Guest Lecture GEO391

Importance of Mesophyll Diffusion of CO_2 for Modeling Terrestrial Carbon Cycle

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Outline

1. **Overview of Global Carbon Cycle**
   Concepts, trends, uncertainties

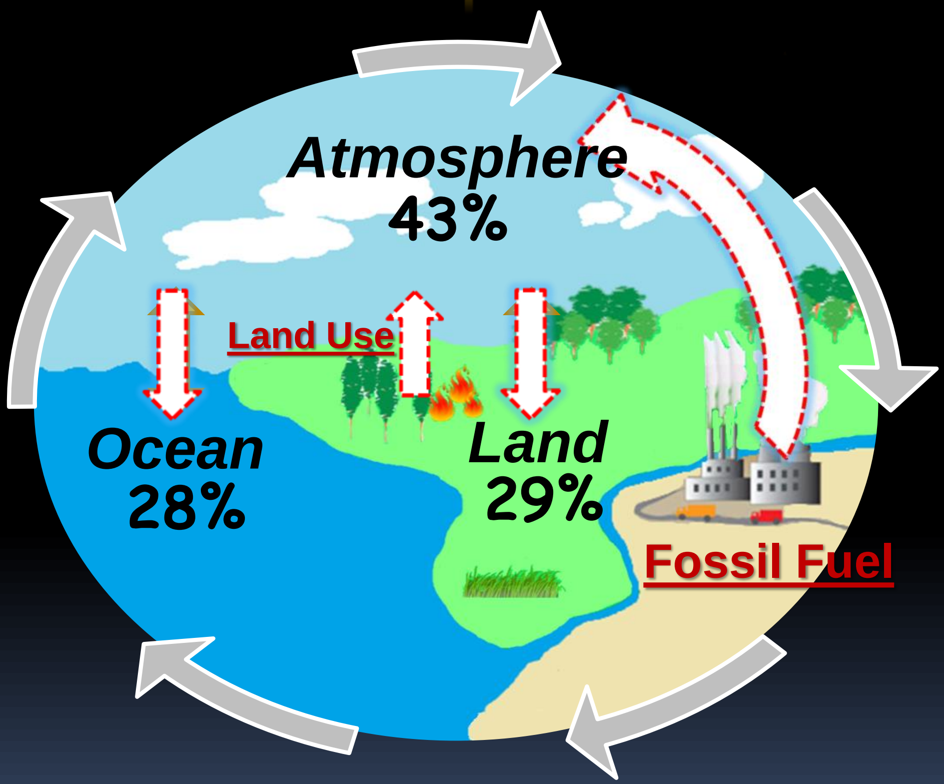
2. **Photosynthesis and Mesophyll Diffusion**
   Mechanisms and modeling at leaf scale

3. **Global Impact of Mesophyll Diffusion**
   CO_2 fertilization of vegetation productivity on land

4. **Conclusions**

Carbon Cycling and Partitioning

Sources↑ & Sinks↓

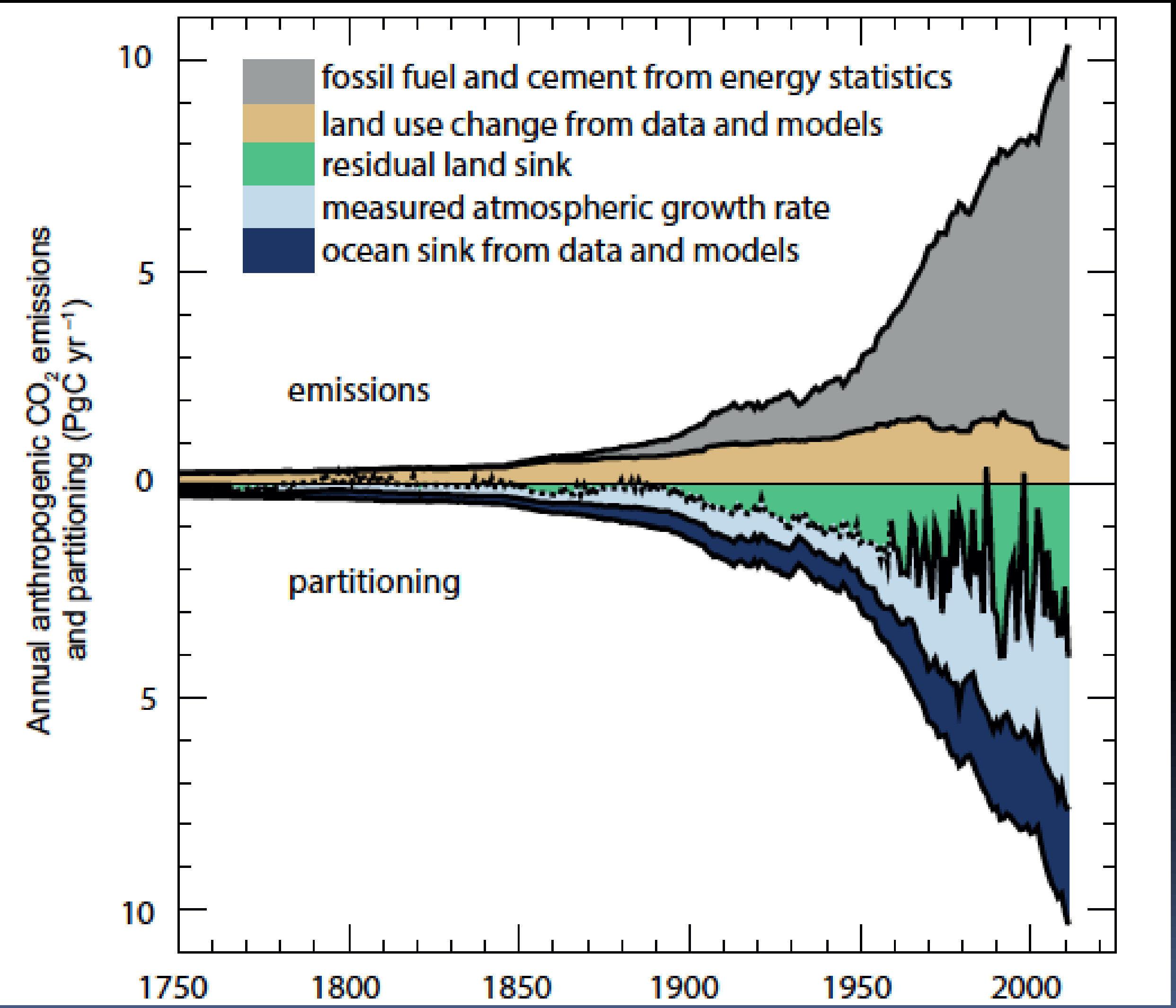


Global Anthropogenic CO_2 Budget

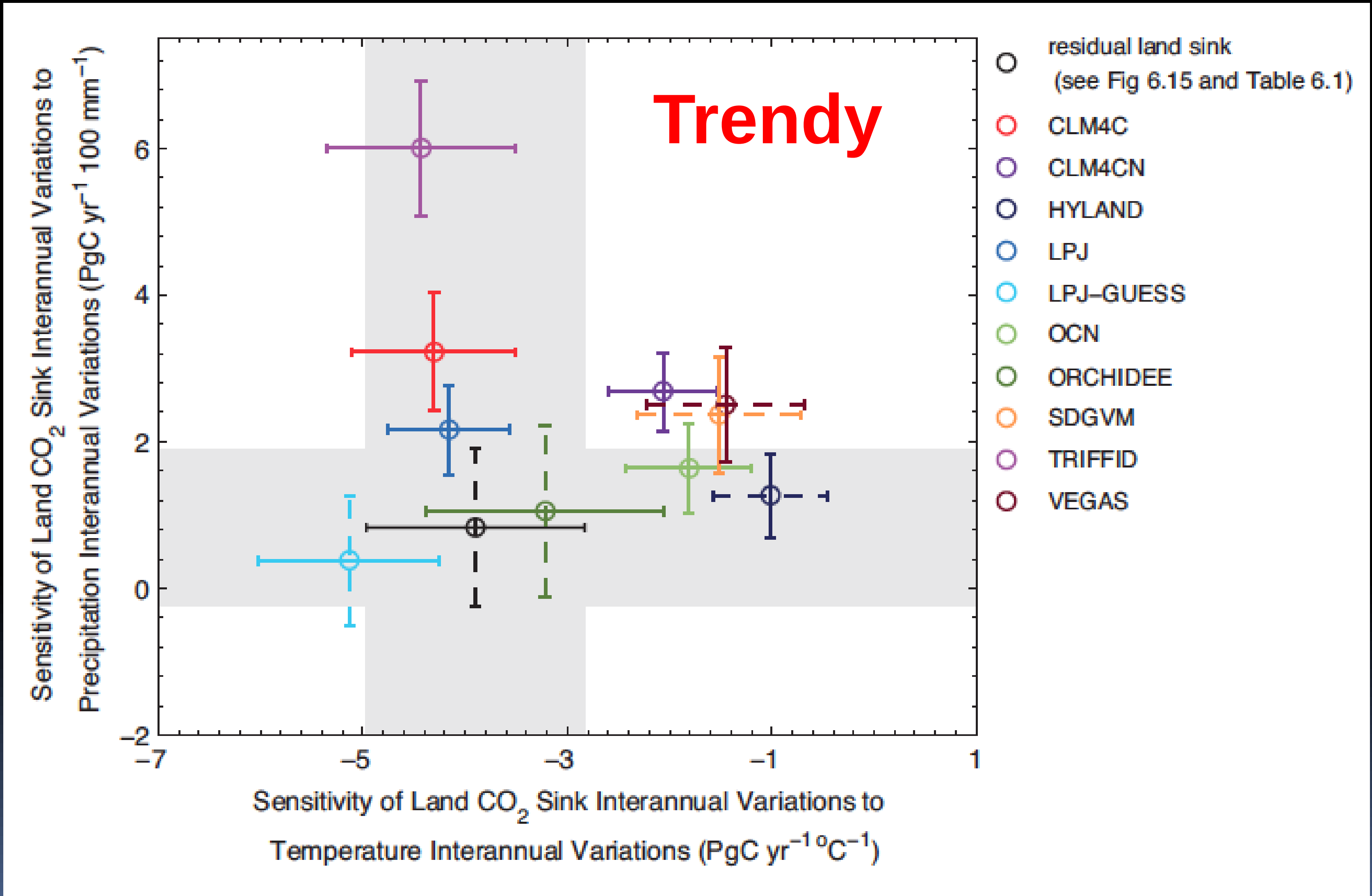
	1750–2011 Cumulative PgC
Atmospheric increase[a]	240 ± 10[f]
Fossil fuel combustion and cement production[b]	375 ± 30[f]
Ocean-to-atmosphere flux[c]	–155 ± 30[f]
Land-to-atmosphere flux	30 ± 45[f]
Partitioned as follows	
Net land use change[d]	180 ± 80[f,g]
Residual land sink[e]	–160 ± 90[f]

