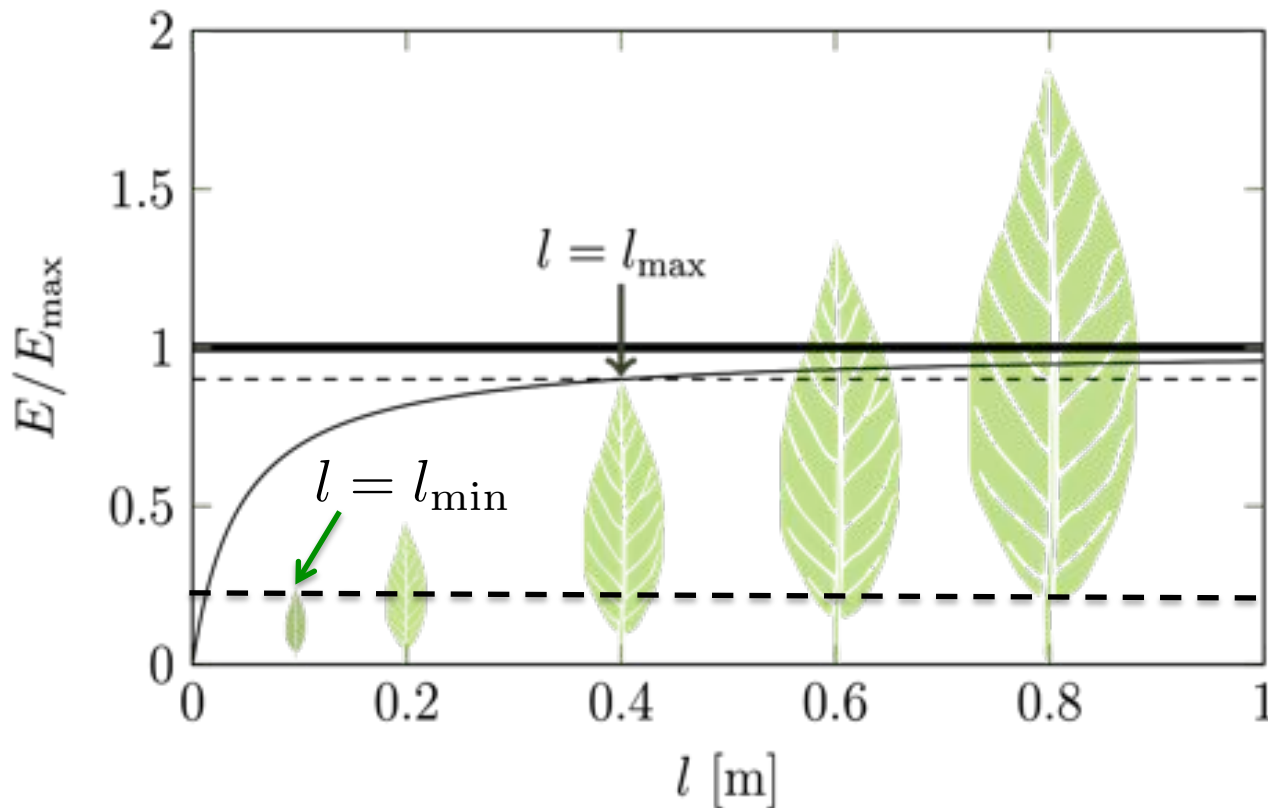
$$\bar{u} = \frac{L_p l r^2}{r^3 + 8L_p \eta l h} \Delta p$$





Limits to Leaf Size

- Energy flux $E = kcu = \frac{2r^2 L_p l}{r^3 + 16L_p \eta l h} kc\Delta p$.

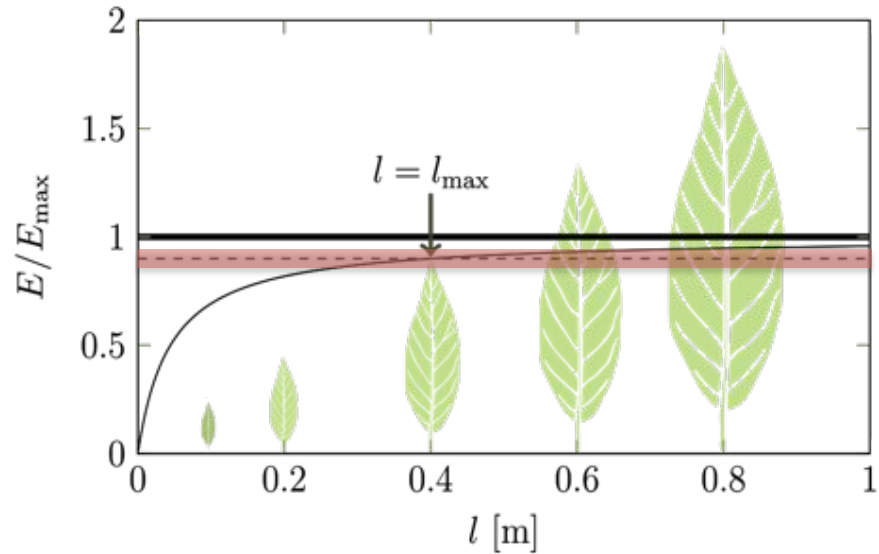


$$E_{\max} = \frac{1}{8} \frac{r^2}{\eta h} kc\Delta p.$$

Upper limit to leaf size

- Large leaf, fast flow
 - Cost of maintaining vasculature

$$C = \gamma l \pi r^2$$



$$E - C = 0 \Rightarrow l_{\max} = \frac{1}{16} \frac{2r^2 L_p k c \Delta p - \gamma r^3}{\gamma L_p \eta} \frac{1}{h}$$

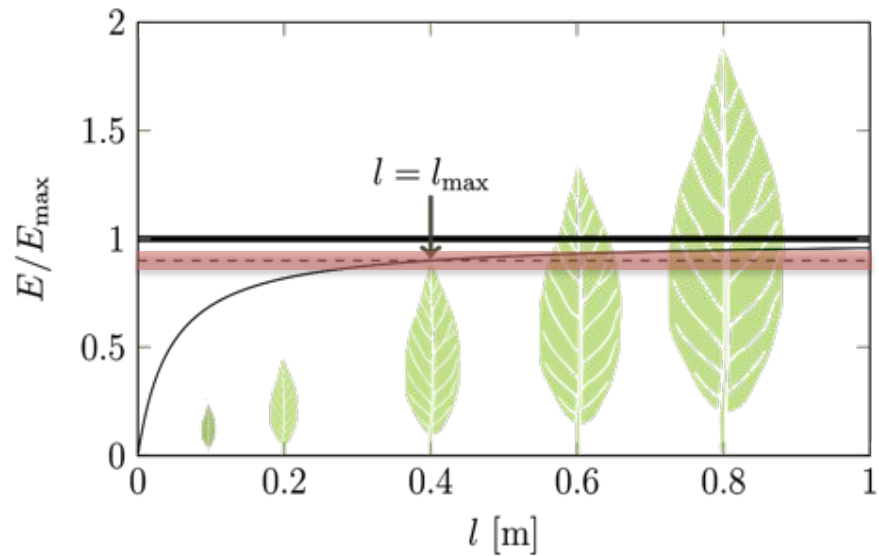
$$l_{\max} \sim \frac{1}{h}$$

Upper limit to leaf size

- Large leaf, fast flow
 - Stop growth when close to max output

$$E \sim (1 - \tau)E_{\max} \quad \tau \ll 1$$

$$l_{\max} = \frac{1}{16} \frac{r^3}{\tau L_p \eta} \frac{1}{h}$$



$$l_{\max} \sim \frac{1}{h}$$

Lower limit to leaf size

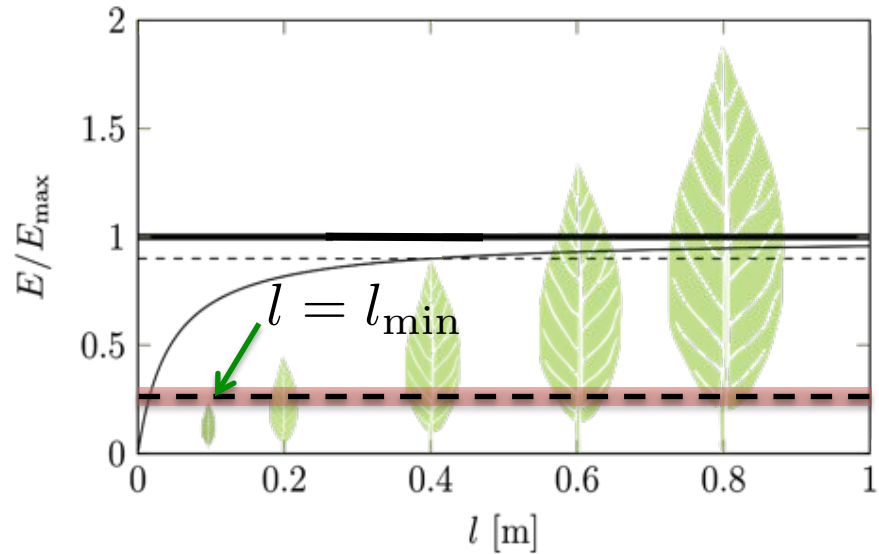
- Small leaf, slow flow
 - Bulk flow faster than diffusion

