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On the air permeability of Populus pit

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What is a pit?

- Bordered pits = cavities in cell walls of xylem conduits used for water-transport system

- Two parts:
  - Pit membrane: porous membrane that allows water to pass between xylem conduits but limits the spread of embolism
  - Pit wall: overarching cell wall with a narrow aperture to the pit chamber
Introduction

• Problematics
  – How is sap hydrodynamics controlled by « pits »?
  – How do pit junctions regulate the sap flow and stop embolism?
  – How does pit porosity adjust the flow under negative pressure and stop the air bubble diffusion?

• Approach
  – Quantitative study of pit properties at the nanometric scale
  – Study of hydrodynamics of the Populus branches
I- Quantitative study of pit properties at the nanometric scale

Atomic Force Microscopy (AFM)

Agilent 5500 Scanning Probe Microscope

- Surface structure images
- Nano-mechanics
  - Dry pits
    - Nano-indentation
  - Swelled by water pits
    - Membrane flexion
    - Nano-indentation
### Vessel and pit architectures

#### Pit microstructure

<p>| | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Pit diameter (AFM)</td>
<td>7 μm</td>
</tr>
<tr>
<td>Membrane diameter (AFM)</td>
<td>1.5 μm</td>
</tr>
<tr>
<td>Pit wall thickness (AFM)</td>
<td>1.60 μm</td>
</tr>
<tr>
<td>Vessel diameter in the branches (AFM)</td>
<td>11.2 μm</td>
</tr>
<tr>
<td>Thickness of the pit membrane (TEM)</td>
<td>311 nm</td>
</tr>
</tbody>
</table>

#### AFM images of pits

[Images of AFM images showing PM, PW1, and PW2]
Young’s moduli on dry sample

Indentation of vessel wall

Hertz model:
\[ E = \frac{3\chi k}{4R^{1/2}} = 7.89 \pm 0.39 \text{ GPa} \]

Force-displacement curves

Indentation curve

Flexion of PM

Flexion model:
\[ E = \frac{\chi L^2}{4ad^3} \left[ \frac{3(2 - \nu)(1 - \nu^2)}{\pi} \right] = 3.63 \times 10^2 \pm 40 \text{ MPa} \]

Log-log representation of the force-distance curve with a linear fit

Force-displacement curve

Indentation curve
Viscoelastic behavior of water swelled pits

- Zener viscoelastic model:
  \[ \sigma = E_1 \varepsilon + \eta \dot{\varepsilon} \left(1 - \exp \left(-\frac{\varepsilon}{\tau \dot{\varepsilon}}\right)\right) \]
  - relaxation time \( \tau \)
  - two Young’s moduli, \( E_1 \) and \( E_2 \)

<table>
<thead>
<tr>
<th></th>
<th>PM</th>
<th>PW1</th>
<th>PW2</th>
</tr>
</thead>
<tbody>
<tr>
<td>( E_1 ) (GPa)</td>
<td>0.41</td>
<td>1.66</td>
<td>0.43</td>
</tr>
<tr>
<td>( E_1 + E_2 ) (GPa)</td>
<td>0.95</td>
<td>3.35</td>
<td>0.84</td>
</tr>
<tr>
<td>( \tau ) (s)</td>
<td>0.99</td>
<td>63.3</td>
<td>6.2</td>
</tr>
</tbody>
</table>
II- Study of hydrodynamics of the Populus branches

Air seeding experiments

Diagram of the experiment

First results
- Critical pressure: $P_c = 18 \times 10^5$ Pa
- Critical length: $L_c = 15$ cm
- Open pore diameter
  \[ d_{\text{open pore}} \approx \frac{4\sigma \cos(\theta)}{\Delta P} \]
  \[ d_{\text{open pore}} \approx 162 \text{ nm} \]
Deformation study

- PM deformation:
  \[
  \begin{pmatrix}
    ( ) & ( ) & ( ) \\
  \end{pmatrix}
  \]
- Maximal deformation at 18 bar: 
  \[4.43 \times 10^{-6} \, \mu m\]
- \(d_{\text{closed pore}} \approx 96 \, \text{nm}\)
Experimental flow rate

- \( \Delta P \in [\Delta P_C; 3MPa] \)

- Permeability \( K \) of the samples:
  \[
  K = \frac{Q_T\mu L_b}{A \Delta P}
  \]
  - \( \mu \) is the water viscosity
  - \( \Delta P \) is the pressure difference
  - \( L_b \) is the branch length
  - \( A \) is area of the branch section

- Total flow rate \( Q_T \) for \( n \) capillaries:
  \[
  Q_T = n_{cap} \frac{\pi \Delta P}{128\mu L_b} d_{cap}^4
  \]
Flow rate through a pit

Modeling of the flow rate

Numbers of capillaries, pits and open pores variation
Conclusion

- Study of the structure and the mechanical properties of pits at nanoscale
  
  **Dry pits moduli**
  
<table>
<thead>
<tr>
<th>Material</th>
<th>Modulus (GPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vessel wall</td>
<td>7.89</td>
</tr>
<tr>
<td>PM</td>
<td>3.62 $10^2$</td>
</tr>
</tbody>
</table>

- Swelled by water pits Zener elements

<table>
<thead>
<tr>
<th>Material</th>
<th>$E_1$ (GPa)</th>
<th>$E_1 + E_2$ (GPa)</th>
<th>$\tau$ (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PM</td>
<td>0.41</td>
<td>0.95</td>
<td>0.99</td>
</tr>
<tr>
<td>PW1</td>
<td>1.66</td>
<td>3.35</td>
<td>63.3</td>
</tr>
<tr>
<td>PW2</td>
<td>0.43</td>
<td>0.84</td>
<td>6.2</td>
</tr>
</tbody>
</table>

- $E_{membrane} \ll E_{vessel\ wall}$
- No difference in mechanical properties between dry and water swelled pit membranes
- Membrane is deformed by injected air
- $d_{closed\ pore} \approx 100$ nm found by air seeding experiments
- Membrane is deformed until 2.3 MPa with a constant number of pores, pore diameters are growing with membrane deformation
Thank you for your attention