LNAS model for wheat with soil coupling

Pierre Carmier
Equipe Digiplante, Laboratoire MAS, CentraleSupelec, France
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The main idea behind this model is to introduce allocation functions which describe how the daily produced biomass is allocated to the different organs of the plant. It is a rather simple model in which the plant can be seen as a black box which converts environmental resources (provided on a stochastic basis) into biomass. With respect to sugarbeet, wheat represents more of a challenge to modelize due to the larger number of organs involved in the growth process (see Fig. 1). In the following, we shall provide a detailed yet simple model which describes the coupling of shoot and root processes and enforces the balance of water and biomass at all times.

A. Shoot part

The compartmental circulation of biomass for organ $o = \{\mathbf{g}\text{rain}, \mathbf{s}\text{tem}, \mathbf{r}\text{oot}, \text{green } \mathbf{l}\text{eaf}\}$ obeys the following equation:

$$Q_o^{(n+1)} = (1 - \beta_o^{(n)} - \gamma_o^{(n)})Q_o^{(n)} + \alpha_o^{(n)} q^{(n)} \ , \tag{1}$$

with α, β, γ respectively allocation, remobilisation and senescence functions. The case of $\mathbf{y}$ellow leaves is special, since it thrives on the senescence of green leaves and receives no allocation from the biomass pool: $Q_y^{(n+1)} = (1 - \gamma_y^{(n)})Q_y^{(n)} + \gamma_l^{(n)} Q_l^{(n)}$. The various functions responsible for biomass circulation depend on the thermal time $\tau(t) = \tau_d^{-1} \int_0^t dt' \max[0, \mathrm{T}(t') - T_c]$, such that

$$\tau^{(n+1)} = \tau^{(n)} + \max[0, \underline{\mathrm{T}}^{(n)} - T_c] \tag{2}$$

where T_c is a cultural-dependent base temperature. For example, assuming that allocation to grain only starts after a characteristic time τ_g and is asymptotically exhaustive, one can parametrize the corresponding allocation function as a cumulative log-normal distribution:

$$\alpha_g^{(n)} = F_{\log \mathcal{N}(\mu_g, \sigma_g)}(\tau^{(n)} - \tau_g) = \frac{1}{2}\left(1 + \mathrm{erf}\left[\frac{1}{\sigma_g \sqrt{2}} \log\left(\frac{\tau^{(n)} - \tau_g}{\tau_{1/2} - \tau_g}\right)\right]\right) \ , \tag{3}$$

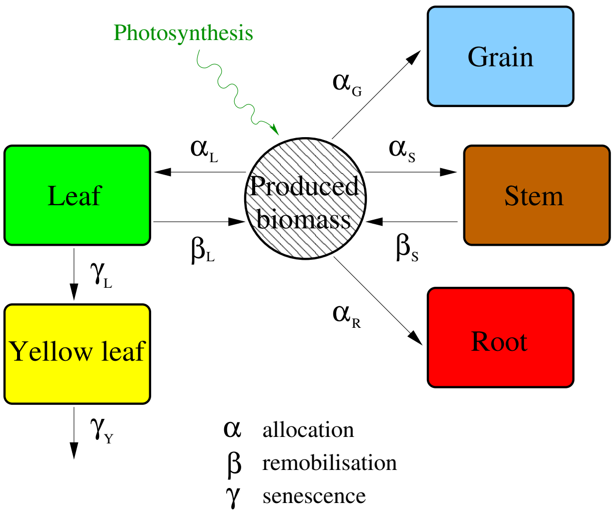

Figure 1: Circulation of biomass inside the plant modeled as different organ compartments, in terms of allocation, remobilisation and senescence functions.

