

A dynamic model system to couple the organ length and mass dynamics specified for spring barley (*Hordeum vulgare* L.)

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Introduction

An important goal in developing functional-structural plant models (FSPMs) is a reliable and adequate description of the inherent interactions between processes controlling plant growth and formation of plant architecture. Several architectural models have been introduced for specific crops using temperature-driven descriptive models based on the phyllochron / plastochron philosophy (Dornbusch et al., 2007; Drouet, 2003; Evers et al., 2005; Fournier et al., 2003; Prévot et al., 1991; Watanabe et al., 2005). In order to couple those architectural models to process models, which lastly compute the amount of mass assimilated by the photosynthetically active organs, an interface between mass dynamics and the formation and growth of new organs needs to be developed. Fournier et al. (2005) introduced a model to describe the length dynamics of leaf blades and leaf sheaths of wheat (*Triticum aestivum* L.). Here we propose an extension of this model to describe the length dynamics coupled with the corresponding mass dynamics of barley (*Hordeum vulgare* L.) organs (blades, sheaths and internodes) based on experimental data. The proposed model includes a set of coupled ordinary differential equations (ODEs). The model performance is demonstrated by simulation studies.

Model description

Fournier et al. (2005) describe the organ length dynamics of blades and sheaths using cell fluxes between three cell pools: i) the cell pool in the division zone (D), ii) the cell pool in the elongation-only zone (E) and iii) the cell pool in the mature zone (M). Here we introduce a different notation for the state variables in the model by Fournier et al. (2005):

$$\frac{dZ_D}{d\tau} = R_{Z,D} - F_{Z,D \rightarrow E}, \quad R_{Z,D} = K_1 \cdot Z_D, \quad (1)$$

$$\frac{dZ_E}{d\tau} = R_{Z,E} + F_{Z,D \rightarrow E} - F_{Z,E \rightarrow M}, \quad R_{Z,E} = K_2 \cdot Z_E, \quad (2)$$

$$\frac{dZ_M}{d\tau} = \quad + F_{Z,E \rightarrow M}, \quad (3)$$

with the initial conditions:

$$Z_D(\tau = 0) = Z_{D0}, \quad Z_E(\tau = 0) = 0, \quad Z_M(\tau = 0) = 0, \quad (4)$$

where τ = phyllochronic time. The state variables Z_D , Z_E and Z_M are vectors and define the length Z of the zones D, E, and M of blades, sheaths and internodes. The total organ length equals to $Z_T = Z_D + Z_E + Z_M$. The vector R is the increase in length in the respective zone and F the length fluxes between them. K_1 and K_2 are defined in Eq. (6) and (7). To couple the mass and length dynamics of each organ, we introduce a function CF , which controls the availability of assimilates required for building up the structure of an organ. Using the assimilated carbon $m_{C,ass}$ and the dry mass m_{tiller} of a tiller and introducing the concentration C defined as $C = m_{C,ass} / m_{tiller}$ we formulate the control function CF as:

$$CF(\tau, C) = \frac{C}{K_C + C} \cdot (\tau > \tau_0), \quad CF(\tau \leq \tau_0) = 0, \quad 0 \leq CF \leq 1. \quad (5)$$

The parameter K_C is a model parameter stating a critical concentration of available carbon, below which no organ growth is initiated, and τ_0 is the phyllochronic time where fluxes into a respective organ are initiated. Using the model parameters k_1 and k_2 (cf. Fournier et al. 2005) the functions K_1 and K_2 are defined as:

$$K_1(\tau) = k_1 \cdot CF, \quad (6)$$

$$K_2(\tau) = k_2 \cdot CF. \quad (7)$$

The production terms $R_{Z,D}$ and $R_{Z,E}$ characterize cell division and cell elongation rates (cf. Eq. (1) and (2)). The cell exchange fluxes $F_{Z,D \rightarrow E}$ and $F_{Z,E \rightarrow M}$ between two cell pools are defined as:

