Coupling carbon and water cycles in global vegetation models

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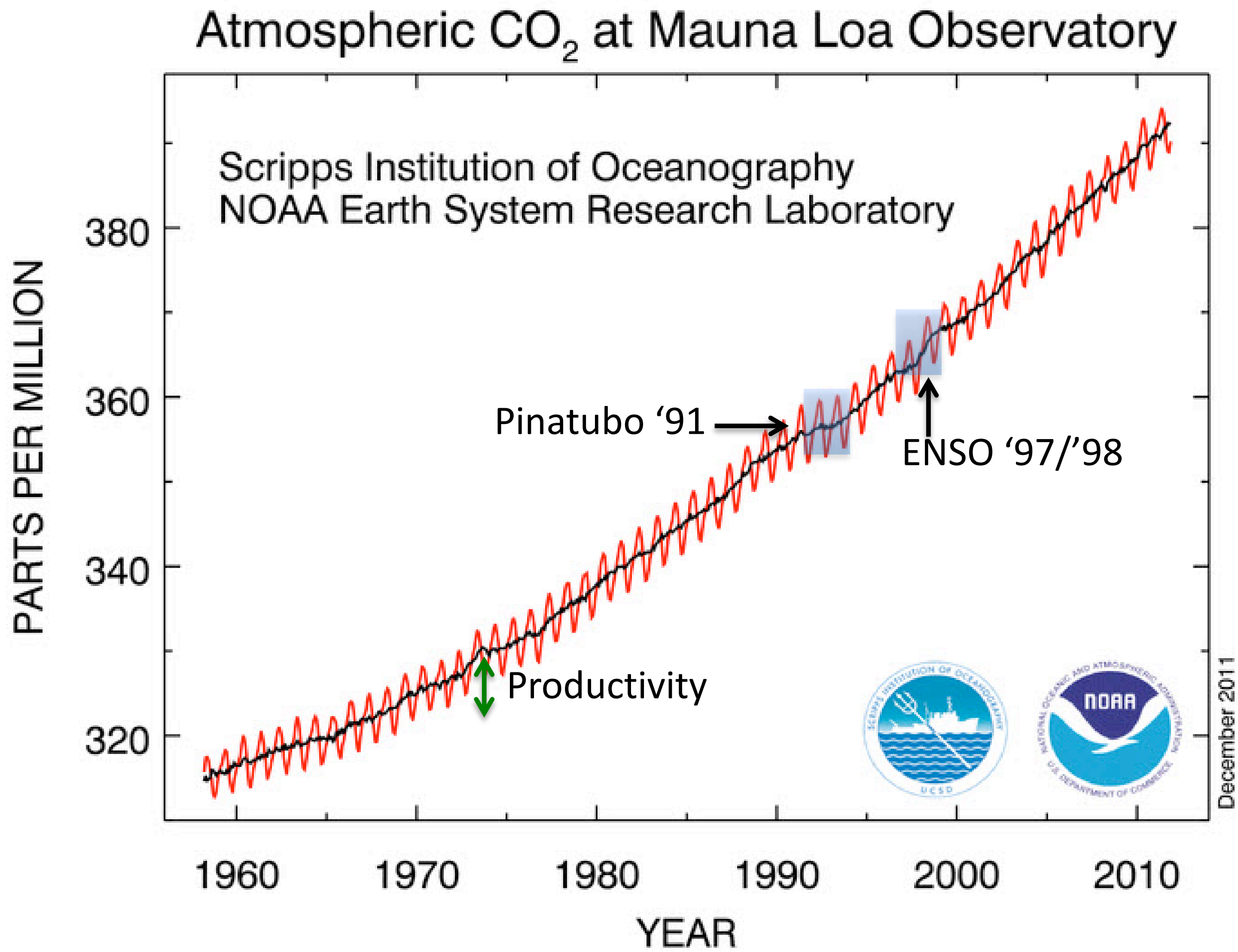
Carbon and water cycling



Goal of lecture

- Conceptual
    - Canopy processes
    - Photosynthesis
    - Conductance

- Technical
    - Approaches for modeling photosynthesis
    - Coupling photosynthesis and conductance