$$Pe = \frac{uL}{D} \geq 1$$

Péclet number

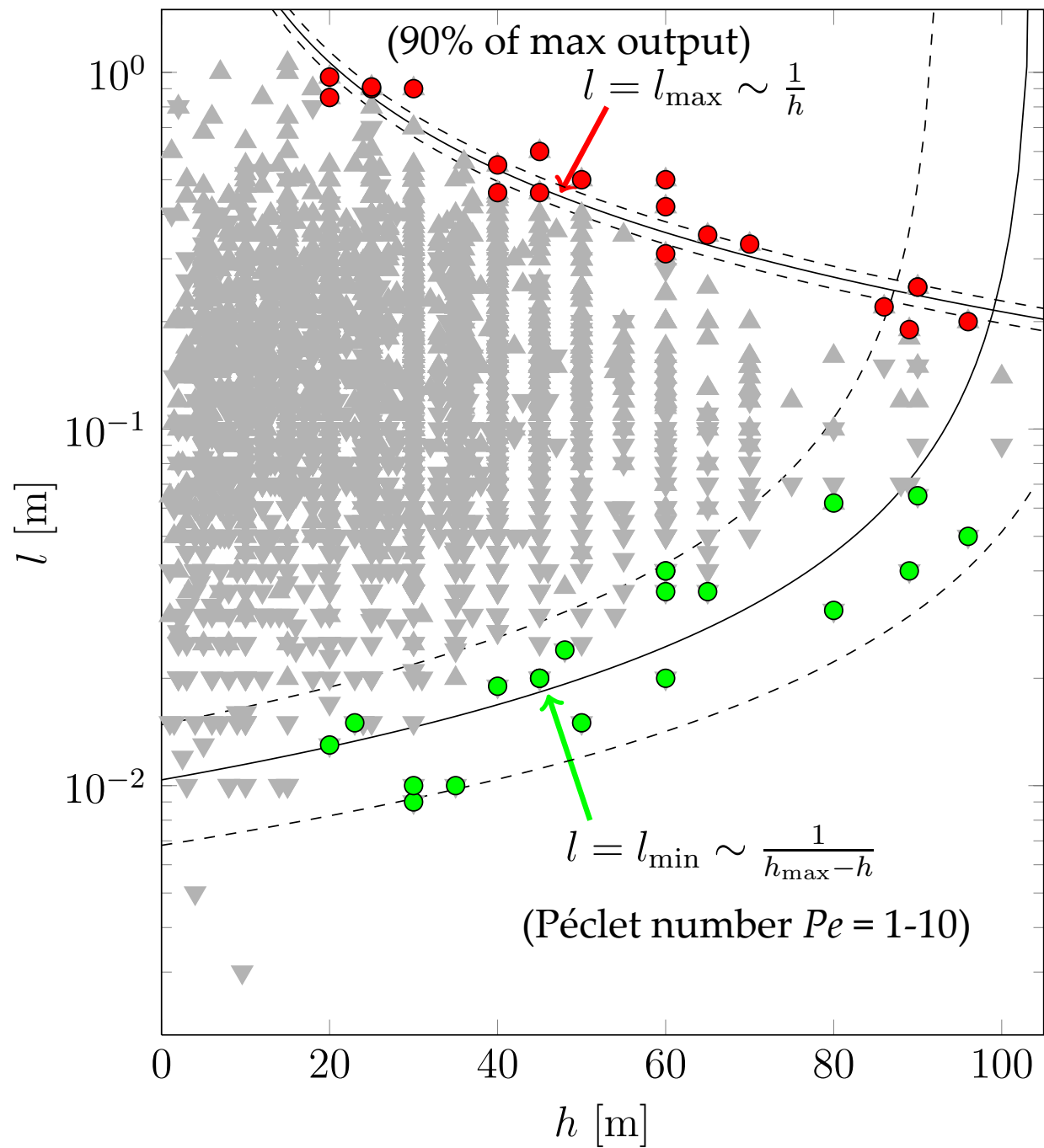
L Characteristic cell-to-cell distance (10-100 μm)