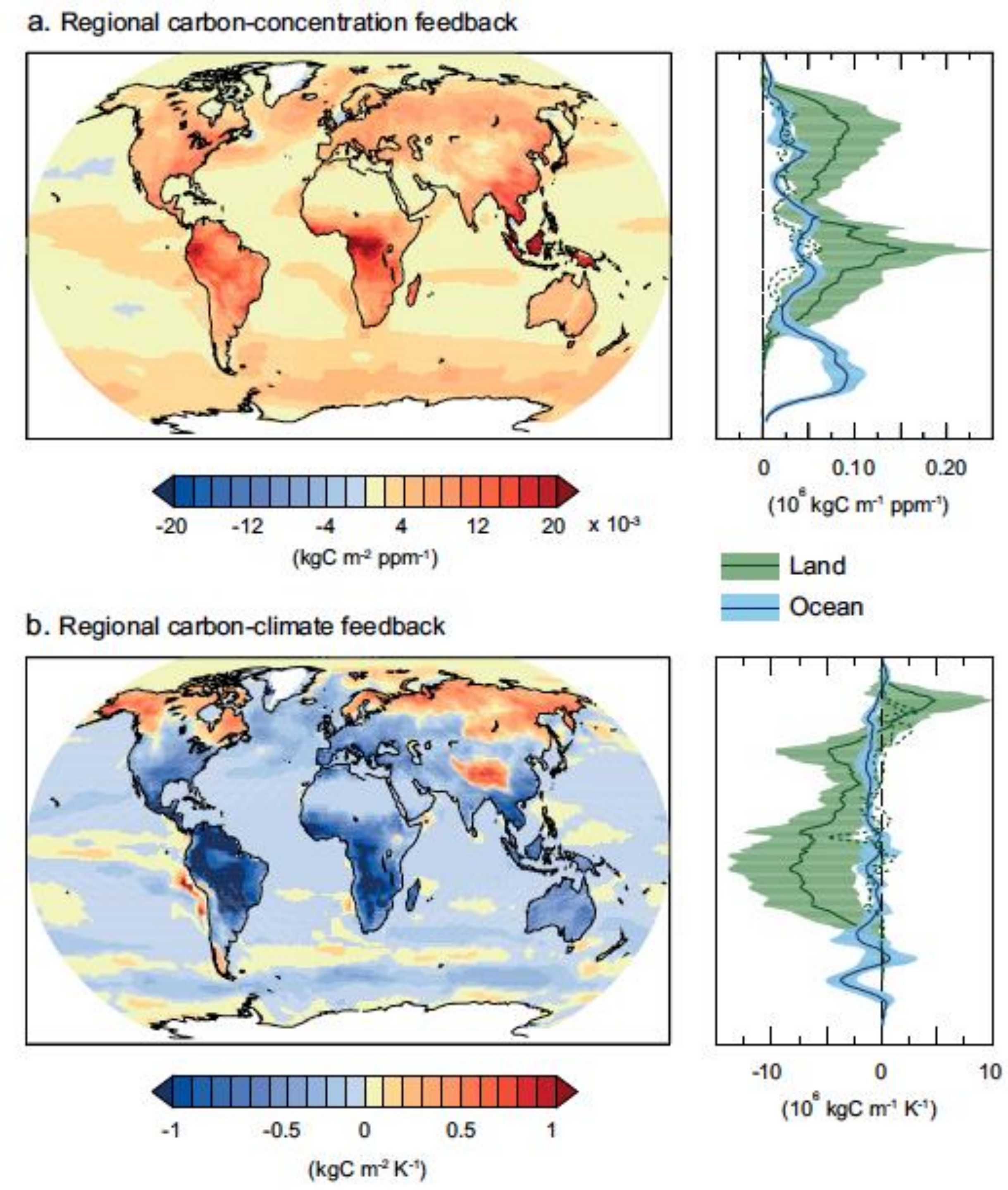
(IPCC AR5)

Trend of Carbon Partitioning



Large Uncertainty of Land C Sink to Climate by model simulation (historical)

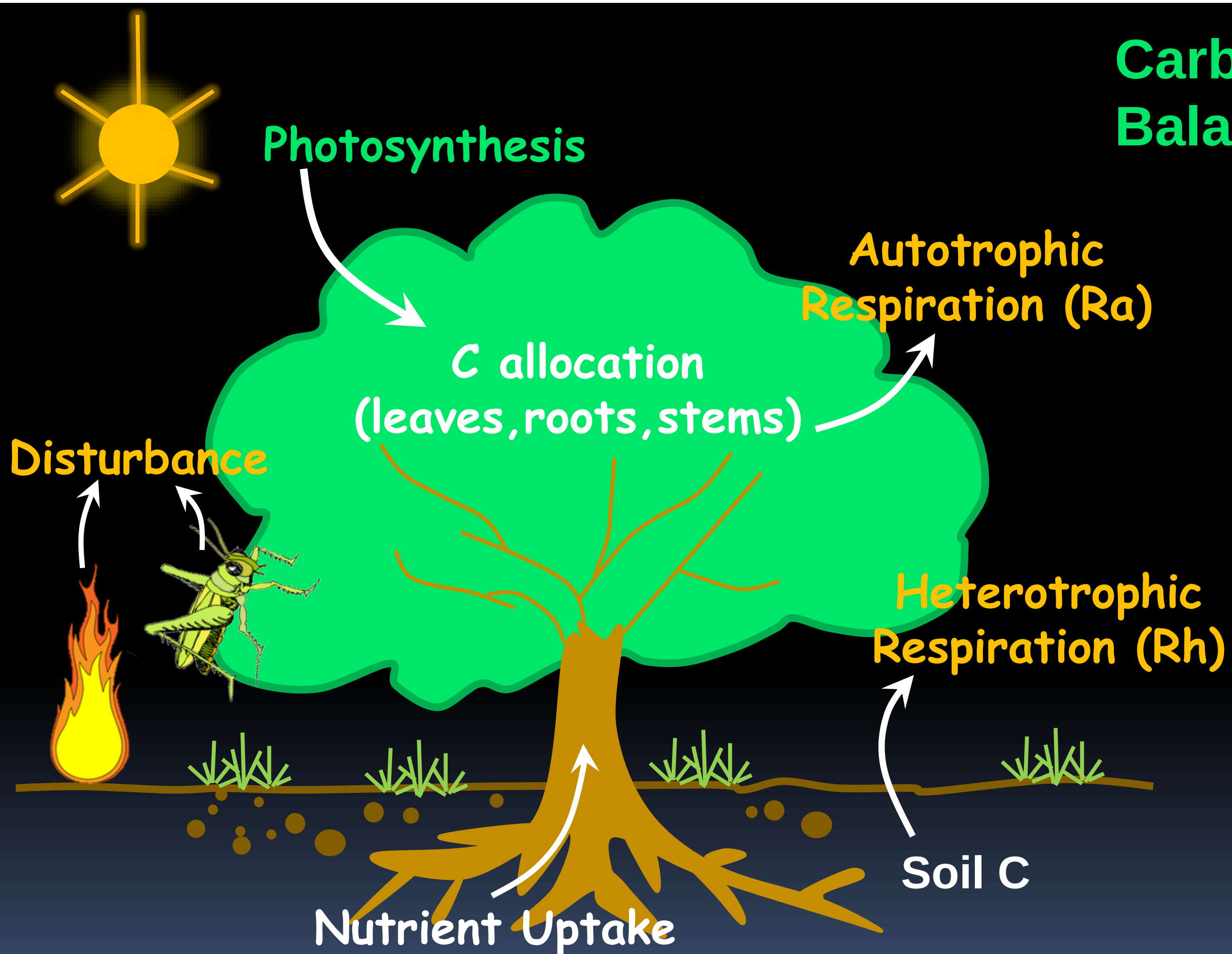




CMIP5

Large Uncertainty of Land C Sink to CO_2 increase and Climate (Projection)

Terrestrial Carbon Cycle: Concepts



Carbon Balance = Gain↓ − Loss↑

Gross Primary Production (GPP)

↓ -Ra

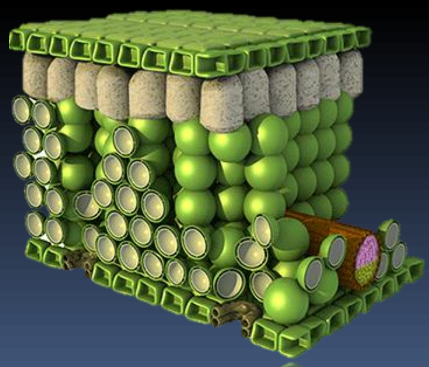
Net Primary Production (NPP)

↓ -Rh

Net Ecosystem Production (NEP)