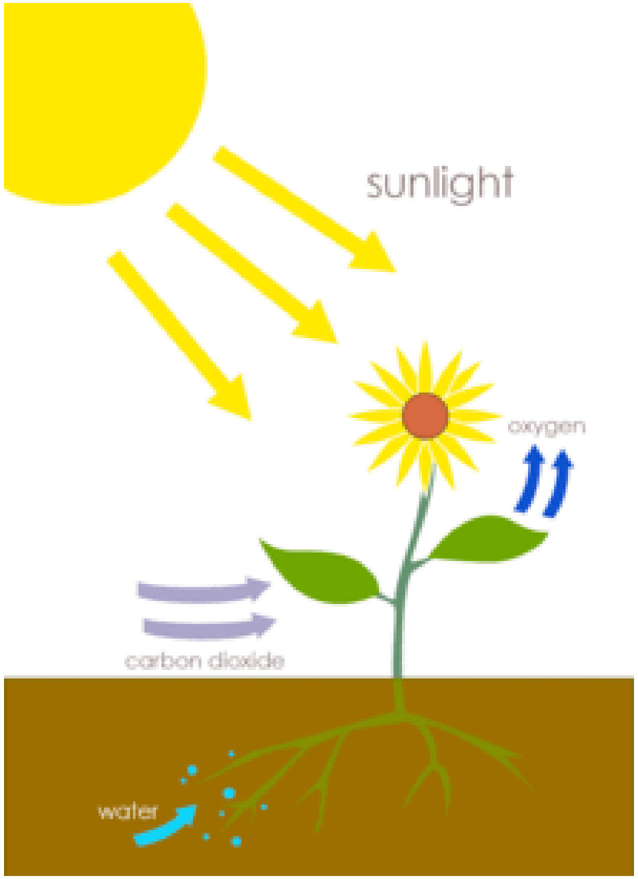
Some variables

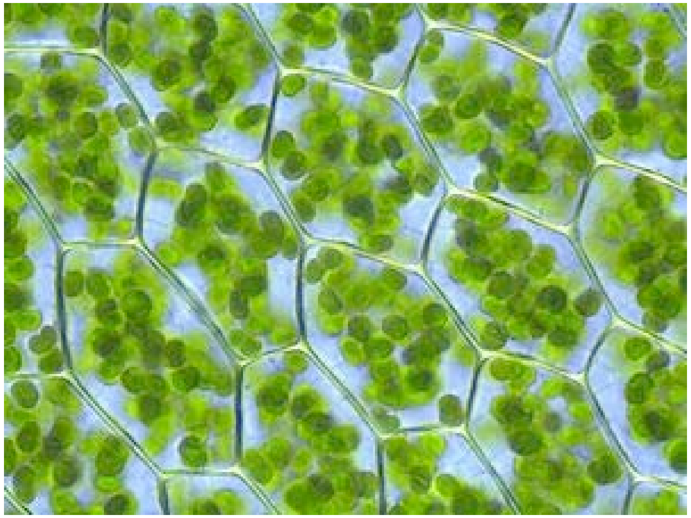
- A (µmol m^{-2} s^{-1}): gross photosynthesis
- Anet (µmol m^{-2} s^{-1}): photosynthesis – Rd
- Rd (µmol m^{-2} s^{-1}): leaf respiration
- gs (mol m^{-2} s^{-1}): stomatal conductance
- gc (mol m^{-2} s^{-1}): canopy conductance
- VPD (kPa): vapor pressure deficit
- RH (%): relative humidity
- Ci (ppm): leaf internal CO_2 concentration
- Ca (ppm): atmospheric CO_2 concentration

Photosynthesis

- Conversion of CO_2 to organic compounds (mainly sugars) using energy from sunlight
- 3.5 billion year old process
- Conducted by plants, algae, ba
- Oxygen (O_2) is a waste product
- Globally, captures 100 Terawat
- Global NPP 100-115 PgC

