MODELLING SPRING BARLEY DEVELOPMENT USING CANONICAL FUNCTIONAL MODEL. PRELIMINARY RESULTS

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Summary

We present a preliminary mathematical model of the biomass resources production and redistribution in the spring barley. It is based solely on the quantitative data describing changes in the dry matter weight of the spring barley stem, leaves and ear with grain. Data were collected for the Rasbet and Rastik spring barley cultivars. The model focuses on description of the accumulation of the biomass reserves in the stem and leaves and its redistribution to the grain during the grain filling. The so-called canonical approach is applied.

Key words and phrases: spring barley, plant development, biomass, modelling

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1. Introduction

Mathematical modelling of plants development is a very interesting topic. Most works in this field concern trees. Their models are widely used in computer graphics and forestry. In the recent years we observe growing interest in the agricultural application of modelling. The farming plants concerned are: cotton, wheat, barley, maize, tomato and others. In general the models describe the production and allocation of the plant biomass.

There exist three approaches to the plant modelling each used for different applications: the structural plant models (SPM), process-based models (PBM) and functional-structural plant models (FSPM). The SPM can be also called an architectural model as it is used to describe the plant developing structure basing only on measurements of the sizes, shapes and angles of the plant organs. On the contrary the PBM is used to model the physiological processes within a plant without an interest in its detailed morphology. A large group of PBMs are the so called source-sink models in which various plant organs play role of the sources of the biomass or their sinks. The combining of the two model types leads to the FSPMs which are the most sophisticated approaches to describe a plant growth.

Though there already exist a few works on barley growth modelling describing highly developed models (Buck-Sorlin, 2005; Buck-Sorlin, 2007; Alam, 2006; Wernecke, 2007) we present preliminary results for a new approach which is far less precise but much simpler in developing and moreover does not require large amount of experimental observations. In our model we focus on the source-sink relations between a stem with leaves and a developing ear with grain. We are interested in the biomass production, storage and redistribution before and after the anthesis.

The article is divided into six sections. In its second part we describe the materials collected during the experiment and the tools used in their analysis. In the following section we introduce the notion of the canonical modelling. In fourth part the important facts about the allocation and redistribution of biomass resources within the barley are given. The details of the applied mathematical model are described in the fifth section. Next, the results of the analysis are presented. The article ends with conclusions.
2. Materials and methods

In this work we analyse data collected during year 2002. Two barley varieties, Rasbet and Rastik were sown in the optimal timing each on four experimental fields of the 12x2.5 m size. Six times during the vegetation the sample individuals were randomly picked from one 30 cm long row. Dry matter weight was measured; the number of plants and total number of their stems were calculated. The aboveground biomass was split into three parts: dry weight of leaves, stems and ears with grain. The total values were divided by the number of stems in order to obtain the dry mass weight development for an individual barley stem. In the case of both barley varieties we observe that results obtained from one of the experimental fields differ strongly from the remaining ones which may be caused by different soil conditions or other unknown factors. We remove the protruding results and calculate the model input data as the mean of the dry weight masses measured in the three remaining fields. The standard deviations of the means stand for data uncertainties. In our analysis we utilize the Rasbet variety results for which final data are presented in Fig.1.

![Fig. 1](image)

**Fig. 1.** The experimental data for the Rasbet barley variety. Dry mass weights calculated for a mean individual plant as described in text. Averages and standard deviations calculated using measurements from the experimental fields 1, 2 and 3. The moment 0 corresponds to the first day of measurements. The interpolation curves obtained with Excel.
The parameters of the models applied in the article were computed by minimizing the $\chi^2$ function:

$$\chi^2 = \sum_{i=1}^{n} \left( \frac{f_{\text{theor},i} - f_{\text{exp},i}}{f_{\text{exp},\text{error},i}} \right)^2,$$

(2.1)

where $n$ is the number of the experimental points and $f_{\text{theor},i}$, $f_{\text{exp},i}$, and $f_{\text{exp, error},i}$ are the theoretical and experimental function values and the experimental value errors, respectively. We applied the variable metric optimization algorithm published simultaneously in 1970 by Broyden, Fletcher, Goldfarb and Shanno (for code description see Nash, 1990).

The main tool for calculations was the R Statistical Computing environment (version 6.2.1). Large amount of computations was performed on the computer cluster of the Faculty of Experimental Design and Bioinformatics of the Warsaw University of Life Sciences.

3.Canonical modelling

In order to model the barley growth using solely the dry weight data we apply the so called “canonical model” which allows incorporating physiological source-sink relations within a plant without considering in detail the processes which govern them. This approach has been applied with success for description of the growth of the mountain birch (Kaitaniemi, 2000; Renton, et al. 2005b), the amaranth plant (Renton, 2004; Renton, et al., 2005a) or the cotton stand (Thornby, 2004; Renton, et al., 2005a). It was developed in 1969 by M.A. Savageau for the purpose of modelling the biochemical processes (Savageau, 1969). It is based on the power-law assumption.