D Diffusivity

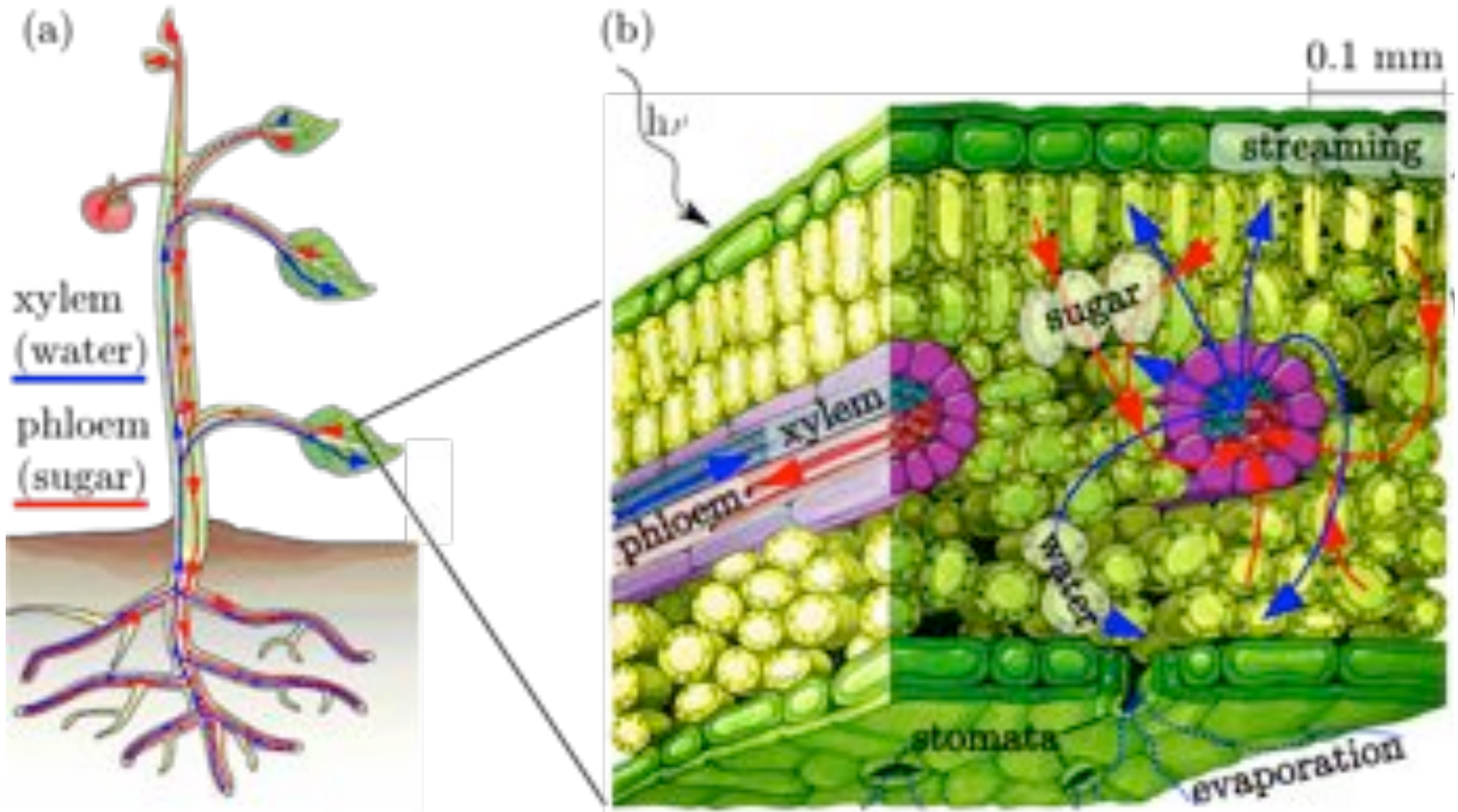


$$l_{\min} = \frac{1}{16} \frac{r^3}{L_p \eta} \frac{1}{(h_{\max} - h)}$$

$$h_{\max} = \frac{r^2 L \Delta p}{8 \eta D} \frac{1}{Pe}$$



Physical challenges



Engineering challenge #2: Mapping the vascular architecture

Serial light micrographs

X-Ray Computed tomography

Zwieniecki *et al.*
Plant, Cell & Environment **29** (2006)

Brodersen *et al.* New Phytologist **191** (2011)
Lee *et al.* Microscopy Res. Tech. **76** (2013)

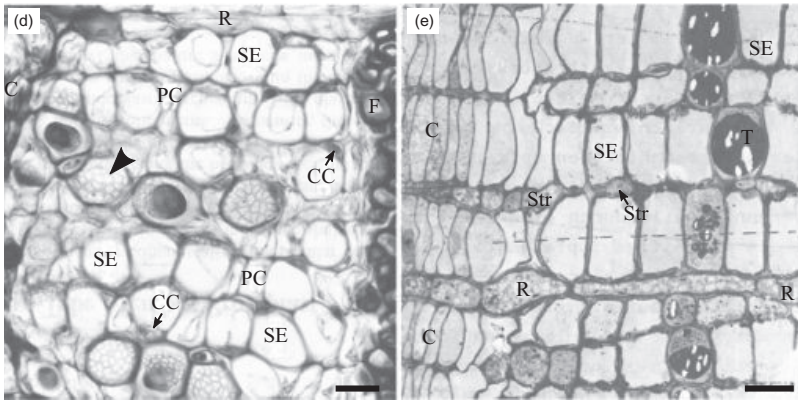
Size of individual phloem tubes

Black locust

Norway spruce

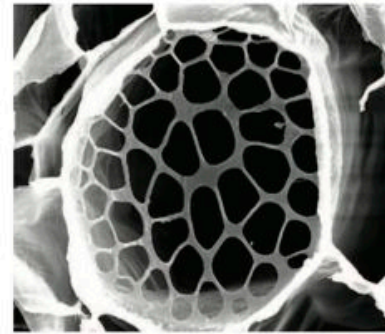
Squash

Bamboo

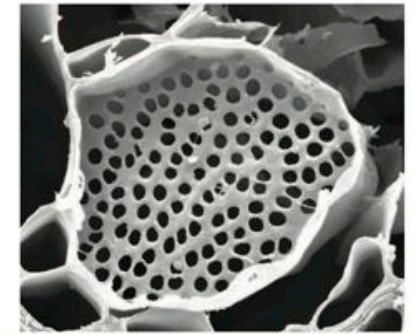


20 μm

30 μm

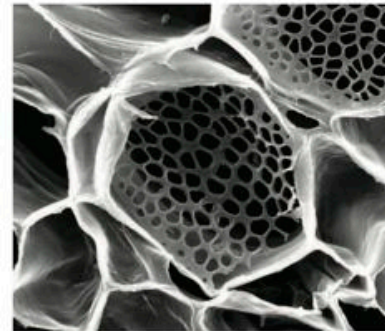


10 μm



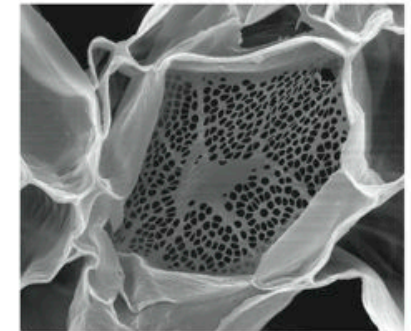
Green bean

10 μm



Castor bean

20 μm



Mullendore *et al.* Plant Cell 22 (2010)

Jensen, Liesche, Bohr, Schulz. Plant, Cell & Environment 35 (2012)

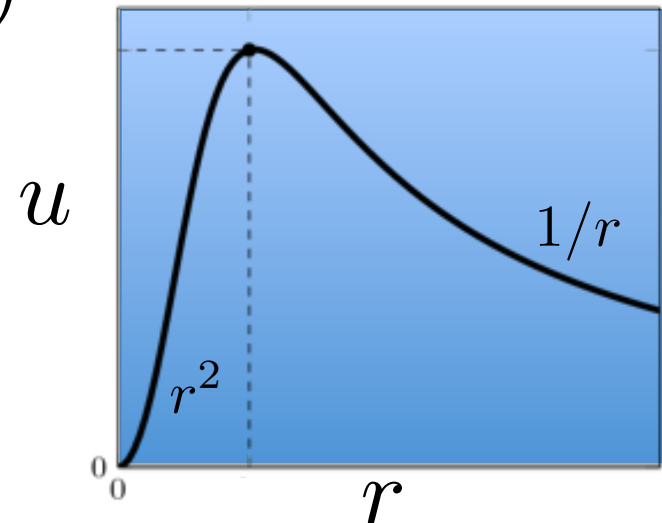
Jensen, Mullendore, Holbrook, Bohr, Knoblauch. Front. Plant Sci. 3 (2012)

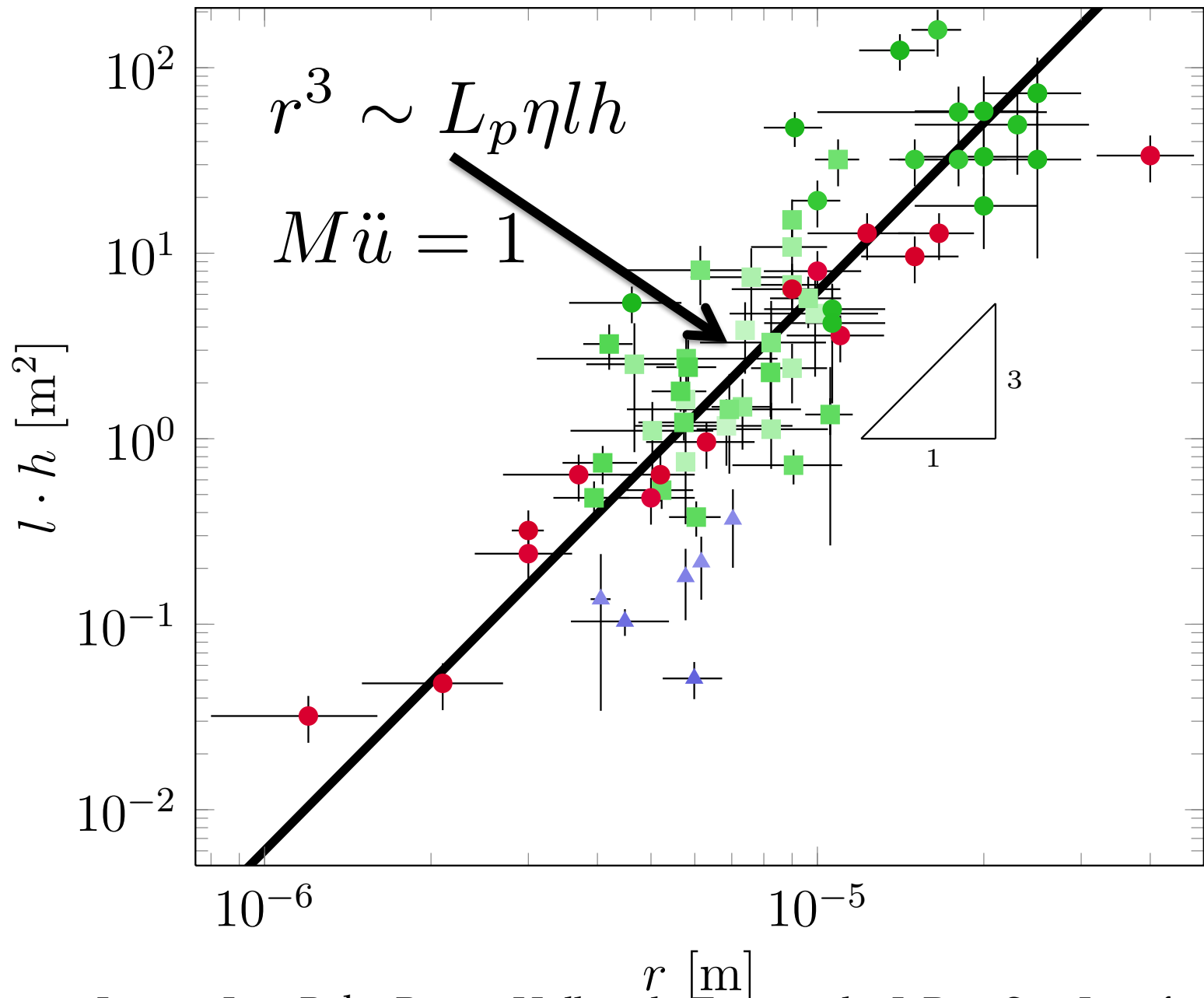
Sugar speed depends on the phloem tube size