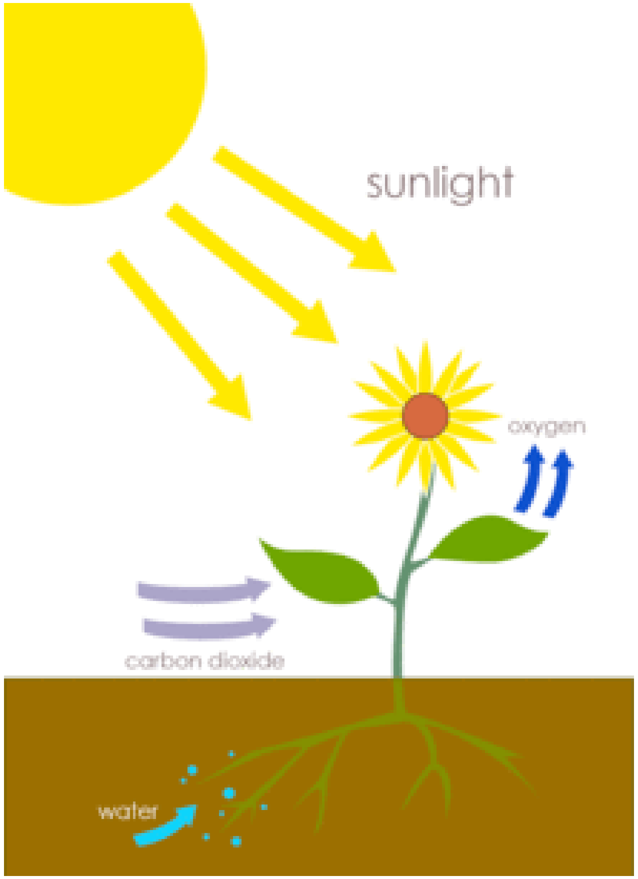
Photosynthesis

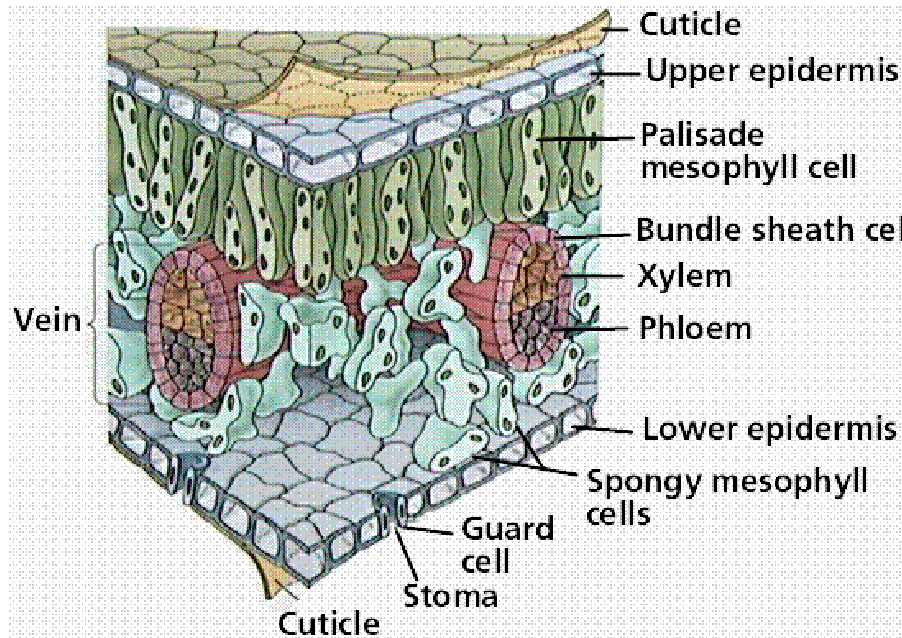




$$CO_2 + H_2O + light \rightarrow CH_2O + O_2$$

Photosynthesis

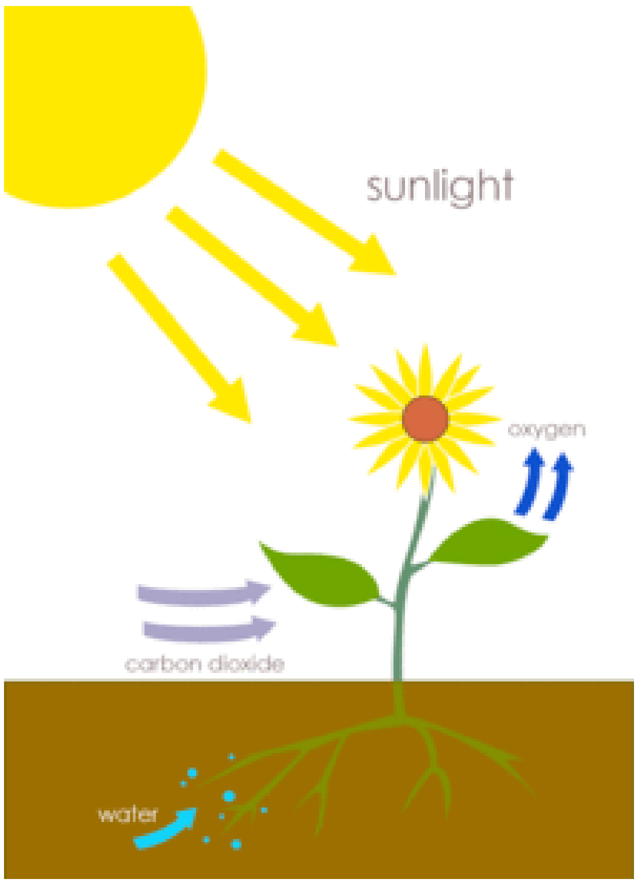


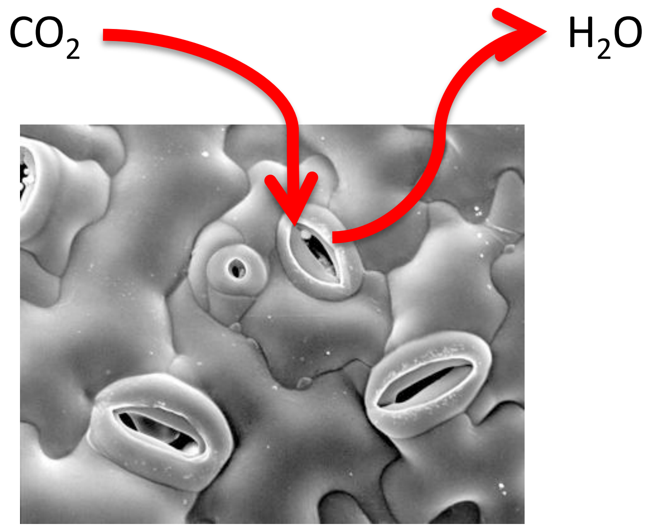


$$CO_2 + H_2O + light \rightarrow CH_2O + O_2$$

Carbon and water cycling

Photosynthesis



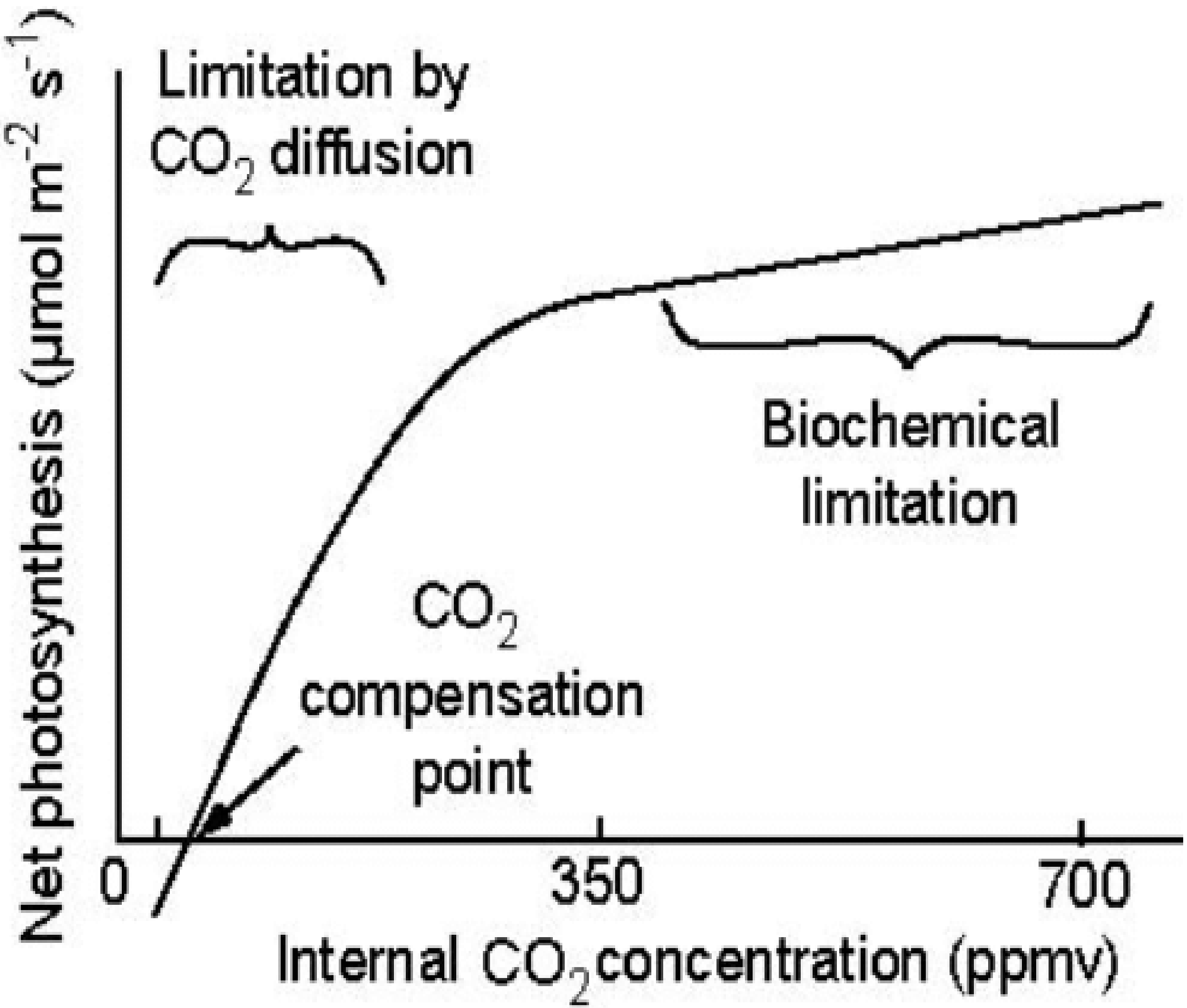


Trade off:

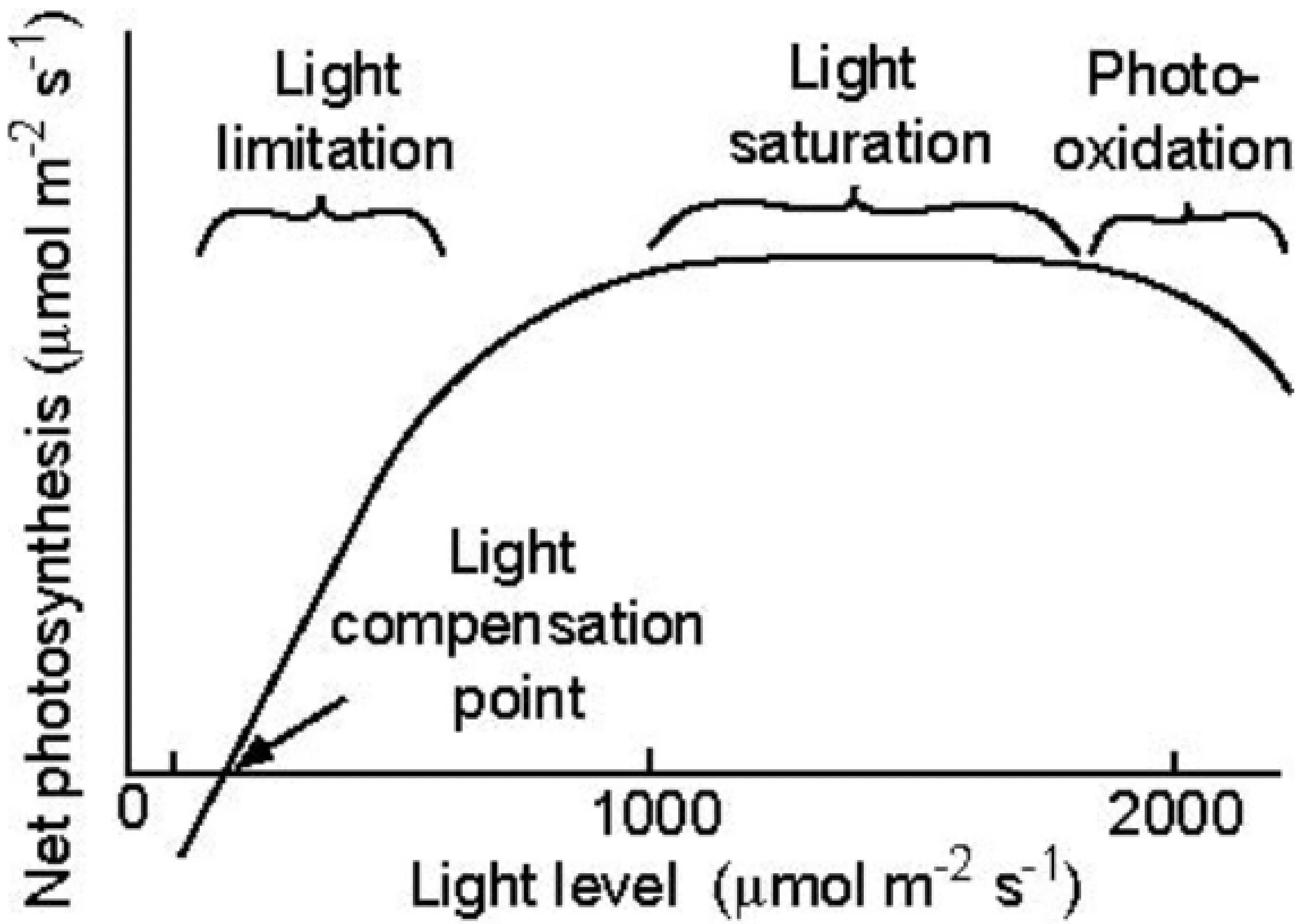
Gain carbon and water loss

$$CO_2 + H_2O + \text{light} \rightarrow CH_2O + O_2$$

CO_2 response curve of photosynthesis



Light response curve of photosynthesis

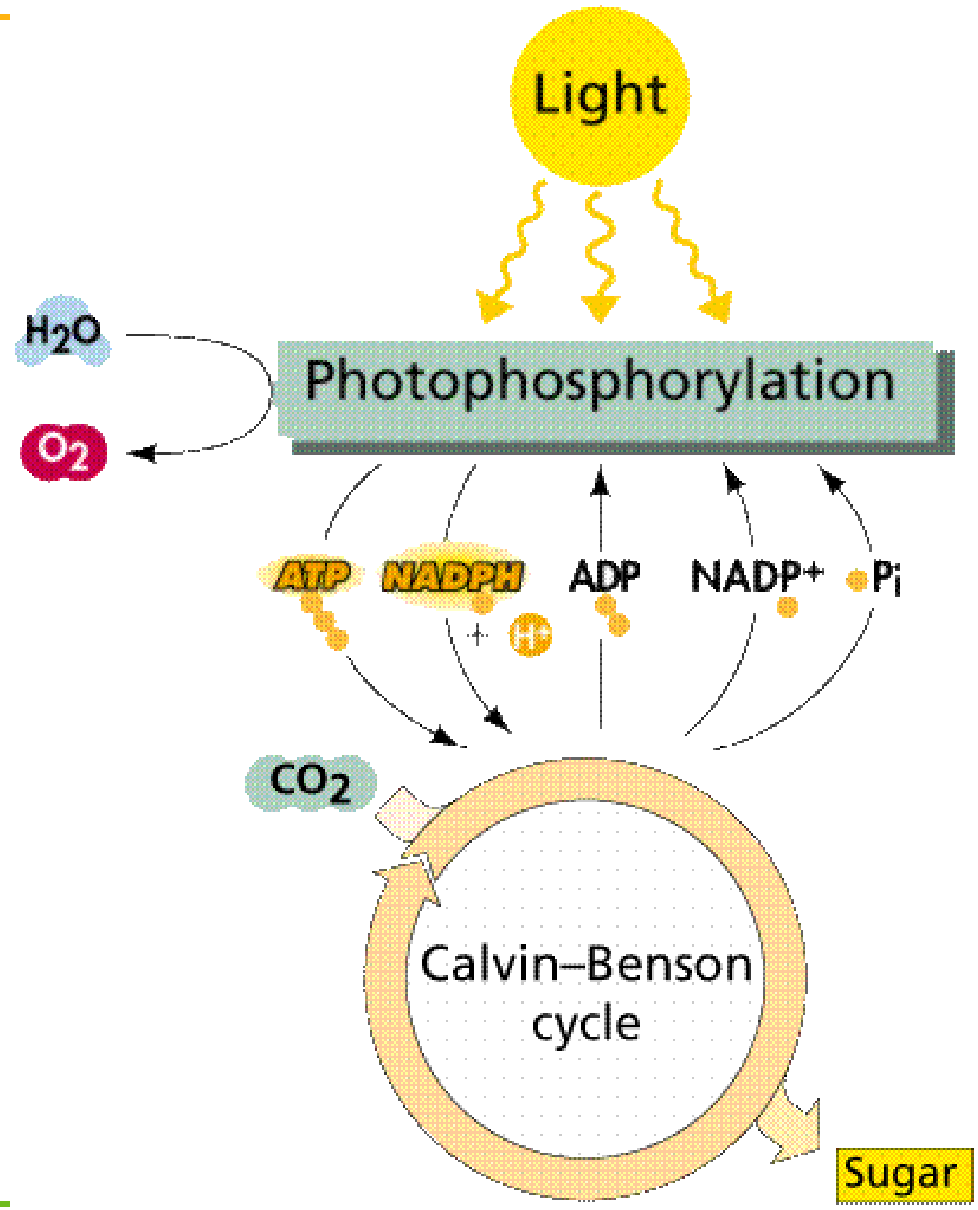


Calvin cycle

Photosynthesis
Two sets of reactions:

Light harvesting
- converts light energy to chemical energy (ATP, NADPH)
- splits H_2O and produces O_2 as byproduct

Carbon fixing
- uses ATP and NADPH from light reactions to fix CO_2 into sugar