Any plant can be described as a set of compartments which can play role of sources, sinks or both. The compartment variables are usually associated with such quantities as biomass of various plant organs. They are connected by fluxes of biomass and the so called influences which describe impact of various compartments on fluxes. Given flux is calculated as a constant multiplied by the product of the source compartment for that flux and all its influencing compartments, each raised to some different constant. The fluxes describe variation in time of the compartment variables. For each variable one takes into account all incoming and outgoing fluxes and obtains a set of the ordinary differential equations governing development of a plant. The graphical illustration of the
structure of an exemplary canonical model with its set of the ordinary differential equations is presented in Fig. 2.

\[ f_1 = \alpha_1 x_2^{k_{12}}, \quad \frac{dx_1}{dt} = f_1 - f_2 - f_3, \]
\[ f_2 = \alpha_2 x_1^{k_{21}} x_3^{k_{23}}, \quad \frac{dx_2}{dt} = f_2, \]
\[ f_3 = \alpha_3 x_1^{k_{31}}, \quad \frac{dx_3}{dt} = f_3. \]

**Fig. 2.** Graphical illustration of the structure of an exemplary canonical model with three compartment variables (circles), three fluxes (solid lines) and two influences (dotted lines). The equations form a set of ordinary differential equations governing the development of the modelled plant.

### 4. Spring barley growth – allocation and redistribution of resources

Let us concentrate on the details of the barley development interesting for the purpose of the biomass allocation and redistribution. As can be seen in Fig. 1 the spring barley growth can be divided into three phases: pre-anthesis (approximately measurements till the third experimental point), grain filling (from third till fifth point) and final senescence (after the fifth point). During the first phase both stem and leaves grow very quickly. During anthesis ear emerges and begins its rapid development, the grain filling starts. At similar time senescence of other organs begins. The leaves of barley grow in a hierarchical way. They are successively formed at the apex and also successively initiate senescence. While the primary leaf already starts to decay the new top leaves are being formed (Wiedemuth et al., 2005). At the final stage before harvest all spring barley organs loose their dry mass weight.

It was observed already in 1869 (Pierre, 1869) that the pre-anthesis period of the development of barley is used to accumulate the biomass resources which are utilized in the later phase of grain filling. That long term phenomenon allows for effective development of the grain during periods of insufficient pho-
tosynthesis. The resource storage occurs also on short term, diurnal scale as required to allow for the overnight grain filling. For review on the barley carbohydrate storage and redistribution see (Schnyder, 1993).

In the case of canonical modelling of the spring barley growth where the interesting time scale is given in days we concern only the long term biomass storage and its later redistribution. Those processes are very complicated and not yet experimentally well established (see for instance Przulij et al., 2003). The storage occurs mostly in the form of water soluble carbohydrates. Their accumulation in stem and leaves is not competitive with the grain filling and lasts until 10-20 days after anthesis (Schnyder, 1993).

5. Model

The simplest method to model barley growth is to divide its organs into three parts: leaves, stem and ear with grain, and the development time into three periods described in detail in previous section. One can analyse each organ growth independently in each of time periods (with the continuity constraint put on the weight functions for each organ). Such approach leads to the analysis of nine models. In each of them the only compartment variable must be related with the dry matter weight of the analysed barley organ. In that case the incoming flux is governed (influenced) by the compartment mass as shown in Fig. 3. Such models are called the unbounded growth models. Their application to our data gives very precise results, see Fig. 4. Unfortunately that way we do not gain any insight into the physiological processes occurring during the barley development.

![Graphical illustration of the unbounded canonical growth model](image)

\[ f = \alpha x^k, \]
\[ \frac{dx}{dt} = f. \]

*Fig. 3. Graphical illustration of the unbounded canonical growth model*
Realistic model of barley plant growth must be based on knowledge of the allocation and redistribution of biomass resources within the plant. Our proposal of such model is graphically presented in Fig. 5. The model consists of two compartments describing biomass of the stem with leaves ($x_{ls}$) and biomass of the ear with grain ($x_{ec}$), respectively. The photosynthesis of both groups of organs has been included through the $f_{ils}$ and $f_{iec}$ input fluxes. The $f_u$ flux represents the biomass redistribution within the plant and the $f_{ls}$ and $f_{ec}$ fluxes describe the loss of the dry weight mass through senescence. The photosynthesis is described in the same way as in the unbounded growth model (we use $1+x_{ec}$ instead of $x_{ec}$). The total number of parameters is 11. We apply additional Boolean variables $x_{b1}$, $x_{b2}$ and $x_{b3}$ necessary to describe noncontinuous behaviour of most of the fluxes. The Boolean variables are defined zero below some time threshold and one above that threshold.
The model is divided into three phases. First applies to the pre-anthesis period, only the leaves and stem develop then \((x_{b1}=x_{b2}=x_{b3}=0)\). Next, after the anthesis ear begins to grow and the redistribution of the biomass resources through the \(f_u\) flux starts \((x_{b3}=1)\). At the same time the senescence of leaves and stem begins \((x_{b2}=1)\). Finally after termination of the grain filling ear commences its senescence \((x_{b3}=1)\).

