Photosynthesis with a twist in a warming world

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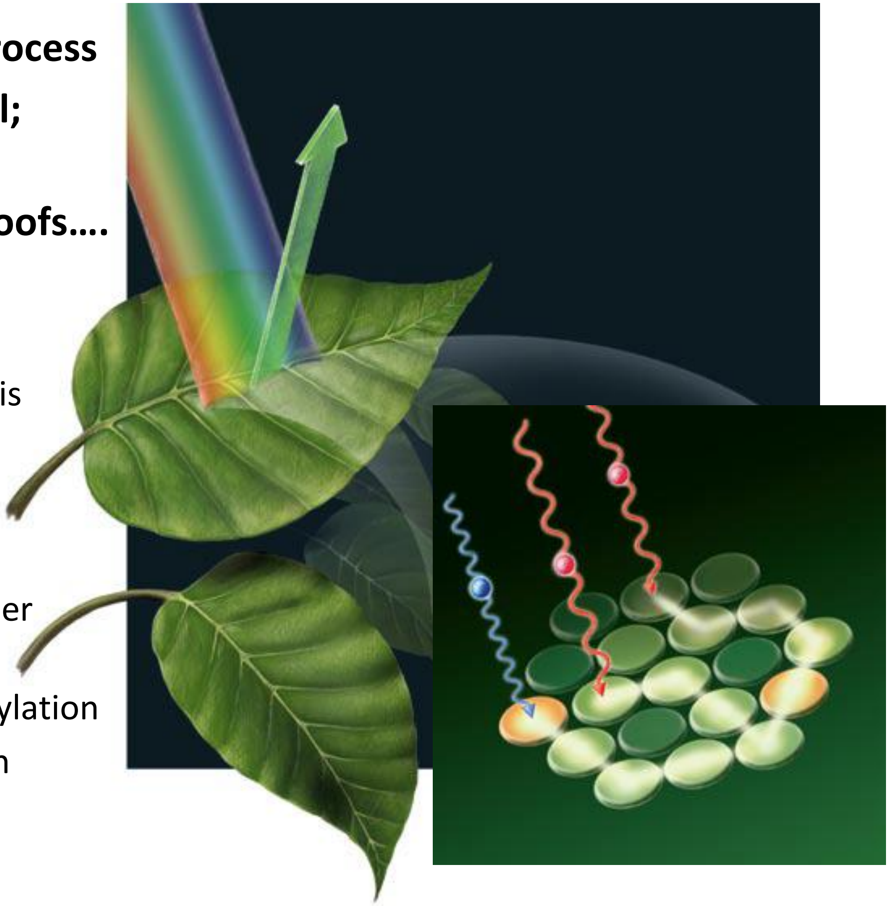
Photosynthesis is the foundation of our biosphere and civilization

- **Food for nearly all life on Earth**
- **Dominant solar energy storage and utilization process**
- **Source of fossil fuels (Carboniferous trees to coal; aquatic organisms to oil and natural gas)**
- **Feedstocks for plastics, dyes, pharmaceuticals, roofs….**
- **Nobel prize winners (all Chemistry)**

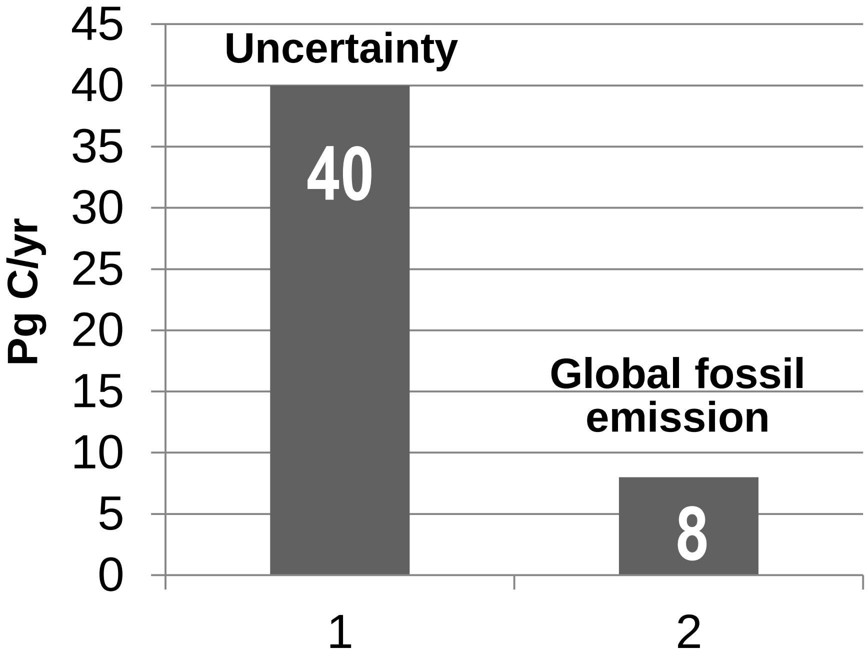
- Wilstatter (1915), chlorophyll purification and structure
- Fischer (1930), chlorophyll chemistry and hemin synthesis
- Karrer (1937), Carotenoid structure
- Kuhn (1938), carotenoids and vitamins
- Calvin (1961), C_3 CO_2 fixation pathway
- Woodward (1965), total synthesis of chlorophyll and other natural products
- Mitchell (1978), Oxidative and photosynthetic phosphorylation
- Michel, Huber and Deisenhofer (1988), bacterial reaction centers
- Marcus (1992), Electron transfer theory
- Boyer and Walker (1997), Enzymatic mechanisms in the synthesis of ATP



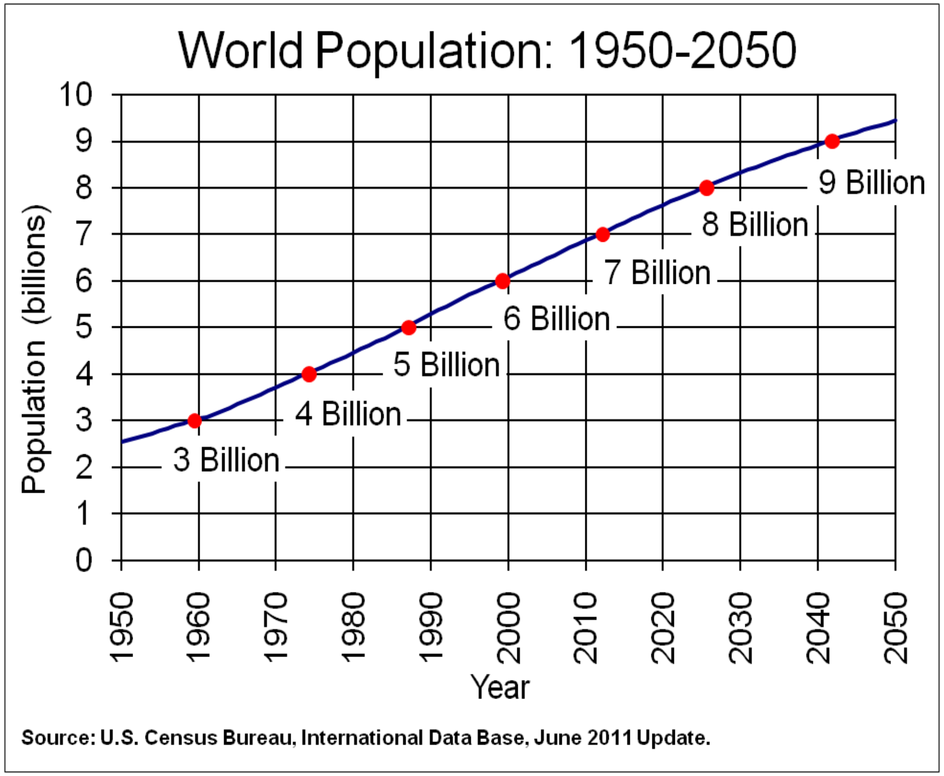
But our understanding of photosynthesis in natural environments remains poor

***Estimates of global photosynthesis*:**

- ***Science* 2010 (329, 834-838): ~ 120 Pg C/yr**
- ***Nature* 2011 (477, 579-582): ~ 160 Pg C/yr**

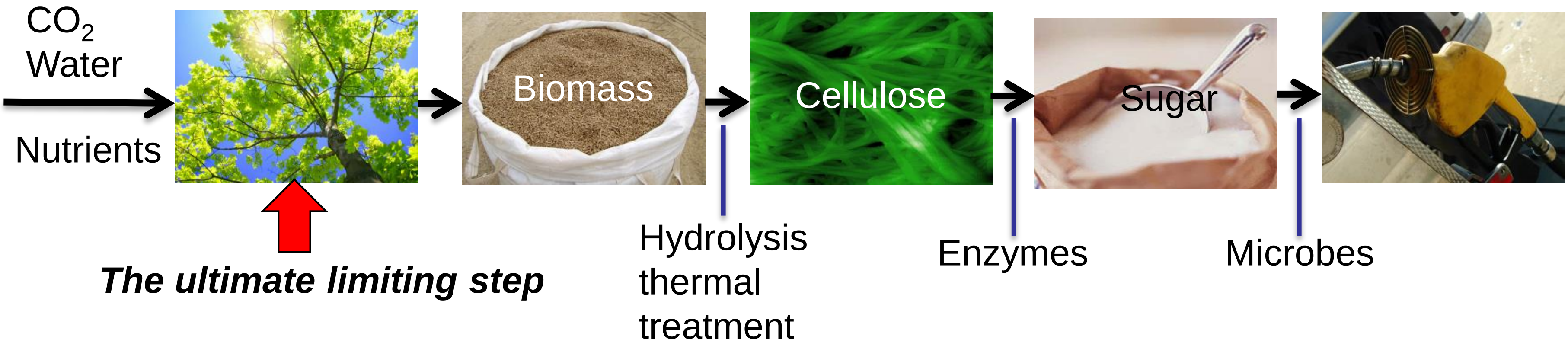


The United Nations Report
‘Food Production Must Double by 2050’



Source: U.S. Census Bureau, International Data Base, June 2011 Update.

Demand for clean bioenergy is increasing



CO$_2$
Water
Nutrients

Biomass

Cellulose

Sugar

Hydrolysis
thermal
treatment

Enzymes

Microbes

The ultimate limiting step

Study of photosynthesis in natural environments is utterly important

- **Innovations to combat hunger**
- **New economy with reduced dependency on fossil energy**
- **Carbon-climate feedbacks**

We need to make sure we deserve this logo

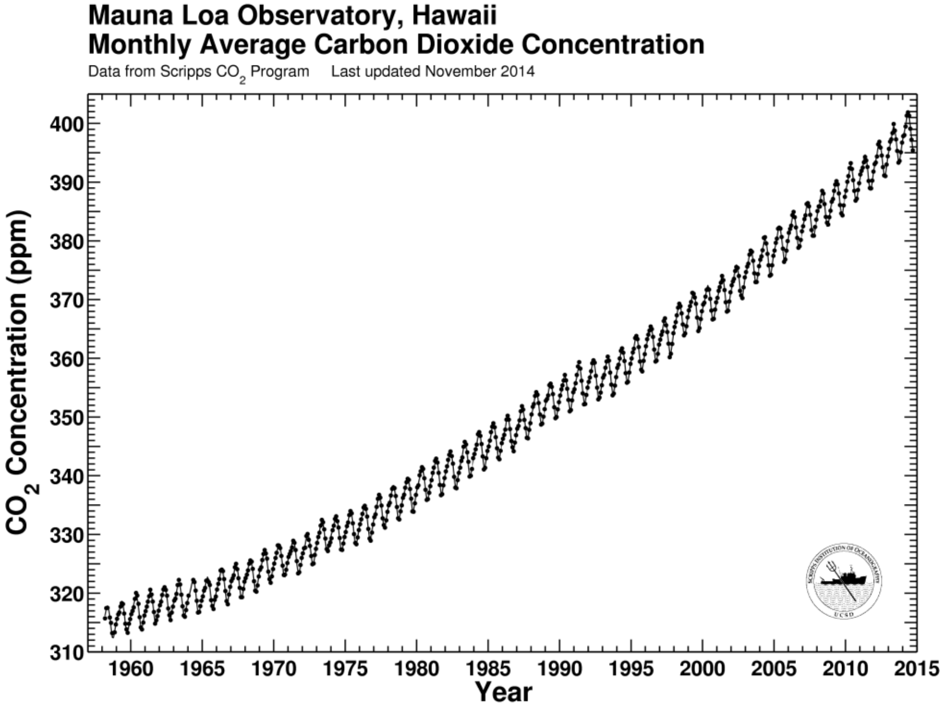
One of the first questions to ask in studying photosynthesis in a natural environment:

What is the CO_2 concentration?