with $\mu_g = \log(\tau_{1/2} - \tau_g)$ and σ_g the mean and variance of the distribution, $\tau_{1/2}$ the time at which $\alpha_g = 1/2$, and $\mathrm{erf}(x) = (2/\sqrt{\pi}) \int_0^x dt\, e^{-t^2}$ the so-called error function. In first approximation, other allocation functions can be taken as complementary to α_g: $\alpha_{s,l,r}^{(n)} = \alpha_{s,l,r}^{(0)}(1-\alpha_g^{(n)})$, with $\alpha_s^{(0)} + \alpha_l^{(0)} + \alpha_r^{(0)} = 1$. Remobilisation and senescence functions can likewise be parametrized by lognormal cumulative distributions: $\beta_o = \eta_o F_{\log \mathcal{N}(\mu_l,\sigma_l)}(\tau-\tau_l)$, where η_o is the fraction of biomass asymptotically involved in the process, $\gamma_l = (1-\eta_l) F_{\log \mathcal{N}(\mu_l,\sigma_l)}(\tau-\tau_l)$ and $\gamma_y = F_{\log \mathcal{N}(\mu_y,\sigma_y)}(\tau-\tau_y)$. Here τ_l and τ_y respectively mark the beginning of the remobilisation/senescence phase and the fall of yellow leaves.

The pool of allocated biomass is itself given as the sum of remobilized biomass and of biomass produced by photosynthesis:

$$q^{(n)} = \mathrm{RUE}\, \min[\mathrm{SSI}^{(n)}, \mathrm{TSI}_\uparrow^{(n)}] \underline{\mathrm{PAR}}^{(n)} (1 - e^{-\lambda \mathrm{LAI}^{(n)}}) + \sum_o \beta_o^{(n)} Q_o^{(n)} \,, \tag{4}$$

with RUE the radiation use efficiency, SSI and $\mathrm{TSI}_\uparrow$ stress indices (defined in section C), PAR the photosynthetically active radiation and $\lambda = \sin\phi$, where ϕ is the average angle between a leaf and the incoming light. The leaf area index $\mathrm{LAI}^{(n)} = S_l^{(n)}/S = \rho_l Q_l^{(n)}$ appears here as a geometrical factor inside the Beer-Lambert law for light interception: $(1 - e^{-\lambda \mathrm{LAI}})$ represents the soil coverage probability for a density LAI of leaves randomly distributed in space (but oriented with angle ϕ with respect to incoming light).

B. Root and soil part

The water balance equation reads

$$\mathrm{R}^{(n+1)} = \mathrm{R}^{(n)} + \underline{\mathrm{W}}^{(n)} - \mathrm{Es}^{(n)} - \mathrm{Tp}^{(n)} - d^{(n)} \,, \tag{5}$$

where W is the daily water input coming from precipitations and irrigation, Es is the water lost by evaporation from the soil, Tp is the water transpired by the plant and d is a drain function which takes into account the fact that the soil can only withhold a certain quantity of water which is bounded by the field capacity $\mathrm{R}_{\max}$. Starting from a continuous description, the soil water content can be expressed as

$$\mathrm{R}^{(n)} = \int_0^{z_M} dz\, \theta^{(n)}(z) \tag{6}$$

with θ the depth-dependent soil humidity and z_M the soil depth. The field capacity is simply $\mathrm{R}_{\max} = \int_0^{z_M} dz\, \theta_{\max}(z)$. Actually, due to the inability of the plant to extract the water from the soil (using capillary forces) below a certain soil humidity threshold $\theta_{\min}$ referred to as the permanent wilting point, one can define the transpirable water content in the soil as $\int_0^{z_M} dz\, \max[0, \theta^{(n)}(z) - \theta_{\min}(z)]$. Daily evaporation and transpiration requirements, given the environmental conditions, are expressed as

$$\mathrm{Espot}^{(n)} = K_s \underline{\mathrm{ET0}}^{(n)} e^{-\lambda \mathrm{LAI}^{(n)}} \,, \tag{7}$$

$$\mathrm{Tppot}^{(n)} = K_c\, \underline{\mathrm{ET0}}^{(n)} \left(1 - e^{-\lambda \mathrm{LAI}^{(n)}}\right) \,. \tag{8}$$