$$u = \frac{2r^2 L_p l}{r^3 + 16\eta L_p l h} \Delta p$$

- Fixed leaf and stem length, speed optimal when $R_s = R_l$ ($M\ddot{u} = 1$)

$$r^3 \sim L_p \eta l h$$





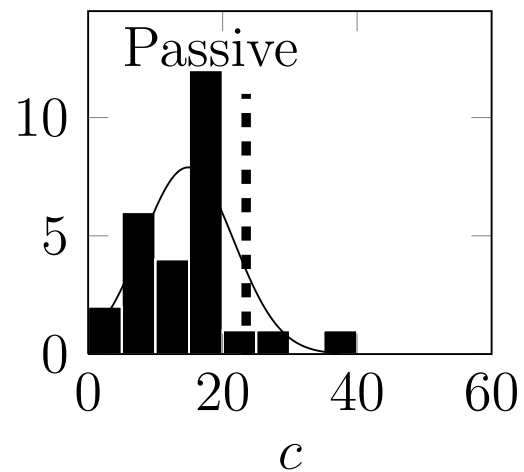
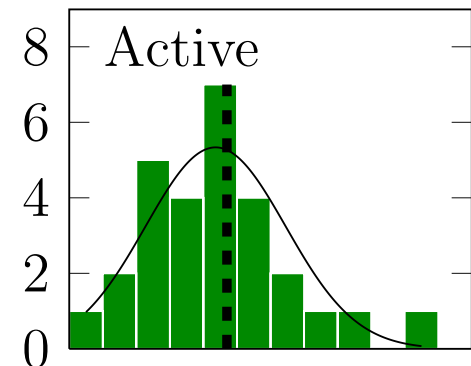
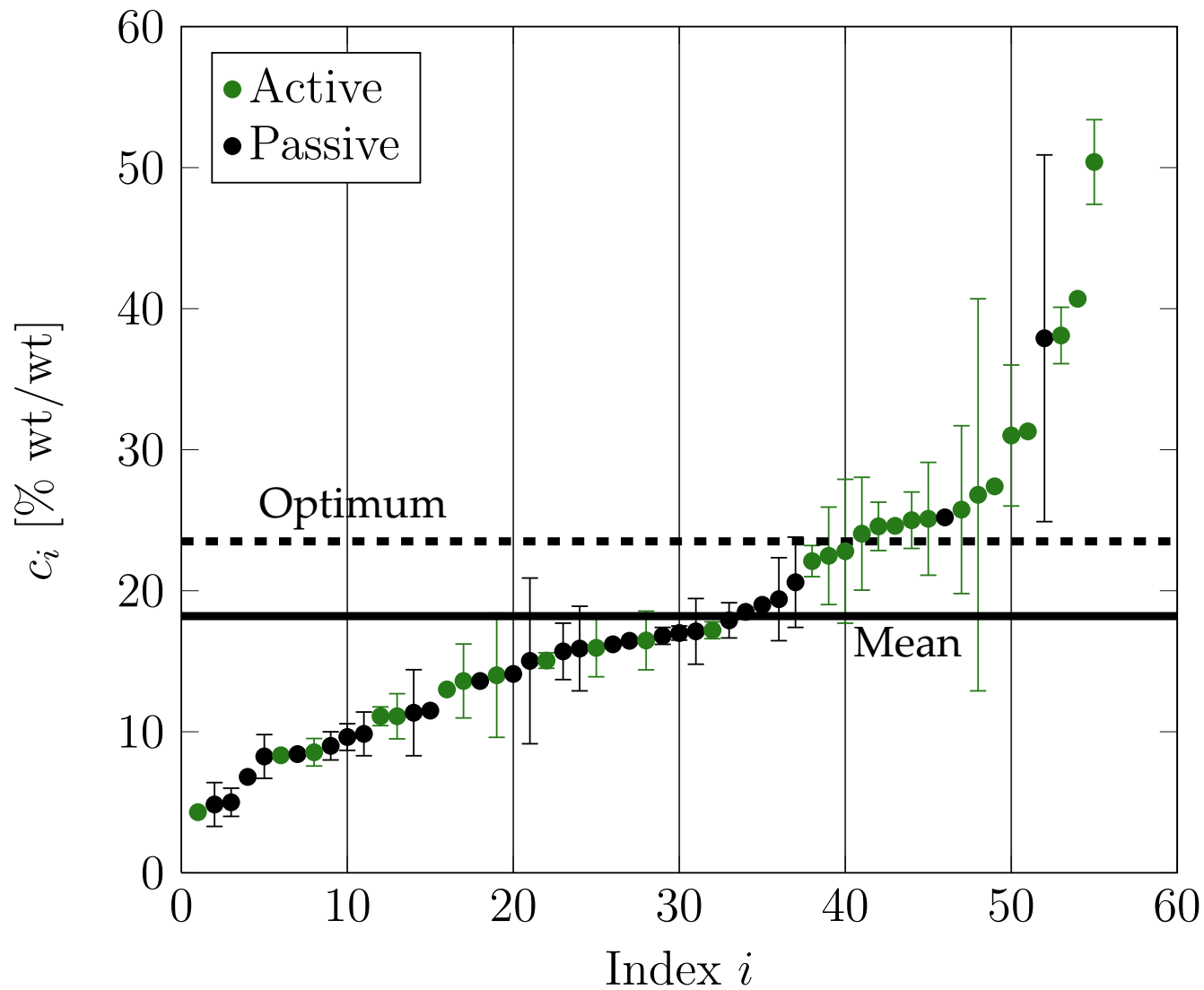
Jensen, Lee, Bohr, Bruus, Holbrook, Zwieniecki. J. Roy. Soc. Interface (2011)

Phloem Sap Composition

- ~ 20 % sugars
 - **sucrose**, glucose, fructose, sorbitol, mannitol, raffinose, stachyose...
- ~ 1 %
 - Proteins, amino acids, hormones, signaling molecules

Engineering challenge #3: Drawing blood from a plant

- Bleeding
- Aphid stylectomy



Jensen, Lee, Holbrook, Bush.
 J. Roy. Soc. Interface **10** (2013)

Jensen, Savage, Holbrook.
 J. Roy. Soc. Interface **10** (2013)