Dark reaction: $CO_2 + 4H^+ + 4e^- \longrightarrow CH_2O + H_2O$

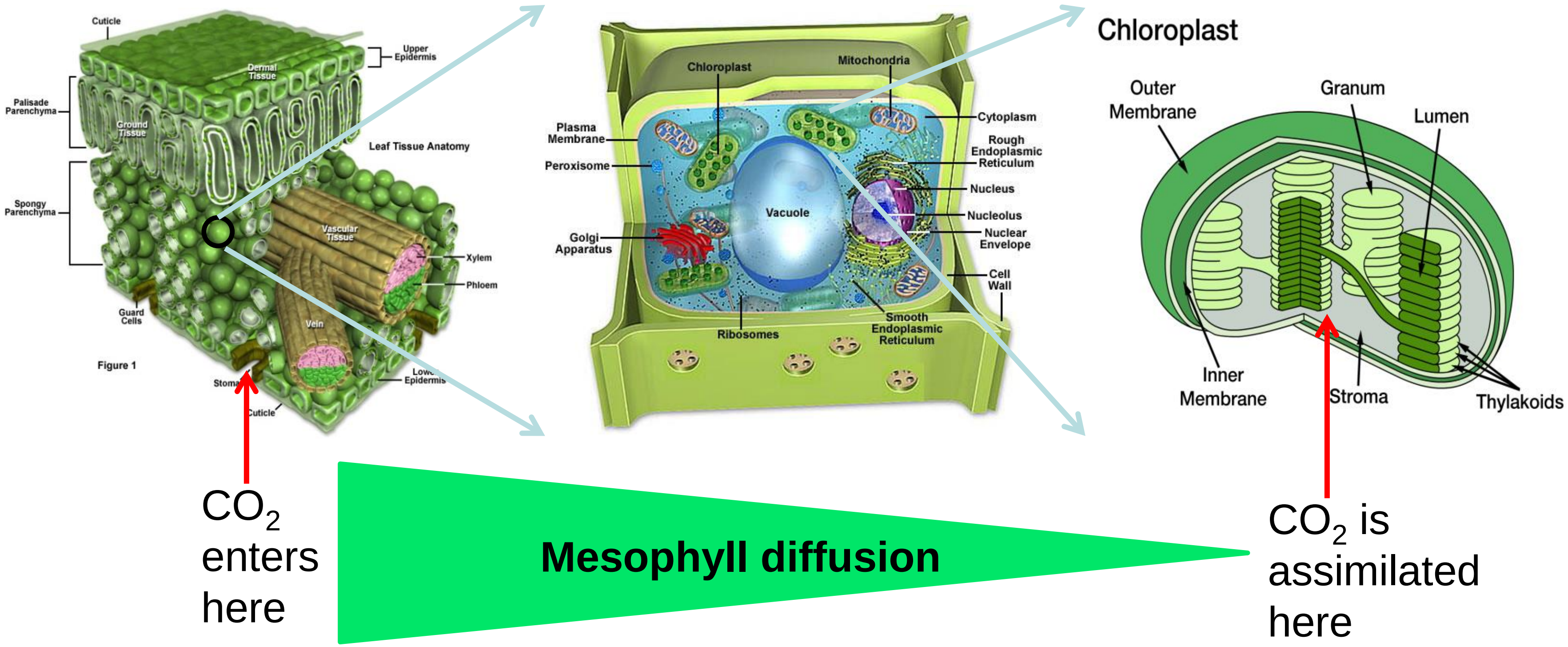
Light reaction: $2H_2O + \text{Light} \xrightarrow{\text{Chl } a} 4H^+ + 4e^- + O_2$

How hard can it be to know CO_2 concentration for photosynthesis?



Photosynthesis does not occur in the air!

The matryoshka dolls of photosynthesis

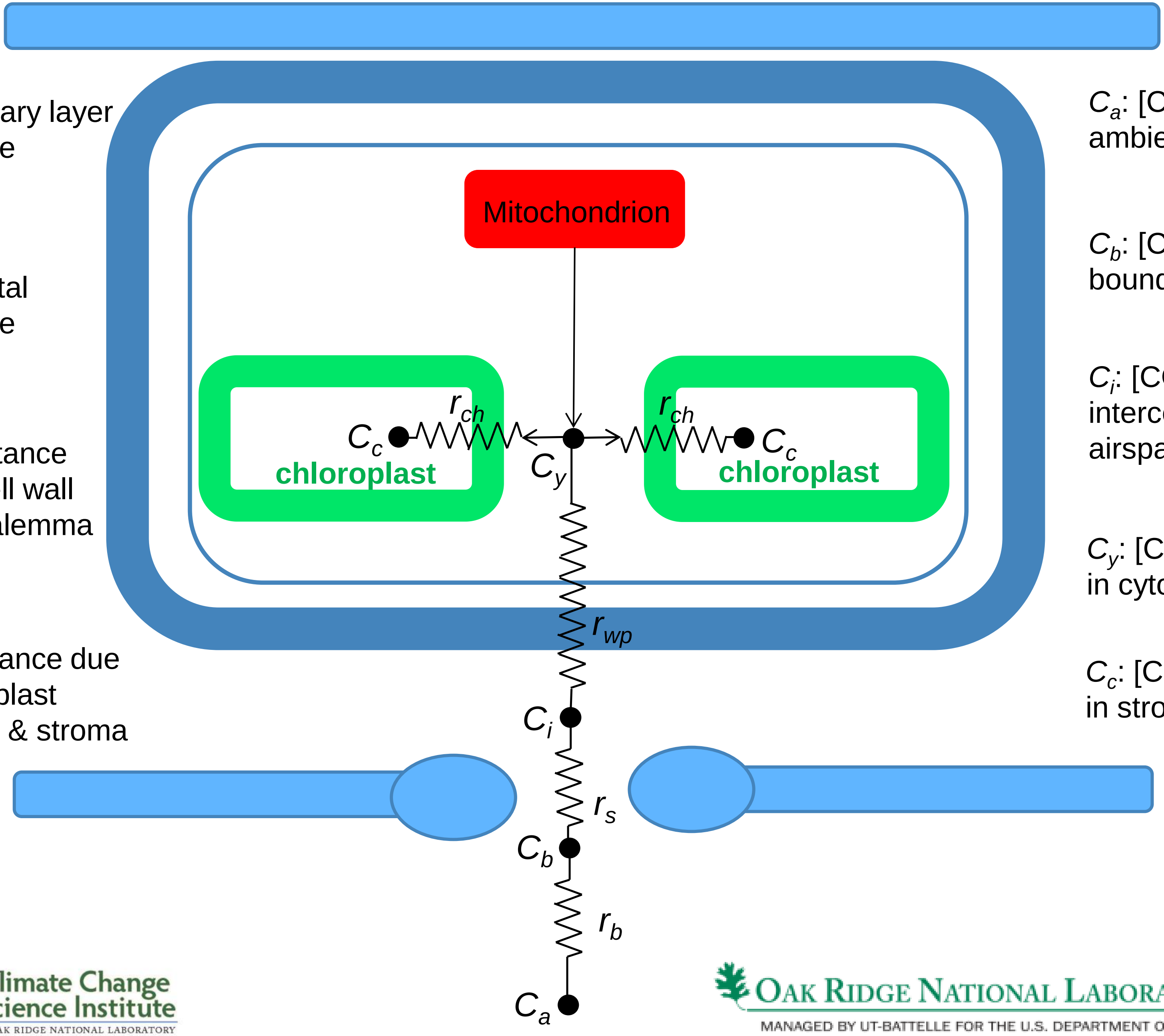


CO_2 enters here

CO_2 is assimilated here

CO_2 is fixed inside the stroma inside the chloroplasts inside the cells inside the leaf inside the boundary layer inside the ambient air

A physicist's rendition of a leaf



r_b: boundary layer resistance

r_s: stomatal resistance

r_{wp}: resistance due to cell wall & plasmalemma

r_{ch}: resistance due to chloroplast envelope & stroma

C_a: [CO_2] in ambient air

C_b: [CO_2] in leaf boundary layer

C_i: [CO_2] in intercellular airspace

C_y: [CO_2] in cytosol

C_c: [CO_2] in stroma

Most photosynthesis studies and ALL carbon-climate models end at the middle matryoshka doll of photosynthesis

C_a C_b C_i C_y C_c

C_a: [CO_2] in ambient air

C_b: [CO_2] in leaf boundary layer

C_i: [CO_2] in intercellular airspace

?

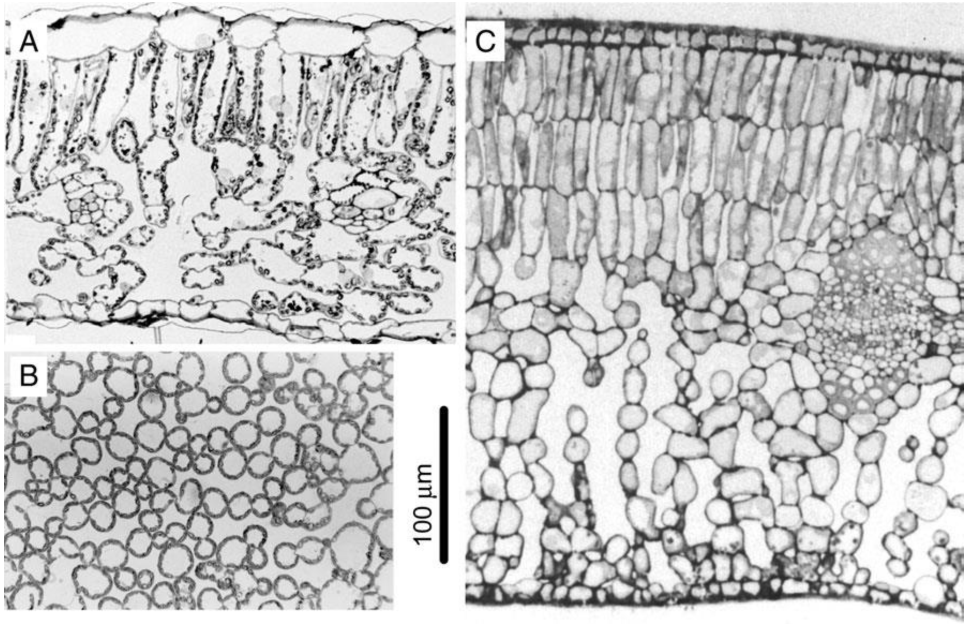
C_y: [CO_2] in cytosol

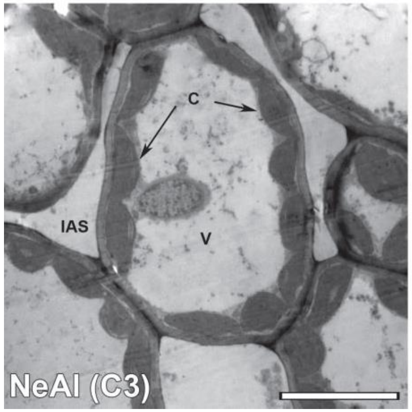
C_c: [CO_2] in stroma

Is it important to know how much smaller the innermost baby is, compared with the outermost figurine in the matryoshka dolls, for understanding and predicting photosynthesis in natural environments?

Evidence that photosynthesis' innermost baby is important: Positioning and sizes of chloroplasts

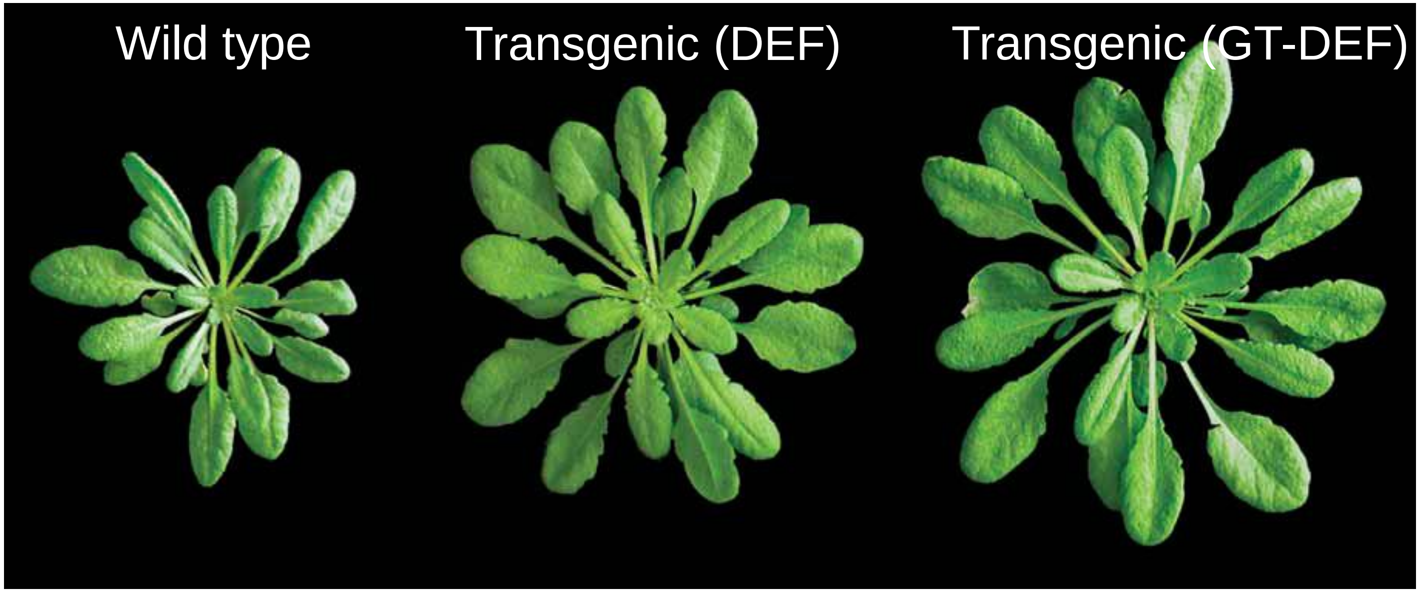
- Photosynthetic cells often have very many small, rather than a few large, chloroplasts.
- Chloroplasts often line up right under cell walls / plasmalemma in C3 plant species



