



Modelling $^{18}\text{O}_2$ and $^{16}\text{O}_2$ unidirectional fluxes in plants. III: Fitting of experimental data by a simple model

Marcel J. André*,¹

154 montée d'Imbert, 04100 Manosque, France

ARTICLE INFO

Article history:

Received 8 July 2012

Received in revised form 24 October 2012

Accepted 24 October 2012

Keywords:

CO_2 transfer

Diffusion resistance

Photorespiration rate

Oxygenation capacity

Atmosphere regulation

Plant-atmosphere coevolution

ABSTRACT

Photosynthetic assimilation of CO_2 in plants results in the balance between the photochemical energy developed by light in chloroplasts, and the consumption of that energy by the oxygenation processes, mainly the photorespiration in C_3 plants. The analysis of classical biological models shows the difficulties to bring to fore the oxygenation rate due to the photorespiration pathway. As for other parameters, the most important key point is the estimation of the electron transport rate (ETR or J), i.e. the flux of biochemical energy, which is shared between the reductive and oxidative cycles of carbon. The only reliable method to quantify the linear electron flux responsible for the production of reductive energy is to directly measure the O_2 evolution by $^{18}\text{O}_2$ labelling and mass spectrometry. The hypothesis that the respective rates of reductive and oxidative cycles of carbon are only determined by the kinetic parameters of Rubisco, the respective concentrations of CO_2 and O_2 at the Rubisco site and the available electron transport rate, ultimately leads to propose new expressions of biochemical model equations. The modelling of $^{18}\text{O}_2$ and $^{16}\text{O}_2$ unidirectional fluxes in plants shows that a simple model can fit the photosynthetic and photorespiration exchanges for a wide range of environmental conditions. Its originality is to express the carboxylation and the oxygenation as a function of *external* gas concentrations, by the definition of a *plant specificity factor* Sp that mimics the *internal* reactions of Rubisco in plants. The difference between the specificity factors of plant (Sp) and of Rubisco (Sr) is directly related to the conductance values to CO_2 transfer between the atmosphere and the Rubisco site. This clearly illustrates that the values and the variation of conductance are much more important, in higher C_3 plants, than the small variations of the Rubisco specificity factor. The simple model systematically expresses the reciprocal variations of carboxylation and oxygenation exchanges illustrated by a “mirror effect”. It explains the protective sink effect of photorespiration, e.g. during water stress. The importance of the CO_2 compensation point, in classical models, is reduced at the benefit of the crossing points Cx and Ox , concentration values where carboxylation and oxygenation are equal or where the gross O_2 uptake is half of the gross O_2 evolution. This concept is useful to illustrate the feedback effects of photorespiration in the atmosphere regulation. The constancy of Sp and of Cx for a great variation of P under several irradiance levels shows that the regulation of the conductance maintains constant the internal CO_2 and the ratio of photorespiration to photosynthesis (PR/P). The maintenance of the ratio PR/P , in conditions of which PR could be reduced and the carboxylation increased, reinforces the hypothesis of a positive role of photorespiration and its involvement in the plant-atmosphere co-evolution.

© 2012 Elsevier Ireland Ltd. All rights reserved.

Abbreviations: P_o , P , net photosynthesis in O_2 (O) or CO_2 , respectively; R , respiration in the light; U , gross O_2 uptake; PR , photorespiration; ETR , electron transport rate, measured by the gross O_2 evolution $E = P_o + U = 1/4 ETR$; Γ^* , true CO_2 compensation point, i.e. measured in the absence of dark respiration; C_x and O_x , crossing points: respective concentrations of CO_2 and O_2 where $P = U$; v_o and v_c , actual rates of oxygenation and carboxylation; WUE, water use efficiency; S_r , S_p , specificity factor for CO_2 , respectively at Rubisco and plant (green shoot parts) level; K_c , K_o , V_c , V_o , kinetic parameters of Sp (i.e. Michaelis–Menten constants and maximum rates of carboxylation and oxygenation at the plant level); C_a , C_i and C_r , respectively CO_2 concentrations in atmosphere, substomatal and at the Rubisco site; RuBP, ribulose-1,5-bisphosphate; Most of gas exchange rates and V_o , V_c are expressed in relative units; K_o and O , in %; C_a , C_r and K_c , in ppm; S_p and S_r , in lab units (% ppm⁻¹).

* Tel.: +33 492 721 128.

E-mail address: aprovinc@club-internet.fr

¹ Formerly: Institut de Biologie Environnementale et de Biotechnologie, Direction des Sciences du Vivant, CEA Cadarache, 13108 Saint-Paul-lez-Durance, France.

1. Introduction

Many models were proposed to explain or to predict photosynthesis. Gaastra's work and model (1959) was a milestone that paved the road to further photosynthetic modelling since the second half of the 20th century (Farquhar et al., 2001; review of El-Sharkawy, 2011). The fitting of CO₂ assimilation vs [CO₂] curves is the most common of their applications, but the existing models have several other purposes:

- to summarise the knowledge of biochemical apparatus;
- to fit curves of data, with several parameters as tools for comparing plant responses;
- to illustrate plant physiology for pedagogic purposes;
- to predict plants' responses to environmental parameters, from field to global level;
- to analyse the conductances of CO₂ transfer.

If the fitting could be easy, with sufficient parameters and plausible hypotheses, it is recommended to have the more rational physiological hypothesis and the more simple and useful application.

Models issued from the equations and the hypotheses of Farquhar et al. (1980) are the most used for all purposes, from the biochemical studies to the global atmosphere analysis. Among a multitude of papers, the properties of the basic model were revisited by von Caemmerer (2000), Sharkey et al. (2007) and von Caemmerer et al. (2009).