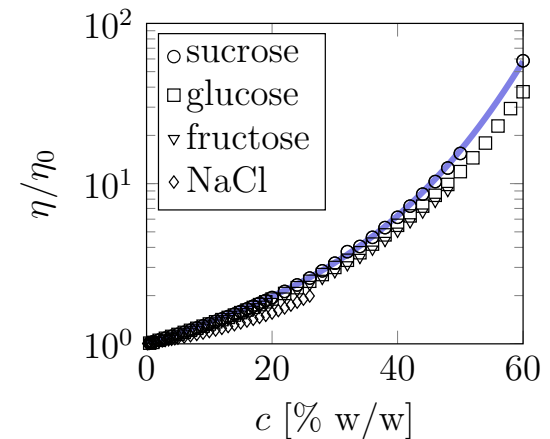
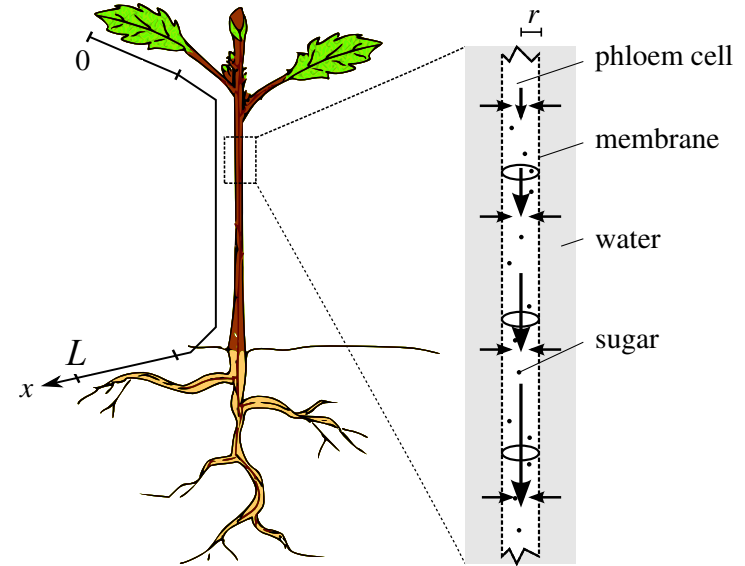
Sugar flow in the stem

- Volume flow

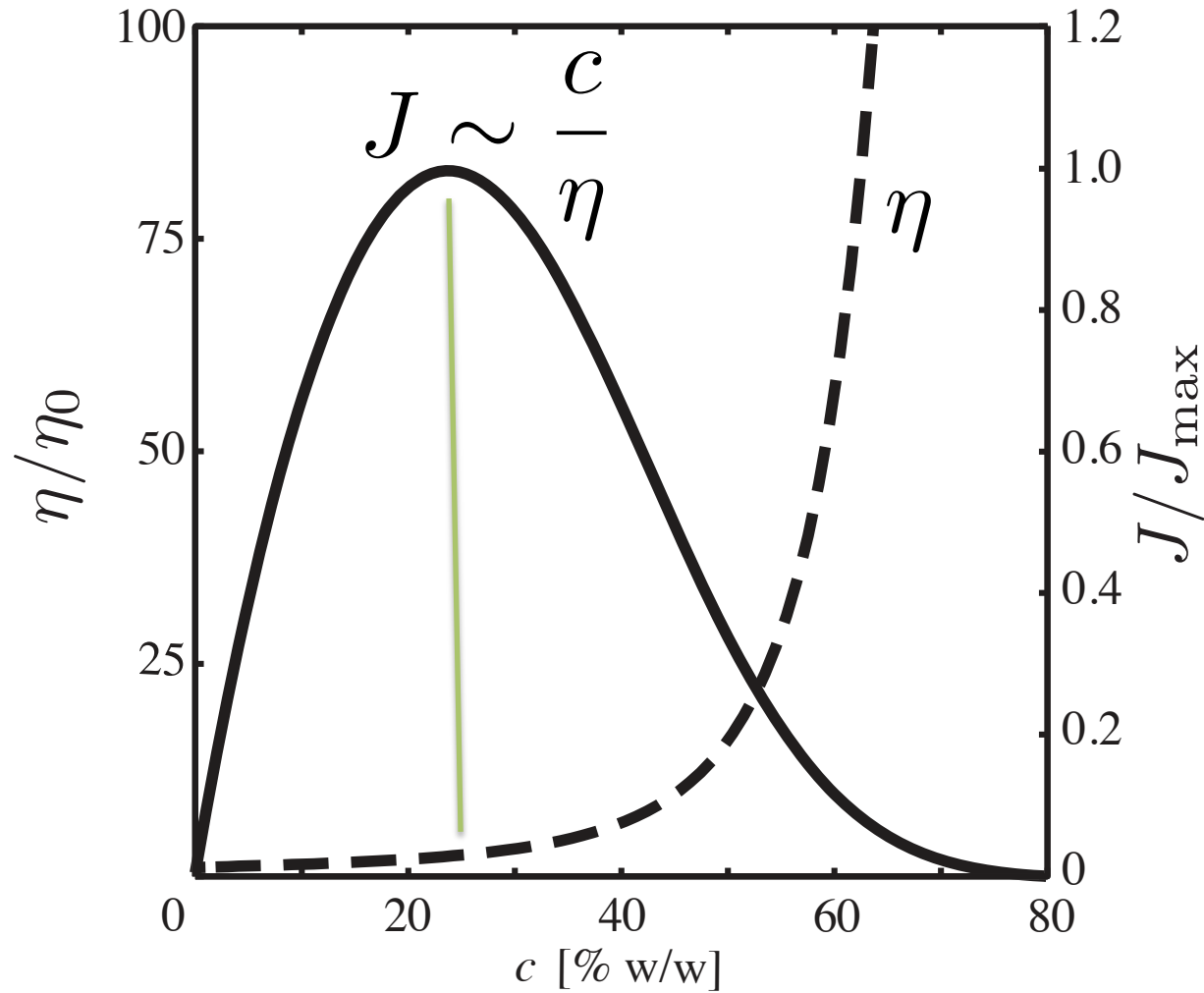
$$Q = \frac{\pi r^4}{8} \frac{\Delta p}{L} \frac{1}{\eta(c)}$$

- Sugar mass flow $J = Qc$

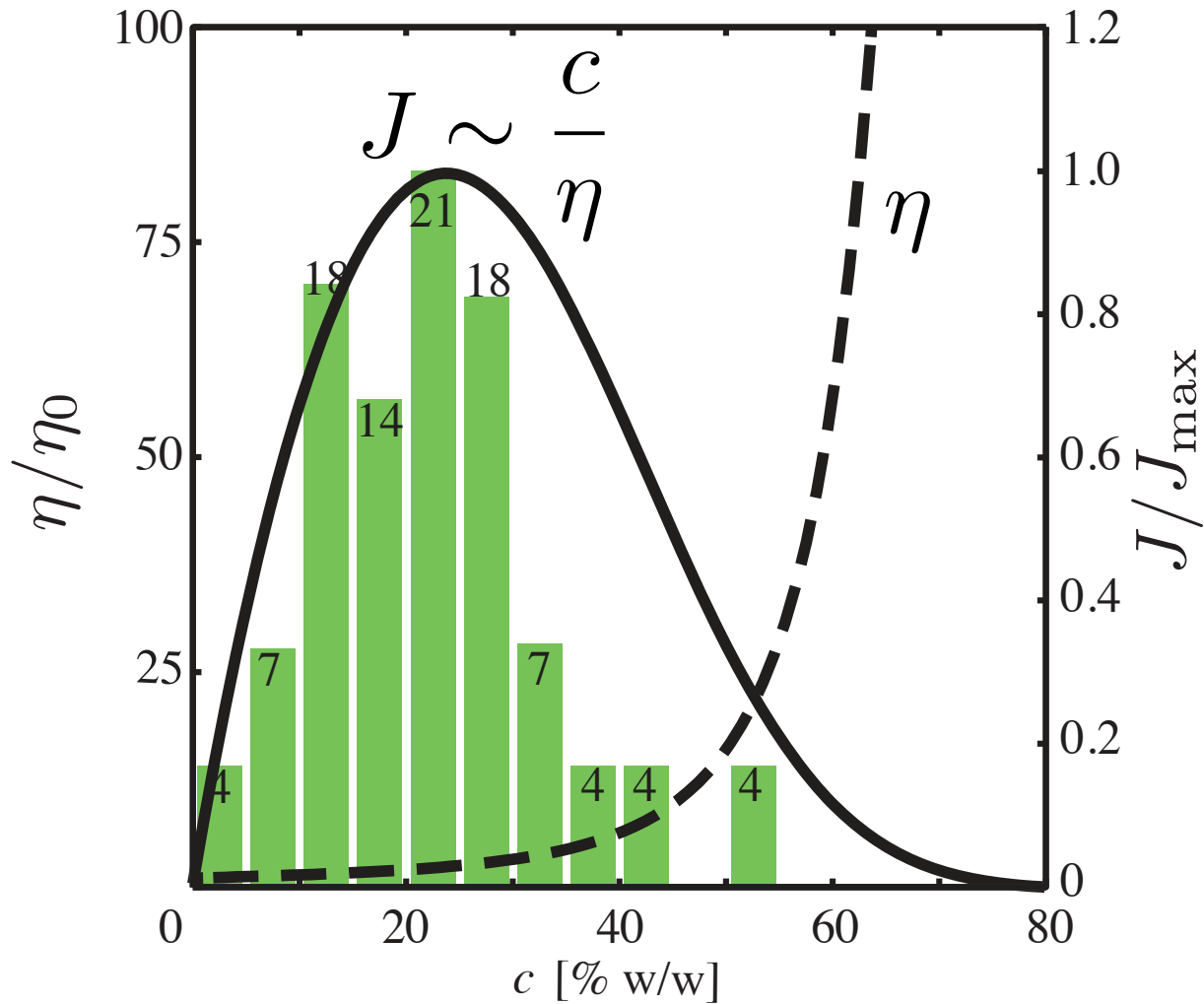
$$J = \left(\frac{\pi r^4}{8} \frac{\Delta p}{L} \right) \frac{c}{\eta(c)}$$



