Equations for a 1-D Lockhart/Ortega model with wall thickening

Cyril Bozonnet

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1 Description

Hereafter I present the equations obtained when considering the classical plant cell elongation problem (Lockhart-Ortega model) with non-constants wall thickness and osmotic potential. It describes growth in the longitudinal direction along with thickening/thinning in the radial direction. Wall thickness dynamic is further related to sugar availability and elongation rate. The cell is supposed to be connected to a water source (at given water potential), and to a sugar source.

2 Equations

2.1 Geometry and kinematics

The total volume of the cylinder is

$$V_t = \pi R^2 L, \tag{1}$$

where R is the **constant** external cylinder radius, and L is its length. The volume of water inside the cylinder is

$$V_h = \pi (R - W)^2 L, \tag{2}$$

with W, the wall thickness. Neglecting the end walls (in $z = 0$ and $z = L$), the wall volume inside the cylinder is

$$V_w = \pi (R^2 - (R - W)^2) L = \pi (2RW - W^2) L \approx 2\pi RWL, \tag{3}$$

where the W^2 term has been neglected to obtain the final expression. Deriving with respect to time the equation for V_h, one gets

$$\frac{\mathrm{d}V_h}{\mathrm{d}t} = \frac{\mathrm{d}}{\mathrm{d}t}\left(\pi(R^2 + W^2 - 2RW)L\right) = \pi(R-W)^2\frac{\mathrm{d}L}{\mathrm{d}t} + \pi L 2W\frac{\mathrm{d}W}{\mathrm{d}t} - 2\pi RL\frac{\mathrm{d}W}{\mathrm{d}t} \approx \pi(R-W)^2\frac{\mathrm{d}L}{\mathrm{d}t} - 2\pi RL\frac{\mathrm{d}W}{\mathrm{d}t}. \tag{4}$$

Normalising the previous relation by V_h gives

$$\boxed{\frac{1}{V_h}\frac{\mathrm{d}V_h}{\mathrm{d}t} = \frac{1}{L}\frac{\mathrm{d}L}{\mathrm{d}t} - \frac{2\pi RL}{V_h}\frac{\mathrm{d}W}{\mathrm{d}t}}, \tag{5}$$

where see that the volume of water increases with the elongation of the cell and decreases with wall thickening.

Now deriving V_w gives

$$\boxed{\frac{\mathrm{d}V_w}{\mathrm{d}t} = 2\pi RW\frac{\mathrm{d}L}{\mathrm{d}t} + 2\pi RL\frac{\mathrm{d}W}{\mathrm{d}t}}, \tag{6}$$

which leads to an equation for the wall thickness:

$$\boxed{2\pi RL\frac{\mathrm{d}W}{\mathrm{d}t} = \frac{\mathrm{d}V_w}{\mathrm{d}t} - 2\pi RW\frac{\mathrm{d}L}{\mathrm{d}t}}, \tag{7}$$

where we see that the wall thickness increases with the increase in wall volume and decreases with cell elongation.

Combining Eqs. (5) and (7), one gets

$$\frac{1}{V_h}\frac{\mathrm{d}V_h}{\mathrm{d}t} = \frac{1}{L}\frac{\mathrm{d}L}{\mathrm{d}t} - \frac{1}{V_h}\left(\frac{\mathrm{d}V_w}{\mathrm{d}t} - 2\pi RW\frac{\mathrm{d}L}{\mathrm{d}t}\right), \tag{8}$$

which can be rearranged as

$$\frac{1}{V_h}\frac{\mathrm{d}V_h}{\mathrm{d}t} = \frac{1}{L}\frac{\mathrm{d}L}{\mathrm{d}t}\left(1 + \frac{2\pi RW}{\pi(R-W)^2}\right) - \frac{1}{V_h}\frac{\mathrm{d}V_w}{\mathrm{d}t}. \tag{9}$$

We can eventually further simplify the previous equation as

$$\boxed{\frac{1}{V_h}\frac{\mathrm{d}V_h}{\mathrm{d}t} = \frac{1}{L}\frac{\mathrm{d}L}{\mathrm{d}t}\left(1 + \frac{2W}{R}\right) - \frac{1}{V_h}\frac{\mathrm{d}V_w}{\mathrm{d}t}}. \tag{10}$$

