

Extending a functional-structural plant model of spring wheat with sub-models for photosynthesis and carbon distribution

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Keywords: spring wheat, architecture, tillering, photosynthesis, sink-source, nitrogen

Introduction

Members of the Poaceae family have been rewarding subjects of research in the field of functional-structural plant modelling (FSPM) (Fournier *et al.*, 2007). Poaceae comprise important cereal crop species such as rice, wheat, and maize, and the plants usually exhibit a regular and co-ordinated development making them particularly suitable for FSPM. The models that have been reported up to now range from descriptive (e.g. Watanabe *et al.*, 2005) to (partially) mechanistic (e.g. Guo *et al.*, 2006; Wernecke *et al.*, 2007).

Here we report on our ongoing work on an FSPM of spring wheat (*Triticum aestivum* L.), of which simulation of growth and development, until recently, have been mainly descriptive. The outgrowth of tiller buds into tillers (branches in Poaceae) has been made dependent on the local ratio between red and far-red light (Evers *et al.*, 2007a). Once the ‘decision’ is taken to develop a particular bud into a tiller, the emergent organs attain more or less predefined properties (e.g. dimensions, shape, etc.). The limitations to this (provisional) approach are (I) source activity is not included and (II) organ outgrowth and dimensions of organs are not subjected to modulation due to sink-source interactions.

The general objective of the current work is to add ‘functionality’, *i.e.* carbon gain and partitioning, to the architectural model in order to obtain a complete FSPM of a canopy of spring wheat plants. Operational objectives of the work include the extension of the current architectural model of spring wheat with provisions that convert radiation absorbed by each element of the 3D structure into photosynthates, and distribute carbon over individual, growing organs.

Approach

The model used in this study is based on the concepts of Fournier *et al.* (2003), and has been calibrated and validated for spring wheat (Evers *et al.*, 2005, 2007b), see Fig. 1 for a visualisation. Details can be found in the papers cited. This model provides a solid basis for extension with sub-models for photosynthesis and carbon distribution.

Data collection

Data to realize the objectives stated, were gathered in two experiments conducted in Wageningen, the Netherlands: one outdoor experiment, and one in a growth chamber. In the outdoor experiment plants were grown at three plant population densities and exposed to two nitrogen treatments (limiting and non-limiting),



Fig. 1: Visualisation of a small simulated wheat plot

and two light treatments (75% shading and full light). In this experiment data were gathered on the distribution of chlorophyll meter values (SPAD) in the canopy, and on plant growth and organ weight by harvesting plants at five stages of development. In the growth chamber experiment, two nitrogen treatments (limiting and non-limiting) were applied. In this experiment a diversity of photosynthesis parameters were assessed (both through gas exchange and chlorophyll fluorescence) and calculated. A calibration curve was created for leaf nitrogen content versus SPAD value. Details on the experimental setups and measurement protocols will follow in later communications.

Source activity

For a given hemispherical distribution of daily incoming solar radiation, the illumination of each plant organ of the canopy structure (leaves, internodes) can be simulated using the wheat architectural model in combination with the nested radiosity model for crop canopies (Chelle and Andrieu, 1998). Using organ-specific reflection and transmission coefficients, PAR absorption by the plant organs was calculated from this illumination on an hourly basis. Subsequently, rate of photosynthesis of each individual organ was modelled by applying an updated biochemical model for C₃ photosynthesis (Yin *et al.*, submitted), based on Farquhar *et al.* (1980), and extended by Yin *et al.* (2004). A (photosynthesis rate), C_i (intercellular CO₂ concentration), and g_s (stomatal conductance) were calculated using an analytical solution to a coupled photosynthesis - stomatal conductance model.