Dickinson, 2012; Bonan, 2008

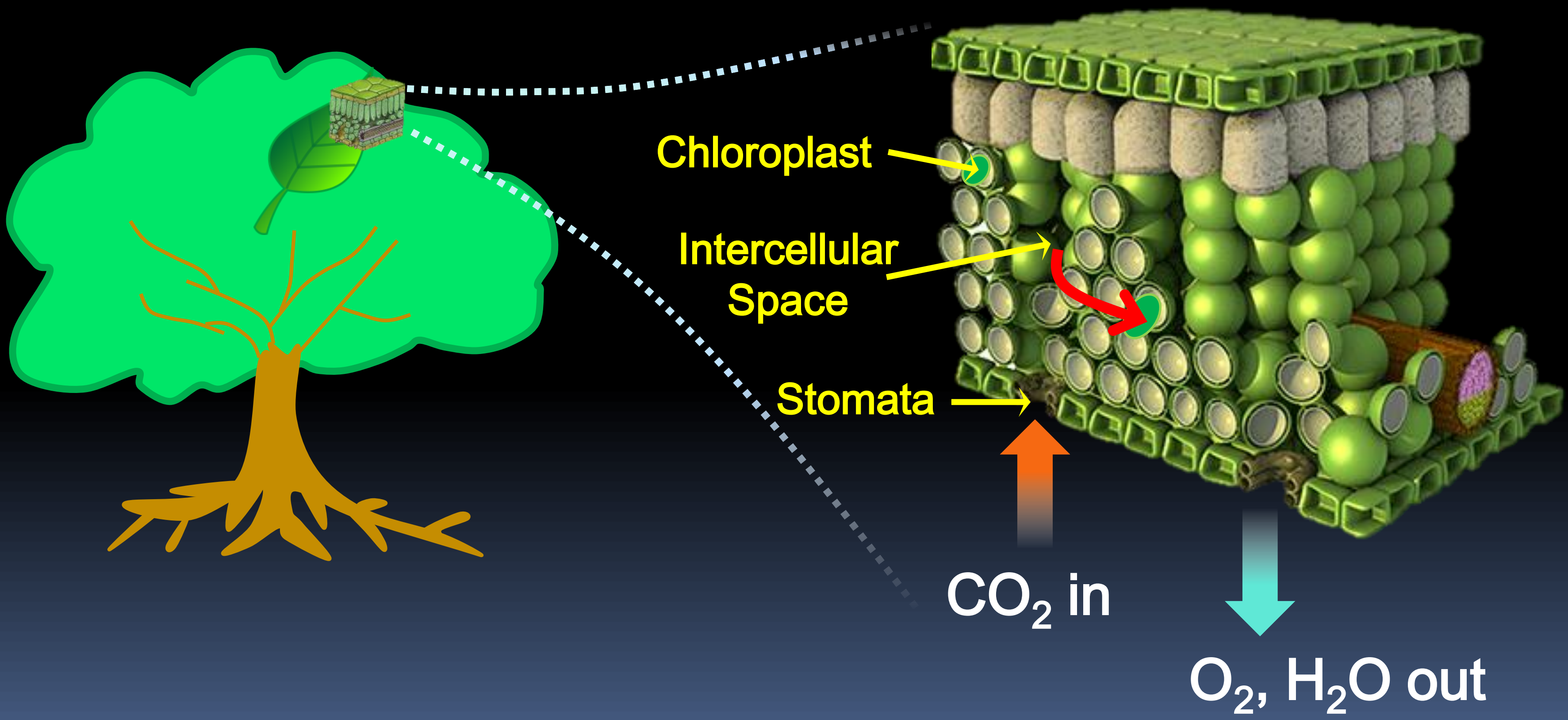
Photosynthesis and Mesophyll Diffusion



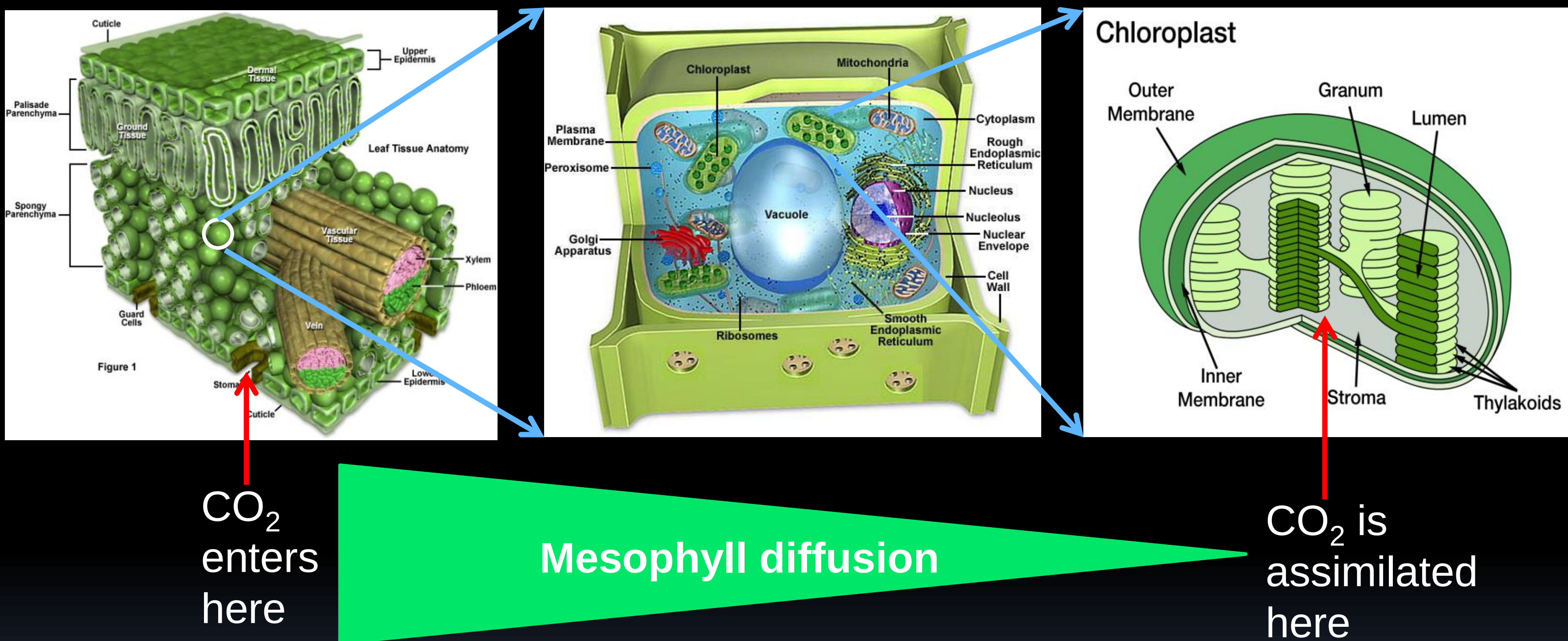
Mesophyll Diffusion of CO2

Mesophyll Diffusion: *(Niinemets, 2009)*

CO_2 diffusion from <u>Intercellular</u> to <u>Chloroplast</u>



CO_2 is assimilated in the stroma inside the chloroplasts



Current carbon cycle models predict photosynthesis as if CO_2 was assimilated inside the substomatal cavities

Stomatal diffusion vs. mesophyll diffusion

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}

Mesophyll layers constitute a major barrier for CO_2 movement inside leaves

Journey of CO_2 inside C3 Plant Leaves

CO_2 drawdown

CO_2 @ Atmosphere

Boundary Conductance

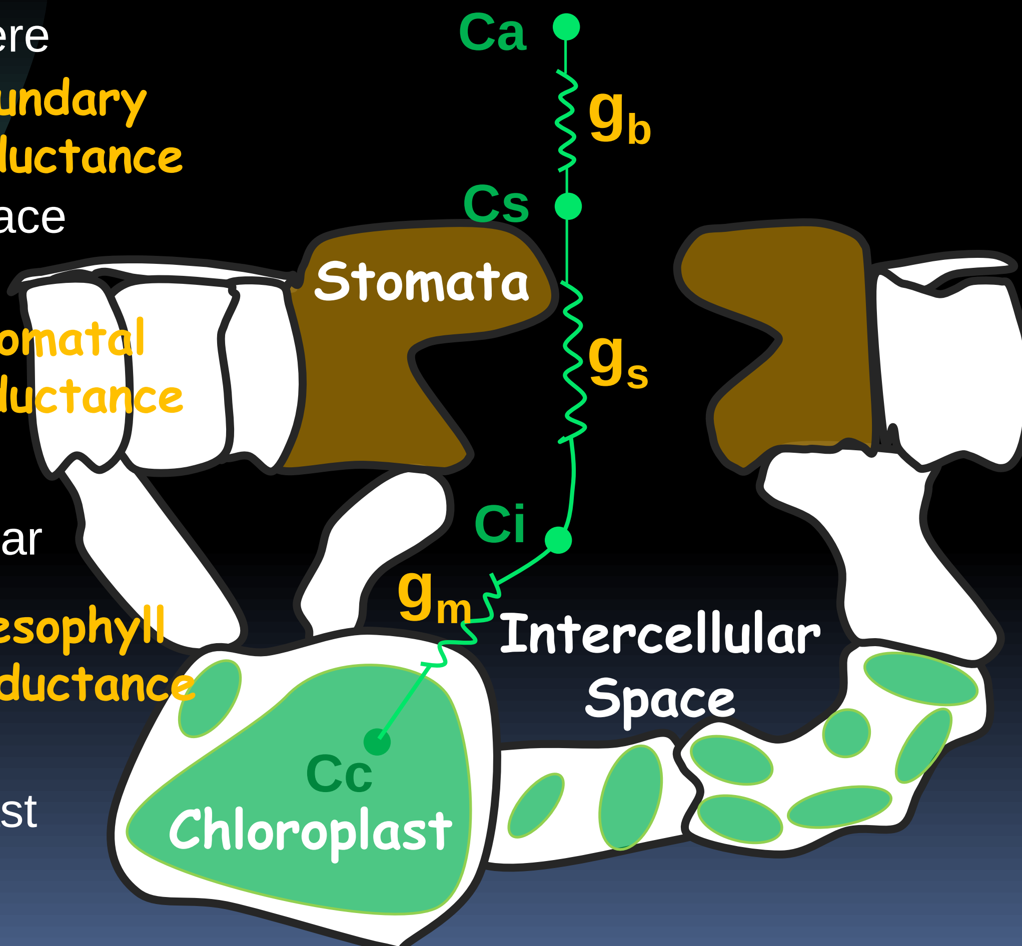
CO_2 @ Leaf Surface

Stomatal Conductance

CO_2 @ Intercellular

Mesophyll Conductance

CO_2 @ Chloroplast



Methods of determining mesophyll conductance

- Chlorophyll fluorescence
  - Variable *J* (Harley et al. 1992; Gu and Sun 2013)
  - Constant *J* (Harley et al. 1992)
- Online carbon isotope discrimination (Evans et al. 1986; Gu and Sun 2013)
- Fitting of leaf gas exchange measurements (A/Ci Curve fitting; Ethier and Livingston 2004; Gu et al. 2010)
  - LeafWeb (leafweb.ornl.gov)

Photosynthesis Model

The Photosynthesis Model

Farquhar, 1980

$$A = \min(A_c, A_j, A_p)$$

A_c: Rubisco-limited (V_{cmax})

A_j: RuBP regeneration-limited (J_{max})

A_p: Export-limited (TPU)

A Variant Photosynthesis Model (co-limilation)

$$aA_i^2 - (A_c+A_j)\,A_i + A_cA_j = 0$$
$$bA^2 - (A_i+A_p)\,A + A_iA_p = 0$$

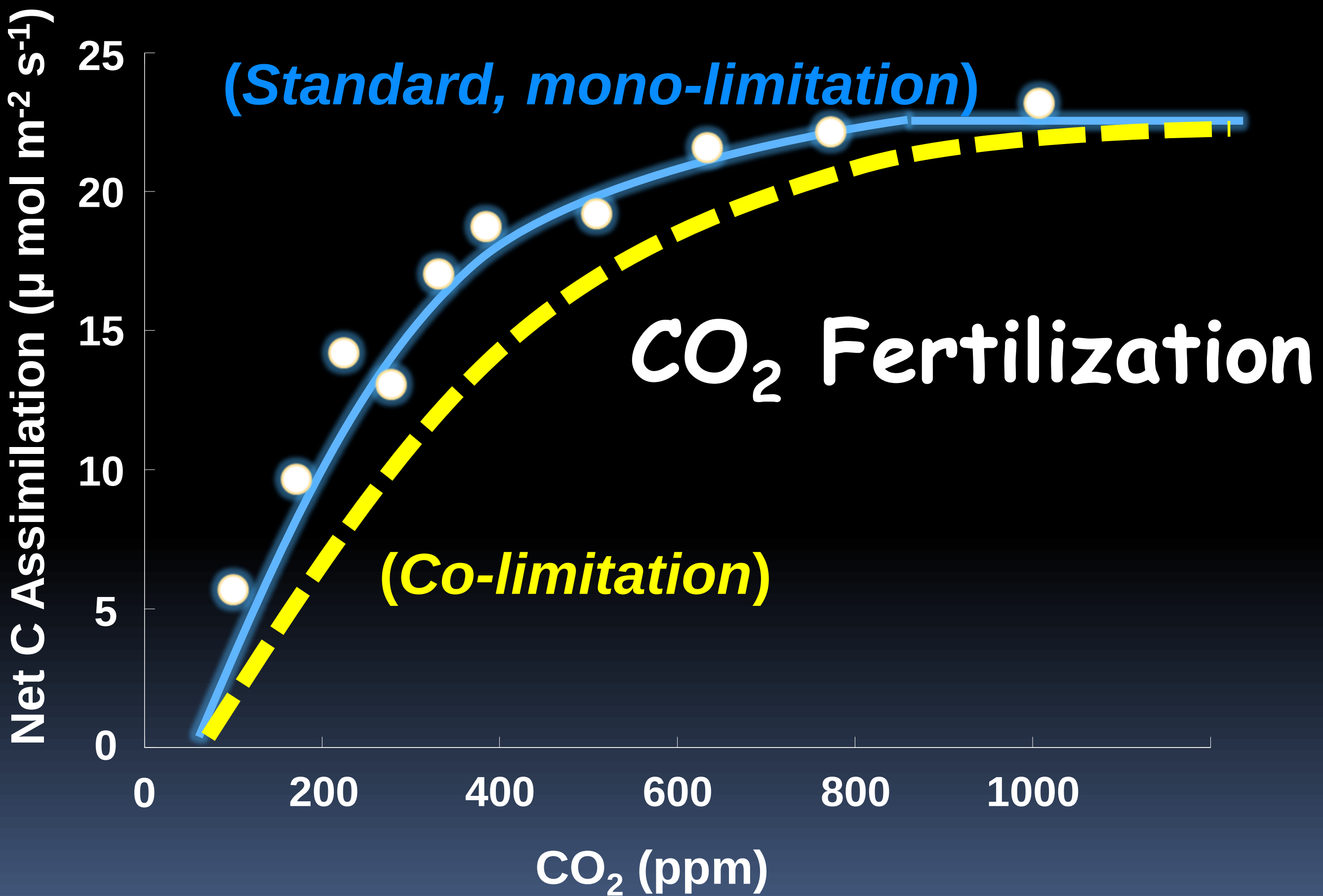
$$A_c = \begin{cases} \dfrac{V_{c\max}(c_i - \Gamma_*)}{c_i + K_c(1 + o_i/K_o)} & \text{for } C_3 \text{ plants} \\ V_{c\max} & \text{for } C_4 \text{ plants} \end{cases}$$

$$A_j = \begin{cases} \dfrac{J(c_i - \Gamma_*)}{4c_i + 8\Gamma_*} & \text{for } C_3 \text{ plants} \\ \alpha(4.6\phi) & \text{for } C_4 \text{ plants} \end{cases}$$

$$A_p = \begin{cases} 3T_p & \text{for } C_3 \text{ plants} \\ k_p \dfrac{c_i}{P_{atm}} & \text{for } C_4 \text{ plants} \end{cases}.$$

