Developmental Stages in Dynamic Plant Growth Models

Heather Maclean[1], Denis Dochain[1], Geoff Waters[2], Michael Stasiak[2], Mike Dixon[2], Dominique Van Der Straeten[3]

[1]*CESAME, Université Catholique de Louvain, 1348 Louvain-la-Neuve, Belgium*
[2]*Controlled Environment Systems Research Facility, University of Guelph, Guelph, Ontario, Canada*
[3]*Laboratory of Functional Plant Biology, Ghent University, 9000 Ghent, Belgium*

Abstract. During the growth of red beet plants in a closed environment plant growth chamber, a change in metabolism was observed (decreasing photosynthetic quotient) which was not predicted by a previously developed simple dynamic model of photosynthesis and respiration reactions. The incorporation of developmental stages into the model allowed for the representation of this change in metabolism without adding unnecessary complexity. Developmental stages were implemented by dividing the model into two successive sub-models with independent yields. The transition between the phases was detected based on online measurements. Results showed an accurate prediction of carbon dioxide and oxygen fluxes.

Keywords: plant modeling, developmental stages, photosynthetic quotient.
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INTRODUCTION AND BACKGROUND INFORMATION

The MELiSSA (Micro-Ecological Life Support System Alternative) project was developed by the European Space Agency with the aim of developing technology for a future regenerative life support system [1]. The central concept is to use microorganisms and plants to produce food, regenerate the atmosphere and recycle some wastes. As part of this initiative, a higher plant compartment has been designed. Dynamic models of plant growth are required for the prediction of important fluxes and the control of this compartment. Most important will be to provide a certain desired flow of high quality edible biomass, however other fluxes (carbon dioxide, oxygen, water, nutrients, etc.) should also be predicted as they are important for the larger life support system.

Models for control should capture the main dynamical features of the system while otherwise remaining very simple. Therefore, a mass balance approach was previously used to develop a simple dynamic model representing photosynthesis and respiration [2]. Our approach emphasized the importance of maintaining model simplicity, identifiability of parameters, and validating the model on independent data. The model is shown in (1) – (5) below.

$$\frac{dM_{\mathrm{d}}}{dt} = Y_1 r \tag{1}$$

$$\frac{dC_{\mathrm{a}}}{dt} = \frac{-r}{V_{\mathrm{chamber}}} + \frac{u_1}{V_{\mathrm{chamber}}} \tag{2}$$

$$\frac{dO_{\mathrm{a}}}{dt} = \frac{Y_2 r}{V_{\mathrm{chamber}}} \tag{3}$$

$$r = v_1 C_{\mathrm{a}} I_{\mathrm{intercepted}} - v_2 O_{\mathrm{a}} I_{\mathrm{intercepted}} - v_3 r_{\mathrm{avg,ps\text{-}pr}} \tag{4}$$

$$I_{\mathrm{intercepted}} = I_0 \left(1 - \exp\left(-k \frac{A_{\mathrm{leaf}}}{A_{\mathrm{ground}}} \right) \right) \tag{5}$$

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In the above equations, M_d is biomass dry mass (g), C_a and O_a are CO_2 and O_2 concentrations in the atmosphere of the chamber (g m^{-3}), r is the reaction rate equation (defined in (4) with the three terms representing the rates of photosynthesis, photorespiration, and mitochondrial respiration respectively), Y_i are the yields (g g^{-1}), $V_{chamber}$ is the volume of the plant growth chamber (29 m^3), u_1 is the rate of CO_2 addition to the chamber for control (g s^{-1}), $r_{avg,ps\text{-}pr}$ is the average rate of photosynthesis less photorespiration over the previous 1 day period (g s^{-1}), $I_{intercepted}$ and I_0 are the intercepted and incident (at canopy height) photon fluxes (μmol PAR m^{-2} s^{-1}), k is the extinction coefficient (0.7, chosen within a feasible range), A_{leaf} is the leaf area (m^2, estimated as proportional to M_d in the model), A_{ground} is the planting area (5 m^2), and v_i are the kinetic rate constants.

