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# **TECHNICAL NOTE: 89.3**

# **MATHEMATICAL MODELS**

# **APPLICABLE TO PLANT**

# **STRESS RESPONSE**

# **PREDICTION**

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## 1. Introduction

The objective of this study is to pursue and extend the higher plant chamber modelling task initiated within the MELISSA framework by Mathieu Favreau and Luis Ordonez Inda.

The model needs to be based on the reaction kinetics of the processes controlling plant growth and development, and on the effects that different stress conditions may have on these processes. Input parameters will be the environmental variables that influence growth and crop yield. This model will be a first attempt to predict whole canopy growth for at least one of the 2 proposed crops (lettuce or table beet), based on parameters to be acquired in the planned plant growth experiments.

This TN reports on the first part of the modelling study dedicated to the literature review and the resulting model structure selection.

This part of the study has been based on a literature review that involves :

- an initial list of references that have been provided by the University of Ghent (UGent-HSB),
- the ESA report with the model of Mathieu Favreau [3],
- an internet bibliographic database search to select possible other papers related to the topic,
- the book on plant modelling by Thornley and Johnson [21].

In the following sections, the relevance of the selected scientific papers and the plant modelling book will be discussed. Then the different aspects of the model of Mathieu Favreau will be highlighted. The model selection and the procedure to be followed in the continuing part of the project will conclude this TN.

## 2. Scientific papers

The number of papers that could be gathered by considering different keywords related to plant growth modelling was quite large. However, most of these papers are not of interest for the present study targeted to reaction kinetics driven models: a further selection was thus needed. From the initial large list, a limited number (25 papers, see papers [1], [2], [4] to [20], [22] to [27] in the reference list) of papers that could be a priori useful in this study has been subsequently chosen.

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The following comments can be made about the papers in this list.

- 1) Most papers are dedicated to specific crops (tomato, potato, maize, lettuce, sugar beet, wheat, olive and conifers) (see Table 1).
- 2) Most papers considers only static relationships (e.g. yields based on various quantitative parameters related to plant growth) but without any considerations of dynamics and time evolution of the plant and its growth. Some of this type of information may be of relevance for modelling plant growth in the present study (as reference yield data) but such static models will not be useful in the present context where the final objective is to run and operate a fully automated plant growth system.
- 3) Although a significant number of papers mention, or at least suggest, the mechanisms that underlie plant growth, most of them lack substantial and deep discussions about these aspects. This is obviously a major drawback if the objective is to build a reliable mass balance based model for plant growth.
- 4) the papers were classified on the basis of their content as follows.
  - a. 5 papers ([2][16][22][23][26]) are indeed general review papers on plant growth modelling, among which two ([2][22]) have a direct link with the book of Thornley and Johnson [21] and the approaches developed therein.
  - b. 2 papers ([1][19]) are related to canopy architecture and its 3-D modelling and simulation.
  - c. 2 papers ([5][25]) are concerned with the link between genomics and plant growth, a topic that goes beyond the interest of the present study.
  - d. 3 papers ([10][12][20]) are linked to soil management and related issues.
  - e. 2 papers ([13][14]) are concerned with the biochemical and biophysical processes at the leaf level and provide only static models.
  - f. Finally, 11 papers ([4][6][7][8][9][11][15][16][17][24][27]) are dedicated to specific applications (see also Table 1).

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tomato	potato	maize	lettuce	sugar beet	wheat	olive	conifer
2	2	2	1	1	1	1	1

Table 1: Number of papers ordered per crop

After analyzing the 25 papers listed above, it was concluded that only three (3) papers ([6], [9], [18]) are potentially of interest for providing useful in this modelling study. In the following paragraphs a quick overview of the 3 papers is given.

### 2.1. Karlberg et al. paper

*“Modelling transpiration and growth in salinity-stressed tomato under different climatic conditions”, by L. Karlberg, A. Ben-Gal, P.E. Jansson & U. Shani [6]*

This paper is mainly concerned with the evaluation of the effect of salinity stress on transpiration and growth of tomatoes. The aim of the paper is to describe models for transpiration, growth and plant salinity stress responses. Two different approaches to salinity stress modelling are tested for two seasons (autumn and spring).