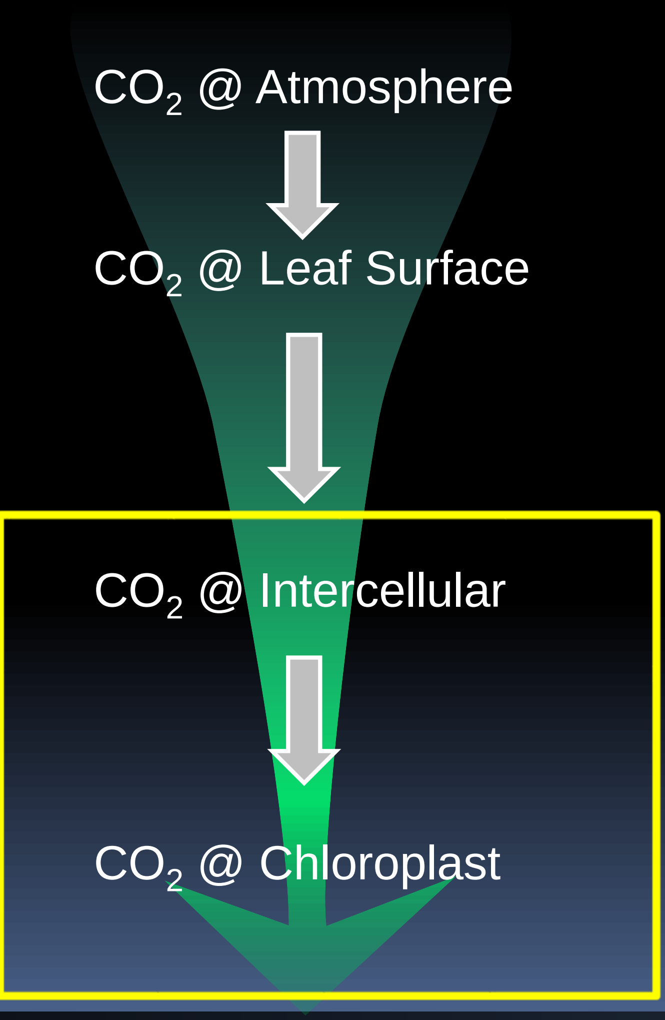
$$A = f\,(V_{cmax}, J_{max}, TPU, CO_2)$$

CO_2 Response Curve (A/C_i Curve)



$A = f\,(V_{cmax}, J_{max}, TPU, C_i) \Rightarrow A = f\,(V_{cmax}, J_{max}, TPU, C_c)$

CO_2 drawdown



$$C_c = C_i - A_n / g_m$$

A_n : **Net C Assimilation (= A - Rd)**

If infinite g_m, $C_c = C_i$

Otherwise, $C_c < C_i$

By assuming an infinite value, g_m is omitted!

Conversion of Fundamental Photosynthetic Parameters

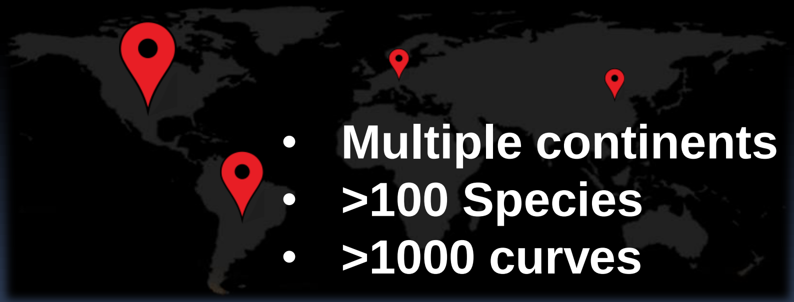
"LeafWeb"
(leafweb.ornl.gov)

$A/C_i \longrightarrow A/C_c$

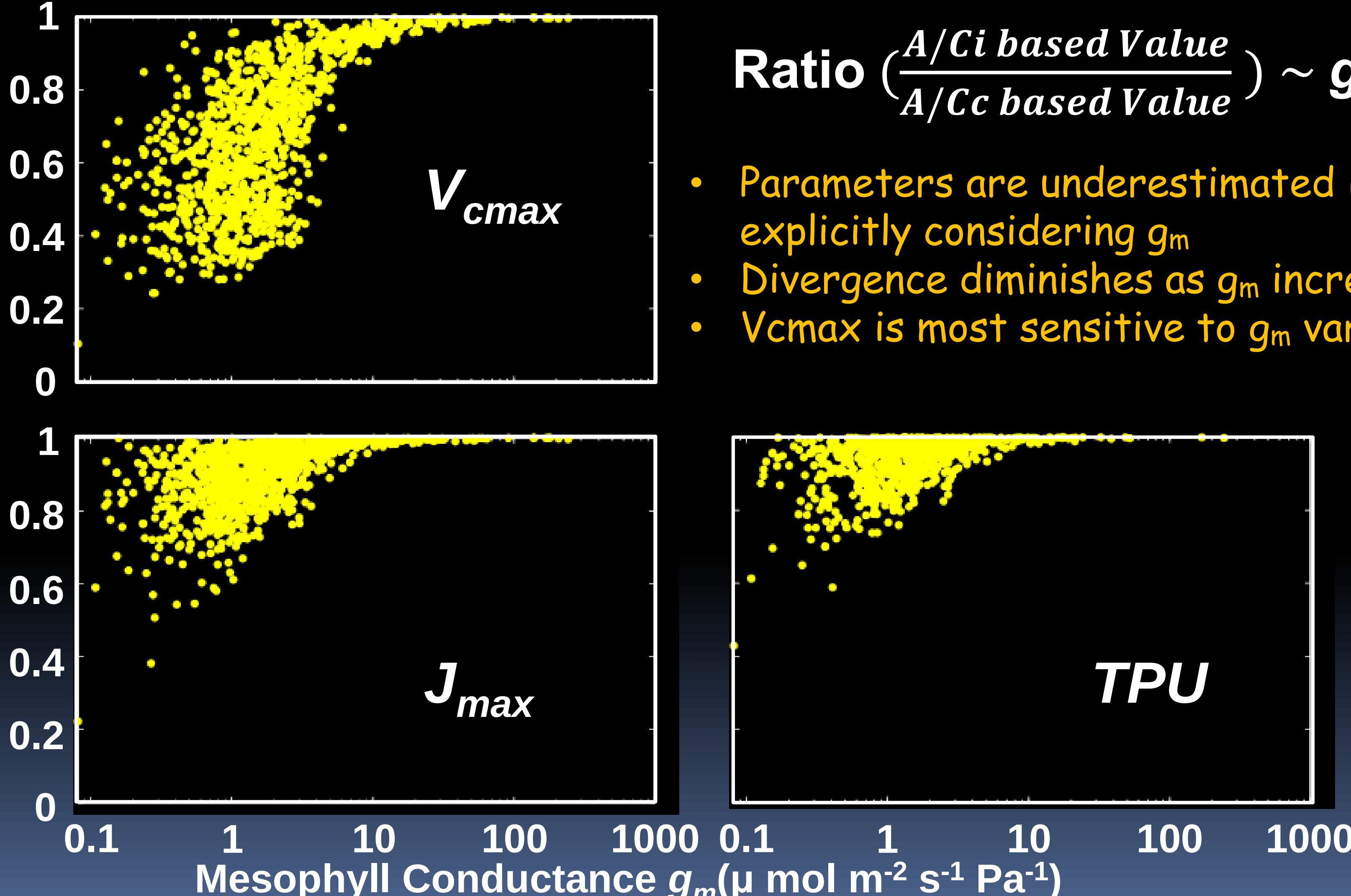
Infinite g_m — Explicit g_m

Apparent V_{cmax}, J_{max}, TPU — **True** V_{cmax}, J_{max}, TPU

Leaf gas exchange measurements



Omission of g_m leads to underestimation of photosynthetic parameters



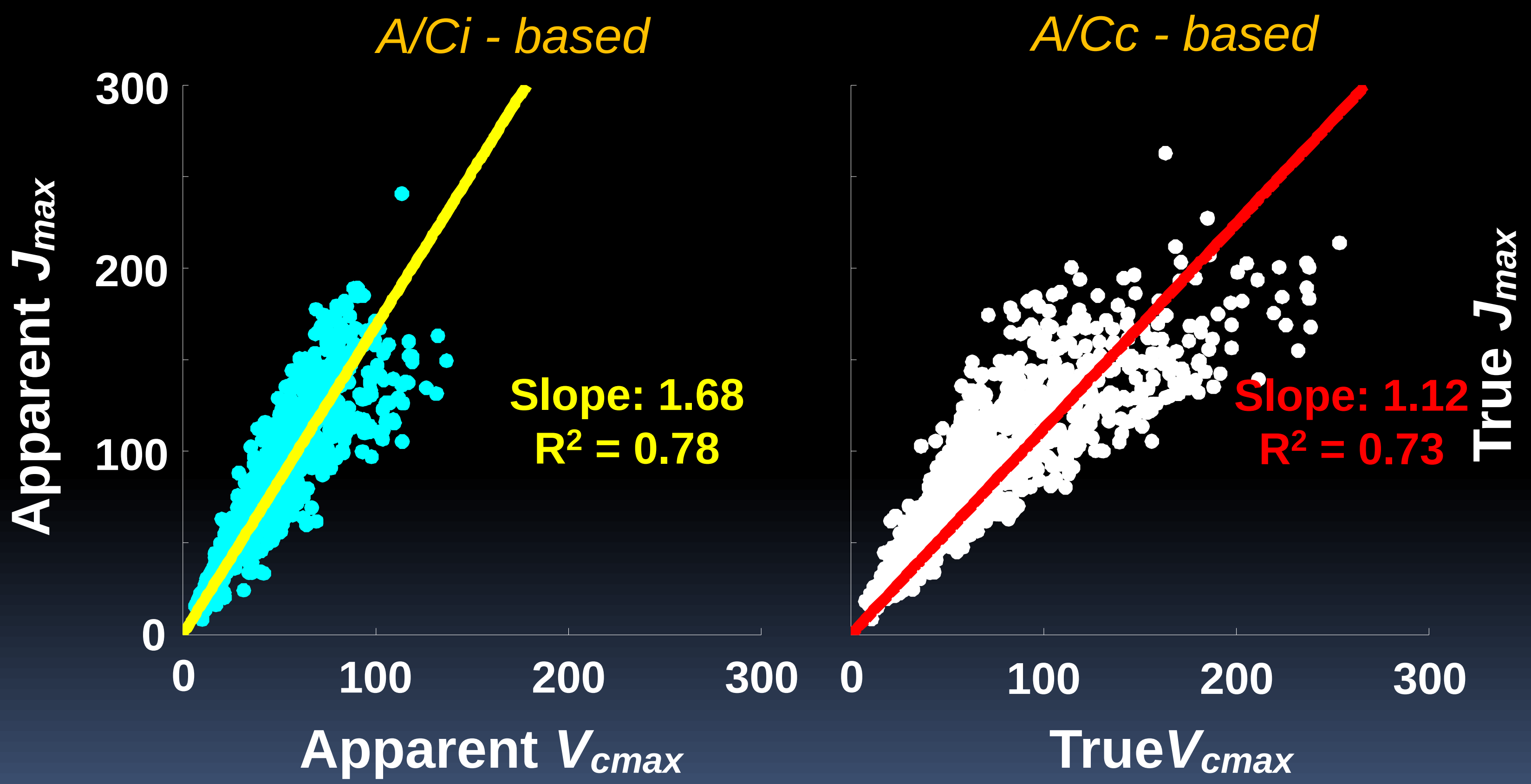
Ratio $\left(\frac{A/Ci\ based\ Value}{A/Cc\ based\ Value}\right) \sim g_m$