Models for photosynthesis

1. Empirical
- **Light-use efficiency**

2. Mechanistic
- Diffusion based

3. Semi-empirical
- Biochemical

Montieth 1977:
Biomass accumulation correlated with light interception

"Conversion efficiency" can be used to estimate gross primary production

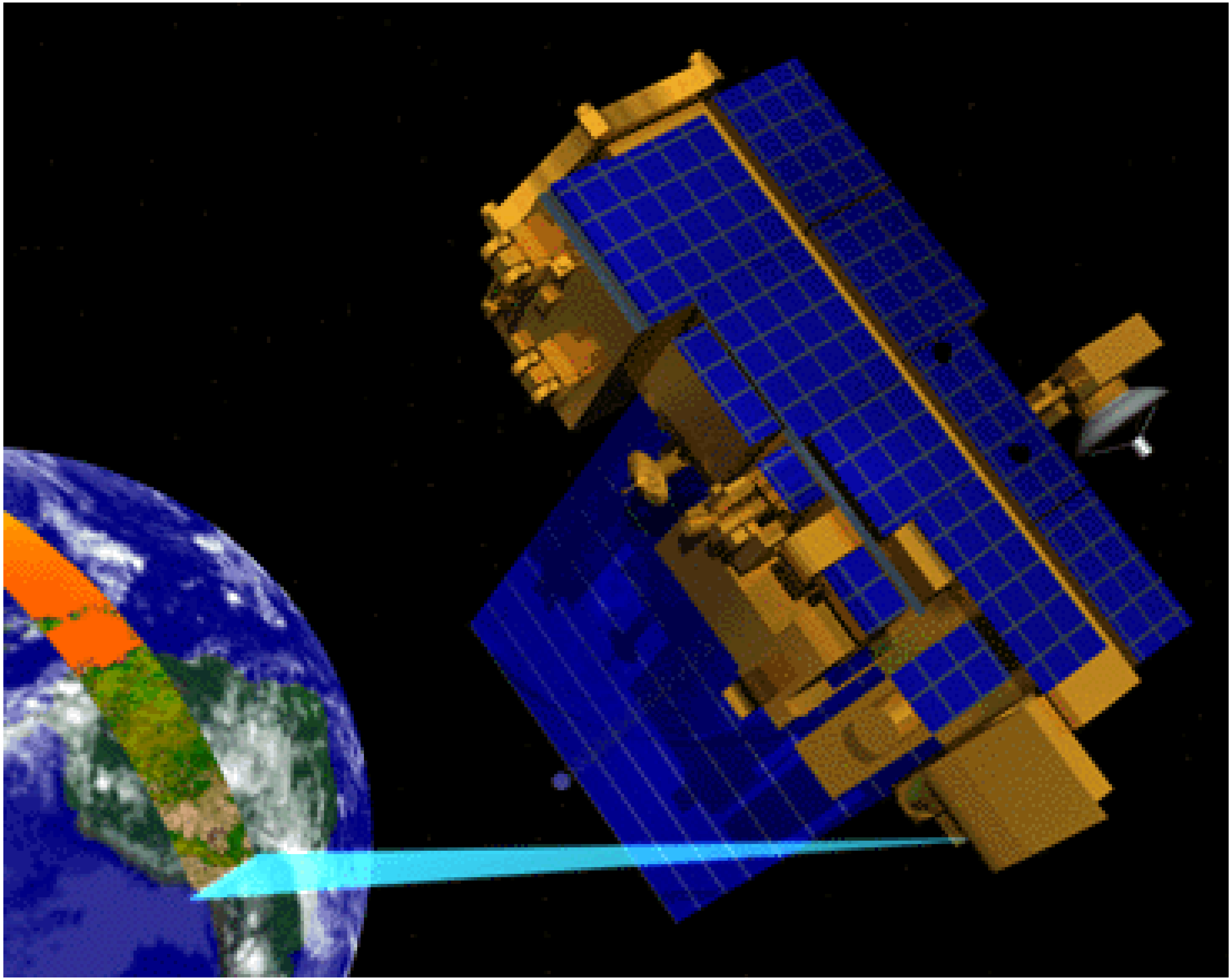
Global estimates first used in CASA (Field et al. 1998, Sellers et al. 1992):

$$\mathrm{NPP} = f(\mathrm{NDVI}) \times \mathrm{PAR} \times \varepsilon^* \times g(T) \times h(W)$$