Traditionally models have described salinity stress as a decrease in water uptake caused by a low osmotic potential in the soil. Growth reductions caused by soil salinity are commonly explained either on the basis of an osmotic effect or by ion toxicity. When salts accumulate in the root zone, the soil water osmotic potential decreases.

Physiological studies suggest that reduced plant growth observed under saline conditions could be caused by increased respiration, decreased assimilation (photosynthesis) and/or decreased water uptake. The photosynthesis rate is determined by the relationship between the demand for carbon dioxide in the Calvin cycle and the supply of carbon dioxide, which is regulated by stomatal aperture and the canopy layer conditions. An accurate determination of stomatal response to environmental stimuli (e.g. radiation, temperature, soil/plant water status, vapour pressure deficit/humidity, availability of nutrients and presence of pollutants, ambient carbon dioxide concentration, and internal carbon dioxide concentration) is of importance for the determination of transpiration and photosynthesis.

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The model developed in the present paper simulates photosynthesis and respiration over a range of salinities. It is based on two existing models (SOIL and SOIL-N). To account for the effect of vapour pressure deficit (VPD) as well as for radiation saturation at high radiation levels, a biochemical photosynthesis module and a module for stomatal carbon dioxide conductance are incorporated into the model. The explicit calculation of growth and maintenance respiration enables plant salinity response mechanisms to be characterized as an increase in respiration. Optionally, salinity stress can be described as a result of reduced water uptake. In the model, the photosynthesis is regulated not only by radiation and transpiration, but also by air humidity (indicated by VPD), leaf temperature, carbon dioxide availability and leaf nitrogen content. The model has been calibrated and tested on two sets of data corresponding to two seasons, autumn and spring. Yields are a factor of two higher in autumn than in spring, even though transpiration is higher during spring. The model explains this variation as being caused primarily by high levels of radiation and vapour pressure deficits during spring, resulting in lower spring water use efficiency (CO<sub>2</sub> taken up in relation to the amount of water lost, as determined by stomatal control).

The model developed in this paper is indeed highly complex. It contains in particular 50 parameters listed in four categories (plant growth properties, plant physical characteristics, salinity stress parameters, and photosynthesis constants). If there is no doubt that conceptually such a model is clearly of interest to understand the mechanisms due to salinity stress, it is most probably not identifiable (structurally and/or practically) from the (potentially) available data. However, since the mechanisms are described in some details, such an approach is potentially of interest at a later stage, especially with respect to the analysis of the influence and impact of stress conditions on plant growth.

## 2.2. Linker & Johnson-Rutzke paper

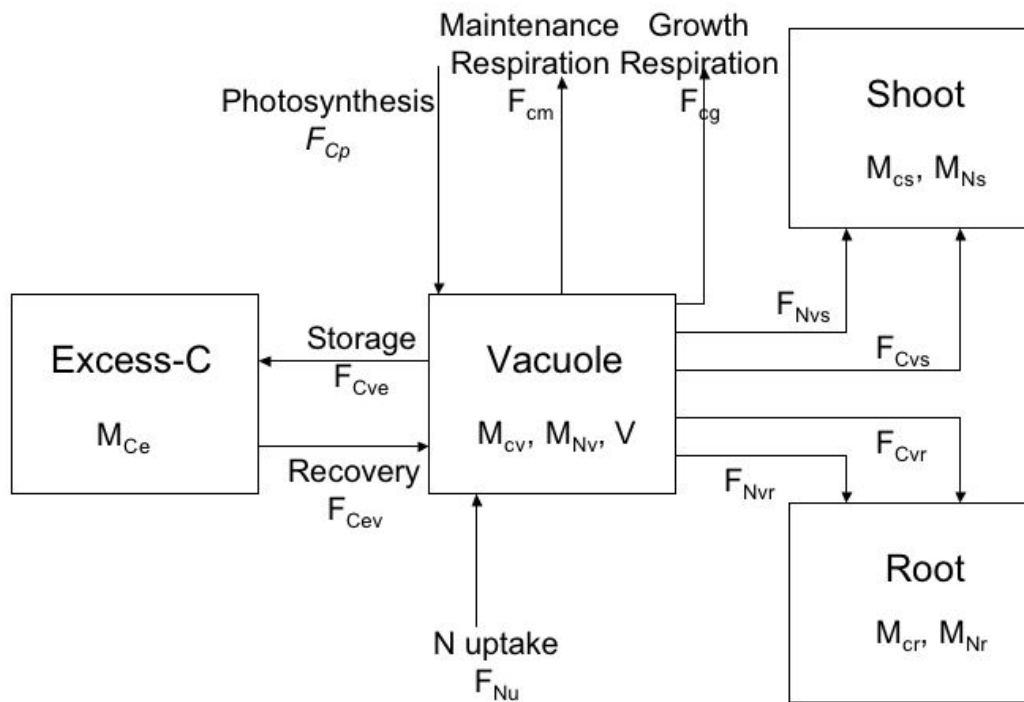
*“Modelling the effect of abrupt changes in nitrogen availability on lettuce growth, root-shoot partitioning and nitrate concentration”, by R. Linker & C. Johnson-Rutzke [9]*