- Parameters are underestimated if not explicitly considering g_m
- Divergence diminishes as g_m increases
- Vcmax is most sensitive to g_m variation

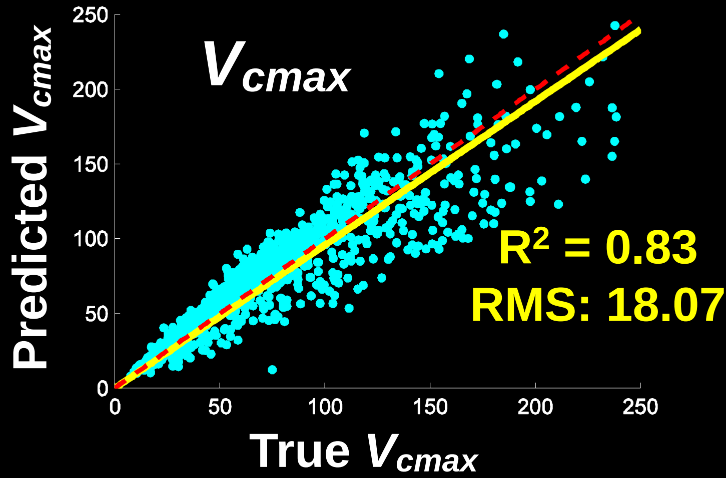
The g_m modifies functional relationships between parameters

Relationships of J_{max} & V_{cmax}

(μ mol m^{-2} s^{-1} Pa^{-1})



"True" parameters can be obtained from A/Ci-based values

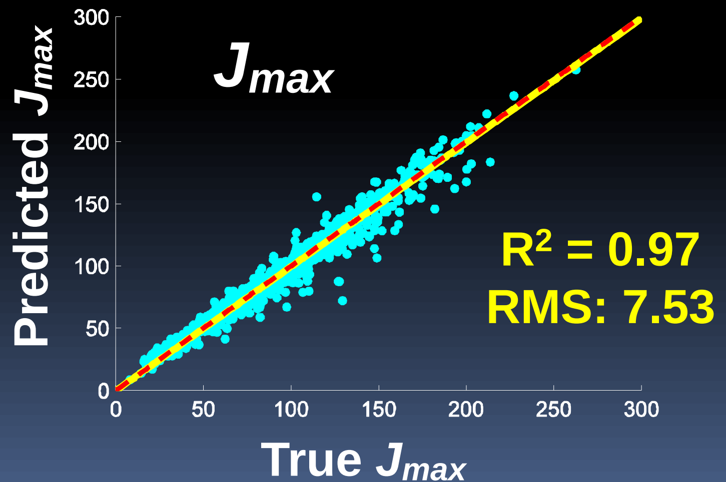


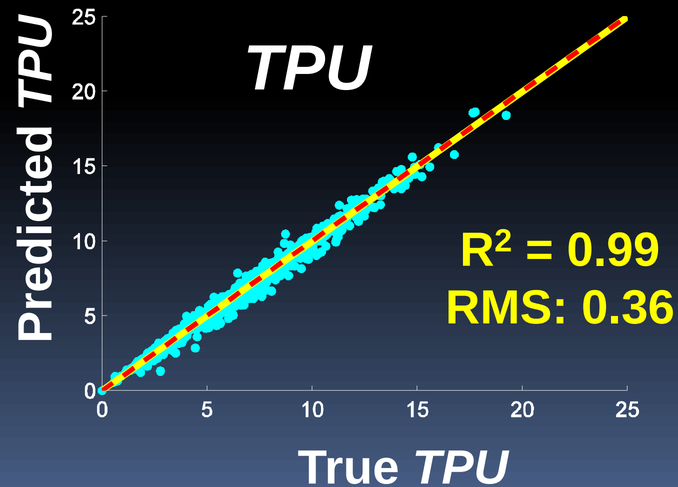
$$\textit{Predicted Value} = f(A/Ci\ Value, gm)$$

$$y = x \exp\left(a \frac{x^c}{g_m^b + d} \right)$$

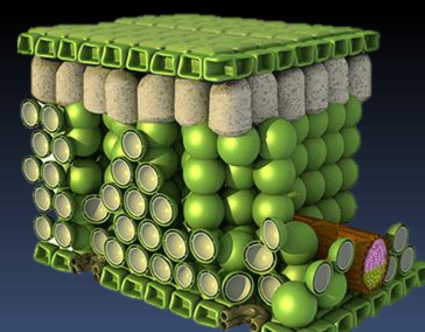
$$\textit{Predicted Value} \sim A/Cc\ Value$$

- *A/Ci* based values can be converted to *A/Cc* based values using an empirical function
- Coefficients differ among *Vcmax*, *Jmax*, *TPU*





Global Impact of Mesophyll Diffusion



A modeling framework for g_m

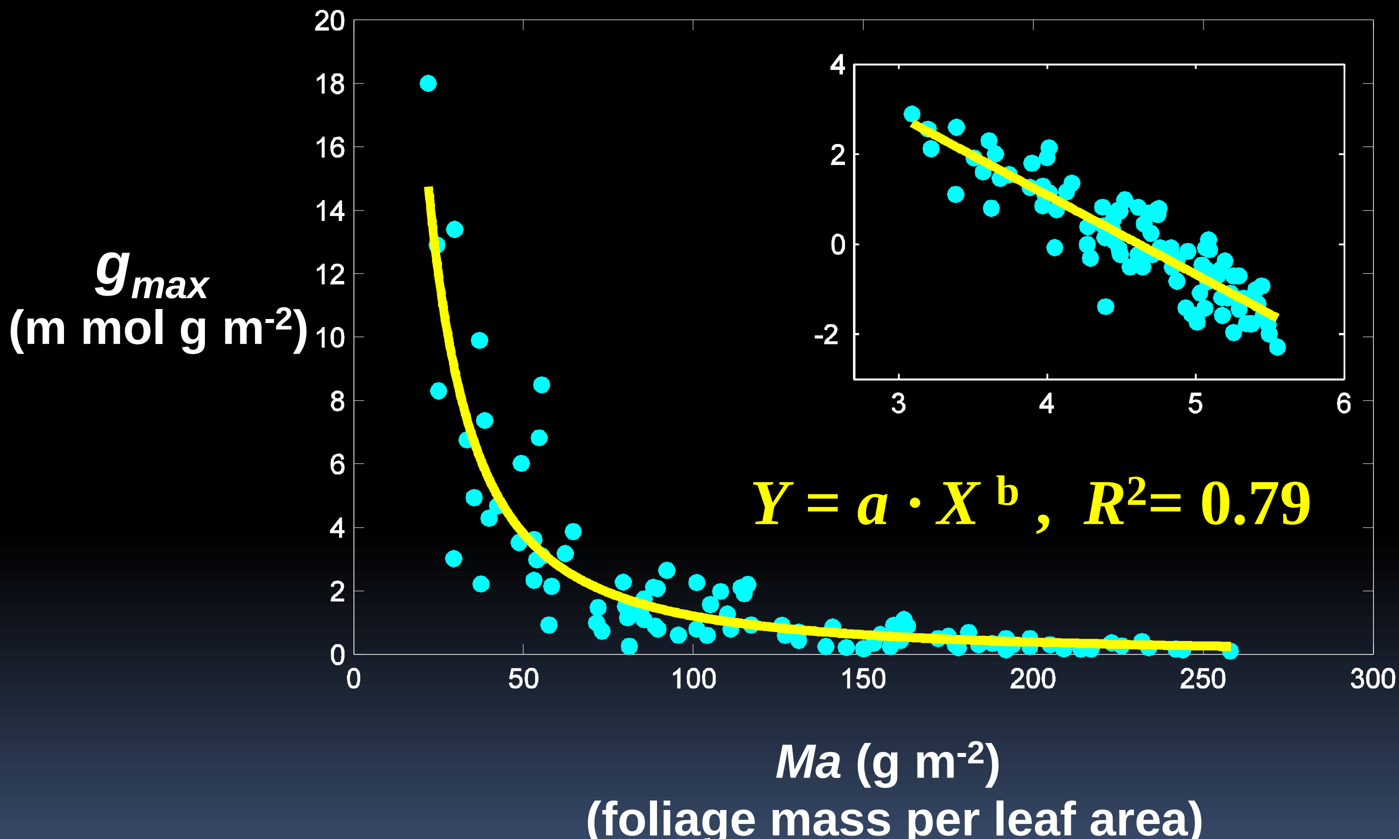
- **Leaf-level parameterization**

$$g_m = g_{max} \cdot f_T(T) \cdot f_w(\theta)$$

- **Scaling up to canopy level**
  - Sunlit leaf
  - Shaded leaf
  - Vertical gradient