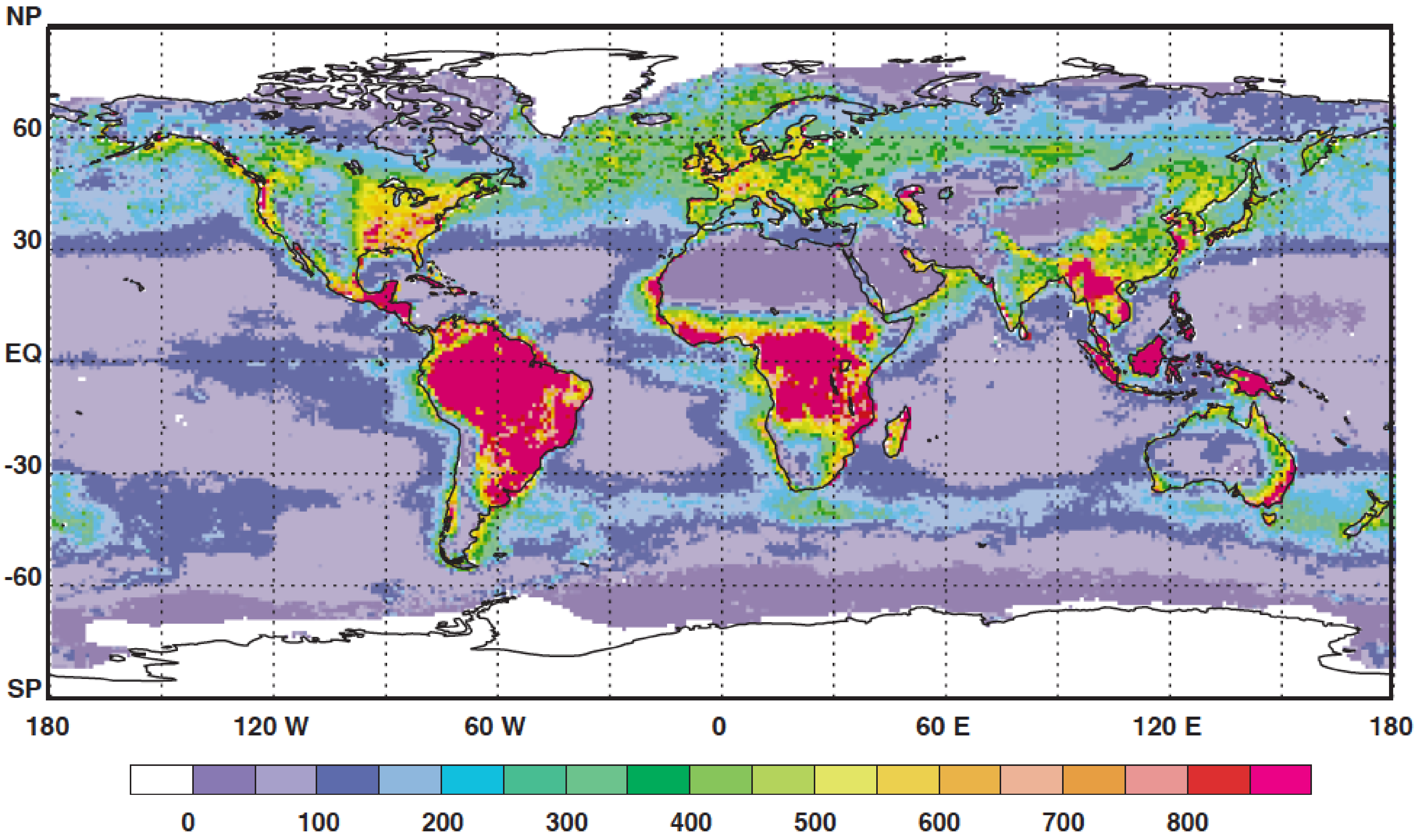
Later used in BIOME BGC and MODIS NPP models