The model was fit independently on beet and lettuce data collected in closed environment experiments performed at the University of Guelph. The yields and kinetic parameters were identified separately (according to a method described by Chen [3]) using a least squares identification. The model was then validated on an independent dataset. The results of this validation on beet data is shown in Figure 3 (b&e).

The model was shown to fit fairly well to carbon dioxide data but there were errors in the oxygen predictions. In this work, potential causes of the discrepancy between the fit of the model on carbon dioxide and oxygen data are examined, and a simple solution is proposed. Our aim is to improve model performance while maintaining relative model simplicity.

THE PHOTOSYNTHETIC QUOTIENT

The discrepancy between the relatively small error in the CO_2 predictions (aside from temporary errors occurring at the transitions between day and night) and the much larger and persistent error for O_2 suggests that there is a problem with either the structure of the model or with the yields. The photosynthetic quotient (PQ), which is the ratio of oxygen produced by the plants over CO_2 consumed, was analyzed to gain insight into the metabolism of the plant. It is typically stated in literature that the photosynthetic quotient (PQ) of a plant should be approximately 1. However, it is known that this value changes with composition [4], nitrogen source [5], and potentially with other factors as well. Figure 1(a) shows the cumulative moles of CO_2 consumed and oxygen produced during a beet experiment. If the photosynthetic quotient has a value of 1 throughout growth, CO_2 consumption should be equal to O_2 production and therefore the two curves should lie on top of each other. However, this is not what is observed in the data. Instead, the PQ seems to be approximately 1 during the first 17 days in the chamber, at which point CO_2 consumption starts to outpace oxygen production, revealing a PQ less than 1 during the second stage of growth.

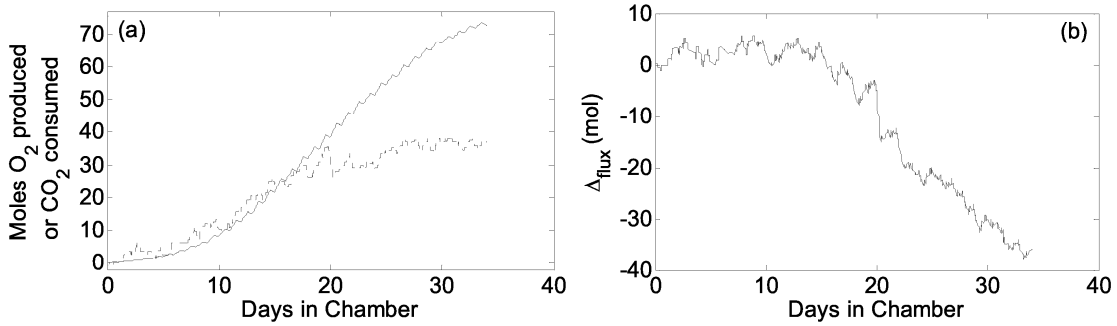

FIGURE 1. (a) Cumulative moles of oxygen produced (dotted line) and carbon dioxide consumed (solid line) during beet experiments in a closed environment chamber and (b) Δ_{flux} (moles O_2 produced – moles CO_2 consumed), the indicator variable used for detection of transition point between the two developmental stage sub-models.

With the limited available data, the ultimate cause of this trend is not clear. Similar results can sometimes be obtained as a result of leakage from the chamber [6]. If this was the case we would expect the divergence between the oxygen and carbon dioxide curves to be triggered by certain oxygen and carbon dioxide concentrations in the chamber. However, based on several experiments (beet and lettuce) this did not seem to be the case. Therefore, it was concluded that the observed change in PQ must have some biological explanation. It could be explained by a change in metabolism either triggered by development (composition, biomass partitioning, volatile production, etc.) or by certain environmental conditions (increasing oxygen concentration causes some physiological response, etc.). Data to test these potential explanations is currently lacking, and therefore no conclusion has so far been reached about the biological explanation for the change in PQ.