$$F_{Z,D \rightarrow E}^{BL} = K_1 \cdot a(\tau) \cdot (Z_D^{BL} + Z_D^{SH}) \cdot Z_D^{BL} \quad \text{for } (Z_D^{BL} > 0),$$

$$F_{Z,D \rightarrow E}^{SH} = K_1 \cdot a(\tau) \cdot (Z_D^{BL} + Z_D^{SH}) \cdot Z_D^{SH} \quad \text{for } (Z_D^{BL} \leq 0), \quad (8)$$

$$F_{Z,E \rightarrow M}^{BL} = K_2 \cdot b(\tau) \cdot (Z_E^{BL} + Z_E^{SH}) \cdot Z_E^{BL} \quad \text{for } (Z_E^{BL} > 0),$$

$$F_{Z,E \rightarrow M}^{SH} = K_2 \cdot b(\tau) \cdot (Z_E^{BL} + Z_E^{SH}) \cdot Z_E^{SH} \quad \text{for } (Z_E^{BL} \leq 0), \quad (9)$$

$$a(\tau) = \max(0, p_{a1} \cdot (\tau - \tau_a)), \quad b(\tau) = \max(0, p_{b1} \cdot (\tau - \tau_b)), \quad (10)$$

with the time functions $a(\tau)$ and $b(\tau)$, the model parameters p_{a1} and p_{a2} , and the characteristic times τ_a , τ_b . We propose a flux of carbon mass $F_{m,E \rightarrow M}$ into the organ proportional to the cell flux $F_{Z,E \rightarrow M}$ as:

$$F_{m,E \rightarrow M} \approx p_m \cdot F_{Z,E \rightarrow M}. \quad (11)$$

The proportional factor p_m defines the need of carbon mass per unit length of new organ tissues. The carbon mass flux $F_{m,E \rightarrow M}$ is sink and source limited. On the one hand, if the sink organ cannot be sufficiently supplied with assimilates produced by the source organ (the carbon concentration in the source organ decreases), the control function CF in Eq. (5) approaches zero and, thus, one gets a source limitation. On the other hand, the number of cells (organ length in the elongation zone) determines the sink limitation.

Organ senescence causes some outflow of carbon F_{sens} . We set this flux proportional (factor p) to the carbon mass of the organ as a function of phyllochronic time $f(\tau)$ (cf. Eq. (15)):

$$F_{sens} = p \cdot f(\tau) \cdot m_C. \quad (12)$$

The balance equation for the carbon masses m_C of organs is given by:

$$\frac{dm_C^{BL}}{d\tau} = F_{m,E \rightarrow M}^{BL} - F_{sens}^{BL}, \quad F_{m,E \rightarrow M}^{BL} = p_1^{BL} \cdot F_{Z,E \rightarrow M}^{BL} + p_2^{BL} \cdot F_{Z,E \rightarrow M}^{SH}, \quad (13)$$

$$F_{sens}^{BL} = p_3^{BL} \cdot f(\tau) \cdot m_C^{BL},$$

$$\frac{dm_C^{SH}}{d\tau} = F_{m,E \rightarrow M}^{SH} - F_{sens}^{SH}, \dots F_{m,E \rightarrow M}^{SH} = p_1^{SH} \cdot F_{Z,E \rightarrow M}^{SH}, \quad F_{sens}^{SH} = p_3^{SH} \cdot f(\tau) \cdot m_C^{SH}, \quad (14)$$

$$f(\tau) = \max(0, \min(p_4 - \tau, \tau)), \quad (15)$$

where only carbon mass of leaf blades m_C^{BL} and leaf sheaths m_C^{SH} are presented here. The first term on the right side of the ODEs (Eq. (13) and (14)) describes the contribution of organ growth proportional to the cell fluxes from blade and sheath organ. The senescence flux F_{sens}^{BL} and F_{sens}^{SH} in (Eq. (13) and (14)) is proportional to the organ carbon mass and its magnitude is determined by the time function $f(\tau)$ (Eq. (12)). The parameter p_4 determines the phyllochronic time of the onset of organ senescence. Knowing the carbon masses by solving the ODE system, then the dry mass m_T can be computed as:

$$m_T = k_{C2M} \cdot m_C, \quad (16)$$

with k_{C2M} being the unit dry mass per unit carbon mass.