Sugar mass flow



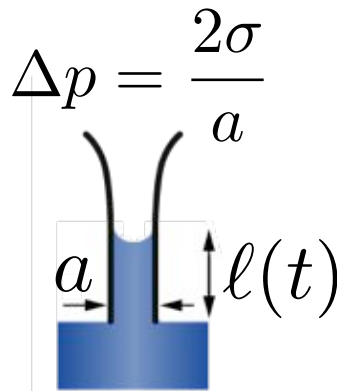
Sugar mass flow



Nectar Drinking

Hummingbirds

- Surface tension
 - Drink through cylindrical tube formed by folding tongue



Sugar uptake

$$J = c \frac{\pi a^2 \ell(T)}{T + T_0}$$

$$\pi a^2 \frac{d\ell}{dt} = \frac{\pi a^4}{8\eta l} \Delta p$$

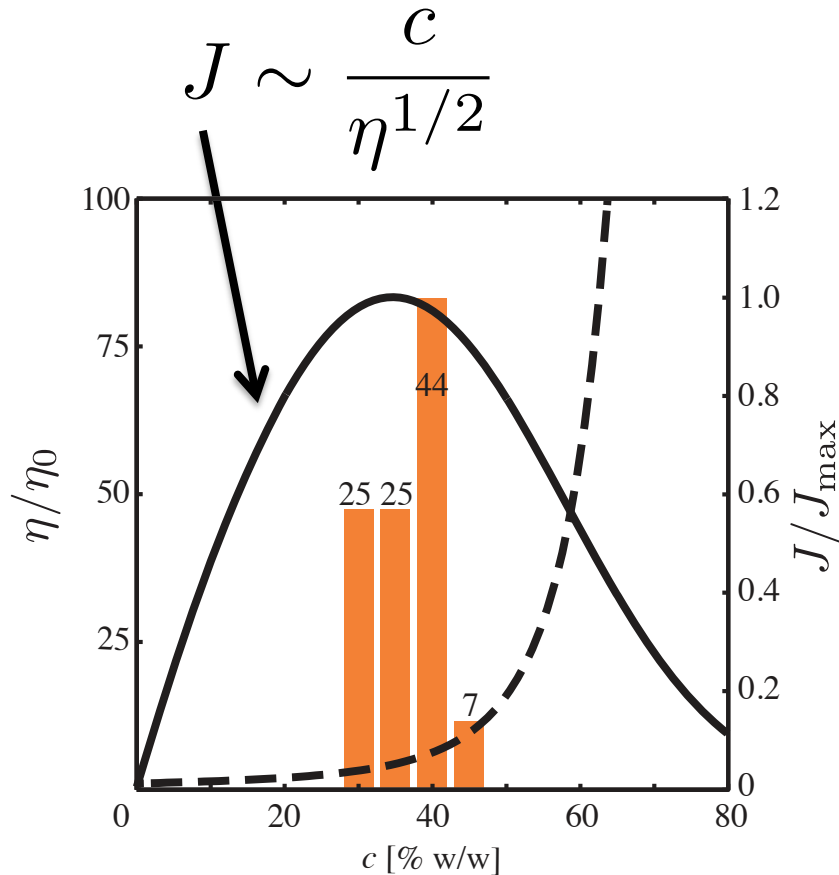
$$\ell = \left(\frac{a\sigma t}{2\eta} \right)^{1/2}$$