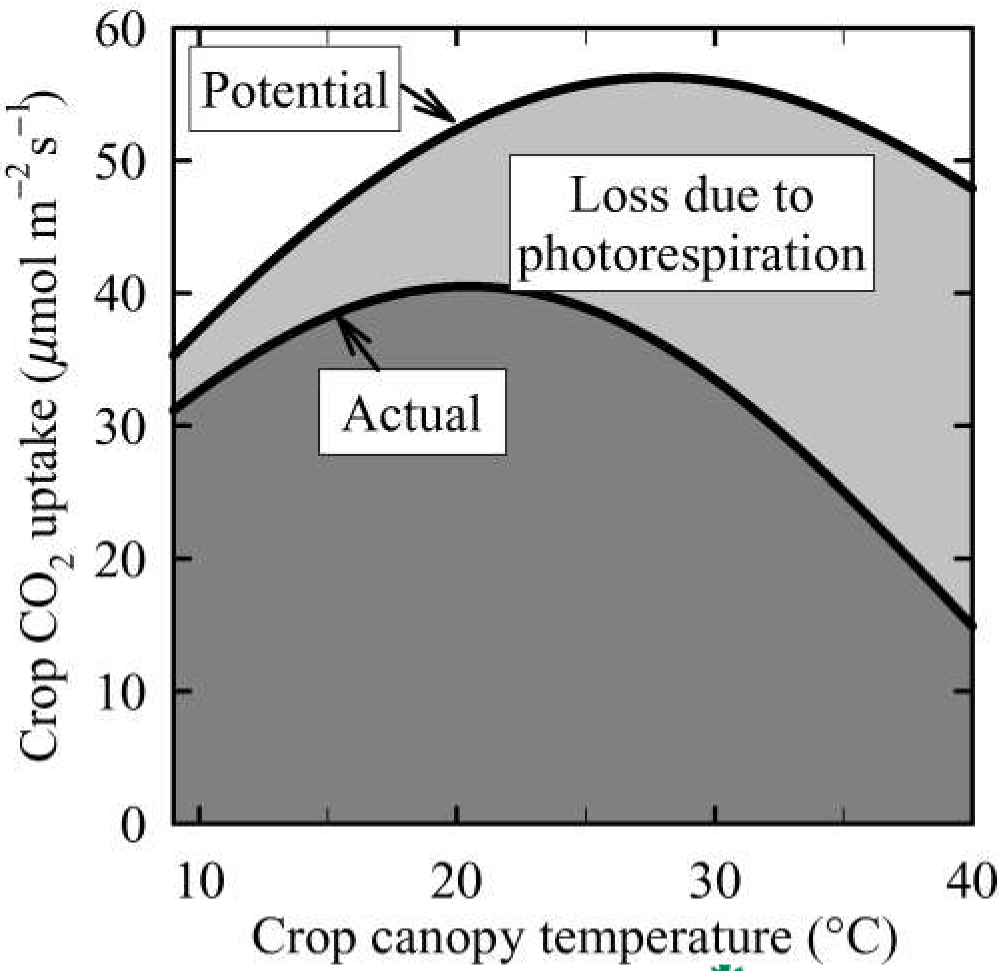


Evidence that photosynthesis' innermost baby is important: Chloroplastic photorespiratory bypass study with transgenic plants

Photorespiratory bypass increases photosynthesis and biomass production in *Arabidopsis thaliana* (Kebeish et al. 2007)

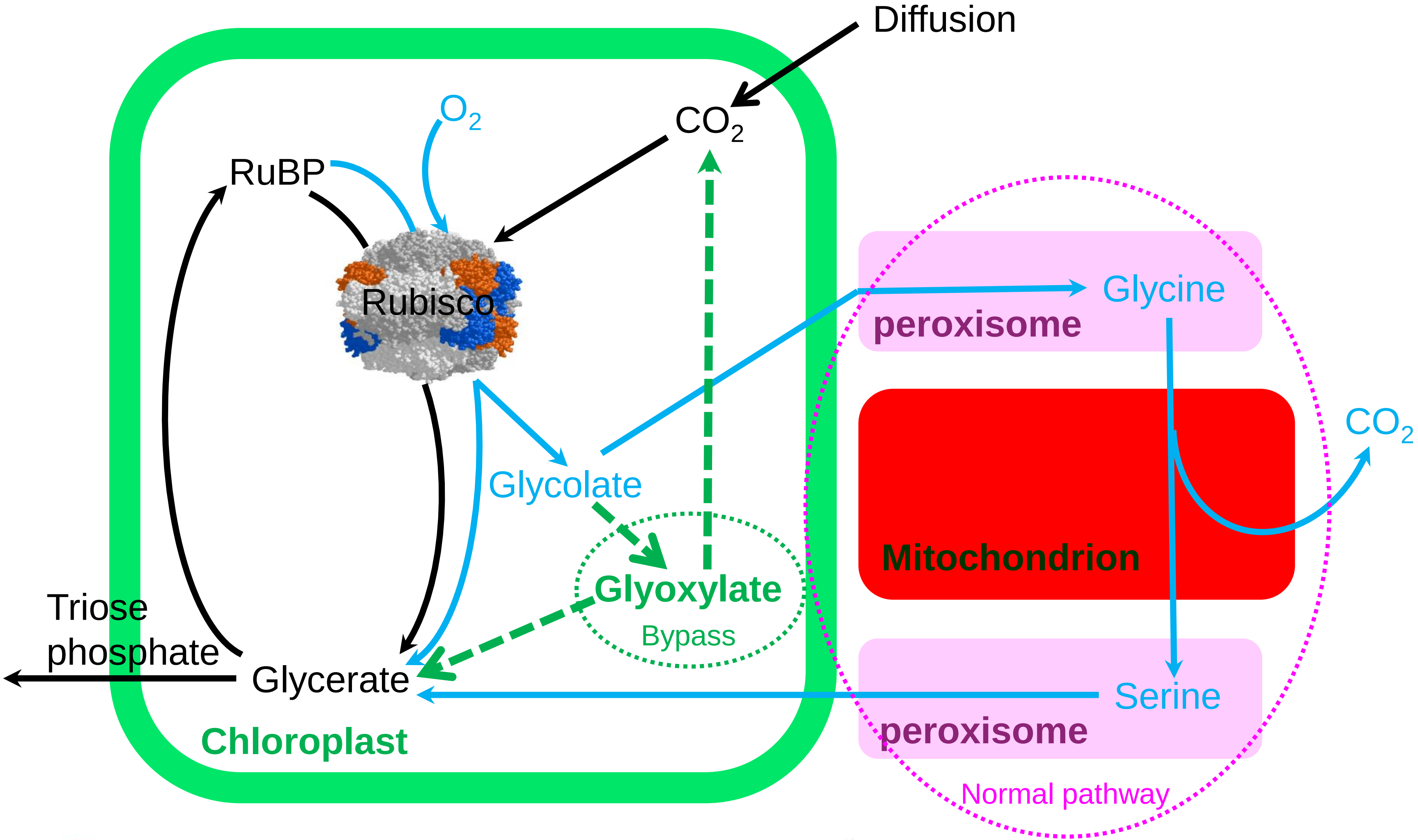


Carbon losses due to photorespiration in C_3 plants



Long et al. (2006)

Chloroplastic photorespiratory bypass increases plant growth by enhancing CO_2 concentration inside chloroplasts



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How did plants end up with a structure of photosynthetic machinery that is so inefficient for its function?

- Photosynthesis originated 2.4 billion years ago when there was essentially no oxygen in the atmosphere and the wastefulness of Rubisco in fixing oxygen posted no disadvantage
- By the time atmospheric oxygen rose to substantial levels, the central role of Rubisco in photosynthesis had been solidly established (too late to change)
- Plants evolved from algae which originated when an heterotrophic cell engulfed and retained, rather than digested, a free living, photosynthetic cyanobacterium in a process called endosymbiosis; this engulfed cyanobacterium later became chloroplast
- This explains the stovepipes and compartments inside plant photosynthetic cells that hinder the efficiency of CO_2 movement and utilization

Lynn Margulis

A scientific rebel

Evidence that photosynthesis’ innermost baby is important: Comparison of CO_2 diffusivities in air, water and lipids

Stomatal diffusion: **Gas phase only**

Mesophyll diffusion: Liquid and lipid phases – cell walls, plasmalemma, cytosols, chloroplast envelopes, and stroma

CO_2 diffusion in liquids and lipids is several orders of magnitude slower than in air

CO_2 diffusivity in different media

Medium	Diffusivity (m^2s^{-1})
Air	1.381×10^{-5}
Cell wall	1.7×10^{-9}
Plasmalemma	10^{-14} - 10^{-11}
Cytosol	1.7×10^{-9}
Chloroplast envelope	10^{-14} - 10^{-11}
Stroma	1.7×10^{-9}

Important questions for understanding the matryoshka dolls of photosynthesis

- **What are the true biochemical capacities of chloroplasts?**
- **How large are the resistances to CO_2 movement along the mesophyll diffusion pathways?**
- **What is the gradient of CO_2 concentration along the mesophyll diffusion pathways?**
- **How to model mesophyll diffusion process?**
- **What are the consequences for modeling global photosynthesis in a world with ever increasing atmospheric CO_2 concentrations?**

Funding, proper tools (*models), data, supporters and collaborators are all needed to* answer these questions!

Missouri AmeriFlux (MOFLUX) Site

Paul Hanson
ORNL

Steve Pallardy
Univ. of Missouri

- l profiles for nd environmental cterization
- Eddy covariance systems at canopy top and forest floor
- High precisio concentration a tower

- Common meteorological measurements
- Plant litter and coarse woody debris production
- Soil CO2 efflux and heat flux
- Soil temperature and moisture at different depth

- Leaf gas exchange and chlorophyll fluorescence
- Leaf nutrient contents
- Leaf water potential
- Phenology

- Opportunistic studies (droughts, heat waves, freeze, ice storms, etc)

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A physicist’s leaf

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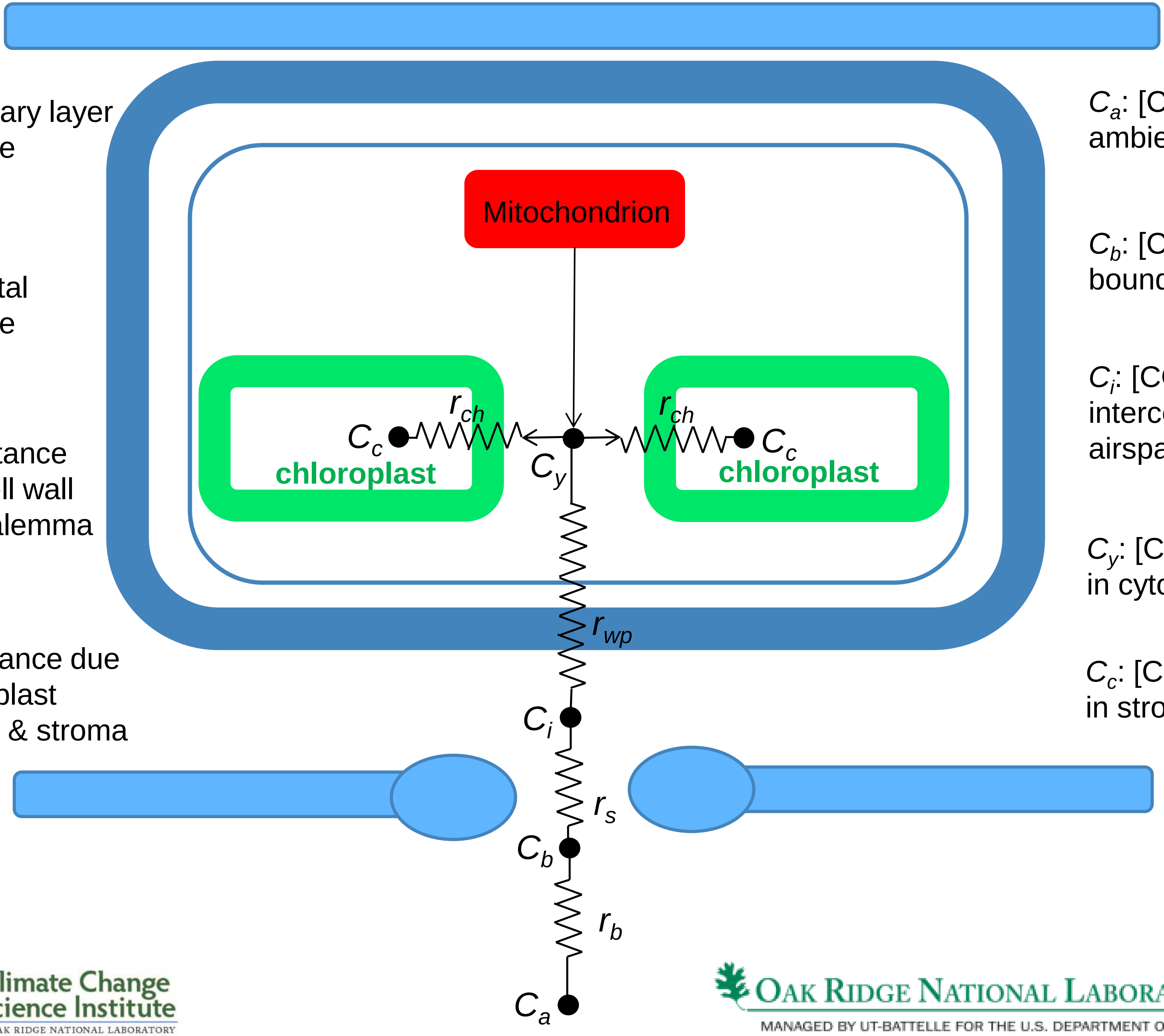