The objective of this paper is to propose a model that investigates the effect of abrupt changes in nitrogen availability on lettuce growth. The starting point is that lettuce models are available that explicitly include nitrate concentrations. Such models are able to predict the effect of nitrogen stress

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on shoot growth, but, since they do not include a root compartment, they do not account for the increase of the root-to-shoot ratio (RSR) that is associated with nutrient stress. The objective of this paper is therefore more precisely to examine if the addition of a root compartment and root-shoot portioning mechanism is advantageous for predicting dry weight and nitrate concentration.

The model is based on four compartments (Figure 1) : the root, the shoot, the vacuole and the carbon compartment labelled “excess-C”. The variable-sized excess-C compartment allows for variations in water content and N-to-C ratio on a dry-mass basis.



**Figure 1:** Four compartment scheme

The model consists of mass balance equations for the four compartments and is based on the following assumptions.

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- 1) Nitrate is not present in the excess-C compartment.
- 2) The amount of reduced-N in the root and shoot compartments is proportional to the size of each compartment.
- 3) The size of the vacuole, and hence the amount of water in the plant (see Figure 1, vacuole compartment,  $V$  for volume) is proportional to the combined size of the root and the shoot.

The model results basically in 7 differential equations (4 for carbon, 3 for nitrogen) and contains 21 parameters. Sensitivity analysis has been used to reduce the number of parameters to 5.

Subsequently the model was further simplified by imposing a constant root to shoot ratio, and compared with the output of the original model with variable RSR.

The conclusion were that a constant root-to-shoot ratio had almost no consequence on the predictions of shoot fresh mass, dry matter content, nitrate concentration, and reduced nitrogen content, except in the extreme case where almost no nitrogen was supplied for the whole growing period.

The interesting points of this paper are the mechanistic modelling and the emphasis on the influence of (another type of) stress on plant growth. The compartmental approach is clearly quite convenient.

### 2.3. Ramirez et al. paper

*“Calibration and validation of complex and simplified tomato growth models for control purposes in the southeast of Spain”, by A. Ramirez, F. Rodriguez, M. Berenguel & E. Heuvelink [18]*

This paper briefly (8 pages) presents two mechanistic models based on photosynthesis: a reduced-order model and an aggregated model. The context and objective of the derivation, calibration and validation of these models is the control of a greenhouse used for tomato growth. More precisely, the control strategy is a three-level approach in which the middle level is concerned with physiological states.

The first model is derived from a model called TOMGRO which originally had between 69 and 574 state variables. The reduced-order model considers only five state variables:

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- the number of nodes  $N$ , i.e. points on a stem at which the leaves are inserted,
- the leaf area index LAI,
- the fruit dry matter  $W_F$ ,
- the above-ground biomass accumulation  $W$ ,
- the mature fruit biomass accumulation  $W_M$ .