Here ET0 is the potential evapotranspiration evaluated using the Penman-Monteith formula for grass, and $K_s(K_c)$ are cultural coefficients (adapting the formula for wheat). On the other hand, daily maximal evaporation and transpiration, given the available water resources, are expressed as

$$\mathrm{Esmax}^{(n)} = \int_0^{z_M} dz \left(\min[\theta^{(n)}(z), \theta_{\min}(z)] e^{-z/z_S} + \frac{\max[0, \theta^{(n)}(z) - \theta_{\min}(z)] e^{-z/z_S}}{\max[1, e^{-z/z_S} + e^{-z/z_r^{(n)}}]} \right) \,, \tag{9}$$

$$\mathrm{Tpmax}^{(n)} = \int_0^{z_M} dz\, \frac{\max[0, \theta^{(n)}(z) - \theta_{\min}(z)] e^{-z/z_r^{(n)}}}{\max[1, e^{-z/z_S} + e^{-z/z_r^{(n)}}]} \,, \tag{10}$$

with z_S the surface layer of the soil and $z_r^{(n)} = \rho_r Q_r^{(n)}$ the root horizon at day n. Water partition in the soil can then be described sequentially at each time step:

1) Update the water content after input and possible drainage: $\mathrm{R}^{(n)} = \min[\mathrm{R}^{(n)} + \underline{\mathrm{W}}^{(n)}, \mathrm{R}_{\max}]$. In other words, this amounts to finding $z_W^{(n)}$ such that $\underline{\mathrm{W}}^{(n)} = \int_0^{z_W^{(n)}} dz\ (\theta_{\max}(z) - \theta^{(n)}(z))$, and update $\theta^{(n)}(z) = \theta_{\max}(z)$ for $z \leq \min[z_W^{(n)}, z_M]$.

2) Update the water content after evaporation and transpiration: $\mathrm{R}^{(n+1)} = \mathrm{R}^{(n)} - \mathrm{Es}^{(n)} - \mathrm{Tp}^{(n)}$, with

$$\mathrm{Es}^{(n)} = \min\left[\mathrm{Esmax}^{(n)}, \mathrm{Espot}^{(n)}\right] \ , \tag{11}$$

$$\mathrm{Tp}^{(n)} = \min\left[\mathrm{Tpmax}^{(n)}, \mathrm{Tppot}^{(n)}\right] \ . \tag{12}$$

In other words, this amounts to finding $z_{\mathrm{Es}}^{(n)}$ and $z_{\mathrm{Tp}}^{(n)}$ such that $\mathrm{Es}^{(n)} = \int_0^{z_{\mathrm{Es}}^{(n)}} dz$ ... and $\mathrm{Tp}^{(n)} = \int_0^{z_{\mathrm{Tp}}^{(n)}} dz$ ..., and update $\theta^{(n)}(z)$ accordingly.

C. Effect of hydric and thermal stresses

Hydric stress can be accounted for using the stomatal stress index

$$\mathrm{SSI}^{(n)} = \frac{\mathrm{Tp}^{(n)}}{\mathrm{Tppot}^{(n)}} = \min[1, \frac{\mathrm{Tpmax}^{(n)}}{\mathrm{Tppot}^{(n)}}] \ , \tag{13}$$

which describes the falling of the transpirable water reserve in the soil below the daily requirement. The main impact of hydric stress will be to reduce the daily produced biomass in Eq. (4). Recalling that root horizon is proportional to root biomass, such that $z_r^{(n+1)} = z_r^{(n)} + \rho_r \alpha_r^{(n)} q^{(n)}$, hydric stress could also favor root growth by having an impact on allocation functions, for example taking

$$\frac{\alpha_r^{(n)}}{1-\alpha_g^{(n)}} = 1 - (1-\alpha_r^{(0)})\mathrm{SSI}^{(n)} \ , \ \frac{\alpha_{l,s}^{(n)}}{1-\alpha_g^{(n)}} = \alpha_{l,s}^{(0)}\mathrm{SSI}^{(n)} \ . \tag{14}$$