$$J \sim \frac{c}{\eta^{1/2}}$$

Nectar Drinking

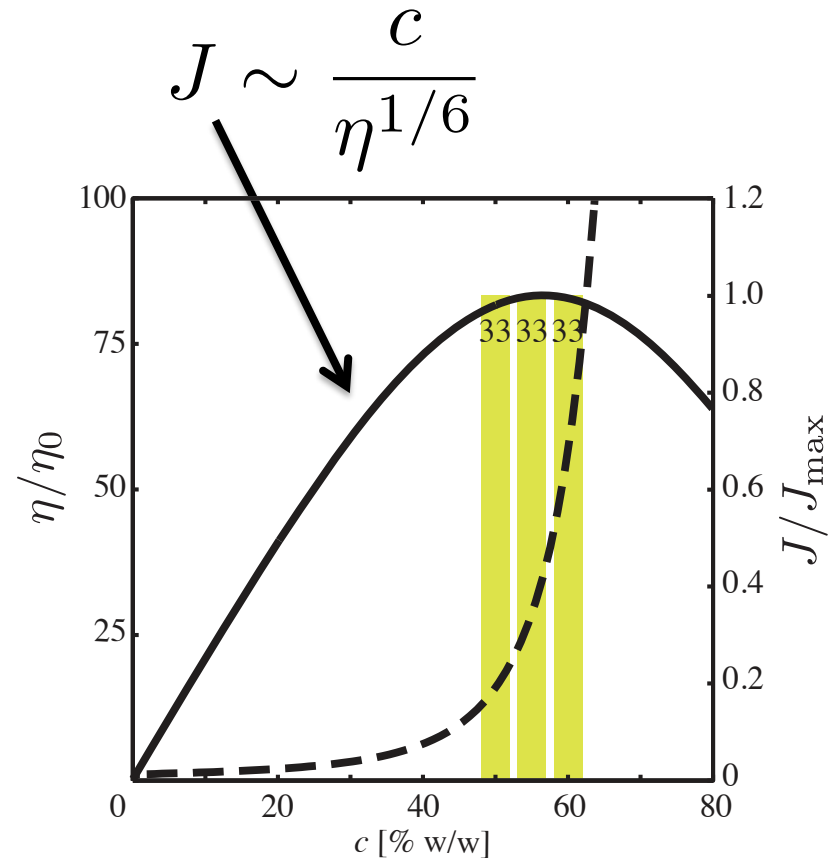
Hummingbirds

- Surface tension



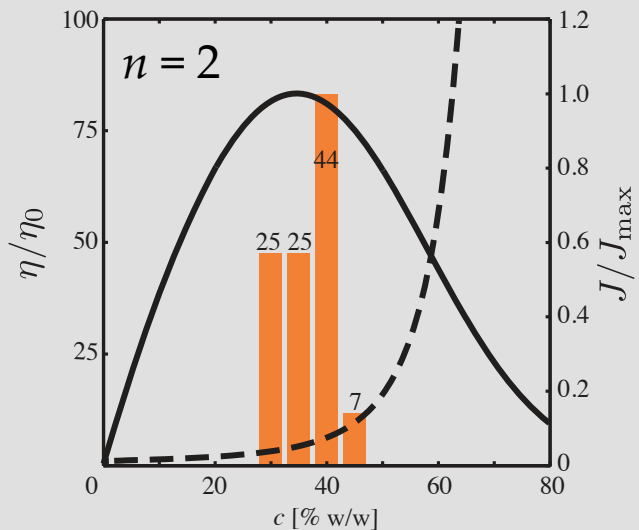
Bees

- Viscous dipping

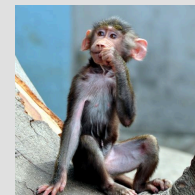
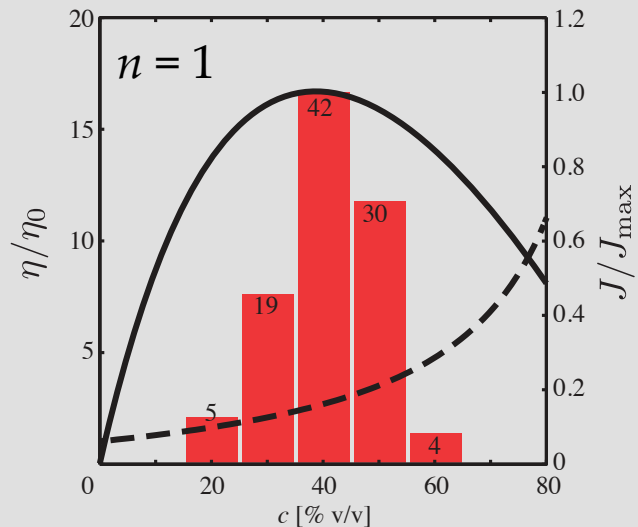


$$J \sim \frac{c}{\eta^{1/n}}$$

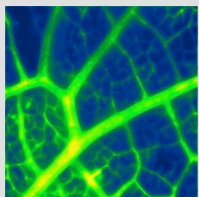
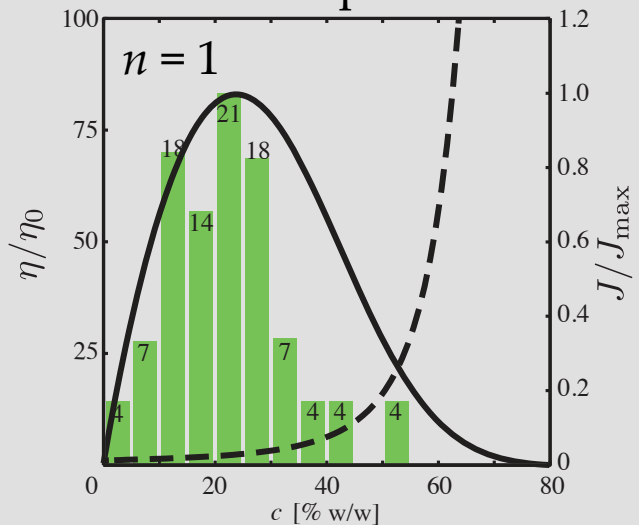
Surface tension



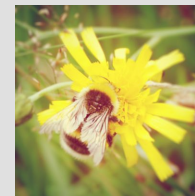
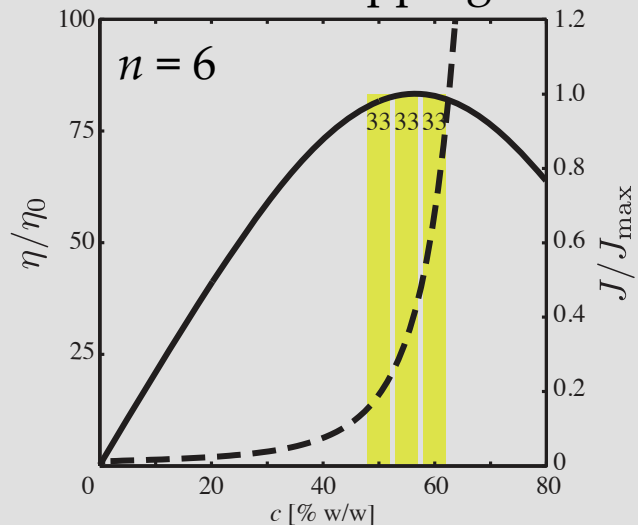
Blood flow



Plant sap flow



Viscous dipping



Simple Model for Flow Impeded by Concentration

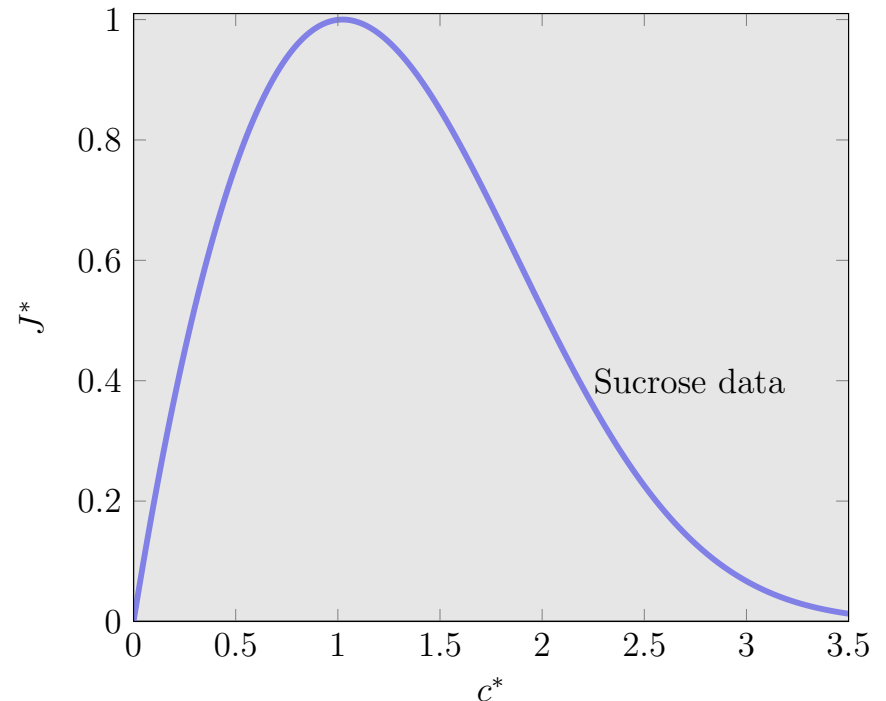
$$c^* = \frac{c}{c_{\text{opt}}} \quad \eta^* = \frac{\eta}{\eta(c_{\text{opt}})} \quad J^* = \frac{J}{J(c_{\text{opt}})}$$