Results and discussion

Based on experimental data for organ length and masses of spring barley organs, values for the parameters in the ODEs were estimated. Using the parameterized ODEs, it was possible to describe the organ dynamics (blades, sheaths, internodes) from the day of planting until ripeness of organs.

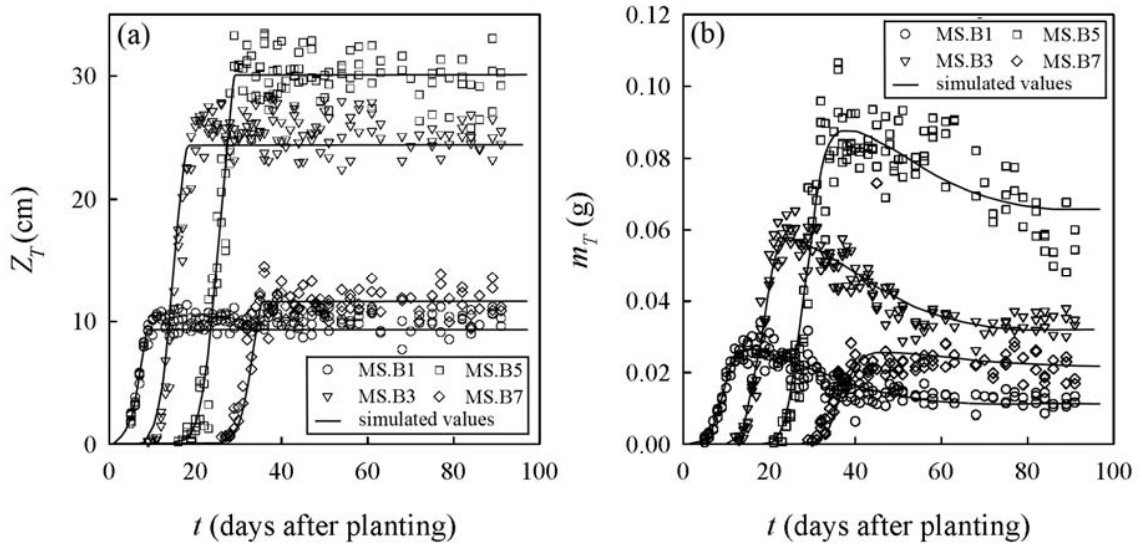


Figure 1: a) Measured values of leaf blade length (Z_T) on the main stem (MS) vs. time (t); some leaf ranks (B2, B4 and B6) were left out for clarity; b) measured values for leaf blade dry mass (m_T) on the main stem vs. time (t); the solid lines represent the approximation of Z_T and m_T with the proposed model.

To demonstrate the performance of the model we present two examples. First, the length dynamics of leaf blades on the main stem are presented in Fig. 1a. All model parameters (values not shown) are estimated based on experimental data. Second, we tested the new approach to describe the mass dynamics of the same organs based on the formulated balance equations, fluxes and senescence rates (Fig. 1b). Results indicate that the model is capable to simulate the organ mass dynamics on the main tiller as a result of cell division, cell elongation, and mass transport to and from each plant organ.

The simulated dynamics depends on ontogenetic events. If an organ state switches from the cell division state to the state of cell elongation, a new sink creates mass fluxes towards this new organ proportional to the corresponding cell fluxes. The following questions need to be addressed in future work. How robust is the length and mass dynamics of an organ depending on the carbon supply (as e.g. influenced by the radiation conditions inside the canopy)? Which key processes can be incorporated into the model to synchronize the architecture and mass dynamics not only on the basis of characteristic times (e.g. parameters τ_a , τ_b), but on the basis of characteristic concentrations of key substrates?

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