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Accurate modelling of photosynthetic light responses of C_3 and C_4 species

Zhou, S-X[1]; Yang, X-L[2]; Ye, Z-P[3]; Han, G-D[4]

[1]Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia; [2]School of Life Sciences, Nantong University, Nantong, China; [3]Maths & Physics College, Jinggangshan University, Ji'an 343009, China; [4]Department of Grassland Science, Inner Mongolia Agricultural University, Hohhot 010018 Inner Mongolia, China

Abstract

Industry-oriented research innovations during the past decades have significantly contributed to the productivity, profitability and sustainability of pastoral industries. Key examples of these innovation efforts include (1) sensor, IoT and machine learning technologies facilitating automation of data collection, data integration and model simulation towards digital decision tools for farmers, and (2) simulating the consequences of changed environment and/or management practices on rangeland and pastoral systems through integrating biological, physical and digital properties and processes across leaf, whole-plant and paddock levels. However, there are fundamental physiological processes which are not well reproduced by models, partly due to the challenge of bridging the advancement of cross-disciplinary knowledge. This paper reviewed recent experiment-modelling-integration efforts towards the accurate model representation on light-response of photosynthesis, in particular: the performances of two models – the most widely used non-rectangular hyperbolic model (NH model) and a more recently developed mechanistic and nonasymptotic model (Ye model) – in reproducing plant photosynthetic light response across light-limited, light-saturated and photoinhibitory light intensity levels. The accuracy of Ye model, and its consistency of model framework, in reproducing the light responses of concurrent photosynthetic functions (i.e., photosynthesis, electron transport rate, stomatal conductance and water use efficiency), make it ideal to be adopted by the current and future experiment-modelling-integration efforts on global rangeland, pastoral and/or broadacre production systems.

Introduction

Plants growing in natural or semi-natural systems experience fluctuating light environments over time scales extending from seconds to hours, largely due to cloud movements and self-shading. Accurate characterization of light-response curve of photosynthesis at leaf scale is fundamental for quantifying crop light relations at whole-plant and community scales. An accurate model should be robust in reproducing light-response curve of photosynthesis (PN–I curve) over light-limited, light-saturated and photoinhibitory I levels, and ideally returning key quantitative traits defining the curves, including initial slope of increase (α), dark respiration rate (RD), the maximum net photosynthetic rate (PNmax) and the corresponding saturation intensity (Isat).

A few models have been developed to characterize the light response of photosynthesis of higher plants, including biochemical models, rectangular and non-rectangular hyperbolic models, negative exponential equations, and nonasymptotic function models. The non-rectangular hyperbolic model (NH model) is the most widely used (Holley, 2022).

The FvCB model (Farquhar, von Caemmerer and Berry, 1980) has been widely used to characterize leaf gas exchange. In the FvCB model, the NH model is a sub-model to characterize the light response of electron transport rate (*ETR–I* curve, using the same function as the above P_N–*I* model) besides estimating the maximum electron transport rate (ETR_{max}) (Farquhar & Wong, 1984). Unavoidably, due to its asymptotic function, the NH model overestimates ETR_{max} when the model is fitted against observations. Besides, since early years, the NH model has been reported on its failure in reproducing the *ETR–I* curve at photo-inhibitory *I* levels (Ögren & Evans, 1993).

This paper reviewed recent studies comparing the performances of two different models (NH model and Ye model) in reproducing the light response curves of *ETR and* P_N.

Methods

NH model on the light response of photosynthesis and electron transport rate

The NH model describes the P_N–*I* function as below (Thornley 1976, Ögren and Evans 1993, Thornley 1998):

$$P_N = \frac{\alpha I + P_{Nmax} - \sqrt{(\alpha I + P_{Nmax})^2 - 4\theta\alpha I P_{Nmax}}}{2\theta} - R_D \quad (1)$$

where P_N is net photosynthetic rate, P_{Nmax} is the maximum net photosynthetic rate, α is the initial slope of curve, *I* is light intensity, θ is the curve convexity (dimensionless), and R_D is the dark respiration rate.

ue to its asymptotic function, the NH model can only indefinitely approach to, but never reach, a maximum net photosynthetic rate (and thus cannot return the corresponding saturation *I*). This means that (1) the P_{Nmax} generated by fitting the NH model will be unavoidably overestimated, and (2) the NH model cannot reproduce the curve section at and after the saturation *I* (where photoinhibition occurs).

