Advances in the Response of Leaf Photosynthetic Physiology to Environmental Factors Based on the FvCB Model: Postprint

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Abstract

To enhance leaf photosynthetic rates and better understand the response mechanisms of leaf photosynthetic physiology to variations in environmental factors, the FvCB model (C3 plant photosynthetic biochemical model) is commonly utilized to analyze CO2 response curves under diverse environmental conditions and predict the intrinsic status of photosynthetic systems in living leaves. This paper systematically introduces the fundamental theories of the FvCB model' s establishment, development, and fitting methodologies, and reviews research applications of the model in elucidating the response mechanisms of leaf photosynthetic physiology to changes in environmental factors such as light, CO2, water, temperature, and nitrogen nutrition. To further improve the FvCB model and deepen understanding of how photosynthetic systems in living leaves respond to environmental factor variations, future research should strengthen investigations into: 1) the relationship between carboxylation rate and photosynthetic electron transport rate; 2) the specific components of mesophyll conductance and their influence on FvCB model parameter estimation; 3) the regulatory mechanisms of leaf stomatal conductance and mesophyll conductance in response to environmental factor changes.

Full Text

Preamble

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Title: Advances in Photo-Physiological Responses of Leaves to Environmental Factors Based on the FvCB Model

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Abstract

Biochemical models of leaf photosynthesis are invaluable tools for exploring the photo-physiological responses of leaves to environmental factors and identifying potential targets to improve the efficiency of CO fixation. The Farquhar-von Caemmerer-Berry (FvCB) model can be used to fit CO response curves developed under different environmental conditions and predict underlying photosynthetic biochemistry. However, to do this successfully, it is important to improve chloroplast electron transport modeling and gain a better understanding of internal CO diffusion limitations and the mechanisms of stomatal (g) and mesophyll (g) conductance responses to environmental factors. This paper reviews the FvCB model and its application in determining the photo-physiological responses to environmental factors such as light, CO , water, temperature, and nitrogen nutrition. To improve the veracity of parameter estimations and reveal the mechanisms of photo-physiological responses, future studies should emphasize: (1) the relationship between the carboxylation rate of Rubisco and chloroplast electron transport rate; (2) CO diffusion limitations in mesophyll cells and their effect on parameter estimations; and (3) the regulation of g and g responses to different environmental conditions.

Keywords: C plants; photosynthesis; FvCB model; photosynthetic physiology; environmental factors

1. FvCB Model Theory for C Plants

The FvCB model reveals how photosynthetic biochemistry changes under different environmental conditions by analyzing CO response curves and predicting internal changes in the photosynthetic system of living leaves. The model simulates internal photosynthetic biochemical reactions and has been widely applied to study response mechanisms to environmental factors such as light, CO , water, temperature, and nitrogen nutrition. It also helps establish crop yield prediction models, stomatal conductance models, and plant growth models.

1.1 Three Limitation Stages

In the carbon reduction cycle, Rubisco catalyzes both carboxylation and oxygenation reactions. When CO concentration is low, the ratio of oxygenation to carboxylation increases. At high light and low CO , photosynthesis is limited by Rubisco activity. At low light and high CO , it is limited by RuBP regeneration rate. A third limitation occurs when triose phosphate utilization (TPU) rate is limiting.

Rubisco Activity-Limited Stage:
At high light and low CO , photosynthesis is limited by Rubisco activity. Based on enzyme kinetics, the carboxylation rate (V_c) and oxygenation rate (V_o) are:

$$V_c = \frac{V_{cmax} \cdot C_c}{C_c + K_c(1 + O/K_o)}$$

$$V_o = \frac{V_{cmax} \cdot O}{O + K_o(1 + C_c/K_c)}$$

where V_{cmax} is maximum carboxylation rate, C_c is CO concentration at Rubisco carboxylation sites, O is O concentration, and K_c and K_o are Michaelis-Menten constants for carboxylation and oxygenation, respectively.

The net assimilation rate (A) is:

$$A = V_c - 0.5V_o - R_d$$

where R_d is day respiration rate. The CO compensation point without day respiration (Γ*) is:

$$\Gamma* = \frac{0.5V_{cmax} \cdot K_c \cdot O}{V_{cmax} \cdot K_o} = \frac{0.5K_c \cdot O}{K_o}$$

RuBP Regeneration-Limited Stage:
When light is limiting, the regeneration rate of RuBP is insufficient. The electron transport rate (J) is related to irradiance (I) by:

$$J = \frac{\alpha I + J_{max} - \sqrt{(\alpha I + J_{max})^2 - 4\theta\alpha I J_{max}}}{2\theta}$$

where is leaf absorptance, J_{max} is maximum electron transport rate, and is curvature factor. The assimilation rate becomes:

$$A_j = \frac{J(C_c - \Gamma*)}{4.5(C_c + 2\Gamma*)} - R_d$$

TPU-Limited Stage:
When triose phosphate export from chloroplast is limiting, assimilation is:

$$A_p = 3T_p - R_d$$

where T_p is the triose phosphate export rate.