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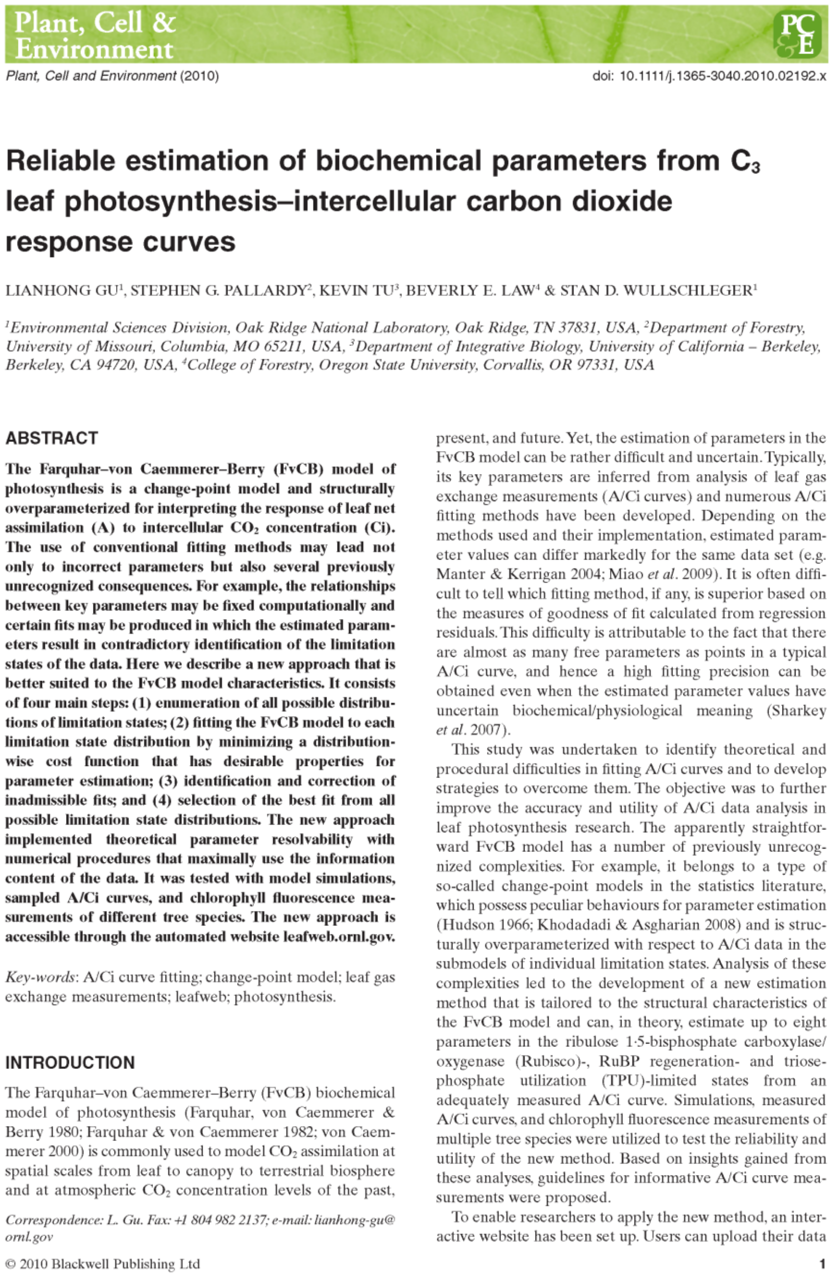

Plant, Cell & Environment

PC&E

Plant, Cell and Environment (2010) doi: 10.1111/j.1365-3040.2010.02192.x

Reliable estimation of biochemical parameters from C_3 leaf photosynthesis–intercellular carbon dioxide response curves

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ABSTRACT

The Farquhar–von Caemmerer–Berry (FvCB) model of photosynthesis is a change-point model and structurally overparameterized for interpreting the response of leaf net assimilation (A) to intercellular CO_2 concentration (Ci). The use of conventional fitting methods may lead not only to incorrect parameters but also several previously unrecognized consequences. For example, the relationships between key parameters may be fixed computationally and certain fits may be produced in which the estimated parameters result in contradictory identification of the limitation states of the data. Here we describe a new approach that is better suited to the FvCB model characteristics. It consists of four main steps: (1) enumeration of all possible distributions of limitation states; (2) fitting the FvCB model to each limitation state distribution by minimizing a distribution-wise cost function that has desirable properties for parameter estimation; (3) identification and correction of inadmissible fits; and (4) selection of the best fit from all possible limitation state distributions. The new approach implemented theoretical parameter resolvability with numerical procedures that maximally use the information content of the data. It was tested with model simulations, sampled A/Ci curves, and chlorophyll fluorescence measurements of different tree species. The new approach is accessible through the automated website leafweb.ornl.gov.

Key-words: A/Ci curve fitting; change-point model; leaf gas exchange measurements; leafweb; photosynthesis.

INTRODUCTION

The Farquhar–von Caemmerer–Berry (FvCB) biochemical model of photosynthesis (Farquhar, von Caemmerer & Berry 1980; Farquhar & von Caemmerer 1982; von Caemmerer 2000) is commonly used to model CO_2 assimilation at spatial scales from leaf to canopy to terrestrial biosphere and at atmospheric CO_2 concentration levels of the past, present, and future. Yet, the estimation of parameters in the FvCB model can be rather difficult and uncertain. Typically, its key parameters are inferred from analysis of leaf gas exchange measurements (A/Ci curves) and numerous A/Ci fitting methods have been developed. Depending on the methods used and their implementation, estimated parameter values can differ markedly for the same data set (e.g. Manter & Kerrigan 2004; Miao *et al*. 2009). It is often difficult to tell which fitting method, if any, is superior based on the measures of goodness of fit calculated from regression residuals. This difficulty is attributable to the fact that there are almost as many free parameters as points in a typical A/Ci curve, and hence a high fitting precision can be obtained even when the estimated parameter values have uncertain biochemical/physiological meaning (Sharkey *et al*. 2007).

This study was undertaken to identify theoretical and procedural difficulties in fitting A/Ci curves and to develop strategies to overcome them. The objective was to further improve the accuracy and utility of A/Ci data analysis in leaf photosynthesis research. The apparently straightforward FvCB model has a number of previously unrecognized complexities. For example, it belongs to a type of so-called change-point models in the statistics literature, which possess peculiar behaviours for parameter estimation (Hudson 1966; Khodadadi & Asgharian 2008) and is structurally overparameterized with respect to A/Ci data in the submodels of individual limitation states. Analysis of these complexities led to the development of a new estimation method that is tailored to the structural characteristics of the FvCB model and can, in theory, estimate up to eight parameters in the ribulose 1·5-bisphosphate carboxylase/oxygenase (Rubisco)-, RuBP regeneration- and triose-phosphate utilization (TPU)-limited states from an adequately measured A/Ci curve. Simulations, measured A/Ci curves, and chlorophyll fluorescence measurements of multiple tree species were utilized to test the reliability and utility of the new method. Based on insights gained from these analyses, guidelines for informative A/Ci curve measurements were proposed.

To enable researchers to apply the new method, an interactive website has been set up. Users can upload their data

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Comment from Graham Farquhar:

"I am very interested……as are the reviwers"

Comments from anonymous reviewers:

"…… a very significant advance…… could be the definitive solution…...might be of even broader importance, in the study of change-point models in general. "

"Given the potential value of this work, and the very real possibility that the authors have achieved a remarkable breakthrough……

Tom Boden

LeafWeb.ornl.gov

Steve Parham

- **Objectives**

  - Provide plant physiologists and photosynthesis researchers a reliable tool for analyzing leaf gas exchange measurements

  - Develop a global database of critical leaf biochemical and physiological parameters for ecosystem and land surface models

- **Approach**

  - Web-based automated <u>SE</u>rvice in <u>E</u>xchange for <u>D</u>ata <u>S</u>haring (SEEDs)

ORNL LDRD support for pre-NGEE Tropics research

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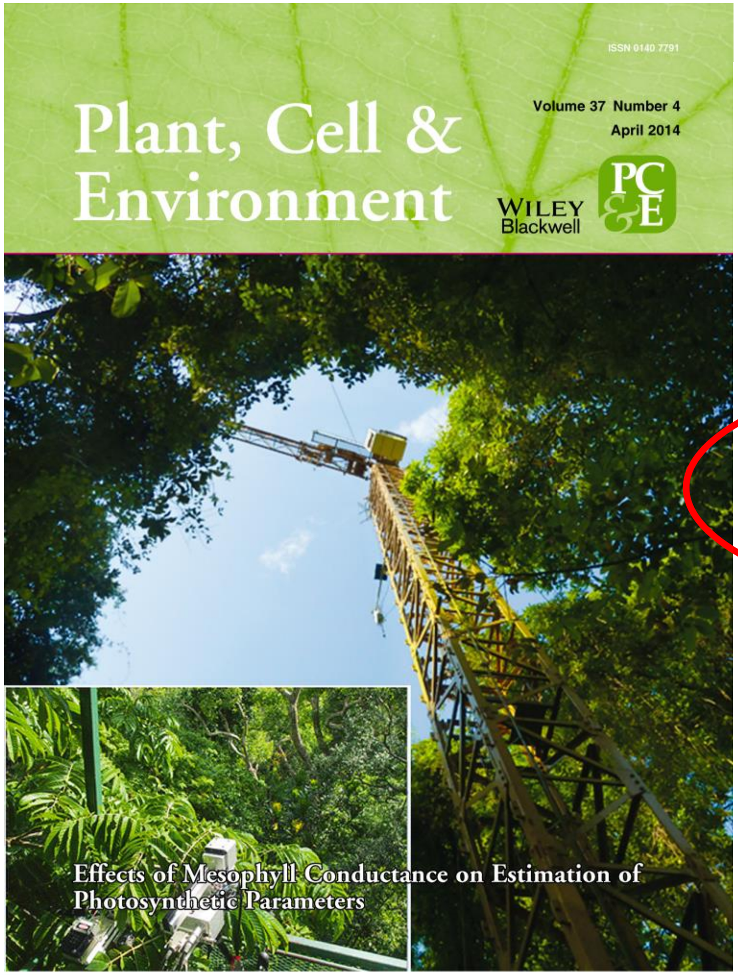
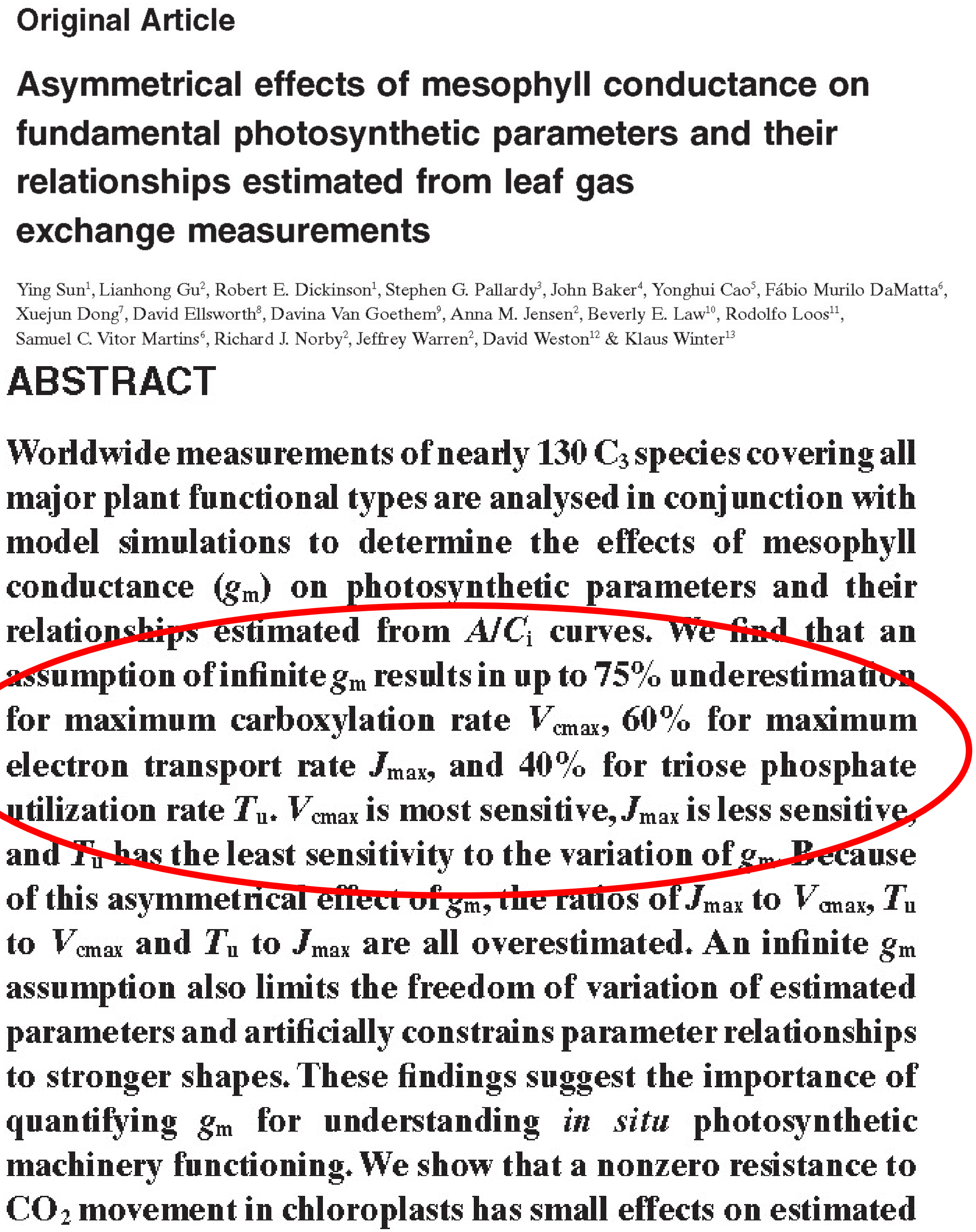
A collaboration started in an AGU party