New Advances from field studies

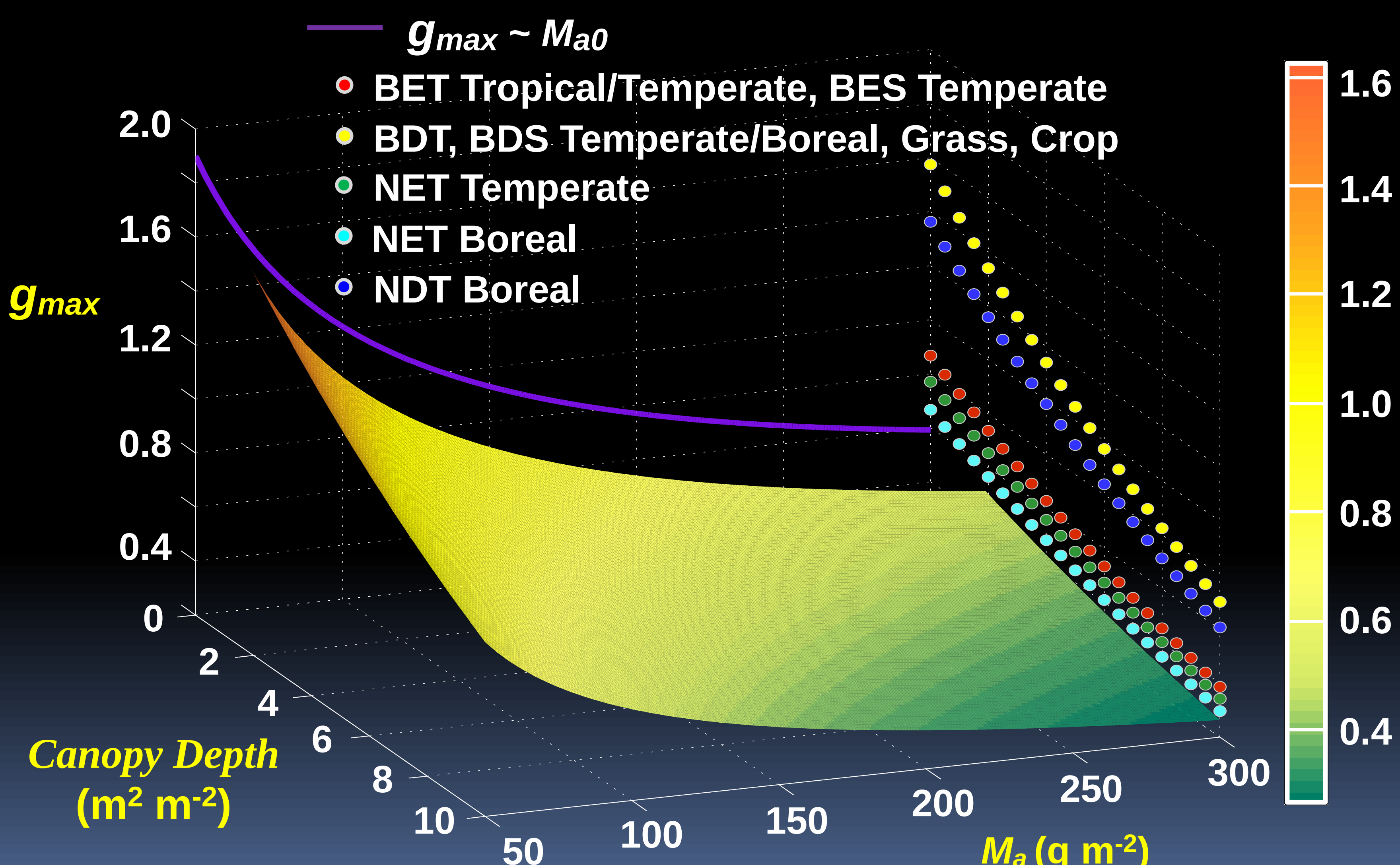
Maximum g_m (no stress)



- A Meta-analysis for > 100 species
- No Stress (T,water,light)

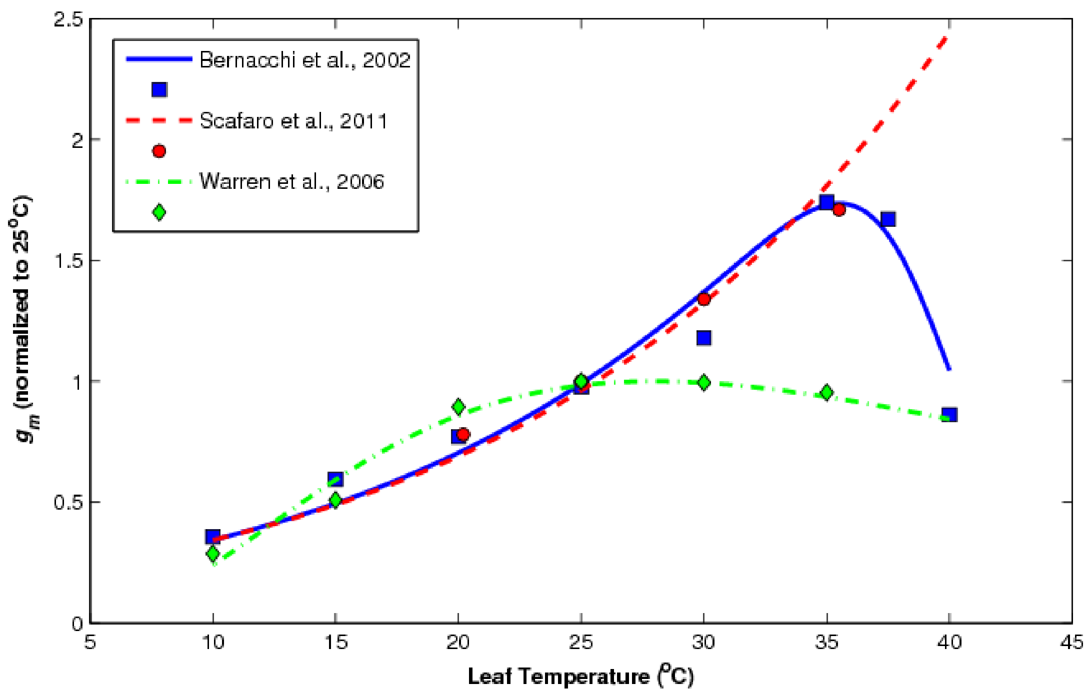
Niinemets, 2009

Variation of g_m with Ma & canopy depth



Environmental Modifiers

- T Response Function
- Water Stress factor



- β_{tran} Calculated in host model CLM4.5
- β_{tran} Scaled to 0 to 1

Implementation of global mesophyll conductance model in CLM4.5

- Structural Updates:

  Inclusion of mesophyll conductance model

  Photosynthesis model based on Cc instead of Ci

- Parameter Recalibration:

  Transformation of apparent photosynthetic parameters (V_{cmax}, J_{max} and *TPU*) to corresponding true values using "conversion function" developed by "LeafWeb"

- Pair Comparison:

  Differences in dynamic behaviors between with and without explicit representation of mesophyll diffusion

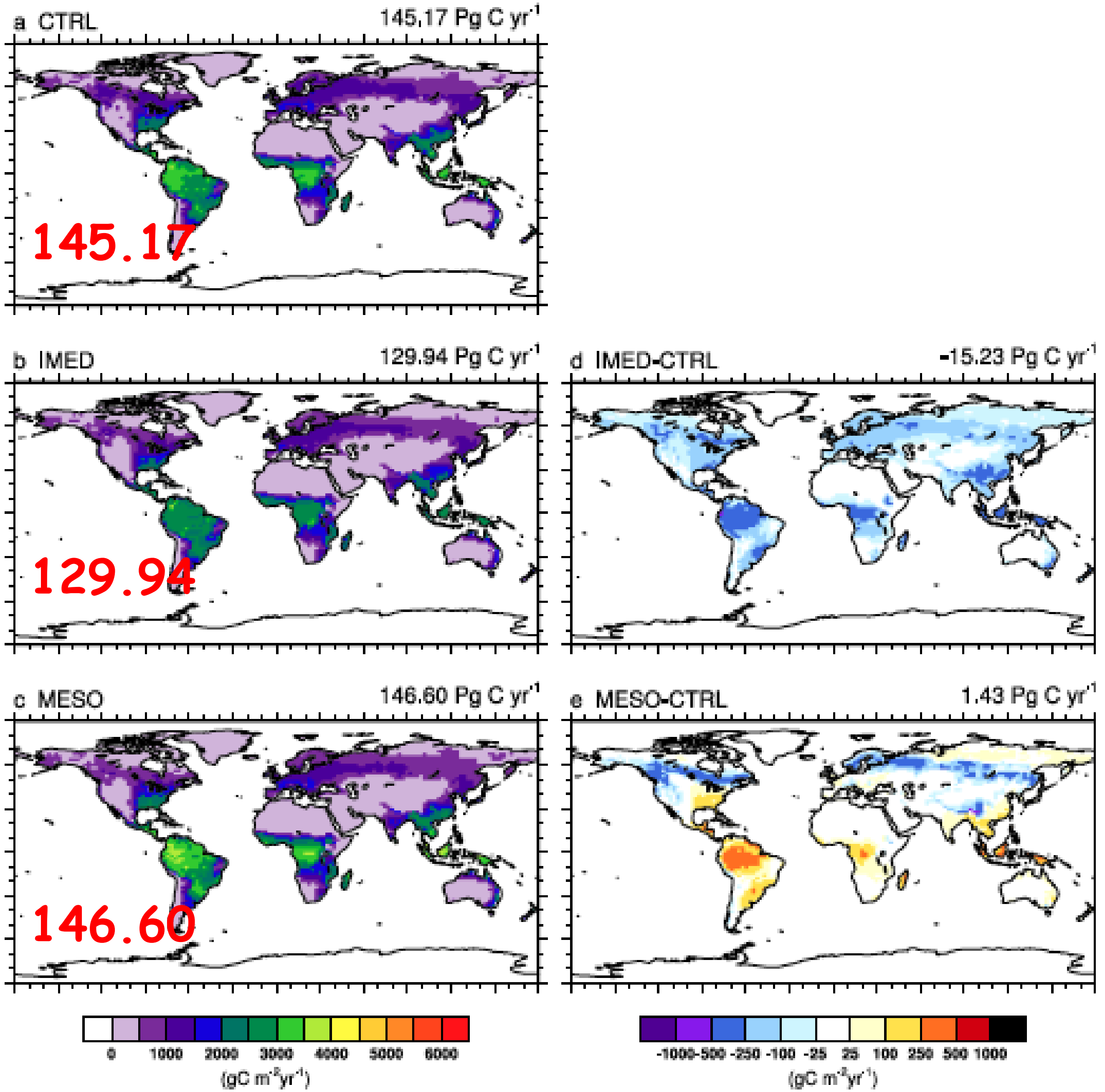
Simulation protocols

Simulation	Description
Transient CO_2 simulations	
CTRL	Control simulations with the default CLM4.5
IMED	Intermediate simulations that use CLM4.5 with the mesophyll conductance (g_m) model only, but retain the original phenomenological (g_m-lacking) photosynthetic parameters
MESO	Fully updated simulations that use CLM4.5 with the g_m model and the g_m-including photosynthetic parameters
Constant CO_2 simulations	
CTRL_cCO_2	Same as CTRL, but with a constant atmospheric CO_2 concentration (296 ppm at 1901)
MESO_cCO_2	Same as MESO, but with a constant atmospheric CO_2 concentration (296 ppm at 1901)

The MESO simulations are repeated with the colimiting and monolimiting conversion functions.