\[
\begin{align*}
    f_{ls} &= \alpha_{ls}x_{ls}e^{k_{ls}t} \\
    \frac{dx_{ls}}{dt} &= f_{ls} - f_u - f_{ls} \\
    f_{ec} &= \alpha_{ec}(1 + x_{ec})e^{k_{ec}t}x_{b1} \\
    \frac{dx_{ec}}{dt} &= f_{ec} + f_u - f_{ecs} \\
    f_{ss} &= \alpha_{ss}x_{ls}e^{k_{ss}t}x_{b2} \\
    f_{ecs} &= \alpha_{ecs}x_{ec}e^{k_{ecs}t}x_{b3}
\end{align*}
\]

Results of the proposed model after fitting its parameters are presented in Fig. 6. Fig. 7 shows the changes of fluxes in time. Their integrated values are given in Table 1. First we observe that after the stem and leaves senescence begins it nearly equals the biomass photosynthesis and the net biomass production by those organs is very small. That can be partly explained by the scheme of the leaves production in barley. While the top leaves emerge the low ones

![Graphical representation of the model for the resource allocation and redistribution in the spring barley](image)
already decay. We also notice that the dry mass redistribution from the stem and leaves into the ear and grain is an important part (about 42%) of the dry mass allocated during the grain filling. Finally, we present plots showing the predicted contributions of the stem with leaves and ear with grain to the total plant photosynthesis. Since anthesis till the harvest the ear and grain contribution grows from 10% to over 35%.

**Fig. 6.** Development of a stem with leaves and of an ear with grain predicted by the model expressed as the biomass change over the time. The moment 0 corresponds to the first day of measurements.
Fig. 7. Change of the flux values over time. The moment 0 corresponds to the first day of measurements.
Table 1. Values of the fluxes integrated over time (in g)

<table>
<thead>
<tr>
<th>Flux</th>
<th>$f_{ls}$</th>
<th>$f_{ec}$</th>
<th>$f_{lu}$</th>
<th>$f_{ls}$</th>
<th>$f_{ec}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Integrated value</td>
<td>4.21</td>
<td>0.76</td>
<td>0.54</td>
<td>3.44</td>
<td>0.65</td>
</tr>
</tbody>
</table>

Fig. 8. The model predicted contributions of the stem with leaves and ear with grain to the total spring barley plant photosynthesis

6. Conclusions

Model of the spring barley growth has been presented. The approach utilizes solely the dry mass data of the spring barley organs. We applied the so-called canonical functional model which is a nonlinear source-sink approach built of compartments and fluxes of biomass. The current knowledge on the physiological processes of the biomass allocation and redistribution within a barley plant was used to construct necessary fluxes. As an outcome of the model we obtained predictions for all fluxes and for the contributions of the stem with leaves and ear with grain to the total plant photosynthesis.

Though, as we believe, we propose a consistent model which results agree with the current knowledge on the barley development it is still a preliminary model. It should be expanded in a few ways. First, separate compartment variables for the stem and leaves should be introduced with appropriate fluxes. Second, more data points should be used in order to obtain more reliable thresholds for the model phases and more precise fits. That requires new dedi-
cated field experiments. Finally, we should consider roots in the barley growth description which most probably requires a laboratory experiment.

References


MODELOWANIE ROZWOJU JĘCZMIEŃA JAREGO Z WYKORZYSTANIEM FUNKCJONALNEGO MODELU KANONICZNEGO. WYNIKI WSTĘPNE

Streszczenie

W pracy przedstawiamy wstępny model matematyczny opisujący produkcję i redystrybucję zapasów biomasy w jęczmieniu jarym. Model bazuje wyłącznie na pomiarach suchej masy pędów, liści oraz kłosów z ziarnem wykonanych dla odmian Rasbet i Rastik jęczmienia jarego. Skupiamy się na opisie akumulacji zapasów biomasy w pędzie i liściach i ich późniejszej redystrybucji na etapie wypełniania ziaren. W pracy stosujemy tak zwany model kanoniczny.

Słowa kluczowe: jęczmień jary, rozwój roślin, biomasa, modelowanie

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