Robert Dickinson
University of Texas - Austin

Ying Sun
University of Texas - Austin

Previous studies have significantly underestimated the true biochemical photosynthetic capacities of chloroplasts





Original Article

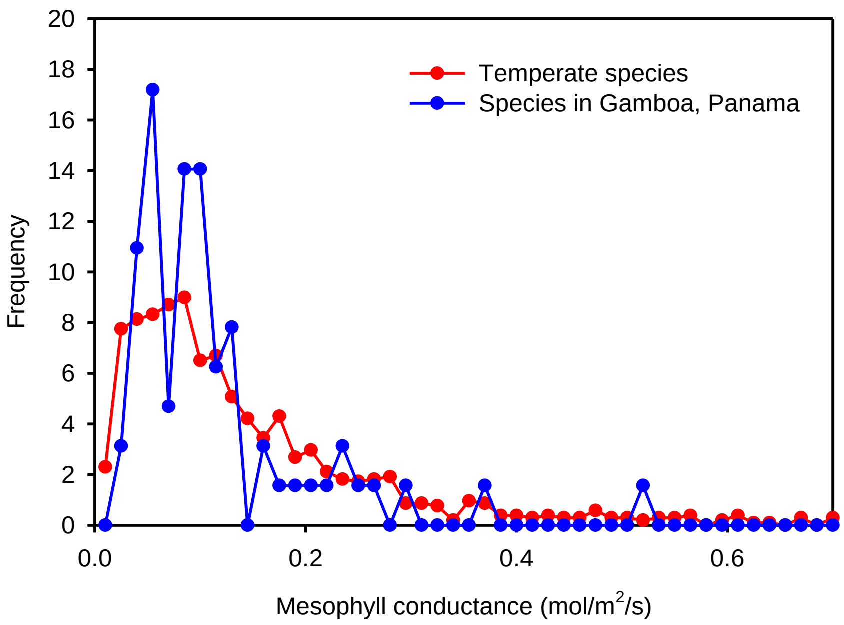
Asymmetrical effects of mesophyll conductance on fundamental photosynthetic parameters and their relationships estimated from leaf gas exchange measurements

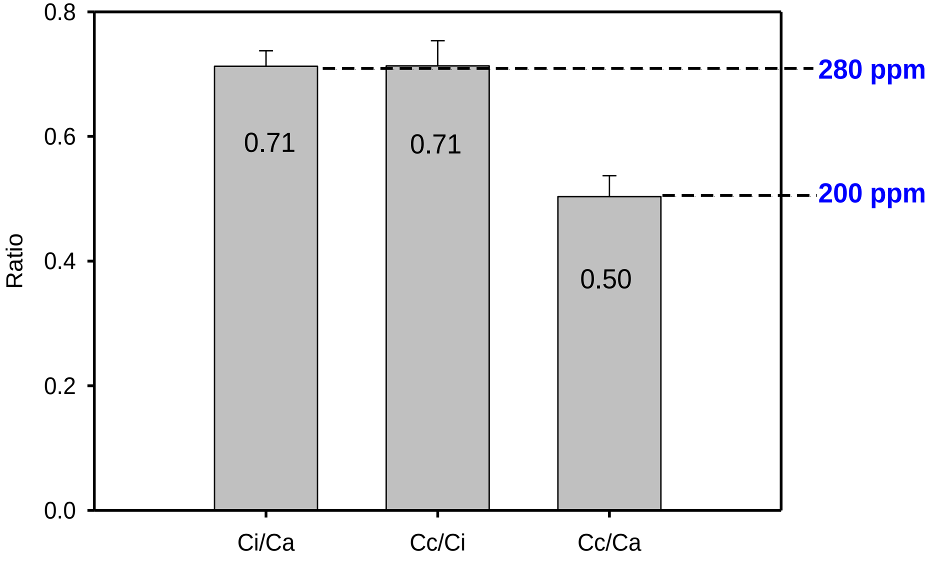
Ying Sun[1], Lianhong Gu[2], Robert E. Dickinson[1], Stephen G. Pallardy[3], John Baker[4], Yonghui Cao[5], Fábio Murilo DaMatta[6], Xuejun Dong[7], David Ellsworth[8], Davina Van Goethem[9], Anna M. Jensen[2], Beverly E. Law[10], Rodolfo Loos[11], Samuel C. Vitor Martins[6], Richard J. Norby[2], Jeffrey Warren[2], David Weston[12] & Klaus Winter[13]

ABSTRACT

Worldwide measurements of nearly 130 C_3 species covering all major plant functional types are analysed in conjunction with model simulations to determine the effects of mesophyll conductance (g_m) on photosynthetic parameters and their relationships estimated from A/C_i curves. We find that an assumption of infinite g_m results in up to 75% underestimation for maximum carboxylation rate V_{cmax}, 60% for maximum electron transport rate J_{max}, and 40% for triose phosphate utilization rate T_u. V_{cmax} is most sensitive, J_{max} is less sensitive, and T_u has the least sensitivity to the variation of g_m. Because of this asymmetrical effect of g_m, the ratios of J_{max} to V_{cmax}, T_u to V_{cmax} and T_u to J_{max} are all overestimated. An infinite g_m assumption also limits the freedom of variation of estimated parameters and artificially constrains parameter relationships to stronger shapes. These findings suggest the importance of quantifying g_m for understanding *in situ* photosynthetic machinery functioning. We show that a nonzero resistance to CO_2 movement in chloroplasts has small effects on estimated

Mesophyll resistance to CO_2 movement is large and chloroplasts photosynthesize at a CO_2 concentration much smaller than previously thought





Clearing the path for modeling impact on global photosynthesis

Flexas J. et al. (2007) Rapid variations of mesophyll conductance in response to changes in CO_2 concentration around leaves. *Plant, Cell & Environment* **30,** 1284–1298

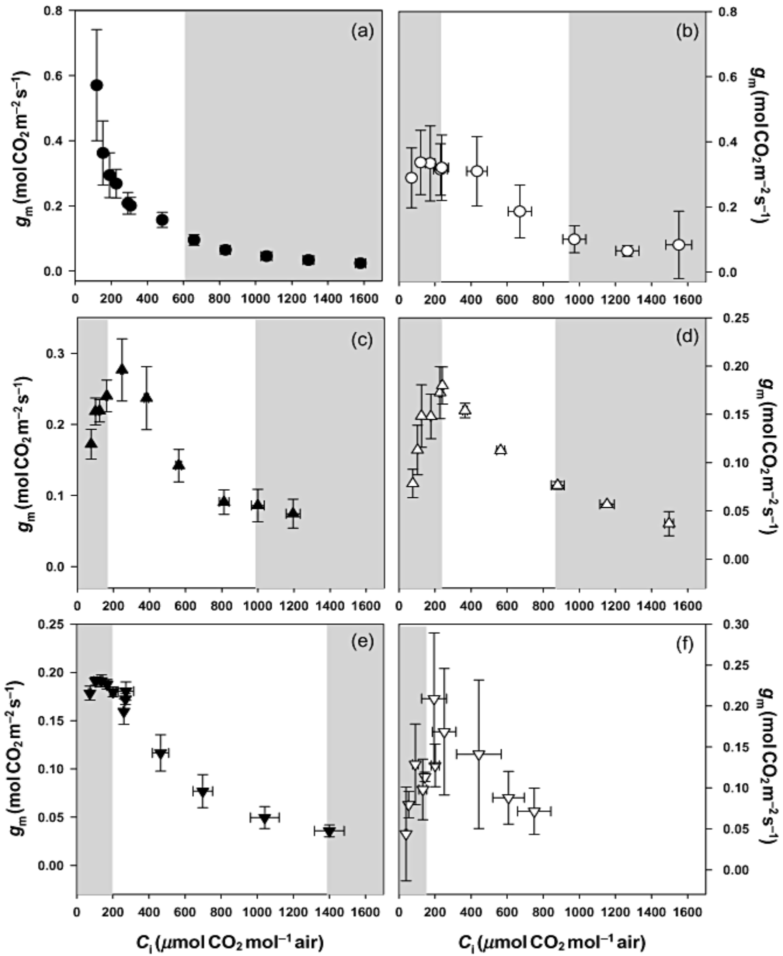
Gu L. & Sun Y. (2014) Artefactual responses of mesophyll conductance to CO_2 and irradiance estimated with the variable *J* and online isotope discrimination methods. *Plant, Cell & Environment* **37,** 1231–1249

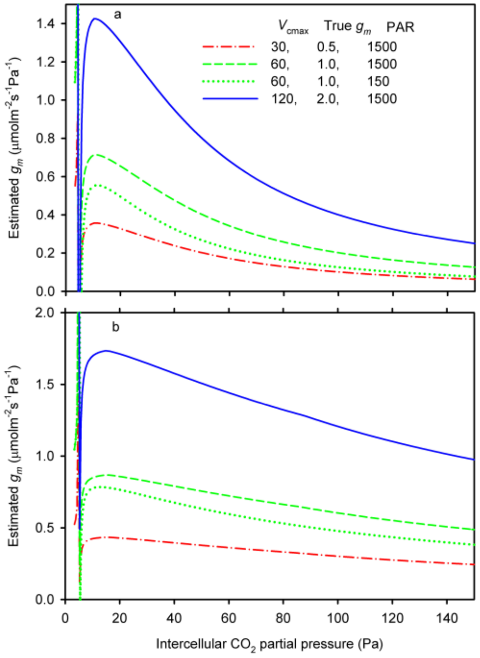
$$\Delta^{13} = \frac{1}{1-t}\left[a_b \frac{C_a - C_s}{C_a} + a_s \frac{C_s - C_i}{C_a}\right] + \frac{1+t}{1-t}\left(a_m \frac{C_i - C_c}{C_a} + b\frac{C_c}{C_a} - \frac{\beta_b}{\beta_f} f \frac{\Gamma^*}{C_a} - \frac{\beta_b}{\beta_e} e \frac{R_d}{A+R_d}\frac{C_c-\Gamma^*}{C_a}\right)$$