1.2 Mesophyll Conductance

Mesophyll conductance (g) represents the resistance to CO diffusion from intercellular air spaces to Rubisco carboxylation sites:

$$g_m = \frac{A}{C_i - C_c}$$

where C_i is intercellular CO concentration. Incorporating g modifies the model equations, requiring solving quadratic equations to relate A to C_i.

1.3 Temperature Dependencies

Temperature affects all biochemical parameters. The Arrhenius equation is used:

$$P(T) = P_{25} \exp\left[\frac{E_a}{R}\left(\frac{1}{298} - \frac{1}{T}\right)\right]$$

where P(T) is the parameter at temperature T (K), P_{25} is the value at 25°C, E_a is activation energy, and R is the gas constant.

Table 1 shows standard parameter values at 25°C.

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2. Applications in Studying Environmental Responses

2.1 Light

Under different light intensities, leaf morphology and biochemistry change. Sun leaves have higher contents of cytochrome f, ATP, and Rubisco than shade leaves, leading to greater V_cmax and J_max. Sun leaves also show higher g and g due to: - Greater chloroplast surface area exposed to intercellular air spaces - Shorter diffusion path lengths - Higher aquaporin expression under high light

Instantaneous light intensity affects g but has species-dependent effects on g . Some species show increased g with light, while others maintain constant g .

2.2 CO Concentration

Long-term elevated CO reduces Rubisco content and activity, decreasing V_cmax and J_max. It also reduces g and g , partly due to increased leaf thickness that lengthens the diffusion path. Short-term CO increases cause stomatal closure, reducing g . The relationship between g and short-term CO changes is complex, with some studies showing negative correlation while others find no relationship. Aquaporins and chloroplast movements may mediate rapid g responses.

2.3 Temperature

Temperature directly affects photosynthetic biochemistry. V_cmax, J_max, and T_p increase with temperature up to an optimum. Mesophyll conductance generally increases with temperature, possibly due to: - Increased membrane permeability - Changes in cell wall thickness and liquid-phase diffusion path - Upregulated aquaporin gene expression

2.4 Drought and Salt Stress

Water deficit reduces g through stomatal closure and can decrease g by: - Reducing mesophyll cell size and surface area - Altering cell wall properties - Downregulating aquaporin expression

Salt stress additionally causes ion accumulation in guard cells, interfering with stomatal function.

2.5 Nitrogen Content

Nitrogen is a key component of photosynthetic machinery. Leaf N content positively correlates with: - Rubisco content and V_cmax - Cytochrome f content and J_max - Chlorophyll content - Mesophyll conductance (through effects on leaf anatomy and aquaporin expression)

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3. Research Prospects

Accurate parameter estimation in the FvCB model is crucial for understanding photosynthetic responses and predicting crop yields and climate change impacts. However, several issues require attention:

3.1 Linking Carboxylation and Electron Transport

The relationship between V_c and J is complex. Current models assume linear electron transport and ignore alternative electron flows, which may affect J estimation. Future research should investigate: - Stoichiometry of NADPH/ATP production and consumption - Cyclic electron transport around Photosystem I - Alternative electron sinks

3.2 Mesophyll Conductance Components

g is a composite parameter including resistances from: - Cell walls - Plasma membranes - Chloroplast envelopes - Stroma

Current models treat g as a single parameter, which may introduce errors. Future work should combine: - Microscopic observation of leaf anatomy - Isotopic tracing of CO diffusion - Mechanistic modeling of each resistance component

3.3 Regulatory Mechanisms of g and g

While g and g respond to environmental factors, their regulatory mechanisms remain unclear. Potential mechanisms include: - **Stomatal regulation:** CO sensing via malate and ion channels in guard cells - **Mesophyll conductance regulation:** - Structural changes (cell wall thickness, chloroplast positioning) - Aquaporin-mediated CO transport - Chloroplast movements avoiding high light

Direct experimental evidence is lacking. Future studies should integrate: - Gas exchange measurements - Chlorophyll fluorescence - Molecular biology (aquaporin expression) - Cell biology (chloroplast behavior)

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