The biochemical photosynthesis model was parameterized by fitting the photosynthesis (gas exchange and chlorophyll fluorescence) data derived from the growth chamber experiment, measured for the two nitrogen treatments, two leaf insertion levels and three leaf age categories (Yin *et al.*, submitted). The estimated parameters were maximum carboxylation rate of Rubisco ($V_{c,max}$), maximum rate of linear electron transport (J_{max}), Rubisco CO₂/O₂ specificity factor ($S_{c/o}$), mesophyll conductance (g_m), 'dark' respiration rate in the light (R_d), residual g_s at the light compensation point (g_0), minimum leaf nitrogen content for photosynthesis (N_b), and a parameter for maximum efficiency of light conversion into linear electron flux on incident light basis ($\kappa_{2(LL)}$). Remaining parameter values required by the model of Farquhar *et al.* (1980) are considered to be conservative among C3 species, and taken from Von Caemmerer *et al.* (1994) and Bernacchi *et al.* (2002).

Sink strength

Sink strength is defined as the potential capacity of sink tissues to accumulate assimilates (Marcelis and Heuvelink, 2007). Experimentally, the sink strength can be derived from the growth curve under conditions ensuring abundant source supply, either by removing competing sinks or by enhancing photosynthesis (high radiation and/or CO₂). For the current work, sink strength values were derived using the GreenLab plant modelling approach (Yan *et al.*, 2004). Based on several growth chamber experiments using the same wheat cultivar as in the present study, sink strength values for various organ types (blades, sheaths, internodes, spikes, root system) have been calculated by a non-linear least squares root fitting procedure (Kang *et al.*, in press). These values were used in the present study.

Sink-source relations

To simulate the distribution of assimilates from the sources to the sinks, the semi-mechanistic concept of carbon allocation being determined by the relative sink strengths of competing sinks can be implemented (Heuvelink, 1996; Marcelis, 1996). However, bud break and the appearance of tillers is not straightforward: whether or not particular tillers will appear will not 'automatically' emerge as a result of the simulation. Here extra rules might be needed, e.g. specifying that the local assimilate production of the parent leaf has to be taken into account (Bos, 1999).

It is possible to efficiently implement carbon fluxes between plant components, based on gradients in driving forces (*i.e.* Ohm's law analogy) (Allen *et al.*, 2005; Prusinkiewicz *et al.*, 2007). The virtue of that approach is that local effects and sink priorities become an emergent property. Sink activity is represented by Michaelis-Menten kinetics, the parameters of which

(V_{max} and k_m) are being deduced from the sink strength functions, while resistance is proportional to distance. In the FSPM distance is deduced from organ dimensions and topology that are kept track of. However, it will be examined first whether the semi-mechanistic approach can be used satisfactorily.

Nitrogen distribution

Instead of modelling the entire nitrogen economy of a wheat plant, an empirical function was developed that describes the distribution of SPAD values of the individual leaf blades throughout the development of a wheat plant. The function is a cubic polynomial relation between SPAD value and thermal time, of which the four parameters are themselves linear functions of the cumulative phytomer number of the leaf blade (which is the total number of phytomers from the bottom of the plant until the leaf blade in question):

$$S = (p_a C + p_b) \cdot t^3 + (q_a C + q_b) \cdot t^2 + (r_a C + r_b) \cdot t + s_a C + s_b \quad (\text{Eq. 1})$$

where S is SPAD value (dimensionless), C is cumulative phytomer number of the leaf blade, t is thermal time ($^{\circ}\text{Cd}$), p_a , q_a , r_a , s_a are slope parameters and p_b , q_b , r_b , s_b are intercept parameters fitted to the S - C - t data, for each of the treatments. Subsequently, the calculated SPAD values were converted into nitrogen content per surface area, using the calibration curve obtained from the growth chamber experimental data.

Outlook

The combination of an architectural plant model and sub-models for carbon assimilation and distribution throughout the plant is promising. The added value of taking plant geometry into account will show its strength when phenomena that rely on local processes are simulated (e.g. bud break). This is what the current work is aiming at.

Acknowledgements

We thank the staff of the experimental facilities UNIFARM of Wageningen University, Fleur Sterk, and Guillaume Castel for their contributions to the experiments; Dr. A. Schapendonk, Mr. S. Pot (Plant Dynamics B.V.), Dr. T. Pons and Mr. R. Welschen (Utrecht University) for their support. The C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) and the Instituto Nacional de Investigación Agraria y Alimentaria (INIA) funded this work.

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