A General Expression for the Control of the Rate of Photosynthetic CO₂ Fixation by Stomata, the Boundary Layer and Radiation Exchange

Ian E. Woodrow, J. Timothy Ball and Joseph A. Berry

Department of Plant Biology, Carnegie Institution of Washington, 290 Panama Street, Stanford, California 94305, USA. (CIW-DPB Pub. No. 955)

1. Introduction

Previous descriptions of the "limitation" to the rate of photosynthetic CO₂ assimilation imposed by the stomata and boundary layer have focused on the basic mechanism of CO₂ diffusion and have made use of several simplifying assumptions regarding leaf temperature and transpiration rate. These descriptions are consequently useful under controlled conditions but, in the field, it is impossible to consider the role of the stomata and boundary layer in regulating CO₂ uptake without considering their roles in controlling water and heat exchange and leaf temperature. In the following, we examine a complex leaf system that includes CO₂, water and heat exchange and present expressions quantifying the degree to which each element of the system "limits" the rate of CO₂ assimilation.

2. Materials and Methods

Transpiration rates, CO₂ assimilation rates and leaf temperatures were measured with a compensating gas exchange system similar to that described by Field et al. [2]. Gas exchange parameters were calculated according to Ball [3]. The boundary layer conductance to water vapour ($g_{bw}$) was 3.5 mol m⁻² s⁻¹ distributed equally between the two surfaces of the leaf. The ambient mole fractions of CO₂ and water vapour were 330 μmol mol⁻¹ and 26.6 mmol mol⁻¹, respectively.

3. Description of the Photosynthetic System

The model of photosynthesis (Fig. 1) used in the analysis of the control of the rate of CO₂ assimilation consists of four basic components: (1) the leaf boundary layer, (2) the stomata, (3) radiation exchange, and (4) the photosynthetic biochemistry. The latter component is responsible for fixing CO₂ in the reaction catalysed by ribulose 1,5-bisphosphate carboxylase in C3 plants and phosphoenolpyruvate carboxylase in C4 plants and includes as much of plant metabolism as one wishes as long as there are no feedback mechanisms influencing stomatal conductance other than those reflected by the response of stomatal conductance to $c_i$ [4]. The boundary layer mediates three transfer processes between the bulk atmosphere and the leaf surface: (1) CO₂ diffusion ($C_a=C_s$), (2) water vapour and associated latent heat transfer ($W_a=W_s$), and heat transfer by forced and natural convection ($H_a=H_s$). The stomata also mediate CO₂ diffusion ($C_s=C_i$) and water vapour and associated latent heat transfer ($W_s=W_i$), but in this case between the leaf surface and the intercellular spaces. Heat is transferred in the form of longer wavelength radiation by a process that is independent of both the stomata and boundary layer and depends upon the leaf temperature ($T_l$) and incident flux density of radiation from the surrounding environment. Photosynthetically active radiation (P.A.R.) primarily affects the rate of photosynthetic electron transport and the stomatal aperture.

Internal CO₂, in addition to its involvement in diffusion through the stomata, is a product of photorespiration, a substrate of the carboxylation reaction, an activator of the carboxylase in C3 plants, and a feedback inhibitor of the stomata. Whether the feedback is direct or indirect is not important in the present context because the analysis does not depend upon these mechanistic details. It is assumed that the calculated $c_i$ approximates the concentration of CO₂ in the stroma, but should this not be the case, the control due to CO₂ transfer from the leaf intercellular spaces to the stroma will be attributed to the "biochemistry".

It is also assumed that increases in the rate of transpiration do not change leaf water potential.

Abbreviations: $c_i$, mole fraction CO₂ in the leaf intercellular air spaces; $g_{bw}$, conductance of the boundary layer to water; $T_l$, leaf temperature; $w_s$, mole fraction water vapour at the leaf surface.

such that the capacity of the "biochemistry" for fixing CO₂ is altered significantly. The effects of \( w_s \) and \( T_l \) on stomatal conductance and \( T_l \) on assimilation are considered in the model.

4. Calculation of Control Coefficients

The degree to which the four basic elements of the system control the rate of CO₂ fixation is described using the control coefficient:

\[
C_P = \frac{\partial V}{\partial P} \frac{P}{V}
\]

where \( V \), in the present case, stands for the rate of CO₂ fixation and \( P \) for any parameter (independent variable) whose change causes a change in \( V \). This coefficient reflects the fractional increase in flux brought about by a fractional increase in the independent variable. In the case of stomata, the letter is the maximum stomatal conductance. The control coefficients, which are properties of the whole system, are derived from coefficients that reflect the rate laws of the isolated components. These elasticity coefficients are defined as:

\[
\epsilon = \frac{\partial v}{\partial S} \frac{S}{v}
\]

where \( v \) is the reaction velocity of the isolated component and \( S \) the concentration of any molecular species affecting the rate of that process.