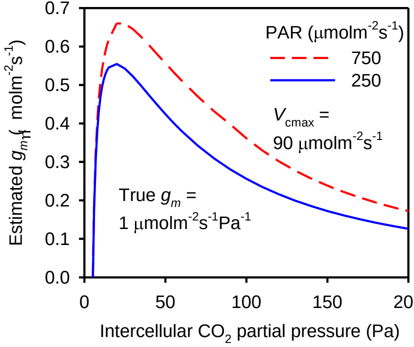
Farquhar’s incomplete equation

$$- \frac{1+t}{1-t}\left(\frac{\beta_{a_m}}{\beta_f} f \frac{A+R_d}{C_c-\Gamma^*}\frac{\Gamma^*}{C_a} + \frac{\beta_{a_m}}{\beta_e} e \frac{R_d}{C_a}\right) r_{ch}$$

Gu & Sun’s complete equation







The first global mesophyll conductance model

Supporting Information

Sun et al. 10.1073/pnas.1418075111

SI Text

Development of a Global Mesophyll Conductance (g_m) Model. A model of mesophyll conductance (g_m) suitable for global applications has not previously been available. We develop such an empirical g_m model by synthesizing the latest advances in field plant physiological studies. Large-scale carbon cycle models generally use the concept of plant functional types (PFTs) to simulate carbon, water, and energy fluxes of terrestrial ecosystems. We use a similar strategy to develop a global g_m model so that it is consistent with large-scale modeling philosophy and applicable broadly to different vegetation types, rather than to particular ecosystems. Field measurements have shown that g_m varies with leaf structures and environmental conditions (1–4). Leaf structures determine the maximum attainable g_m with external environmental forcings modifying this maximum value. This consensus reflects a recent understanding that environmental stress factors (e.g., temperature and water) can induce rapid physiological changes (e.g., hardening of cell walls and aquaporin-mediated alteration of membrane permeability) that cause g_m to vary on time scales of minutes to hours (5–8). Accordingly, we model g_m as

$$g_m = g_{\max 0} \cdot f_I(x) \cdot f_T(T_l) \cdot f_w(\theta), \qquad \textbf{[S1]}$$

where $g_{\max 0}$ is the maximum g_m (i.e., a value of g_m under nonstress conditions, here referring to the presence of ample soil water and a temperature of 25 °C) of a leaf at the canopy top of a PFT; $f_I(x)$ represents the vertical variation of g_m as a function of cumulative leaf area index x from canopy top, driven by light gradient within the canopy; and $f_T(T_l)$ and $f_w(\theta)$ are the response functions of g_m to leaf temperature T_l and to soil moisture θ, respectively.

The present study makes no attempt to represent other potential environmental effects, e.g., salinity, O_3, nutrient availability (4), on g_m because these effects are much less well understood and seldom quantified in field studies. Also we do not consider the potential rapid, direct responses of g_m to changes in ambient CO_2 concentration and irradiance reported in some previous studies as a recent analysis shows that such responses may be due to methodological artifacts in experiments (9). There is also the possibility that the spatial separation between Rubisco and the releasing site of CO_2 from dark respiration and photorespiration (mitochondria) may render g_m to be a composite variable, rather than a stable parameter (10). This possibility can be addressed with a two-component model of mesophyll conductance (10). However, currently there are no data available to parameterize this two-component model. Fortunately, observations often show that in C_3 plant species, mitochondria occupy the center of the cell and are surrounded by chloroplasts that are positioned just under the plasmalemma (11). In such a spatial configuration, CO_2 molecules evolved from mitochondria and released into cytosol must first diffuse through chloroplasts to reach the intercellular air space. From a modeling point of view, this arrangement has the same effect as if Rubisco and mitochondria shared the same compartment (12). Sun et al. (13) and Gu and Sun (9) used simulations to demonstrate that a single g_m model is sufficient for the purpose of modeling photosynthesis. Therefore, in this study, we adopt the framework of a single g_m model.

The $g_{\max 0}$ varies significantly across plant species. A synthesis of measurements for ~100 plant species showed that this term is related to the leaf dry mass per unit area M_a through an empirical power law (2)

$$g_{\max 0} = a \cdot M_{a0}^{b}, \qquad \textbf{[S2]}$$

where M_{a0} represents M_a at canopy top. The constants a = 24.240338 and b = −0.6509 are two empirical parameters that have been determined by fitting compiled data to Eq. **S2** [r^2 = 0.79; $P < 0.001$; see figure 2.1 in Niinemets et al. (2)]. All empirical constants used in our global mesophyll conductance model are listed in Table S1. Similar patterns were also reported in other studies (4, 14) but with fewer species samples. The values of a and b depend on the units of data used for the nonlinear regression of Eq. **S2**. Our study uses μmol/m²/s/Pa for $g_{\max 0}$ and g_m, and g/m² for M_{a0} and M_a. The coefficient b is negative, indicating $g_{\max 0}$ decreases with M_{a0} across PFTs under nonstress conditions. The $g_{\max 0}$ in Eq. **S2** is area based, whereas Niinemets et al. (2) used a mass-based unit. The area- and mass-based $g_{\max 0}$ differ by a factor of M_{a0}. Accordingly, the value of b in our study is a notation on an area basis. In Eq. **S2**, $g_{\max 0}$ is represented as a leaf trait associated with PFTs because it is determined by M_{a0}, which is the product of two important leaf traits: leaf thickness and foliar mass density (2).

Multiple steps are needed to derive an expression for $f_I(x)$, which describes the variation of g_m associated with the prevailing light regime within a plant canopy. The light intensity shapes the mesophyll cell morphology, the number of mesophyll cell layers, and the leaf thickness. These factors are components that determine $M_a(x)$, the leaf dry mass per area at a cumulative leaf area index x (15). They also affect the total surface area of mesophyll cells exposed to intercellular air space per unit leaf area and hence g_m (2, 11). Consequently, g_m tends to change systematically from top to bottom of a canopy (16–22) and scales well with the variation of $M_a(x)$ with canopy depth (18, 21). Therefore, $M_a(x)$ is an important link between g_m and the prevailing light gradient within a canopy. Here this vertical variation of g_m is modeled as follows:

$$g_{\max}(x) = g_{\max 0} \cdot [M_a(x)/M_{a0}]^d, \qquad \textbf{[S3]}$$

where d = 0.8109, an empirical parameter fitted from the data (r^2 = 0.67) in Montpied et al. (21). Rearranging Eq. **S3**, we have

$$f_I(x) = g_{\max}(x)/g_{\max 0} = [M_a(x)/M_{a0}]^d. \qquad \textbf{[S4]}$$

According to Niinemets (15), $M_a(x)$ is related to the seasonally integrated photosynthetic active radiation $I(x)$ via

$$M_a(x) = M_{a0} \cdot [I(x)/I_0]^f, \qquad \textbf{[S5]}$$

where I_0 is the value of $I(x)$ at canopy top; f = 0.221897, a parameter fitted (r^2 = 0.57) from Niinemets (15). Applying the Beer's law

$$I(x) = I_0 \cdot \exp(-k_I \cdot x), \qquad \textbf{[S6]}$$

where k_I = 0.50, a commonly used value for the seasonally averaged light extinction coefficient (23, 24), and substituting Eqs. **S6** and **S5** to Eq. **S4**, we obtain

$$f_I(x) = \exp(-k_I \cdot d \cdot f \cdot x) = \exp(-k_g \cdot x). \qquad \textbf{[S7]}$$

Here, $k_g = k_I \cdot d \cdot f$= 0.08997, a composite parameter that is the product of three empirical coefficients k_I, d, and f. Eq. **S7** shows

Sun et al. www.pnas.org/cgi/content/short/1418075111

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- **Based on empirical data**
- **Leaf functional traits as inputs**
- **Vertical variation in plant canopies to simulate effects of light regimes on leaf morphology**
- **Temperature and water stress dependence to simulate effects of rapid physiological changes (hardening of cell walls and aquaporin-mediated alteration of membrane permeability)**
- **Use in conjunction with the true biochemical photosynthetic capacities of chloroplasts estimated by LeafWeb for hundreds of plant species in the world**
- **Implemented in CLM4.5 to simulate the impact of mesophyll diffusion on global land CO_2 fertilization**

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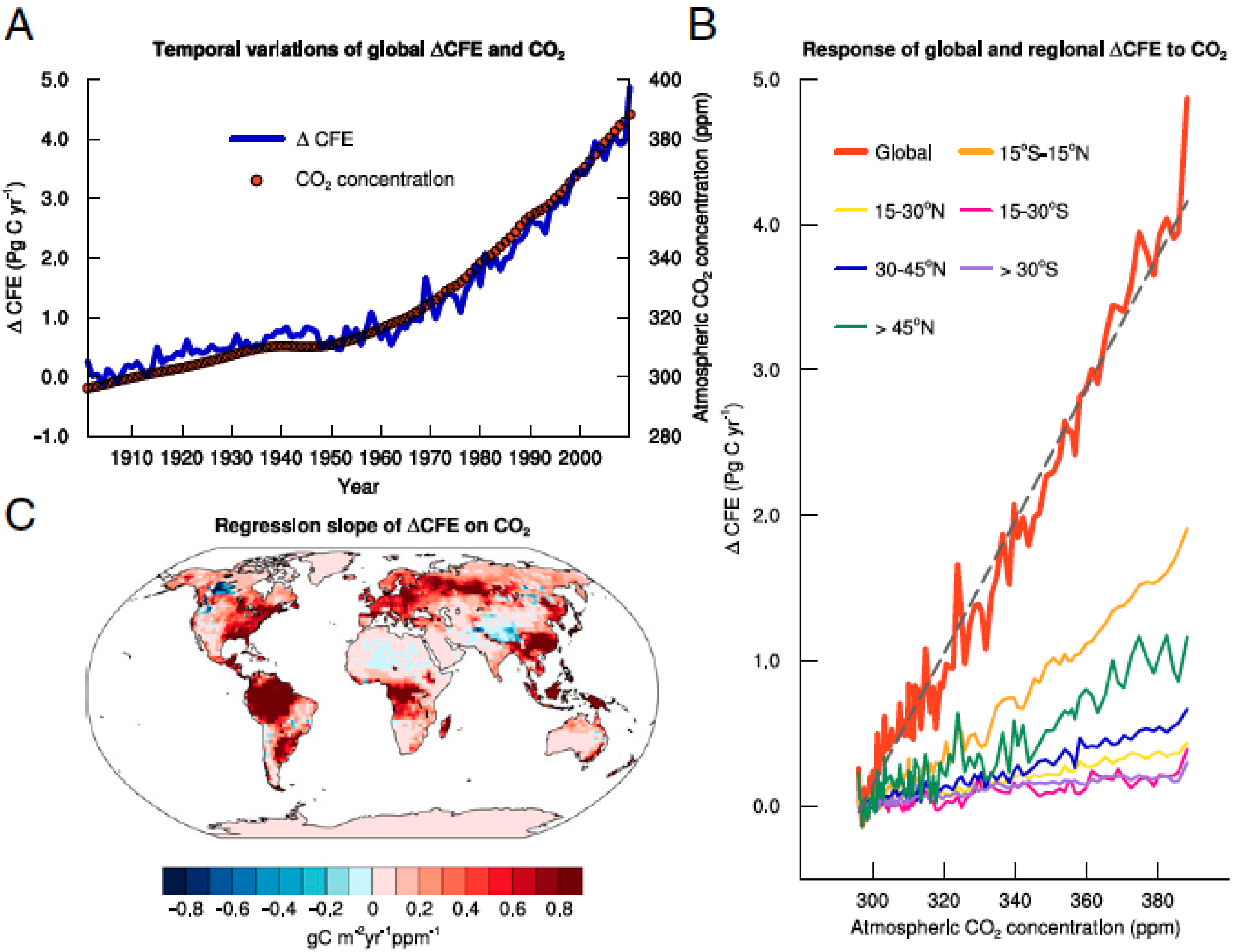
Metrics for quantifying the impact of mesophyll diffusion on global terrestrial CO_2 fertilization

- Model simulations with or without mesophyll diffusion from 1901 to 2010
- Average annual GPP of 1901 to 1910 used as a reference for quantifying the CO_2 fertilization effect (CFE) on global gross primary production (GPP) of the historical anthropogenic carbon emissions
- The difference in CFE (ΔCFE) between the runs with and without mesophyll diffusion in a given year *t*

$$\Delta CFE = \underbrace{GPP_c(t) - GPP_{c,ref}}_{\textbf{CFE with mesophyll}} - \left[\underbrace{GPP_i(t) - GPP_{i,ref}}_{\textbf{CFE without mesophyll}}\right]$$

- The ratio of the beta factors of the with-mesophyll to without-mesophyll runs

$$R(t) = \frac{\beta_c(t)}{\beta_i(t)} = \frac{\left[GPP_c(t) - GPP_{c,ref}\right]GPP_{i,ref}}{\left[GPP_i(t) - GPP_{i,ref}\right]GPP_{c,ref}}$$