The effect of thermal stress on root growth can furthermore be incorporated as $\alpha_r^{(n)} \to \mathrm{TSI}_\downarrow^{(n)}\alpha_r^{(n)}$, with the soil thermal stress index

$$\mathrm{TSI}_\downarrow^{(n)} = \chi_{[0,1]}(\frac{\mathrm{T}_\downarrow^{(n)} - T_{\downarrow c}}{T_{\downarrow\mathrm{opt}} - T_{\downarrow c}}) \ , \text{ with the characteristic function } \chi_{[a,b]}(x) = \left| \begin{array}{ll} x & \text{if } x \in [a,b] \\ 0 & \text{otherwise} \end{array} \right. \ . \tag{15}$$

Soil temperature $\mathrm{T}_\downarrow$ is actually depth-dependent, but we only need its value at root horizon. Its evolution proceeds as $\mathrm{T}_\downarrow^{(n+1)} = \mathrm{T}_\downarrow^{(n)} + (\underline{\mathrm{T}}^{(n+1)} - \underline{\mathrm{T}}^{(n)})e^{-z_r^{(n)}/z_S}$. Note that $\alpha_l^{(n)}$ and $\alpha_s^{(n)}$ will also be impacted by $\mathrm{TSI}_\downarrow^{(n)}$, but with an opposite trend, since biomass conservation ensures that biomass not allocated to the roots must necessarily be allocated to other organs: thus, $\alpha_{l,s}^{(n)} = \alpha_{l,s}^{(0)}(1-\alpha_g^{(n)})[\mathrm{SSI}^{(n)}\mathrm{TSI}_\downarrow^{(n)} + (1-\mathrm{TSI}_\downarrow^{(n)})/(1-\alpha_r^{(0)})]$. Finally, the influence of thermal stress above ground on the daily produced biomass must also be taken care of using:

$$\mathrm{TSI}_\uparrow^{(n)} = \chi_{[0,1]}(\frac{\underline{\mathrm{T}}^{(n)} - T_c}{T_{\mathrm{opt}} - T_c}) \ . \tag{16}$$

D. List of variables and parameters

Main state variables: $\mathbf{X} = \{Q_r, Q_s, Q_l, Q_y, Q_g, \tau, \theta, \mathrm{R}, \mathrm{Es}, \mathrm{Tp}, z_r, \mathrm{SSI}, \mathrm{TSI}_{\uparrow(\downarrow)}\}$
Auxiliary state variables: $\{q, \mathrm{LAI}, \mathrm{Espot}, \mathrm{Tppot}, \mathrm{Esmax}, \mathrm{Tpmax}, d, \mathrm{T}_\downarrow\}$
Environmental variables: $\underline{\mathbf{E}} = \{\mathrm{T}, \mathrm{PAR}, \mathrm{W}, \mathrm{ET0}\}$
Shoot parameters: $\mathbf{P}_\uparrow = \{T_c, T_{\mathrm{opt}}, \tau_g, \mu_g, \sigma_g, \eta_s, \eta_l, \tau_l, \mu_l, \sigma_l, \tau_y, \mu_y, \sigma_y, \mathrm{RUE}, \lambda, \rho_l, K_c(K_s)\}$
Soil and root parameters: $\mathbf{P}_\downarrow = \{\theta_{\max(\min)}, z_S, z_M, \rho_r, T_{\downarrow c}, T_{\downarrow\mathrm{opt}}\}$

E. Initialisation

$\theta^{(0)}(z) = \theta_{\max}(z), \tau^{(0)} = 0, \alpha_{s,r,l}^{(0)} = 1/3, Q_{r,s,l}^{(0)} =?$