To satisfy the analysis of biochemical apparatus, the fitting of data was generally expressed as a function of substomatal internal CO₂ (*C_i*). For a long period of time, the only measured conductance to CO₂ was the stomatal conductance (*g_s*) estimated from the rate of transpiration. The importance of mesophyll conductance (*g_m*) was more and more emphasised (Flexas et al., 2008; Warren, 2008). It is the object of several studies (Barbour et al., 2010; Terashima et al., 2011; Tholen and Zhu, 2011; Kodama et al., 2011; Douthe et al., 2011). Quantitative approaches of physiological regulations of photosynthesis or the measurement of conductances are more difficult (Pons et al., 2009): these authors recommend 22 points of attention, intended to obtain better results by estimating *g_s* and *g_m* using different techniques, and 14 points concerning the gas exchange measurements, curve-fitting and chlorophyll fluorescence methods. In all the models, the most crucial point is the estimation of the value of the electron transport rate (*ETR* or *J*), the flux of biochemical energy, which is shared approximately in equal parts between the reductive and oxidative cycles of carbon (Gerbaud and André, 1979; von Caemmerer, 2000; Pons et al., 2009). The most accessible way is the fluorescence method (Genty et al., 1989), but it is sensitive to several coefficients of absorption and of the gas exchange equations (Yin and Struik, 2009). However, the only reliable method to quantify *J* as the linear electron flux responsible of the production of reductive energy is to directly measure O₂ evolution by ¹⁸O₂ labelling and mass spectrometry, because the splitting of water is the source of the electron transport rate (Gerbaud and André, 1979; von Caemmerer, 2000). It is surprising that ¹⁸O₂ measurement capability is not mentioned in the review of Pons et al. (2009). It is the reason why the gas exchanges data obtained by the ¹⁸O₂ method deserve to be re-analysed. Without contesting the great work made by numerous modellers to satisfy the three first goals of the models, my aim is to contribute to other purposes. In particular, attention would be given to the pedagogic interest as well as the ease of use of modelling for the people who are not familiar with mathematics. Emphasis will be made on the complementary role of photosynthesis and photorespiration in using reductive energy produced by light and, as consequences, the complementary roles of CO₂ and O₂ in the plant atmosphere

co-evolution (André, 2011a,b). The new formulation of the equations of classical biochemical models should be an introduction to a more precise analysis of the regulation effect of conductances (André, 2013).

2. Classical biochemical models

2.1. General laws

The most frequently models used to analyse the response of C₃ plant photosynthesis are issued from Farquhar et al. (1980) model. All versions of the model use the basic property of Rubisco and the relationship between *v_c* and *v_o* by the Eq. of Laing et al. (1974):

$$\frac{v_c}{v_o} = \frac{S_r C_r}{O} \quad (1)$$

where *S_r* is the specificity of Rubisco for CO₂, *C_r* and *O*, respectively CO₂ and O₂ concentrations at the site of Rubisco in chloroplasts, *v_c*, *v_o* are the rates of carboxylase and oxygenase reactions, respectively.

The second basic property of Rubisco is the expression of *S_r* by:

$$S_r = \frac{V_c K_o}{V_o K_c} \quad (2)$$

V_c and *V_o* are the maximum velocities of Rubisco for carboxylation and oxygenation respectively, *K_c* and *K_o* are the Michaelis constants for CO₂ and O₂, in ppm and %, respectively; *S_r* is expressed in % ppm⁻¹.

S_r is only implicit in classical models by:

$$\Gamma^* = \frac{0.5O}{S_r} \quad (3)$$

*Γ** is the "true" CO₂ compensation point in the absence of dark respiration. It is the object of several methods of measurements (Berry et al., 1994).

In this model, two main independent limitations are stated, with actually two fittings of curves. In other words, assimilation is considered as the minimum of two functions based on two limitations. A breaking point is the object of corrective parameters to adjust the transition between the two curves. The equations resulting from the two limitations are presented below, following the explanations of Sharkey et al. (2007) and von Caemmerer et al. (2009).

2.2. Case of low CO₂ – limitation by Rubisco

According the authors mentioned above, when [CO₂] is <200 ppm, CO₂ assimilation is expressed by:

$$P = V_{c_{\max}} \left[\frac{(C_r - \Gamma^*)}{(C_r + K_c(1 + O/K_o))} \right] - R \quad (4a)$$

where *P* is the net assimilation rate. It is generally named *A*. In this work, we choose to use *P*, because our data give access to *P_o*, the net O₂ evolution, both being representative of photosynthesis (*P*); *C_r* is the CO₂ concentration near Rubisco, in chloroplasts.

After rearranging using Eqs. (2) and (3):

$$P + R = V_{c_{\max}} \frac{(C_r S_r / O) - 0.5}{C_r S_r / O + K_c S_r / O(1 + O/K_o)} \quad (4b)$$

The maximum capacity of Rubisco *V_{c_{max}}*

 is obtained by the fitting of the beginning of *P* vs *C_i* curve. This "potential" is shared in two parts by the ratio $(C_r S_r / O - 0.5) / [C_r S_r / O + K_c S_r / O(1 + O/K_o)]$ which depends on *S_r*. The first part (Eq. (4b)) is *P*+*R*. The second part should be the consumption of total oxygenation of the photorespiration pathway, which is only implicit in the classical models.

Download English Version:

<https://daneshyari.com/en/article/10884564>

Download Persian Version:

<https://daneshyari.com/article/10884564>

[Daneshyari.com](https://daneshyari.com)