GPP (1985-2004 mean)

GPP simulation agrees between with and without mesophyll conductance for contemporary period



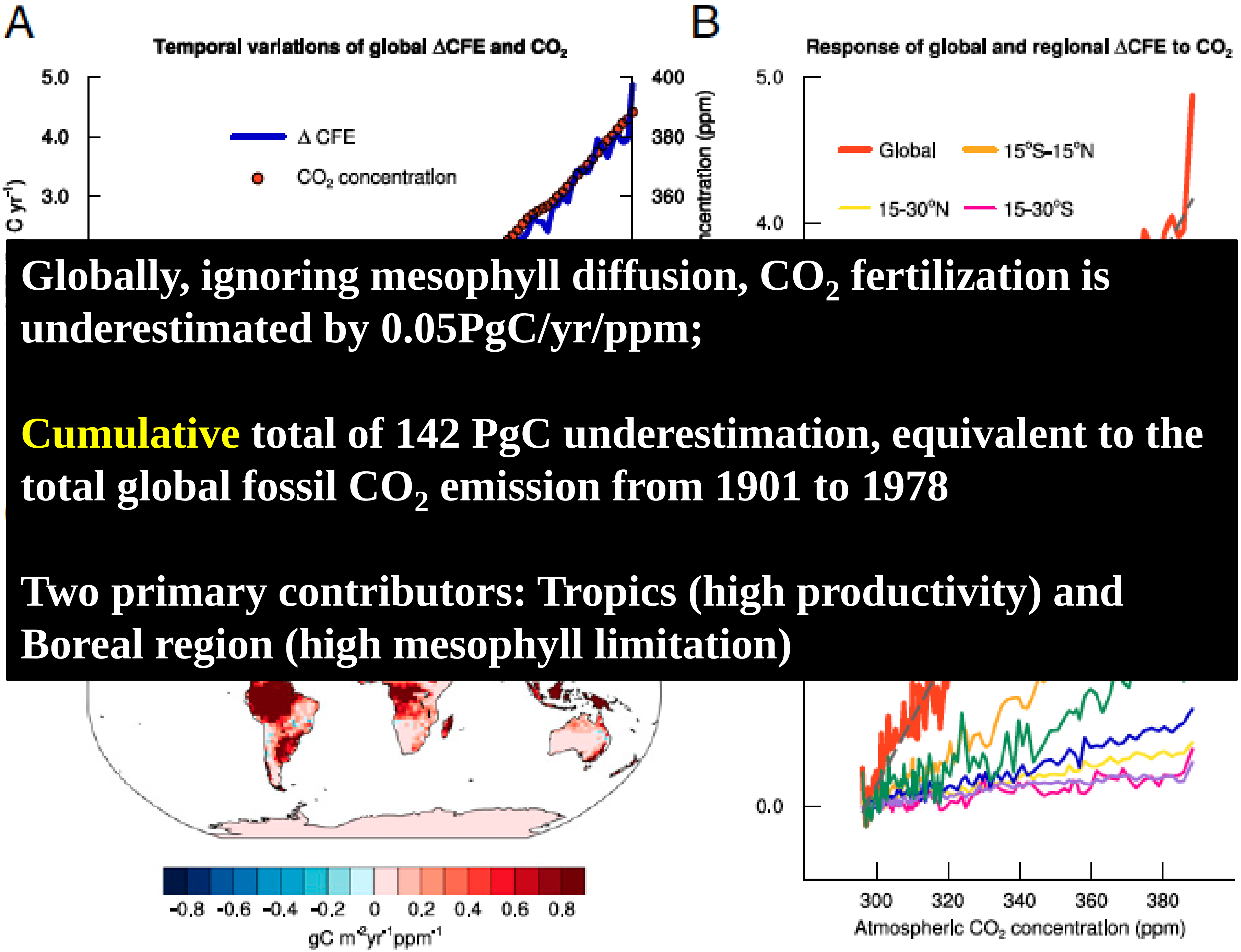
Metrics for quantifying impact of mesophyll diffusion on global terrestrial CO_2 fertilization

- Runs with or without mesophyll diffusion from 1901 to 2010
- Average annual GPP of 1901 to 1910 used as a reference for quantifying the CO2 fertilization effect (CFE) on 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*

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

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

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



Globally, ignoring mesophyll diffusion, CO_2 fertilization is underestimated by 0.05PgC/yr/ppm;

Cumulative total of 142 PgC underestimation, equivalent to the total global fossil CO_2 emission from 1901 to 1978

Two primary contributors: Tropics (high productivity) and Boreal region (high mesophyll limitation)

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1057 - 915 = 142 PgC (16%)

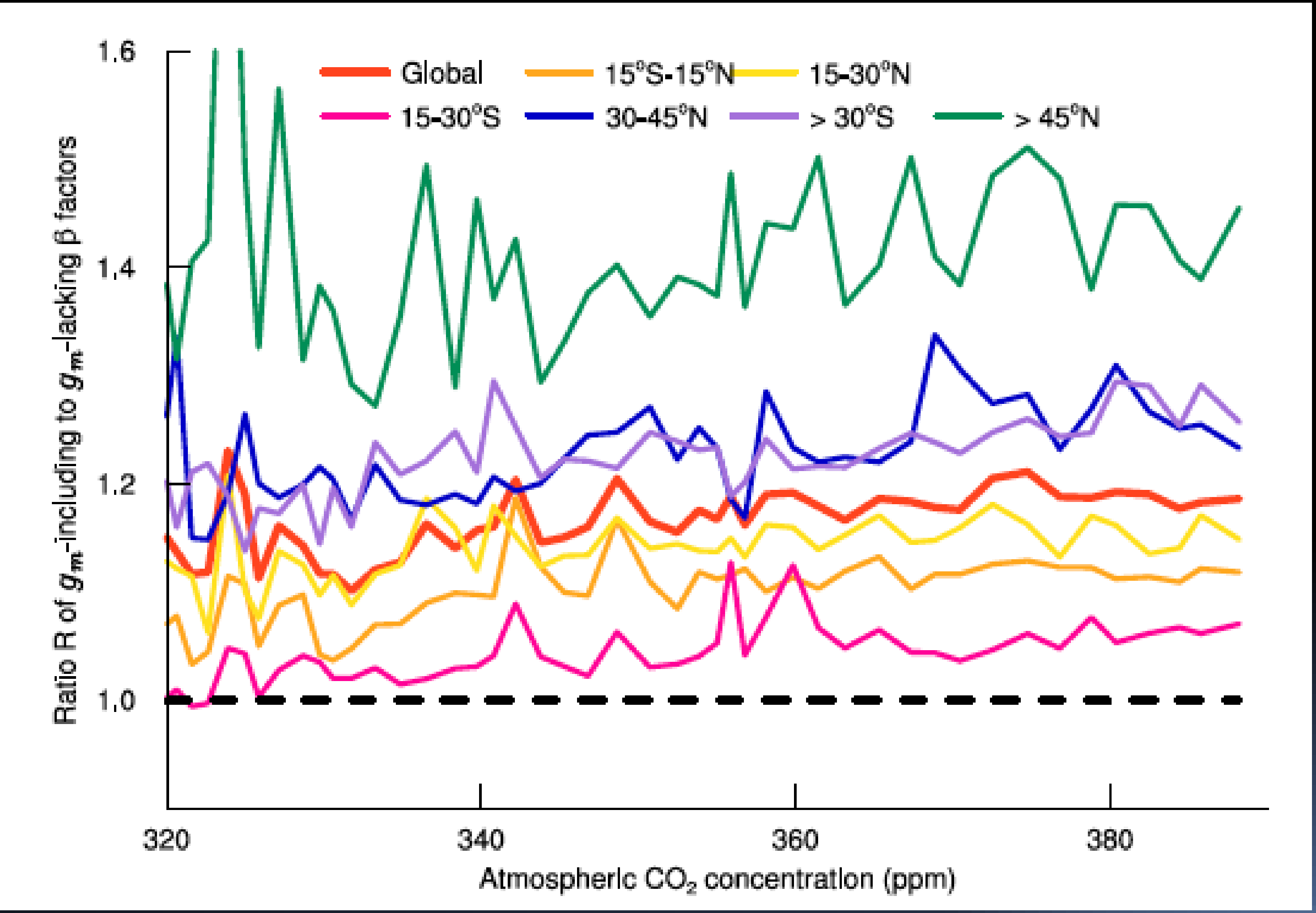
142 PgC ~ 17 ppm (17% overestimation)

Assumption: NPP = 1/2 GPP

1/2 released CO2 stays in atmos

1ppm = 2.123 PgC

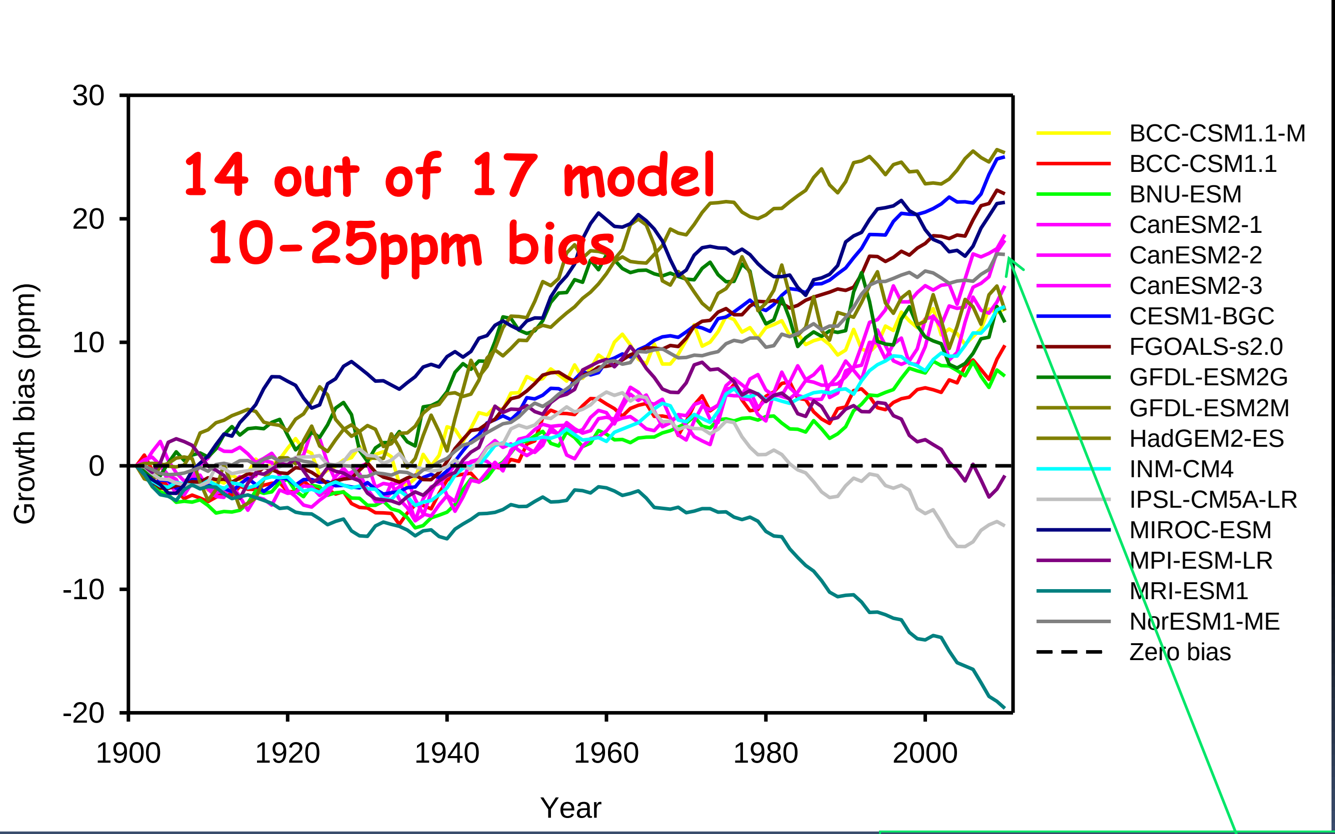
From tropics to boreal, the ratio of the beta factors increases, indicating higher sensitivity of CO_2 fertilization to mesophyll diffusion in higher latitudes (high mesophyll limitation)