The model equations are written as follows:

$$\frac{dN}{dt} = N_m f_{NT}$$

$$\frac{d(LAI)}{dt} = \rho \delta \lambda(T_d) \frac{e^{\beta(N-N_b)}}{1 + e^{\beta(N-N_b)}} N_m f_{NT}$$

$$\frac{dW}{dt} = (GR)_{net} - p_l \rho N_m f_{NT}$$

$$\frac{dW_F}{dt} = (GR)_{net} \alpha_F f_F(T_d) \left[ 1 - e^{-\nu(N-N_{FF})} \right] g(T_{dia})$$

$$\frac{dW_M}{dt} = D_F(T_d)(W_F - W_M)$$

In the above equations,  $N_m$ ,  $f_{NT}$ ,  $\rho$ ,  $\delta$ ,  $\lambda(T_d)$ ,  $T_d$ ,  $\beta$ ,  $N_b$ ,  $(GR)_{net}$ ,  $p_l$ ,  $\alpha_F$ ,  $f_F(T_d)$ ,  $\nu$ ,  $N_{FF}$ ,  $g(T_{dia})$  and  $D_F(T_d)$  hold for the maximum rate of nodes (node/d), a function to modify node development rate, the plant density (plants/m<sup>3</sup>), the maximum leaf area expansion per node (m<sup>2</sup>/node), the temperature function to reduce leaf area, the daily temperature (°C), two coefficients in the expolinear equation ((1/node), and (node)), the net aboveground growth rate (g/m<sup>2</sup>/d), the loss of leaf dry weight per node (g/node), the maximum partitioning new growth to fruit (1/d), a function to modify partitioning to fruit vs average daily temperature, the transition coefficient (1/node), the nodes per plant when first fruit appears (node), a function to reduce growth, and the rate of development of fruit vs daily temperature (1/min), respectively.

The second model is derived from a model called TOMSIM which contains 34 state variables for a crop growing for 100 days. The aggregated model version considers 6 equations with one differential equation for the total dry matter  $W_m$  and one difference equation for the truss (fruit cluster) development stage TDVS :

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$$FR = -a_1 + b_1 \ln(T)$$

$$\frac{dW_m}{dt} = C_f(P_{ge,d} - R_m)$$

$$R_m = R'_m(1 - e^{-f \cdot RGR})$$

$$(TDVS)_t = (TDVS)_{t-1} + (FDVR)_t$$

$$(PGR)_t = \frac{N_f ab \left[ 1 + e^{-b(TDVS_t - c)} \right]^{\frac{1}{d}}}{(d-1)(1 + e^{-b(TDVS_t - c)})}$$

$$(PVGR)_{i,t} = 3.59 e^{-0.168(T-10)}(PFGR)_{i,t}$$

In these equations, FR,  $a_1$ ,  $b_1$ , T,  $C_f$ ,  $P_{ge,d}$ ,  $R_m$ ,  $R'_m$ , f, RGR, FDVR,  $N_f$ , a, b, c, d, PGR, PVGR and PFGR represent the flowering rate (truss/d), two parameters ((truss/d) and (-)), the mean 24h temperature ( $^{\circ}$ C), the conversion efficiency (g dw/g  $CH_2O$ ), the maintenance respiration rate (g $CH_2O$ /m<sup>2</sup>/d), the maximum maintenance respiration rate (g $CH_2O$ /m<sup>2</sup>/d), a regression coefficient parameter, the relative growth rate, the fruit development rate of  $N_f/2$  fruit on the truss (1/d), the number of fruits per truss, four parameters ((g f.d.w./d) and (-)(-)(-)), the potential growth rate of truss (g/d), the potential growth of vegetative unit (g/d), and the potential fruit growth rate (g/d), respectively.

Both models require the identification of a limited number of parameters: 12 ( $N_m$ ,  $N_b$ ,  $\delta$ ,  $\beta$ ,  $V_{max}$ ,  $\alpha$ ,  $\tau$ , CK, CE,  $T_{crit}$ ,  $\alpha_F$ ,  $v$ ) for the first one, 4 (f, CK, Eo,  $\sigma$ ) for the second one.