$$\frac{\partial J^*}{\partial c^*} = A - Bc^*$$

$$J^*(0) = 0$$

$$J^*(1) = 1$$

$$\left. \frac{\partial J^*}{\partial c^*} \right|_{c^*=1} = 0$$



Simple Model for Flow Impeded by Concentration

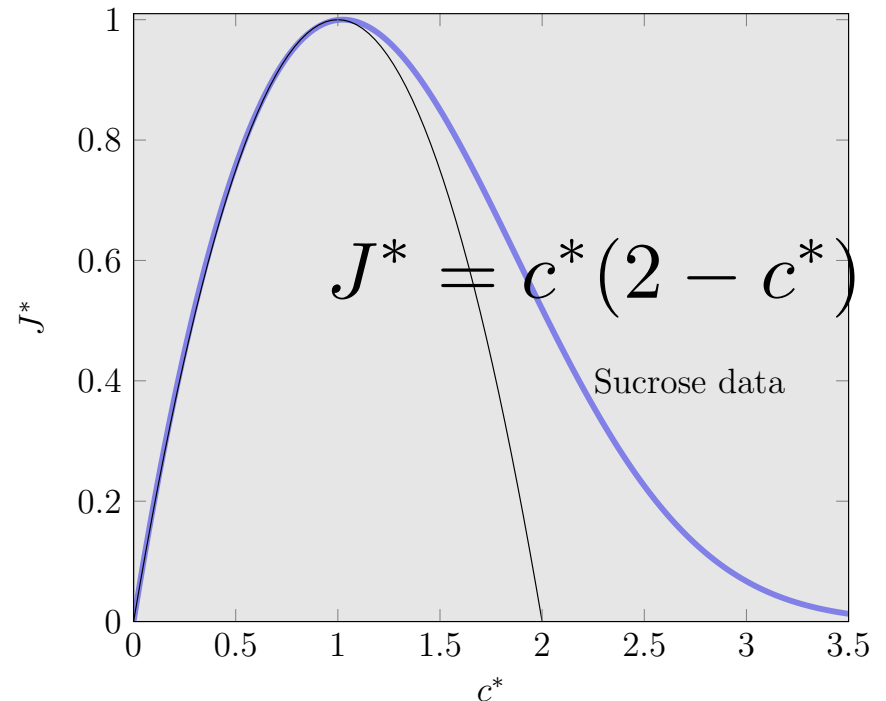
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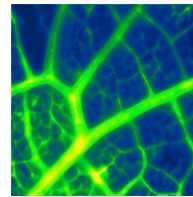
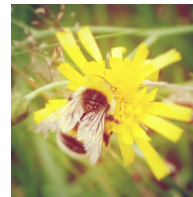
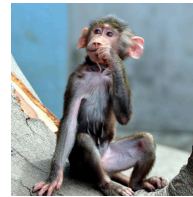
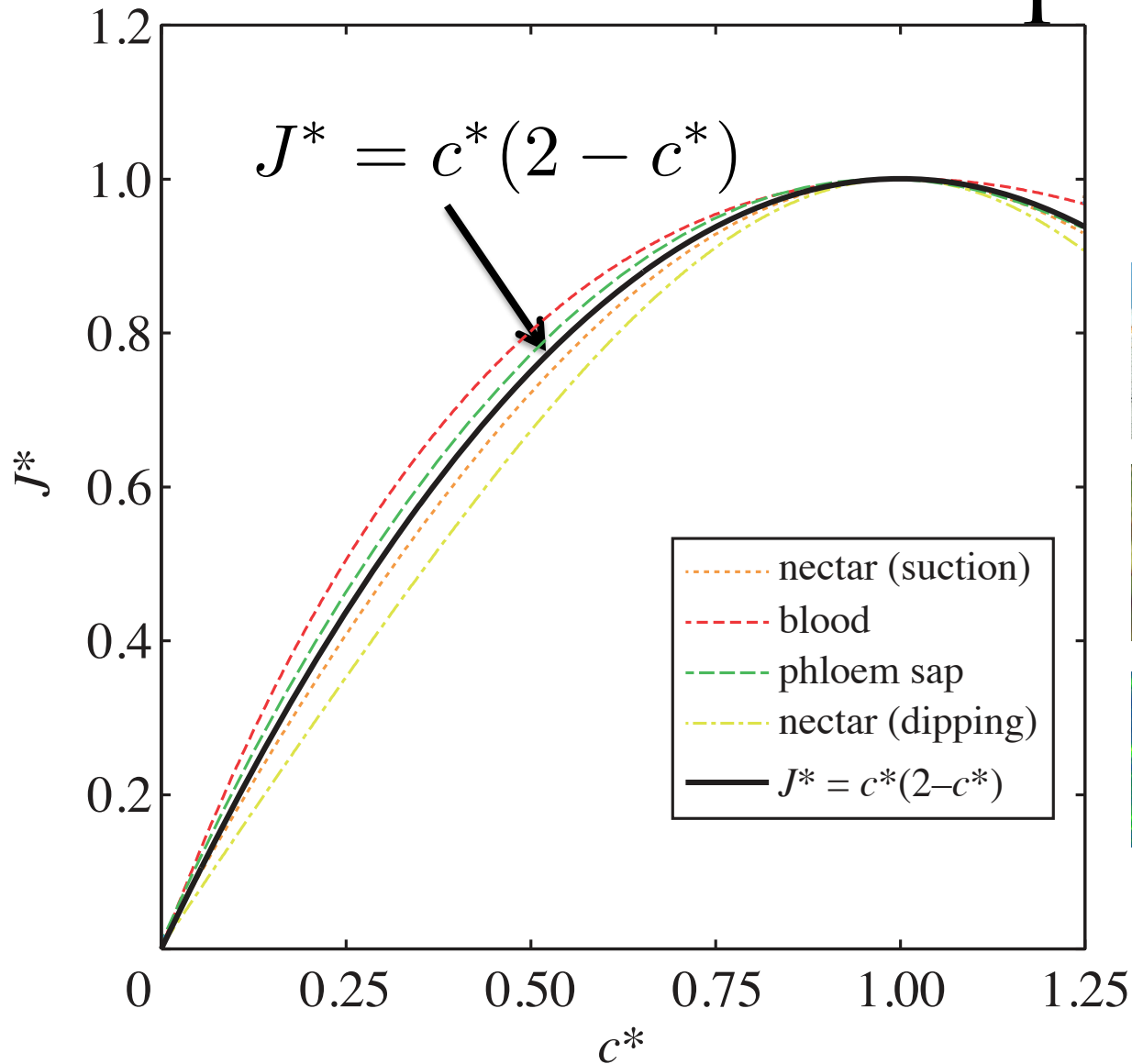
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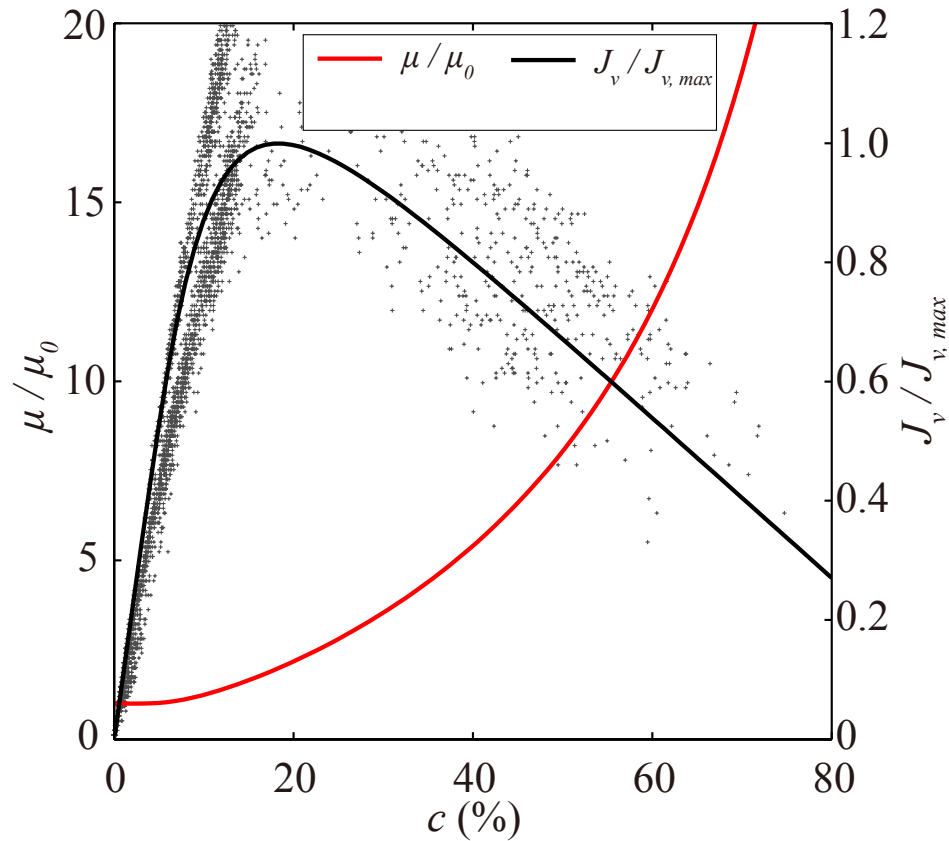


Data collapse

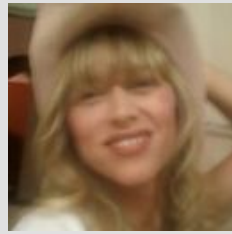


Jensen, Lee, Holbrook, Bush.
J. Roy. Soc. Interface **10** (2013)

Traffic flows



Lighthill and Whitham. Proc. Roy. Soc. A **229** (1955)
Helbing. Rev. Mod. Phys **73** (2001)
Jensen, Lee, Holbrook, Bush. J. Roy. Soc. Interface **10** (2013)



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