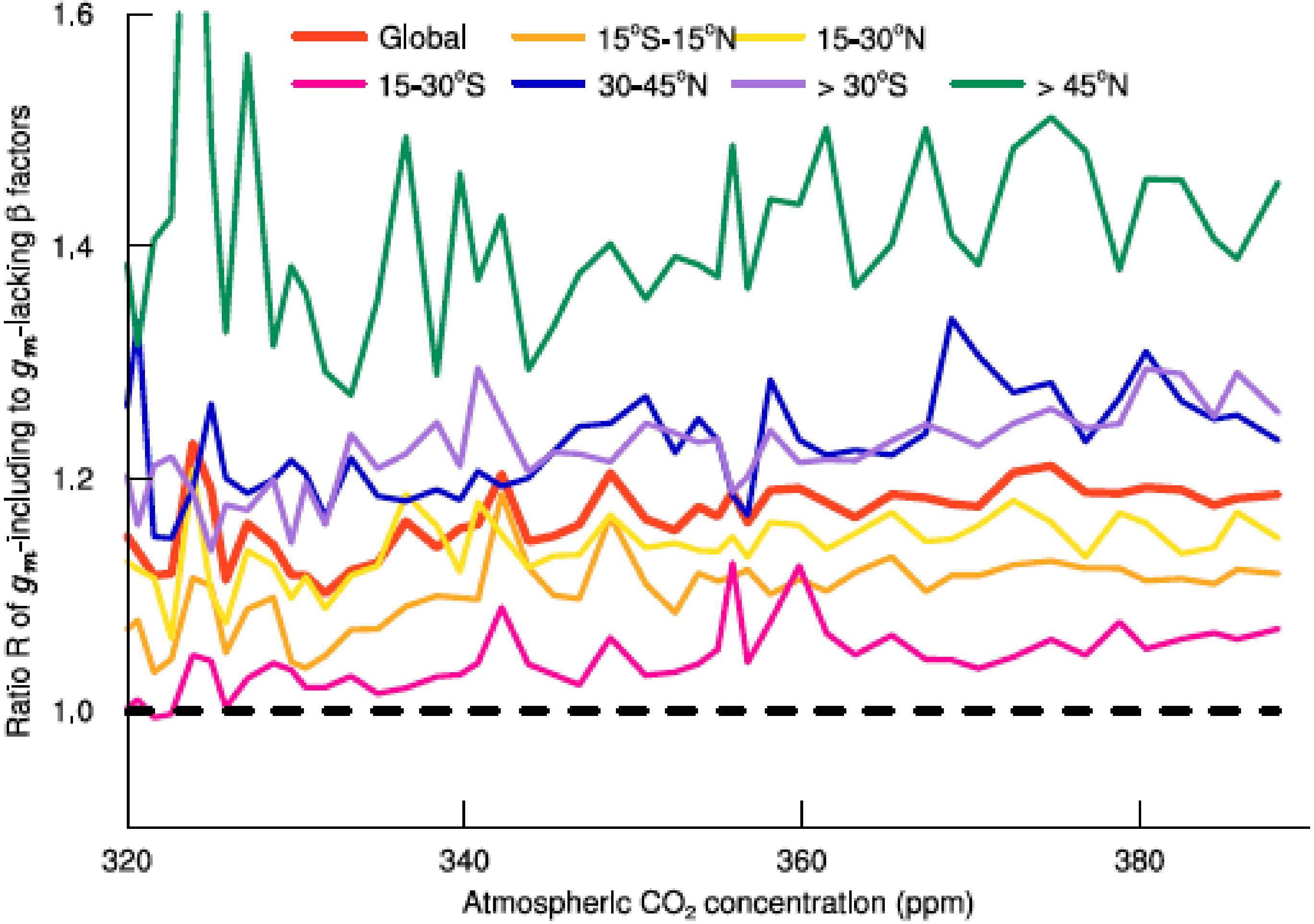


A Temporal variations of global ΔCFE and CO_2

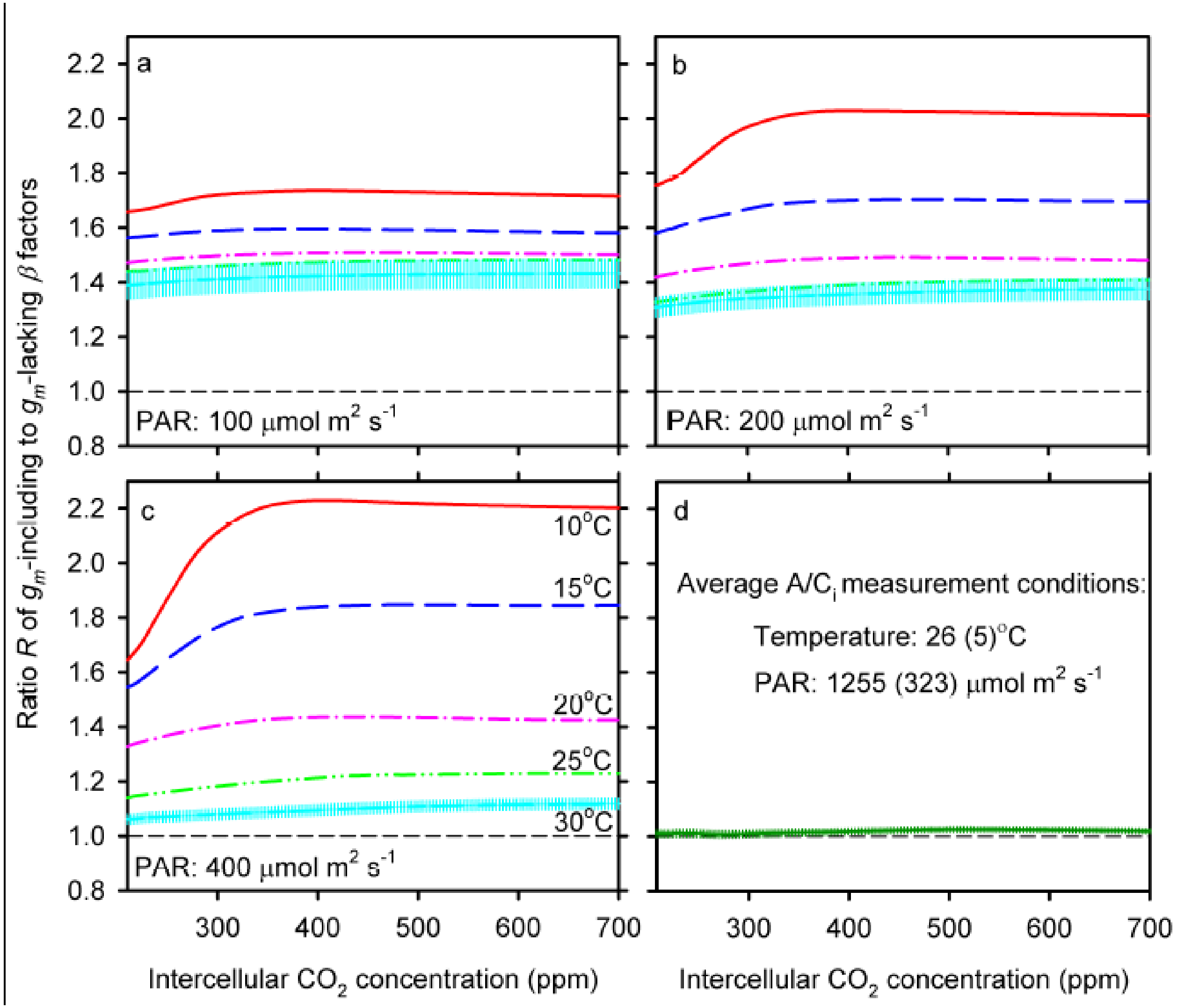
B Response of global and regional ΔCFE to CO_2

C Regression slope of ΔCFE on CO_2

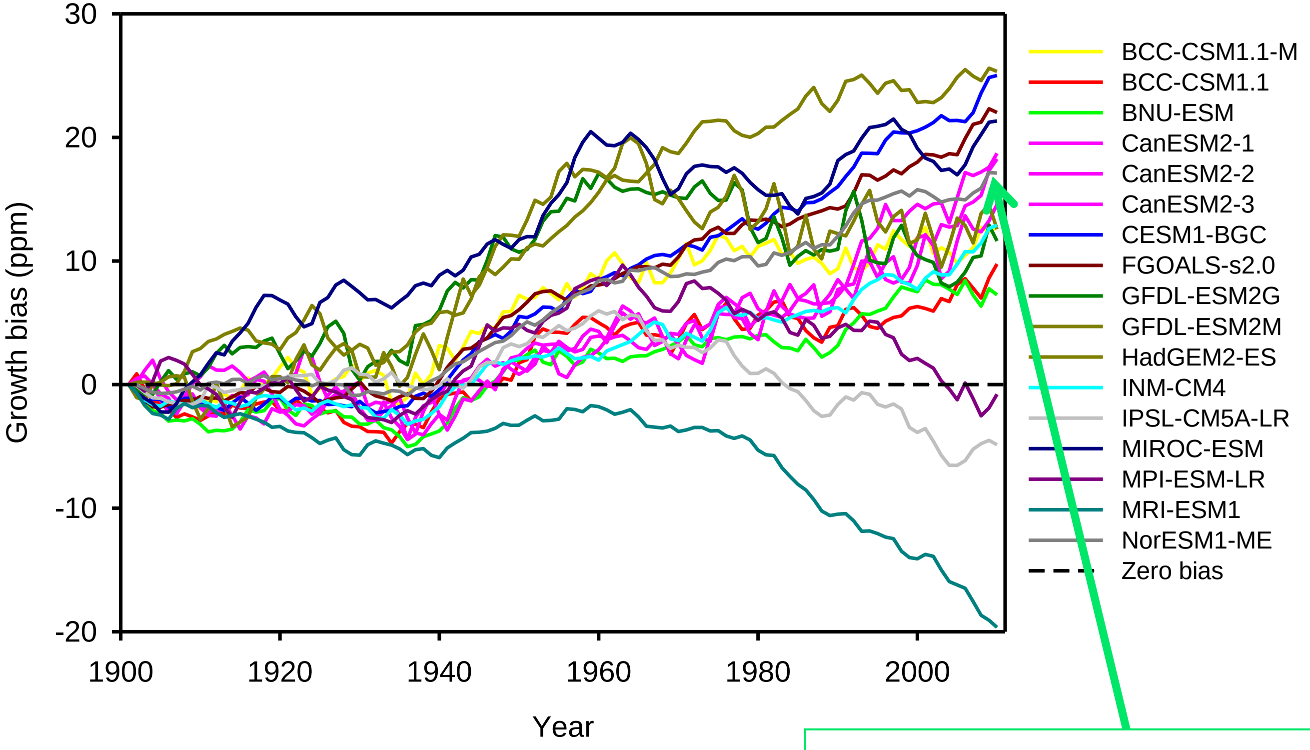
From tropics to boreal, the ratio of the beta factors increases, indicating relatively higher sensitivity of CO_2 fertilization to mesophyll diffusion in higher latitudes



β factor ratio R averaged over 1000 A/Ci curves and 130 plant species from LeafWeb

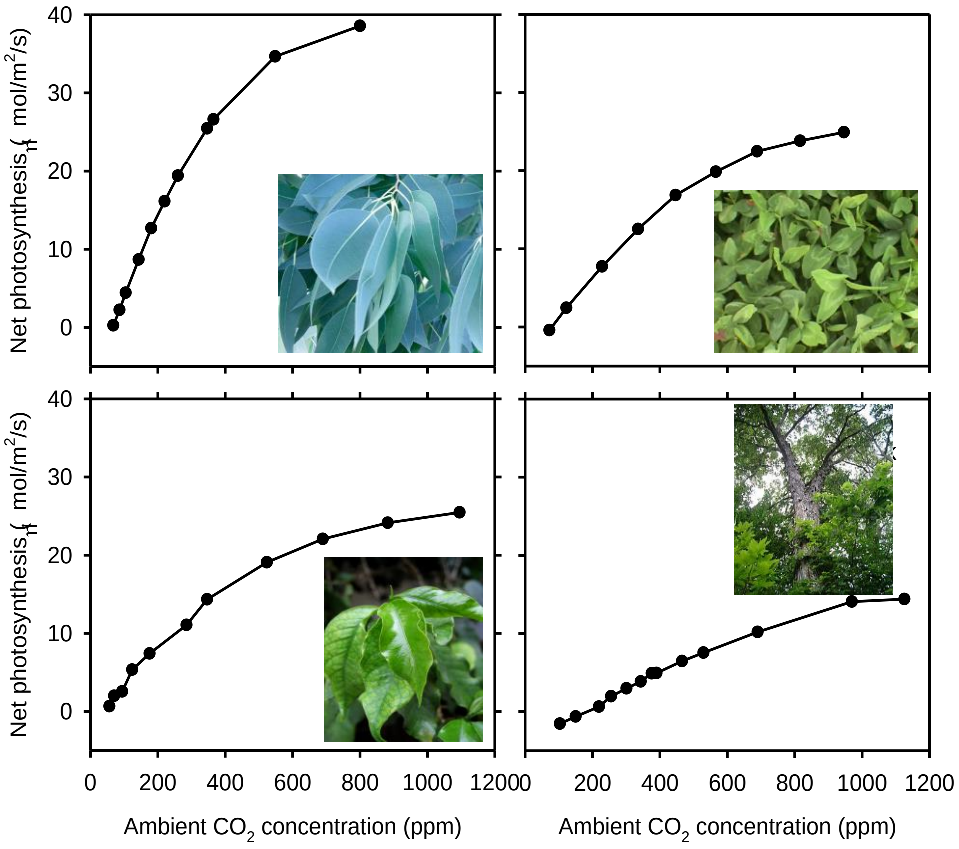


Ignoring mesophyll diffusion, Earth System Models over-predict the growth rate of atmospheric CO_2 due to fossil fuel emissions