2.2 Water fluxes

The changes in the volume of water inside the cell depends on the water fluxes:

$$\frac{\mathrm{d}V_h}{\mathrm{d}t} = AK_h\left(P_{src} - \Pi_{src} - P + \Pi\right), \tag{11}$$

where $A = 2\pi RL$ (neglecting water entry through end walls), K_h, P_{src}, Π_{src}, P and Π are the cylinder external area, the hydraulic conductivity, the pressure potential of the water source, the osmotic potential of water source, the cell turgor pressure and the cell osmotic potential, respectively. Dividing by V_h further leads to

$$\boxed{\frac{1}{V_h}\frac{\mathrm{d}V_h}{\mathrm{d}t} = \frac{AK_h}{V_h}\left(P_{src} - \Pi_{src} - P + \Pi\right) = \Phi_h\left(P_{src} - \Pi_{src} - P + \Pi\right)}, \tag{12}$$

where $\Phi_h = AK_h/V_h \approx 2K_h/R$ is a constant.

2.3 Wall rheology

The rheology of the wall material is described as a Bingham fluid, where the strain rate is related to the wall stress,

$$\boxed{\dot{\varepsilon}_L = \frac{1}{L}\frac{\mathrm{d}L}{\mathrm{d}t} = \frac{(\sigma_L - \sigma_Y)^+}{\mu} + \frac{1}{E}\frac{\mathrm{d}\sigma_L}{\mathrm{d}t}}, \tag{13}$$

for the longitudinal direction, where σ_L is the longitudinal wall stress, σ_Y is the wall yield stress (threshold for plastic deformation), μ is the wall viscosity, and E is the wall Young's modulus. The $(x)^+$ notation is equivalent to $\max(x, 0)$.

2.4 Mechanical equilibrium

As a very first approximation we consider that the new (deposited) walls experience the same stress and strain as the existing walls. Given the geometry, the equilibrium between pressure forces and wall stresses thus leads to

$$\sigma_L = \frac{(P - P_{ext})R}{2W}. \tag{14}$$

The external pressure, P_{ext} can be related to a pressure/stress at the tissue level, to a pressure exerted on the external walls of the cell,... In our case I will assume, we have $P_{ext} = 0$.

2.5 Wall synthesis (following Friend *et al.*, *Nature com.*, 2022)

Changes in wall volume are related to changes in mass, M^w (kg/cell), through ρ_w, the cell wall density (kg/m³):

$$\boxed{\frac{\mathrm{d}V_w}{\mathrm{d}t} = \frac{1}{\rho_w}\frac{\mathrm{d}M_w}{\mathrm{d}t}}. \tag{15}$$

Wall synthesis can be related to sugar availability through a Michaelis-Menten equation, i.e.,

$$\boxed{\frac{\mathrm{d}M_w}{\mathrm{d}t} = \frac{\Delta M_w^{max} n_s/V_h}{n_s/V_h + K_m}}, \tag{16}$$

where ΔM_w^{max} is the maximum speed of wall synthesis (kg/cell/s), n_s is the sugar content (in mol) of the cell and K_m is a kinetic constant (mol/m^3). The maximum speed of wall synthesis could further be related to water volume and temperature using a Bolztmann-Arrhenius equation,

$$\Delta M_w^{max} = \omega V_h e^{\frac{E_w^a}{k}(1/T_0 - 1/T)}. \tag{17}$$

In the previous equation, ω is the normalised rate of cell-wall mass growth (kg/cell/s/m^3) at temperature T_0 (273.15 K), E_w^a is an activation energy for wall building (eV), k is Bolztmann's constant (eV/K) and T is the actual temperature (K).

2.6 Osmotic potential and sugar content

If only one type of osmolytes is present, the cell osmotic potential is

$$\Pi = \frac{n_s R_g T}{V_h}, \tag{18}$$

where R_g is the ideal gas constant. The evolution of the sugar content can be related to wall synthesis and other sugar fluxes through

$$\frac{dn_s}{dt} = -\frac{1}{M_s}\frac{dM_w}{dt} + f_s, \tag{19}$$

where M_s is the sugar molar mass (kg/mol), and f_s is the sum of the sugar fluxes entering or leaving the cell. f_s can be a constant, i.e., a constant sugar flux forced into the cell, or can be computed through a diffusion equation, i.e.,

$$f_s = \eta_s \left(C_s^{ext} - \frac{n_s}{V_h} \right), \tag{20}$$

with η_s the sugar diffusion constant (m^3/s) and C_s^{ext} the external osmotic concentration. This external osmotic concentration can then be used to simulate periods of low or high sugar availability.