MODELLING DEVELOPMENTAL STAGES

Regardless of the cause of the changing photosynthetic quotient, these results indicate that the yields defined in the original simple model ((1)-(5)) can not be considered constant. To account for this, the concept of developmental stages was incorporated into the model. By separating the model into several phases of growth, with transition times linked to measurable data, the changing metabolism of the plant can be represented without adding unnecessary complexity. Each stage should have a unique set of constant yields, and the transition between these stages should be detected according to some criteria which can be analyzed based on online data.

Figure 1(a) shows us that the transition point should clearly be detectable based on carbon dioxide and oxygen data. Therefore, the difference between the oxygen produced and carbon dioxide consumed (called Δ_{flux}, mol) was selected as an indicator variable. The value of this indicator throughout a beet experiment is shown in Figure 1(b). It is clear from this figure that the transition point should be easily detected by a change in the slope of this curve. As an additional requirement, a time constraint was added so that brief variations in the slope (caused by noise or periodic variations) did not incorrectly and prematurely trigger a transition to the next phase. The transition point condition is shown in (6). However, it was found that α and β were correlated, and therefore, for subsequent work β was selected to a conservative value of 1 day, and an appropriate α was identified. This approach was chosen, over the alternative of selecting α and identifying β, because it allowed for the identification of a transition point shortly after the change could be detected, while imposing some conservatism by selecting β. The alternative approach could theoretically be just as effective, however it was considered more simple for the user to choose an appropriate β (based on the observed variability in the data, etc.) than to select α. The transition point condition and the yields were identified concurrently, using a least squares approach. The parameters (α, Y_{2a}, Y_{2b}) were identified on one dataset, and then validated on independent data to ensure model reliability (Figure 2).

Final values were identified using all available data (α=-9.5x10-6 mol s^{-1}, β=1 day, Y_{2a}=0.621 g g^{-1}, Y_{2b}=0.146 g g^{-1}). Values for the yield of biomass on CO_2 (Y_1) during each stage should ideally be identified in the same way as values for Y_2 (yield of O_2 on CO_2). However, due to limited biomass measurements this approach was not possible, and instead Y_1 was estimated assuming a constant yield of biomass on oxygen (g M_d g O_2^{-1}) over the full experiment. Therefore, the final values for Y_1 were calculated to be Y_{1a}=1.261 g g^{-1} and Y_{1b}=0.296 g g^{-1}.

$$\text{Transition if } \frac{d}{dt}\left(\Delta_{\text{flux}}\right) < \alpha \text{ for } \beta \text{ hours} \tag{6}$$