Limited to period of calibration

Carbon and water cycling



Carbon and water cycling

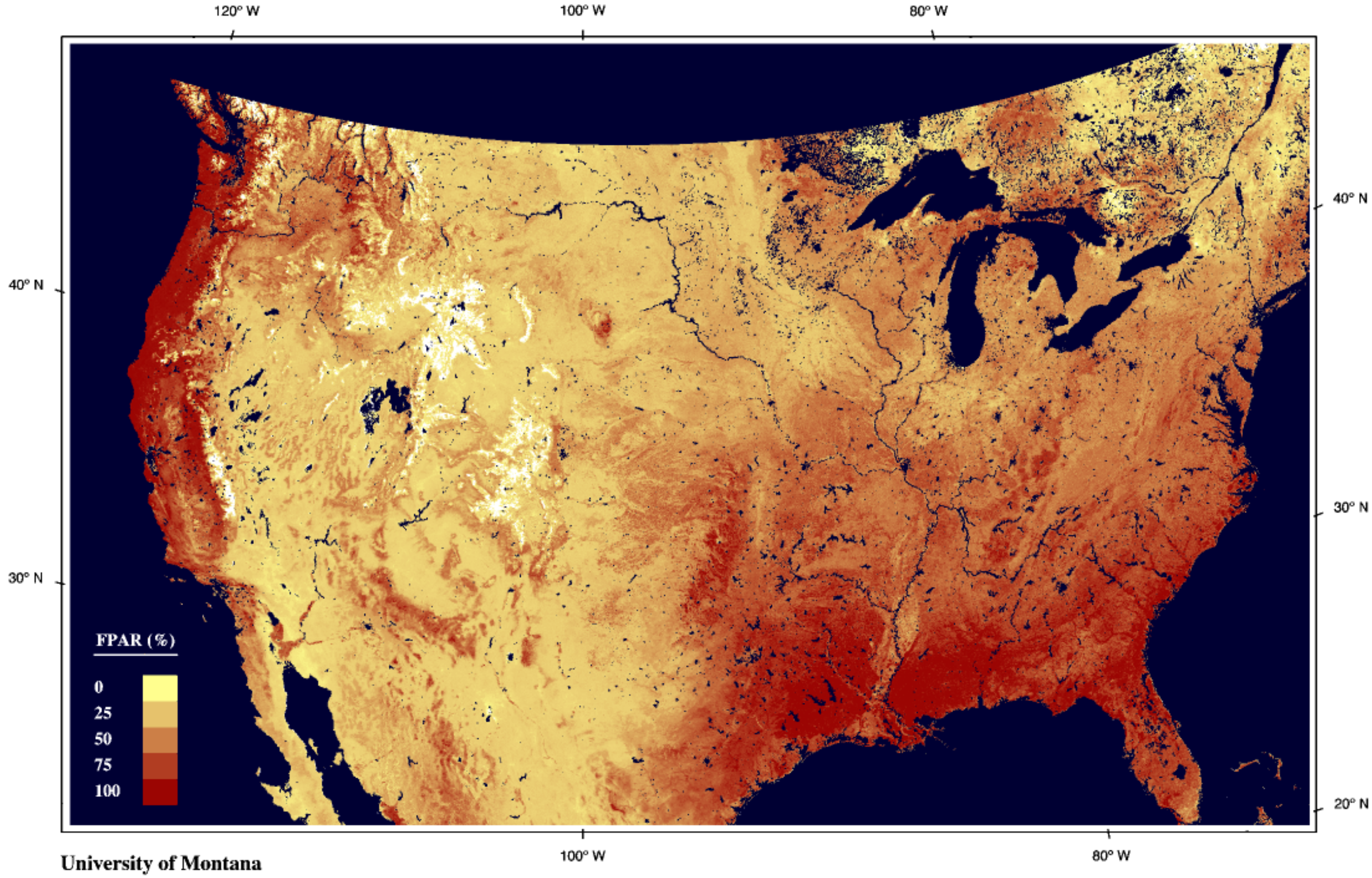


Carbon and water cycling

MODIS FPAR

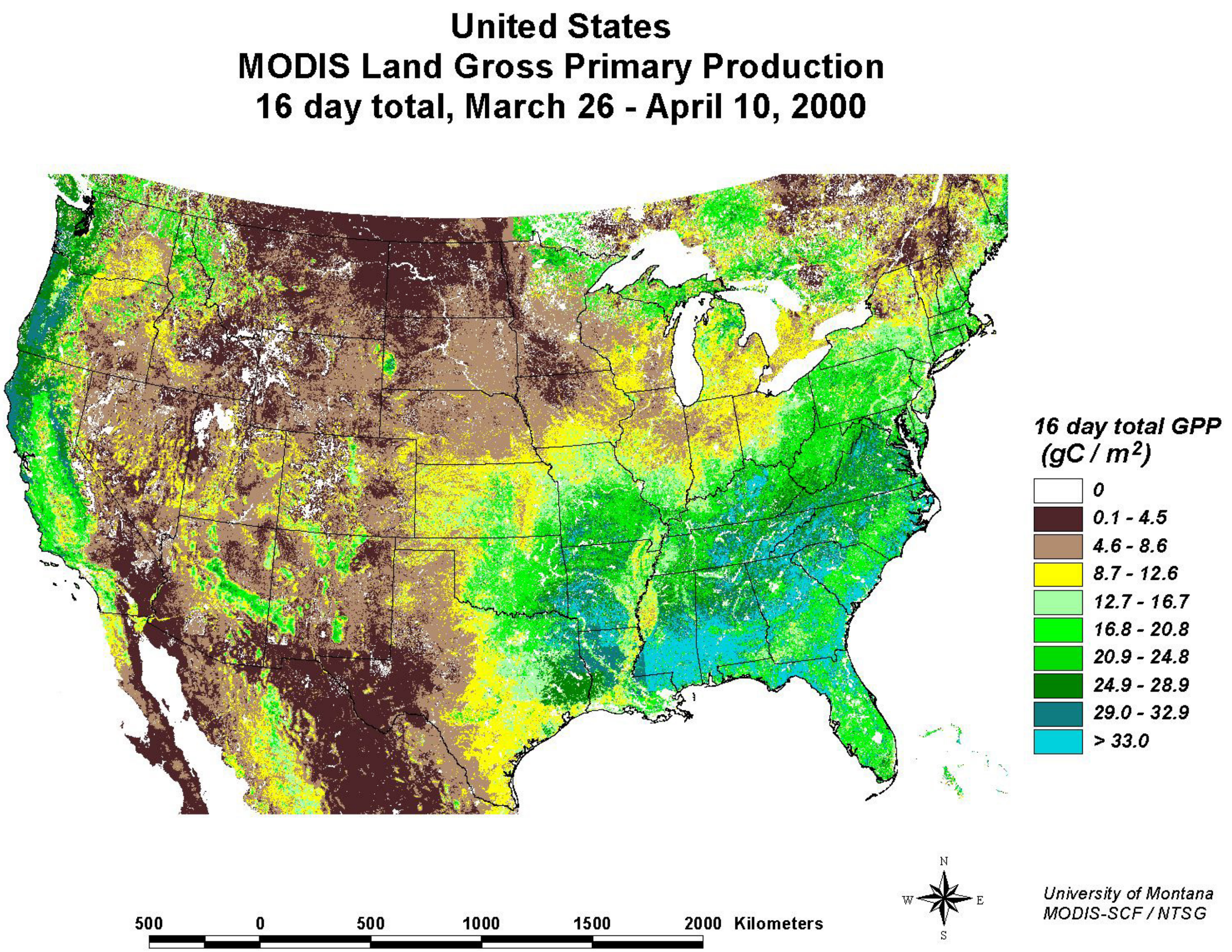
(Fraction of Photosynthetically Active Radiation)