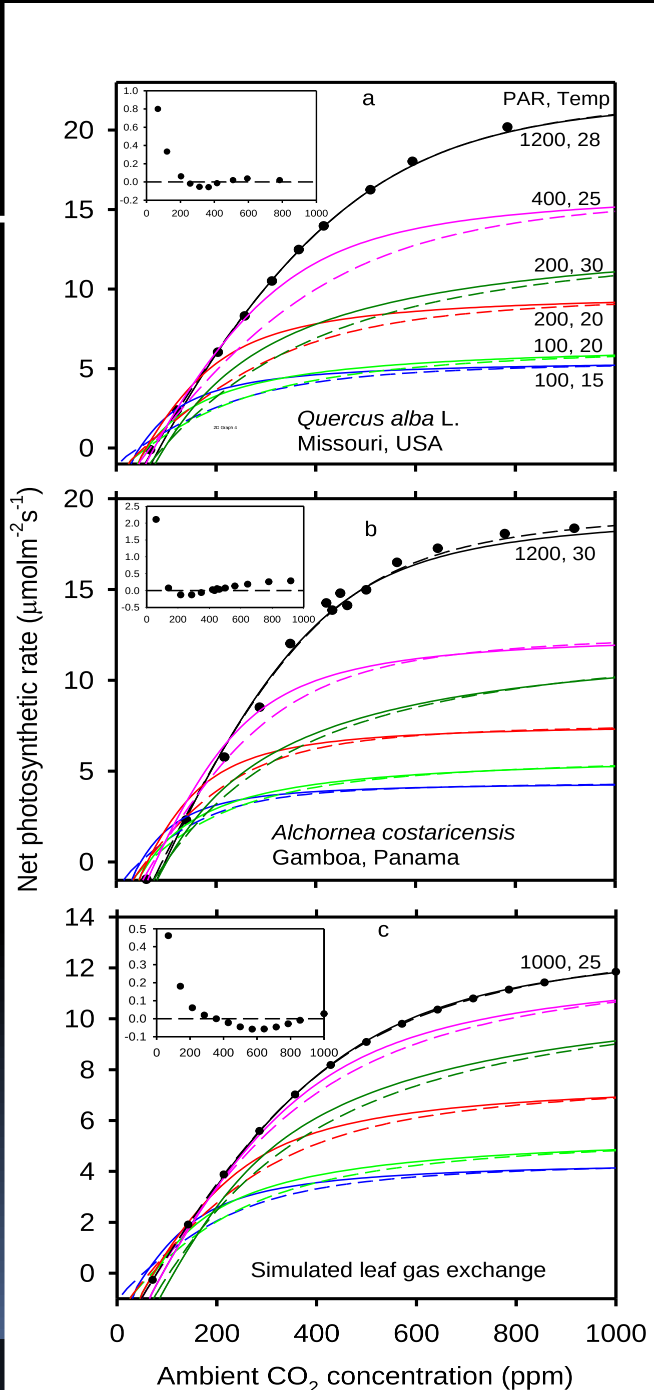
Ignoring mesophyll diffusion, Earth System Models over-predict the growth rate of atmospheric CO2 due to fossil fuel emissions

Bias of atmos CO2 growth rate in CMIP5 simulations

$$= [CO_{2,\,model}(t) - CO_{2,\,model}(ref)] - [CO_{2,\,obs}(t) - CO_{2,\,obs}(ref)]$$



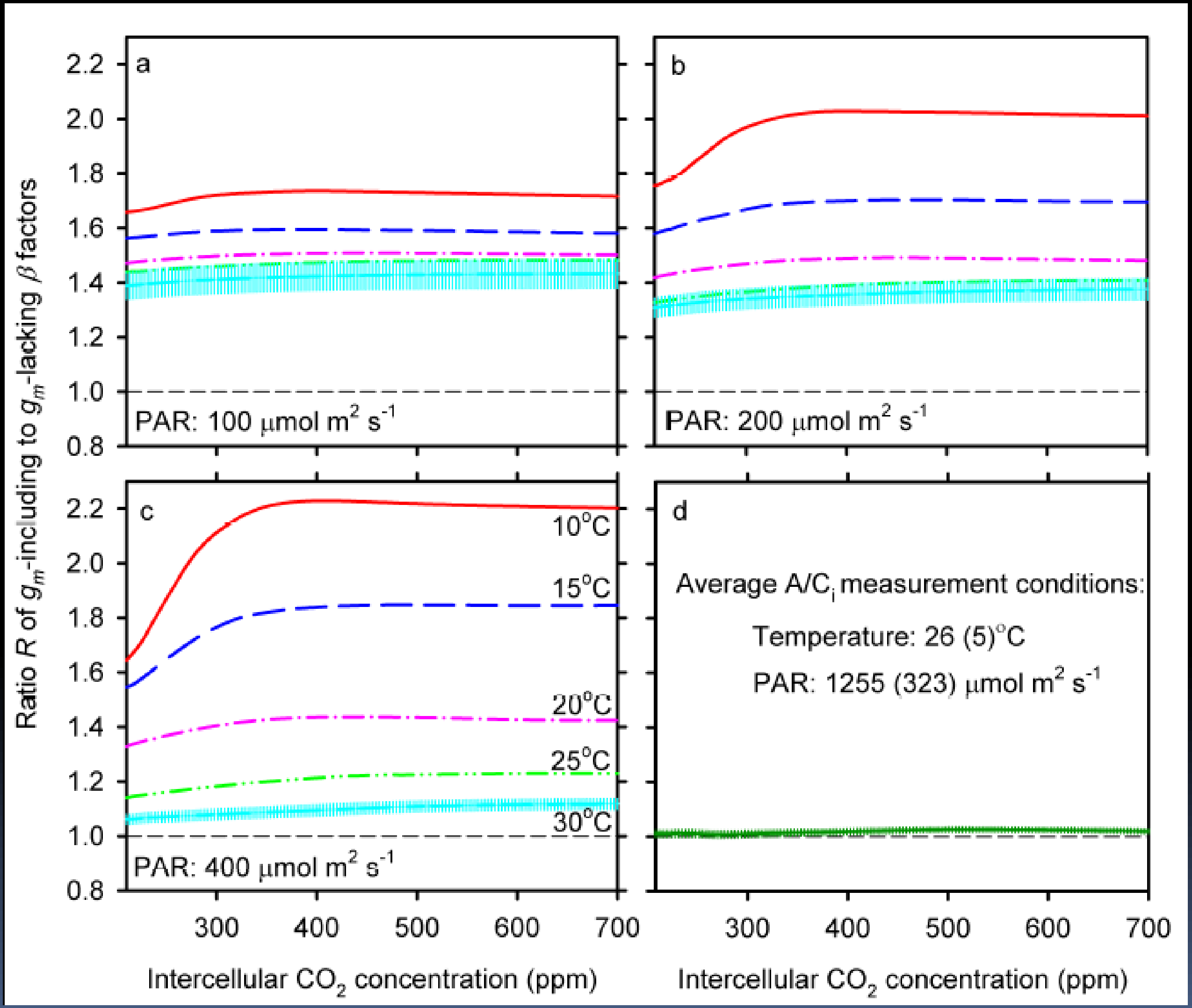
17 ppm (mesophyll correction)

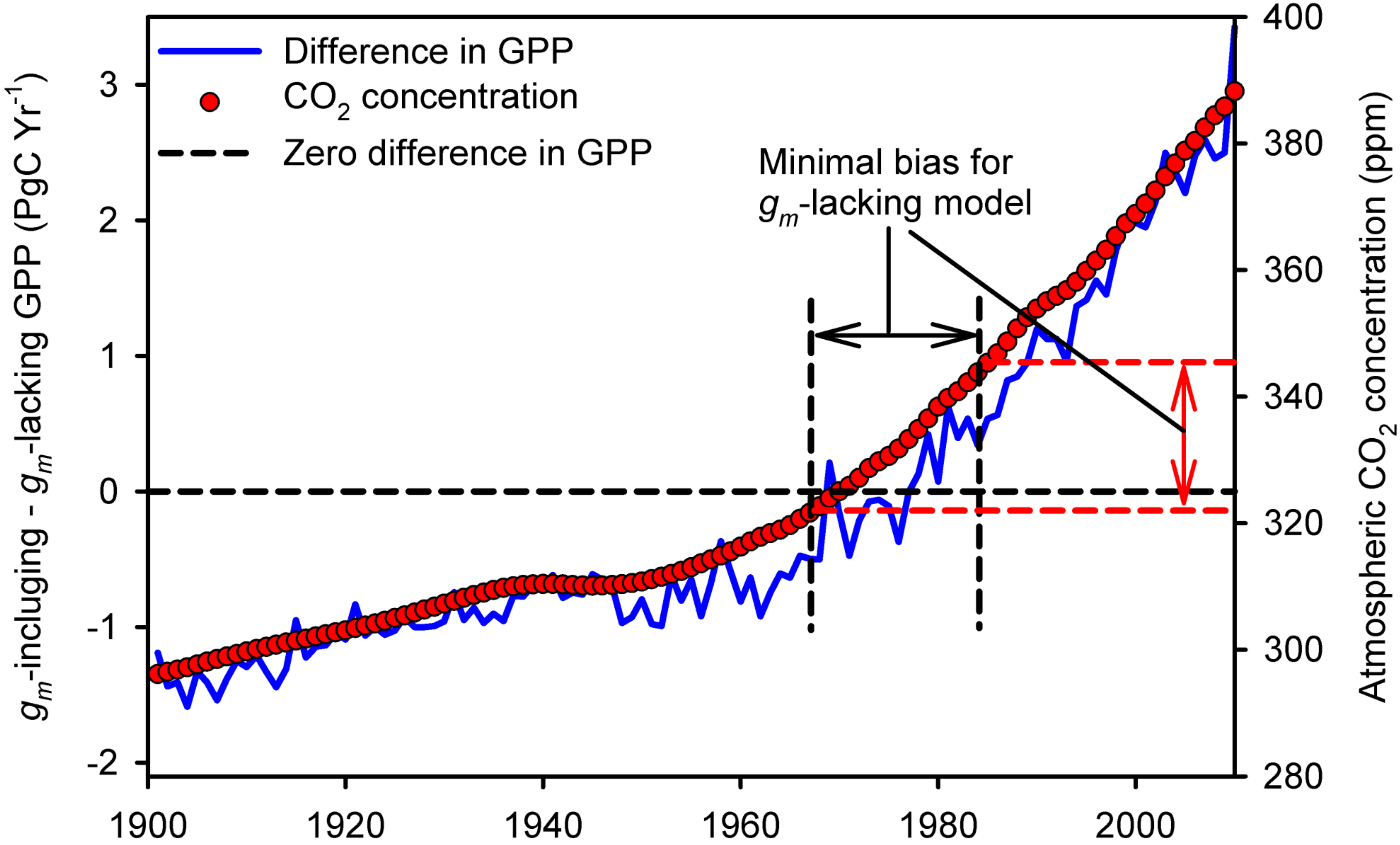


Why lacking mesophyll diffusion underestimate the CO_2 fertilization effect?

- 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
- This model structural deficiency is tentatively compensated for when models are forced to match measurements made at narrowly controlled conditions
- The problem worsens when models run for natural environmental conditions that deviate from the original measurement conditions against which model parameters were tuned

Leaf-scale illustration of Beta factor ratio: Deviation from measurement conditions bias photosynthesis simulation if mesophyll diffusion is ignored




Difference in GPP
CO2 concentration
Zero difference in GPP
Minimal bias for
gm-lacking model
gm-incluging - gm-lacking GPP (PgC Yr-1)
Atmospheric CO2 concentration (ppm)
3
2
1
0
-1
-2
400
380
360
340
320
300
280
1900
1920
1940
1960
1980
2000

Conclusions

1. Terrestrial biosphere may be more CO_2-limited and more responsive to the increase in atmospheric CO_2 concentration than previously thought

2. Current global carbon cycle models may over-predict historical and future growth rates of atmospheric CO_2 concentration

3. Mesophyll diffusion is a key process for modeling terrestrial primary production and must be represented explicitly