Although this paper is rather short and therefore lacks of important details about the procedure for selecting the models, the data collection and the identification procedure, it is attractive in many respects, namely:

- 1) the models are mechanistic,
- 2) the models are control-oriented,
- 3) the models are simple enough,
- 4) the model parameters are apparently estimated in two steps (calibration and validation) and statistical information (confidence intervals) about the parameters values is provided.

## 2.4. The book of Thornley and Johnson

This monograph [21] provides a lot of useful information about the modelling of plant and crops, and, although it does not provide a model structure that

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could be used as such in the context of this study on plant growth, it has to be considered as a major reference and source of inspiration for the future work about plant growth modelling. Important issues related to a large spectrum of plant growth characteristics and phenomena are addressed, ranging from plant growth functions and transport phenomena to phyllotaxis (leaf arrangement within a plant) via leaf and canopy photosynthesis or other issues in plant and crop physiology.

One of the attractive aspects of the book of Thornley and Johnson is the compartmental approach, with a notion of sinks and sources connected by transport links. Compartmental formalism is indeed very convenient for any reaction system. It allows in particular to clearly characterise the different phenomena interacting in the plant growth mechanisms, from reaction kinetics to transport phenomena. A compartment can be, for instance, a reactive element (substrate, for instance) or a part of the plant (e.g. root or shoot). The scientific literature on compartmental systems is abundant and is potentially useful to help to handle the modelling issues of plant growth.

### 2.5. The model of Favreau : the good starting point

The model of Favreau [3] is based on information from the book of Thornley and Johnson ([21], chapter 9, section 9.3, p223). It is based on a reaction scheme that involves two reactions for photosynthesis, one reaction for photorespiration, and on diffusion of external CO<sub>2</sub> into the plant. This model is described in more details below.

#### 2.5.1. Photosynthesis

Consider a homogeneous leaf of thickness  $h$ , uniformly irradiated with irradiance  $I_1$ , and having an uniform internal CO<sub>2</sub> concentration at the photosynthetic sites is  $C_i$ . It is supposed that the light energy in  $I_1$  reacts with some molecular species  $X$  to produce an active form  $X^*$  according to:

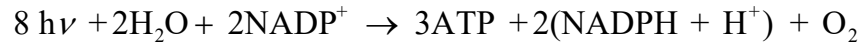


where  $k_1$  is a rate constant. The activate form  $X^*$  reacts with CO<sub>2</sub> within the leaf to synthesize carboydrate {CH<sub>2</sub>O} and to regenerate  $X$ , according to



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where  $k_2$  is a second rate constant. These two reactions can be viewed as a simplified version of :



for the light reactions of photosynthesis in which ATP and NADPH are produced, and then used to drive the  $CO_2$  reduction cycle. The rate of formation of  $X^*$  is then:

$$\frac{dX^*}{dt} = k_1 I_1 X - k_2 X^* C_i$$

Assuming that

$$X_0 = X + X^*$$

is constant and is the total concentration of X. So:

$$\frac{dX^*}{dt} = k_1 I_1 (X_0 - X^*) - k_2 X^* C_i$$

### 2.5.2. Photorespiration

The simple leaf photosynthesis model explain in the previous paragraph can be extended to take into account the photorespiration. Adding to the reactions (1) and (2) a third equation which is



with  $k_3$  a rate constant. Let  $O_i$  be the internal  $O_2$  concentration at the photosynthesis sites. The differential equation for  $X^*$  becomes:

$$\frac{dX^*}{dt} = k_1 I_1 (X_0 - X^*) - X^* (k_2 C_i + k_3 O_i)$$

### 2.5.3. Diffusion of external $CO_2$ into the plant

The limiting effect of the diffusion of the external  $CO_2$  into the leaf is modelled by considering the following expression for the diffusion rate  $r_{D,CO_2}$ :

$$r_{D,CO_2} = \frac{C_a - C_i}{r_d}$$

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where  $C_a$  and  $r_d$  are the external  $CO_2$  concentration and a diffusion resistance coefficient, respectively. A similar expression can be derived to account for the diffusion of  $O_2$ . Such expressions are consistent with the classical transfer rates considered, in particular, in multiphase systems.