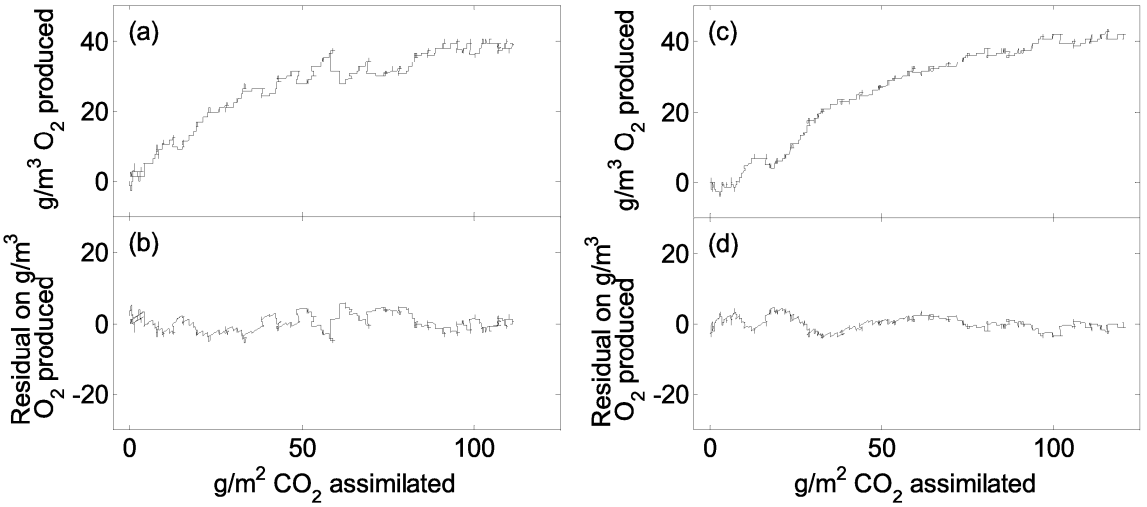

FIGURE 2. Results from joint yield and transition point condition identification (a-b) and validation on independent data (c-d). Plots of measured oxygen production versus carbon dioxide assimilation (a & c) and the residuals between predicted and measured oxygen production (b & d) are shown.

RESULTS OF 2-STAGE APPROACH

The results of the yield identification were then applied to the full model. The model was split into two stages with yields as defined above. The transition point was detected using the condition in (6). The kinetic parameters (v_i in (4)) were first identified on a beet identification dataset, and then the results were validated on a second dataset (Figure 3 (c&f)). The oxygen prediction is much improved by using this two stage approach.

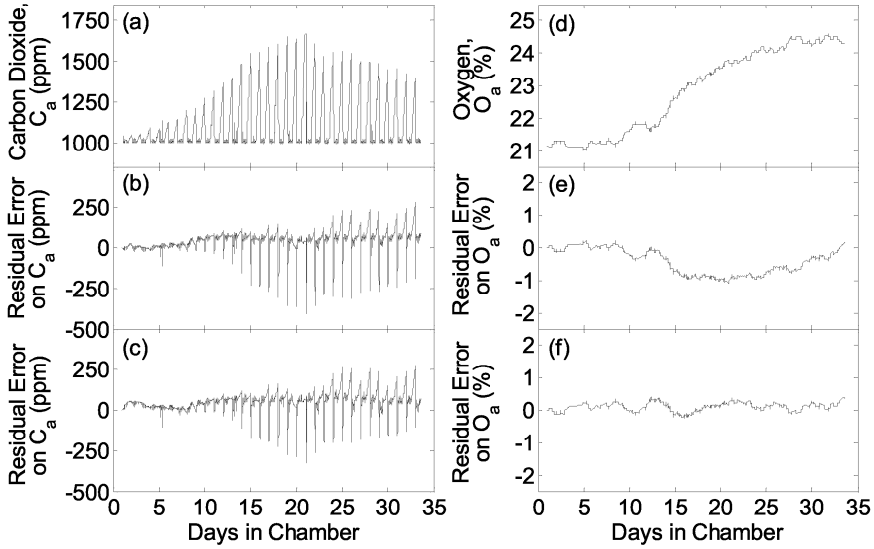

FIGURE 3. Validation of single-stage and two-stage model on an independent dataset not used for kinetic parameter identification. Measured values of carbon dioxide (a) and oxygen (d) are shown along with the residuals between measurements and predictions for the single-stage (b-CO_2, e-O_2) and two-stage (c-CO_2, f-O_2) approaches.

CONCLUSIONS

A decreasing photosynthetic quotient during experiments conducted in a closed environment chamber suggested a changing metabolism that was not accounted for in a basic model of photosynthesis and respiration reactions. By incorporating developmental stages into the model, the changing metabolism of the beet plant was represented without adding unnecessary complexity. Results show a strong improvement in the prediction of oxygen flux, and also gave accurate results for carbon dioxide and biomass (not shown). A similar decrease in the photosynthetic quotient was also observed on lettuce experiments, though the change was more gradual in this case. Efforts are therefore currently underway to apply and potentially adapt this approach for lettuce.

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