The non-rectangular hyperbolic model has been mainly used to fit the *ETR–I* curves of plants, and it has been a sub-model in the FvCB model when irradiance is below the saturation level. In the NH model, the dependence of *ETR* on *I* can be expressed as follows:

$$ETR = \frac{\alpha' \times I + ETR_{max} - \sqrt{(\alpha' \times I + ETR_{max})^2 - 4\theta \times \alpha' \times I \times ETR_{max}}}{2\theta} \quad (2)$$

where α' is defined as the initial slope of the *ETR–I* curve, θ is a degree of curvature, and ETR_{max} is the maximum *ETR*. Because the first derivative of Eqn. 2 is always greater than zero, we cannot use Eqn. 2 to estimate the saturation *I*.

Ye model on the light response of photosynthesis and electron transport rate

The Ye model describes the P_N–*I* function as below (Ye 2007; Ye *et al*. 2013):

$$P_{\mathrm{N}} = \alpha \frac{1-\beta I}{1+\gamma I} I - R_{\mathrm{D}} \tag{3}$$

where α is the initial slope of P_{N}–I curve, R_{D} is the dark respiratory rate, and β and γ are the photoinhibition coefficient and saturation coefficient, respectively (Ye *et al*. 2013). Due to its nonasymptotic function, Ye model can calculate the actual P_{Nmax} and the actual corresponding saturation I (I_{sat}).

According to Ye *et al*. (2013), the photosynthetic electron transport rate (*ETR*) via PSII can be described as:

$$ETR = \alpha_e \frac{1-\beta_e I}{1+\gamma_e I} I \tag{4}$$

Since Eqns. 3 and 4 are of the non-asymptotic function, they have the first derivative. When the first derivative equals to zero, the maximum net photosynthetic rate (P_{Nmax}), the maximum electron transport rate (ETR_{max}) and their corresponding saturation intensities (I_{sat}) can be calculated.

Results

Ye model can accurately characterize the *ETR*–*I* curves (Figure 1) for various C_3 and C_4 species across light-limited, light-saturated and photoinhibitory *I* levels. Its robustness and accuracy in reproducing P_{N}–I curves are consistent at different temperature and CO_2 concentration levels (Figure 2).