### 2.5.4. Comments

The model of Mathieu Favreau concentrates on the basic general mechanisms for the growth of  $C_3$  plants and combines them with a simple view about the transport dynamics (diffusion of  $CO_2$ ). With that respect, the model can be considered as a good starting point for this study.

However many issues have to be discussed and handled before being able to have a reliable model for plant growth that meets the objective of the project as briefly mentioned in the introduction above. The following should be clearly addressed in the future.

- 1) The complexity of the model: the model content has to be defined with respect to the objectives for which it needs to be designed; it has to be as simple as possible while addressing the main (limiting) phenomena appropriately; it needs to be validated. Such issues require measurements of the most important/key variables. The questions that comes, for instance, in mind when looking at the simple model above are : is the model simple enough? Is it complex enough? What assumptions are acceptable or not (e.g. is it valid to assume that  $X_0$  is constant)? Are the proposed mechanisms acceptable or not (e.g., is the two step photosynthesis fitted here? Is the diffusion rate equation appropriate?)
- 2) The predictability properties of the model: the ability of the model to predict correctly the plant growth dynamics depends on the model selection and its validation from experimental data; however a probably open question at this level is the issue of considering a general model for all plants or different models for classes of plants, the complexity of which will be lower and therefore susceptible of better prediction performance. A basic general crop model could be further developed for each chosen crop or crop group.
- 3) The calibration and validation of the model: the quality of the model will highly depend on the quality of the data generated for the calibration of its parameters and their validation, as well as on the experimental planning for generating the experimental data and the

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identification procedure followed to perform parameter estimation and validation.

### 3. Items for a plant growth model

A plant growth model can be schematically represented as in Figure 2. The model of Mathieu Favreau considers in its present form only the first three inputs (light, CO<sub>2</sub>, O<sub>2</sub>). It could be complemented by adding dependences with respect to temperature and, possibly, to humidity. This might be implemented under the form of dependence on kinetic parameters (or other parameters) with respect to these input variables.

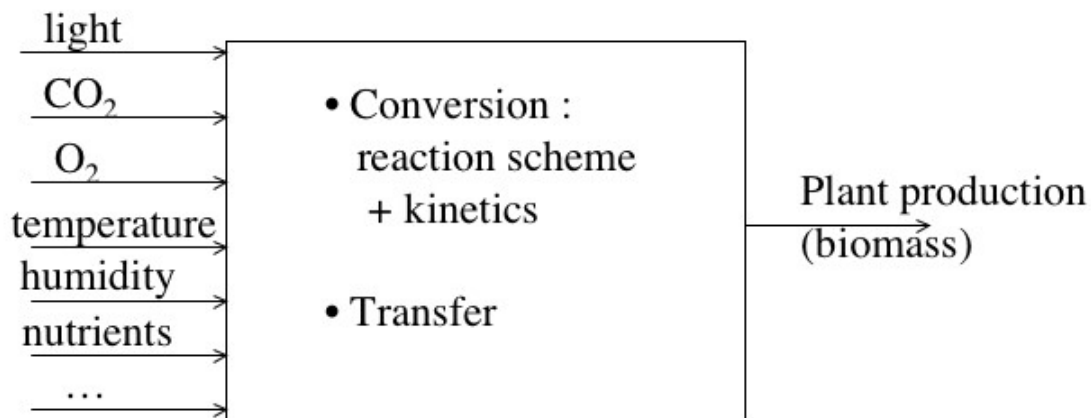


Figure 2: Plant growth model scheme

Another issue would be to identify and formalize the failures (e.g. darkness, pump failures (and associated nutrient and water stress), etc) that will need to be taken into account in the model.

It might also be of interest to include the influence of pre-canopy closure on the system dynamics. Diffusion of CO<sub>2</sub> and light interception are markedly different in pre- and post-canopy closure stages.

### 4. References

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