17 ppm (mesophyll correction)

Why do models without mesophyll diffusion underestimate the CO_2 fertilization effect?
- A simple answer



- Photosynthetic response to CO_2 is a saturating curve
- Larger sensitivity at lower CO_2 than at higher CO_2
- Models without mesophyll diffusion overestimate CO_2 available to Rubisco and thus underestimate its sensitivity to CO2

Why do models without mesophyll diffusion underestimate the CO_2 fertilization effect? - A more complicated answer

Tool for **E**valuating **M**esophyll **I**mpact on **P**redicting **P**hotosynthesis (TEMIPP)

- **The gm-lacking model is fit to an A/Ci curve simulated with finite gm under a given environmental condition (the A/Ci curve condition)**
- **The optimized gm-lacking model is then used to predict photosynthesis under a new condition (the prediction condition)**
- **Compare the predicted and actual photosynthesis and limitation states (Columns AD vs. AE, AU vs. AE). Explore different prediction conditions to see variations**
- **Rerun the Solver (in Data) after changing any input other than the environmental variables of the prediction condition**

*** For details, see TEMIPP Instruction. Contact Dr. Lianhong Gu (lianhong-gu@ornl.gov) or Dr. Ying Sun (suny@jsg.utexas.edu) for questions**

Interactive Section (User Specified Values)

A. Parameters in the FvCB Model	Vcmax25	Jmax25	TPU25##	gm25	Rd25	Kc25	Ko25	Γ*25	Leaf absorptance
	umolm^{-2}s^{-1}	umolm^{-2}s^{-1}	umolm^{-2}s^{-1}	umolm^{-2}s^{-1}Pa^{-1}	umolm^{-2}s^{-1}	Pa	Pa	Pa	Fraction
Parameters @ 25oC to generate an A/Ci curve with finite gm	90	110	10	1	0.5	27.238	16582	3.743	0.85
Parameters @ 25oC for model lacking gm, updated afer executing the Solver (in Data)	48.374	104.778	10.000		0.650	27.238	16582	3.743	0.85

B. Coefficients in Temperature Response Functions			Vcmax25	Jmax25	TPU25	gm25	Rd25	Kc25	Ko25	Γ*25
DHa	Activation energy	kJ/mol	65.33	43.54	53.1	49.6	46.39	80.99	23.72	24.46
DHd	Deactivation energy	kJ/mol	0	0	201.8	437.4	0	0	0	0
DSv	Entropy	kJ/mol/K	0	0	0.65	1.4	0	0	0	0

C. Environmental Conditions	Temperature	PPFD	Pressure	Oxygen
	oC	umolm^{-2}s^{-1}	Pa	Pa

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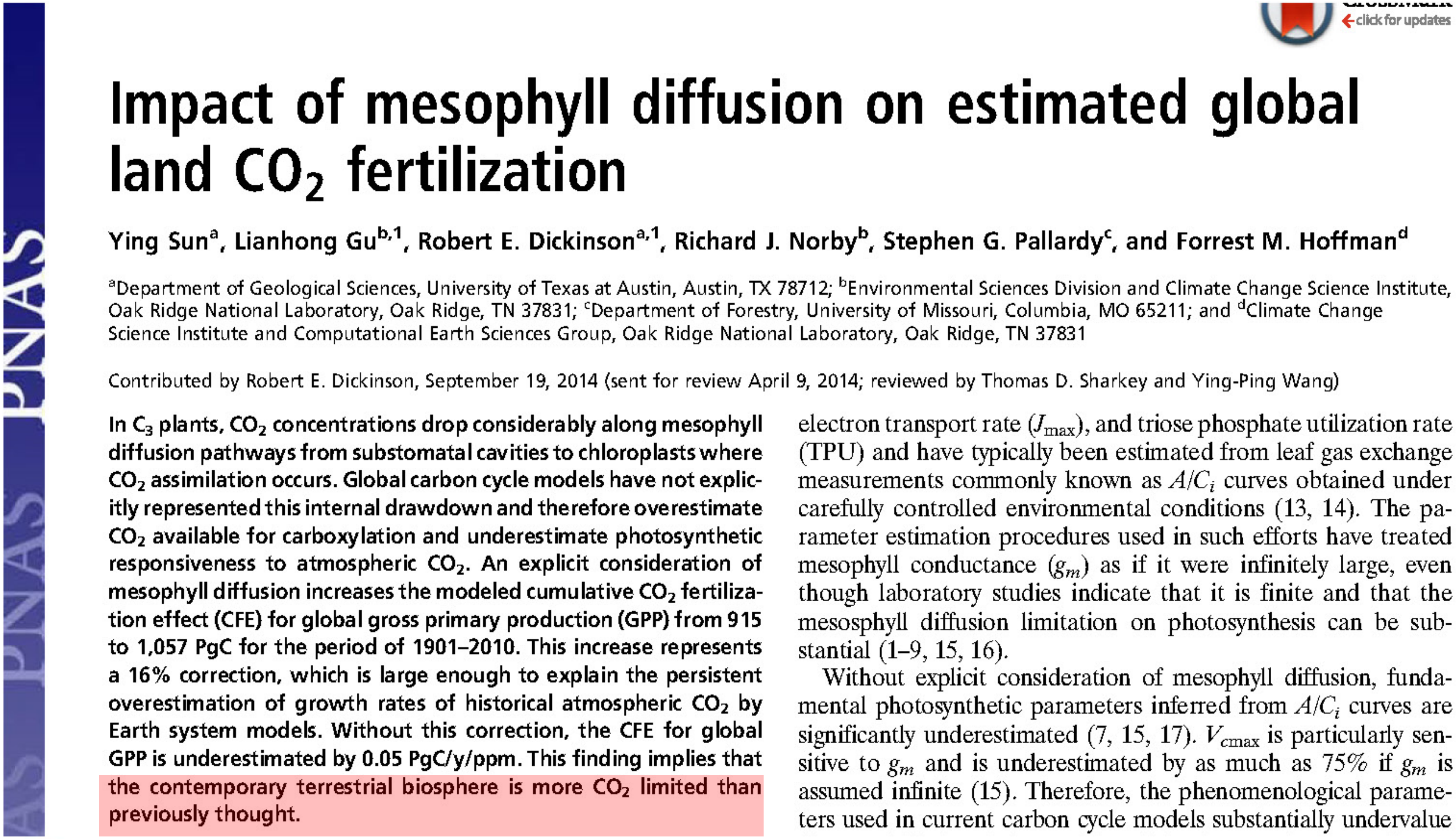
"The contemporary terrestrial biosphere is more CO_2 limited than previously thought"



click for updates

Impact of mesophyll diffusion on estimated global land CO_2 fertilization

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Contributed by Robert E. Dickinson, September 19, 2014 (sent for review April 9, 2014; reviewed by Thomas D. Sharkey and Ying-Ping Wang)

In C_3 plants, CO_2 concentrations drop considerably along mesophyll diffusion pathways from substomatal cavities to chloroplasts where CO_2 assimilation occurs. Global carbon cycle models have not explicitly represented this internal drawdown and therefore overestimate CO_2 available for carboxylation and underestimate photosynthetic responsiveness to atmospheric CO_2. An explicit consideration of mesophyll diffusion increases the modeled cumulative CO_2 fertilization effect (CFE) for global gross primary production (GPP) from 915 to 1,057 PgC for the period of 1901–2010. This increase represents a 16% correction, which is large enough to explain the persistent overestimation of growth rates of historical atmospheric CO_2 by Earth system models. Without this correction, the CFE for global GPP is underestimated by 0.05 PgC/y/ppm. This finding implies that the contemporary terrestrial biosphere is more CO_2 limited than previously thought.

electron transport rate (J_{max}), and triose phosphate utilization rate (TPU) and have typically been estimated from leaf gas exchange measurements commonly known as A/C_i curves obtained under carefully controlled environmental conditions (13, 14). The parameter estimation procedures used in such efforts have treated mesophyll conductance (g_m) as if it were infinitely large, even though laboratory studies indicate that it is finite and that the mesosphyll diffusion limitation on photosynthesis can be substantial (1–9, 15, 16).

Without explicit consideration of mesophyll diffusion, fundamental photosynthetic parameters inferred from A/C_i curves are significantly underestimated (7, 15, 17). V_{cmax} is particularly sensitive to g_m and is underestimated by as much as 75% if g_m is assumed infinite (15). Therefore, the phenomenological parameters used in current carbon cycle models substantially undervalue

Samples of unexpected reactions

BBC News: *'Climate change: Models underplay plant* CO_2 *absorption'*

ABC News: *'Plants absorb* CO_2 *better than models predicted'*

Enviro News: *'Plants* CO_2 *absorption levels underestimated'*

International Business Times: *'Global Warming: Plants absorbed 1000bn tonnes more of* CO_2 *than calculated during last 100 years'*

TechTimes: *'Study contradicts* CO_2 *plant absorption'*

Capital OTC: *'*CO_2 *emissions may have been overestimated by 17%'*

BusinessMirror: *'A TEAM of US scientists has debunked the claim that the Earth is heating up'*

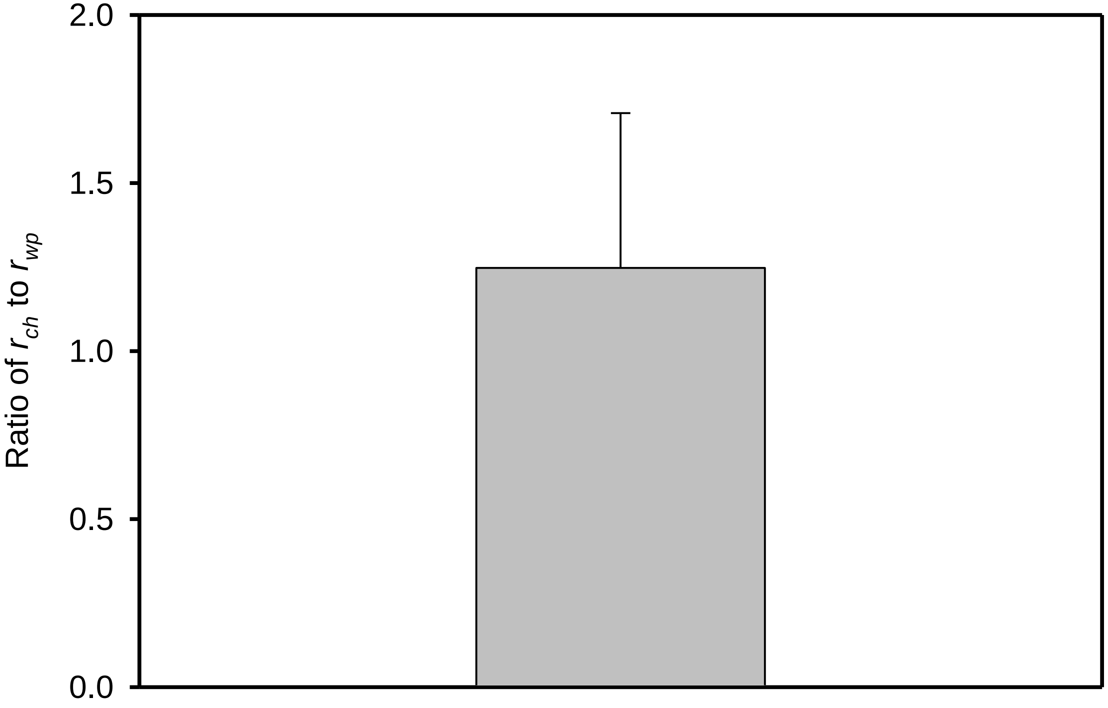
Investigative Headline News: *'Pentagon pins ISIS terror threat on incorrect climate models'*

Efforts to improve the efficiency of photosynthesis in plants

- **Engineer C4 pathway into C3 photosynthesis**
- **Engineer CAM pathway into C3 photosynthesis**
- **Improve Rubisco efficiency**
- **Increase the rate of RuBP regeneration**
- **Improve canopy architecture (diffuse radiation!)**
- **Bypass photorespiration**

CO_2 is only one of the many important factors that affect photosynthesis

Engineering a bare chloroplast could be an important way to boost the efficiency of photosynthesis!



Gu and Weston, unpublished result from *populus* plants