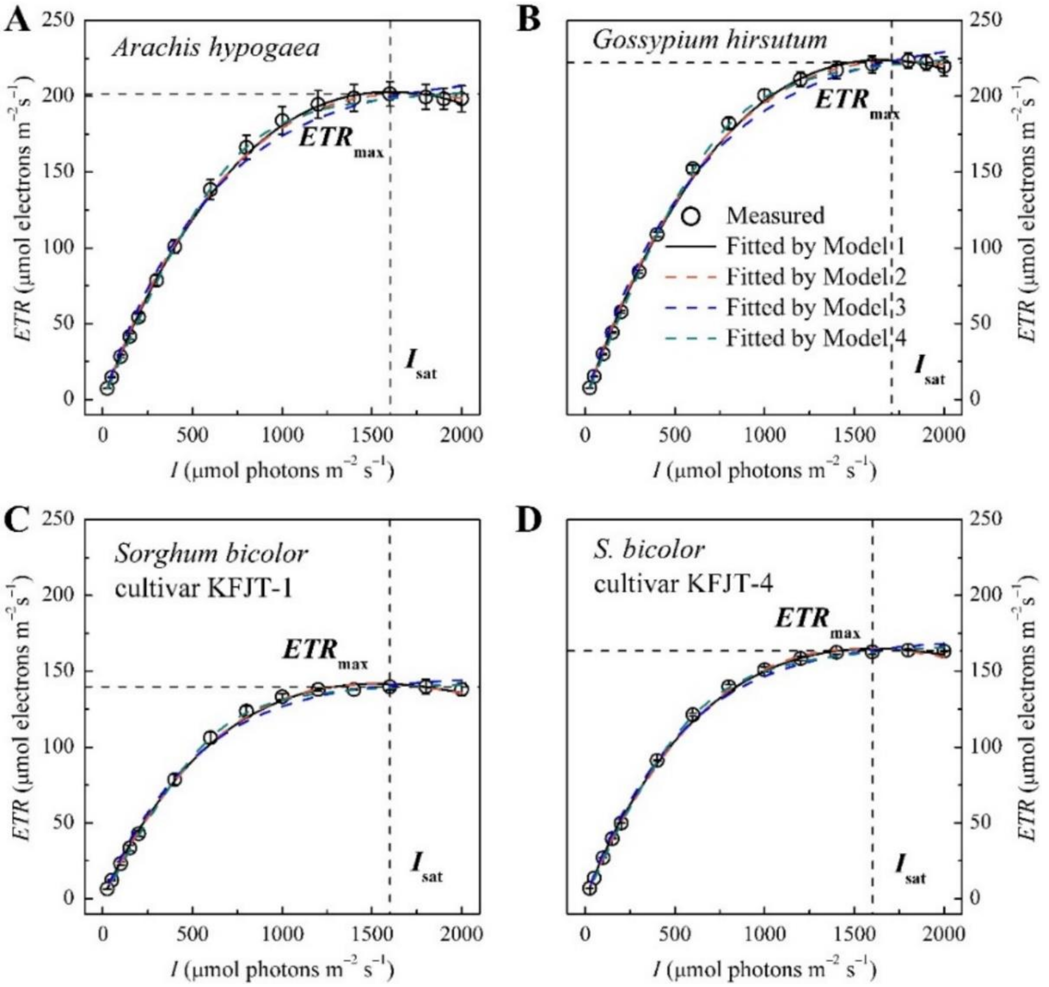

Figure 1. Light-response curves of the electron transport rate (*ETR–I*) for *Arachis hypogaea* (**A**), *Gossypium hirsutum* (**B**), *Sorghum bicolor* cultivar KFJT-1 (**C**) and *S. bicolor* cultivar KFJT-4 (**D**). The curves were simulated by Model 1 (Ye model), Model 2 (negative exponential function), Model 3 (exponential function), and Model 4 (non-rectangular hyperbolic model). A black horizontal dashed line represents the observed value of ETR_{max}, and a black vertical dashed line represents the observed value of I_{sat}. Data is sourced from Yang et al. (2025).

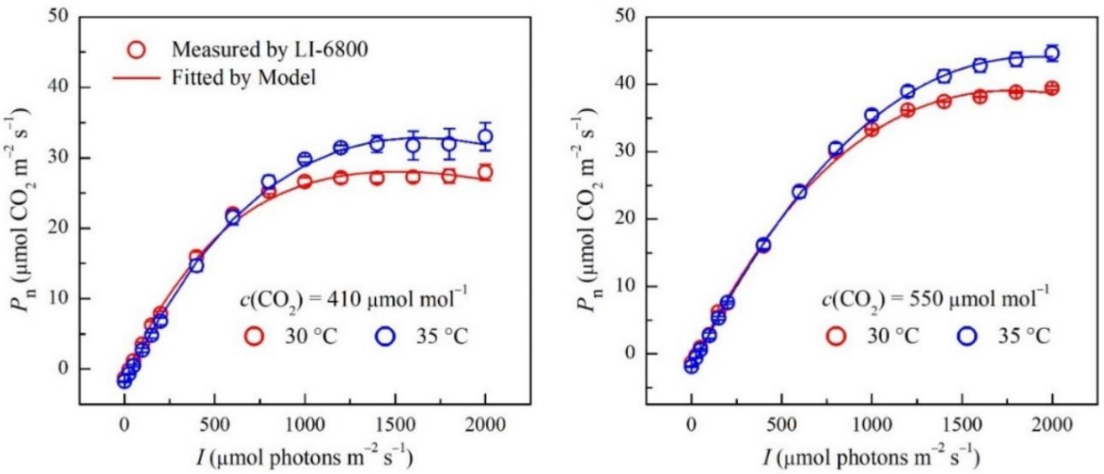

Figure 2. Photosynthetic light response curves fitted by the Ye model for leaves of sweet sorghum under different temperature and atmospheric CO_2 levels (410 and 550 mmol mol^{-1}) and air temperatures (30 and 35°C). Data is sourced from Yang et al. (2024).

Discussion and conclusion

Using an experiment-modelling-integration approach, Ye et al (2021) highlighted that Ye model can well address the limitations of NH model such as (1) underestimation of dark respiration rate (2) overestimation of the maximum net photosynthetic rate and (3) failure in reproducing the photoinhibitory response over both low I levels (i.e., 0–50 µmol m^{-2} s^{-1}) and photoinhibitory I levels (i.e., when I surpassed the cultivar-specific saturation light intensity). Using a consistent model framework as the P_N–I model, Ye et al (2020) reported Ye model can accurately reproduce the *ETR–I* curve, while the NH model significantly overestimated the maximum electron flow for carboxylation but not that for oxygenation, highlighting the reason underlying why the NH model would overestimate P_{Nmax} and ETR_{max}.

This paper reviewed recent research efforts using the experiment-modelling-integration approach to address the long-standing limitations of asymptotic models, and highlighted the long-lasting limitations of the most widely used non-rectangular hyperbolic model (NH model) such as (1) NH model led to underestimation of dark respiration while overestimation of the maximum net photosynthetic rate, and (2) NH model failed in reproducing the photoinhibitory response when light intensity surpassed the species-specific saturation intensity. The more recently developed mechanistic model (Ye model), attributed with its nonasymptotic function, addressed the above limitations of NH model extremely well.

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