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Dynamic properties of foliage photosynthesis

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Highlights: Increasing results illustrate the importance of modelling photosynthesis as a dynamic process where the parameters of the standard photosynthesis curve vary in response to fluctuations in environmental conditions and developmental status of the plant. We describe how engineering approaches to the analysis of dynamic systems can be used and provide information for incorporating the dynamics of photosynthesis into large scale FSPMs.

Keywords: Photosynthesis, stomatal conductance, time constant, dynamic properties.

INTRODUCTION

An achievement of Functional-Structural Plant Modelling (FSPM) has been development of techniques for measurement and representation of the spatial distribution of plant organs and their connections. This in turn has led to a standpoint, expressed by Godin and Sinoquet (2005), that “the growth of the plant continuously modifies the network of components and space occupation, which in turn changes the general balance between organ demand and production.” They refer to this as representing dynamic feedback between structure and function and suggest that its study requires integrating various sources of knowledge into a consistent modelling framework. Photosynthesis is the essential pre-requisite of plant growth and an important question is how to define its dynamics and potentially integrate that understanding in FSPMs. This is a challenge because models for leaf photosynthesis are most frequently designed to simulate instantaneous or short term changes of environmental conditions whereas many FSPMs are designed for longer terms when additional influences must be considered, e.g., sink control (Paul and Foyer 2001).

We consider two related problems. First: How can we measure and model the dynamics of photosynthesis? Increasingly research is showing variation in parameters of standard light saturation and A/C_i curves over daily and seasonal periods. We introduce some techniques used in the analysis of control systems that can aid in understanding such variation. We consider the types of question that may be asked using these techniques, the experiments and measurements that might be made and models that can be used to understand variation found in dynamic responses.

Second: What type of feedback might be expected in the control of photosynthesis? When we say a system is “dynamic” we frequently imply that it responds to change in some form of self-correcting way, which implies some form of “feedback”. Engineers have developed theories of the control of dynamic systems and we examine how they may be applied to study of photosynthesis dynamics.

THE DYNAMICS OF PHOTOSYNTHESIS

Photosynthesis can be defined by its dependence on light and carbon dioxide concentration. There is well established theory that explains these relationships (Taiz and Zeiger 2010): production of ATP and NADPH by light reactions and their utilization in the Calvin-Benson cycle by which carbon from CO_2 is incorporated into organic compounds. The response of foliage photosynthesis to light can be fitted with the non-rectangular hyperbola model (Lambers *et al.* 1998, p27):

$$A = \frac{\phi \cdot Q + A_{\max} - \sqrt{(\phi \cdot Q + A_{\max})^2 - 4 \cdot \phi \cdot Q \cdot \theta \cdot A_{\max}}}{2\theta} - R_d \qquad (1)$$

in which Q is the available incident PPFD, A is the CO_2 assimilation rate, $A_{\max}$ is the assimilation rate at saturating light, ϕ is the apparent quantum efficiency (the initial slope of the linear part of the curve), θ is the convexity of the curve, and R_d is the dark respiration.

Equation 1 represents photosynthesis as an *instantaneous* system—the output of the process, A, the photosynthesis rate, depends upon light. The equation does not take into account whether prior conditions may affect current photosynthesis rate. More complete analyses incorporating the components of gaseous diffusion through stomata, mesophyll and cell have been developed (e.g., Farquhar et al. 2001) but these too consider photosynthesis as a more complex but still an instantaneous system.

Studies of the effects of sunflecks on photosynthesis rate illustrate it does not respond instantaneously to increase in light but that there is an induction period (Way and Pearcy 2012). For example, when sunflecks are simulated experimentally as a step increase in light there is a generally curvilinear increase in photosynthesis rate. Investigators (see Way and Pearcy 2012) have described this rate of increase by calculating a time constant of response. The time constant equation for increase of photosynthesis from base value of zero is:

$$A = A_{max} * (1 - e^{(-t/\tau)}) \qquad (2)$$

where A_{max} is an estimated asymptotic value for maximum photosynthesis rate attained following the step increase in light, t is time, usually measured in seconds, and τ is the time constant and which represents the time it takes for the step response to reach 63.2% of the asymptotic maximum.

We present results and analyses showing that the response described by Eqn 2 is just one example of change in response to changing conditions. Different patterns of increasing photosynthesis in response to step functions of light for shade grown *Abies amabilis* and *Tsuga heterophylla* show leaves to be in different dynamic states associated with the ambient light they are receiving before the step increase. A frequently encountered pattern is represented by addition of two time constant equations one with τ in the range of 8 to 20 seconds and the other with τ in the range of 80 to 150 seconds. Another pattern is overshoot, where A increases to a maximum before settling to a lower value. These are well known response types found in engineering analyses of dynamic systems. For these species control of photosynthesis through variation in stomatal conductance, g_s, tends to occur over considerably longer time intervals with $\tau \sim 600$ s.

DYNAMIC SYSTEMS AND FEEDBACK

Porcar-Castell and Palmroth (2012) draw attention to the requirement for models that take account of the dynamic response of photosynthesis to changing conditions. However, they draw attention to an important problem: "While dynamic models present a substantial improvement compared to steady state models, their parameterization remains a challenge … because parameters change across time and space …"

Dynamic models of leaf photosynthesis are based on theories of chloroplast and leaf function and define pool sizes and conductance of precursors, enzyme characteristics and how these change in response to changes in the environment, particularly light. While recognizing the heuristic value of such models we present a complementary approach with two components: (a) examining the plant through different conditions of its growth and exposing it to changes in weather; while (b) applying step functions and other patterns of changing conditions used in the analysis of dynamic systems (e.g., Franklin et al. 2009). The purpose of this approach is to define variation in the photosynthesis system directly in systems terms i.e., using properties such as time constants of response to changes of different types and estimates of capacitance and resistance to flows of basic components.

Models representing photosynthesis as a series of metabolic pools and processes can make *a priori* assumptions about the type of control system that exists. These are typically open-loop control systems in which control action is dependent on fluctuations in resources and removal of products. This can be contrasted with active control systems such as controlled by transcription processes or removal of enzyme inhibitors which may be analogous to closed-loop control systems in which the control action is dependent on the output. For engineers: **"***Feedback* is a property of closed-loop systems which permits the output to be compared with the input to the system so that appropriate control action may be formed as some function of output and input" (Distefano et al. 2011).

An interesting question for study of dynamics of FSPMs in general and photosynthesis in particular is the extent to which the system can be represented as either a linked collection of open-loop systems with no active control or an active control system, e.g., through sink regulation (Paul and Foyer 2001). We will discuss over what time scales and conditions control of photosynthesis may be considered active or passive.

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