Remark: Are C_s^{ext} and Π_{src} related? In other words, is the osmotic potential of the water source the same as the osmotic potential of the sugar source? If so, sugar fluxes will tend to equilibrate both osmotic potentials, hence removing the osmotic component in the water fluxes, thus stopping water fluxes.

Remark: Simlarly, the same question can be asked about P_{src} (pressure of the water source) and P_{ext} (pressure applied on the walls). In case of a cell immersed in a water bath, we will have $P_{ext} = P_{src}$, and $\Pi_{src} = C_s^{ext} R_g T$, but in case of a cambial cell, the water source could be the xylem, i.e. $P_{src} - \Pi_{src} = \Psi_{src}$, and the phloem being the sugar source, i.e., $C_s^{ext} = C_s^{ph}$. I will additionally consider $P_{ext} = 0$.

2.7 Wall stress equation

One can now reinject some terms in Eq. (10):

$$\Phi_h \left(P_{src} - \Pi_{src} - P + \Pi \right) = \left(1 + \frac{2W}{R} \right) \left(\frac{(\sigma_L - \sigma_Y)^+}{\mu} + \frac{1}{E}\frac{d\sigma_L}{dt} \right) - \frac{1}{V_h \rho^w}\frac{dM_w}{dt}. \tag{21}$$

Rearranging and using the mechanical equilibrium to express the pressure as a function of the longitudinal wall stress, one gets

$$\frac{d\sigma_L}{dt} = \frac{E\Phi_h}{1 + \frac{2W}{R}} \left(\Psi_{src} - \frac{2W}{R}\sigma_L - P_{ext} + \Pi \right) + \frac{E}{V_h \rho^w (1 + \frac{2W}{R})}\frac{dM_w}{dt} - \frac{E}{\mu}(\sigma_L - \sigma_Y)^+. \tag{22}$$

3   To sum-up

Starting from known values of wall thickness, cell length, wall stress and cell sugar content, one can first compute the volume of water in the cell

$$V_h = \pi(R - W)^2 L, \tag{23}$$

and the osmotic pressure

$$\Pi = \frac{n_s R_g T}{V_h}. \tag{24}$$

One can then compute the changes in wall mass,

$$\frac{\mathrm{d}M_w}{\mathrm{d}t} = \frac{\Delta M_w^{max} n_s / V_h}{n_s / V_h + K_m}, \tag{25}$$

which allows computing the changes in sugar content,

$$\frac{\mathrm{d}n_s}{\mathrm{d}t} = -\frac{1}{M_s}\frac{\mathrm{d}M_w}{\mathrm{d}t} + \eta_s\left(C_s^{ext} - \frac{n_s}{V_h}\right), \tag{26}$$

and the changes in wall stress

$$\frac{\mathrm{d}\sigma_L}{\mathrm{d}t} = \frac{E\Phi_h}{1 + \frac{2W}{R}}\left(\Psi_{ext} - \frac{2W}{R}\sigma_L - P_{ext} + \Pi\right) + \frac{E}{V_h\rho^w(1 + \frac{2W}{R})}\frac{\mathrm{d}M_w}{\mathrm{d}t} - \frac{E}{\mu}(\sigma_L - \sigma_Y)^+. \tag{27}$$

One can then compute the changes in cell length,

$$\frac{\mathrm{d}L}{\mathrm{d}t} = L\frac{(\sigma_L - \sigma_Y)^+}{\mu} + \frac{L}{E}\frac{\mathrm{d}\sigma_L}{\mathrm{d}t}, \tag{28}$$

which allows computing the changes in wall thickness,

$$\frac{\mathrm{d}W}{\mathrm{d}t} = \frac{1}{\rho^w 2\pi R L}\frac{\mathrm{d}M_w}{\mathrm{d}t} - \frac{W}{L}\frac{\mathrm{d}L}{\mathrm{d}t}. \tag{29}$$

The values of the different unknowns at the next time step can be obtained by integrating Eqs. (26), (27), (28) and (29).