Composite March 24 - April 8, 2000



University of Montana
Science Compute Facility

Carbon and water cycling



Models for photosynthesis

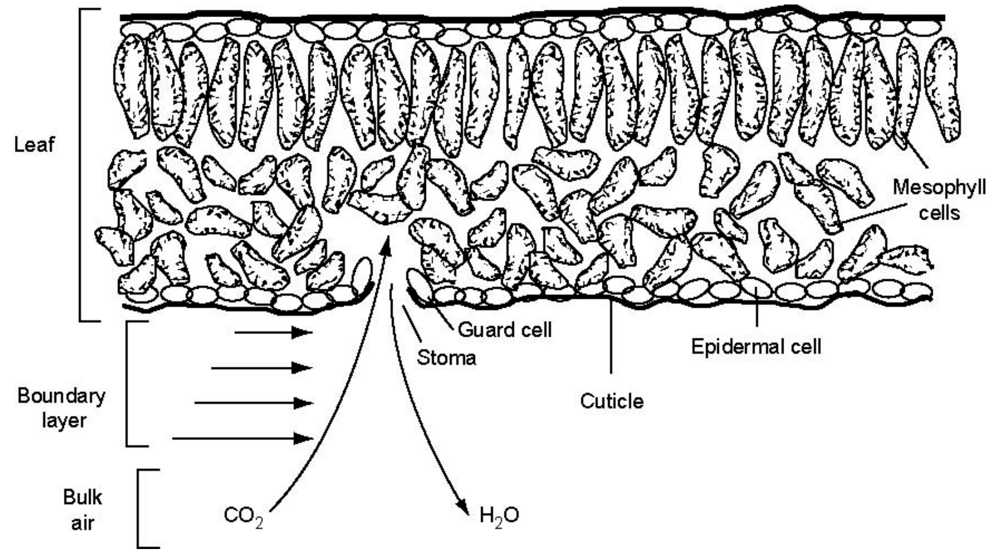
1. Empirical
- Light-use efficiency

2. Mechanistic
- **Diffusion based**

3. Semi-empirical
- Biochemical

Fick's law of diffusion

$$A_{n,leaf} = g_c(C_{ca} - C_{ci})$$



Does not work well for low light & high humidity

Models for photosynthesis

1. Empirical
- Light-use efficiency

2. Mechanistic
- Diffusion based

3. Semi-empirical
- **Biochemical**

$$A = \min\begin{Bmatrix} J_E \\ J_C \\ J_S \end{Bmatrix}$$

$$J_E = \frac{\alpha_p e_m Q_p (C_{ci} - \Gamma^*)}{(C_{ci} - 2\Gamma^*)}$$

$$\Gamma^* = \frac{C_{oa}}{2\tau}$$

$$J_C = \frac{V_m (C_{ci} - \Gamma^*)}{C_{ci} + K_c (1 + C_{oa} / K_o)}$$

$$J_S = V_m / 2$$

Farquhar 1980
Collatz 1991

Models for photosynthesis

1. Empirical
- Light-use efficiency

2. Mechanistic
- Diffusion based

3. Semi-empirical
- **Biochemical**

$$V_m = \frac{V_{m,25}\exp[0.088(T_L - 25)]}{1 + \exp[0.29(T_L - 41)]}$$

$$A = \min\begin{Bmatrix} J_E \\ J_C \\ J_S \end{Bmatrix}$$

$$R_d = \frac{R_{d,25}\exp[0.069(T_L - 25)]}{1 + \exp[1.3(T_L - 55)]}$$

$$K_c, \tau, K_o, V_m, R_d$$

$$k = k_{25}\exp[q(T_L - 25)]$$

Models for photosynthesis

$$A = \min \begin{Bmatrix} J_E \\ J_C \\ J_S \end{Bmatrix}$$

$$J_P = \frac{J_E + J_C - \sqrt{(J_E + J_C)^2 - 4\theta J_E J_C}}{2\theta}$$

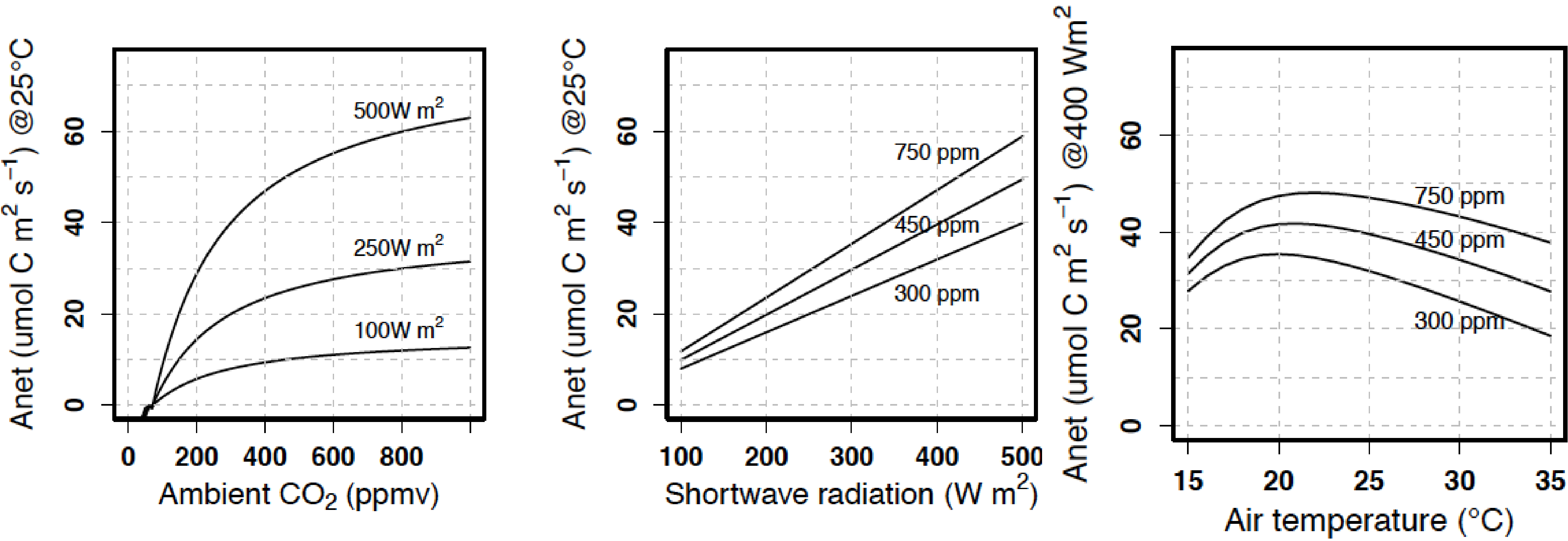
$$A = \frac{J_P + J_S - \sqrt{(J_P + J_S)^2 - 4\beta J_P J_S}}{2\beta}$$

$$A_{net} = A - R_d \qquad R_d = 0.015 V_m$$

Co-limitation rather than sharp transition

- No co-limitation in ORCHIDEE
- Strong colimitation in LPJ (no Js)

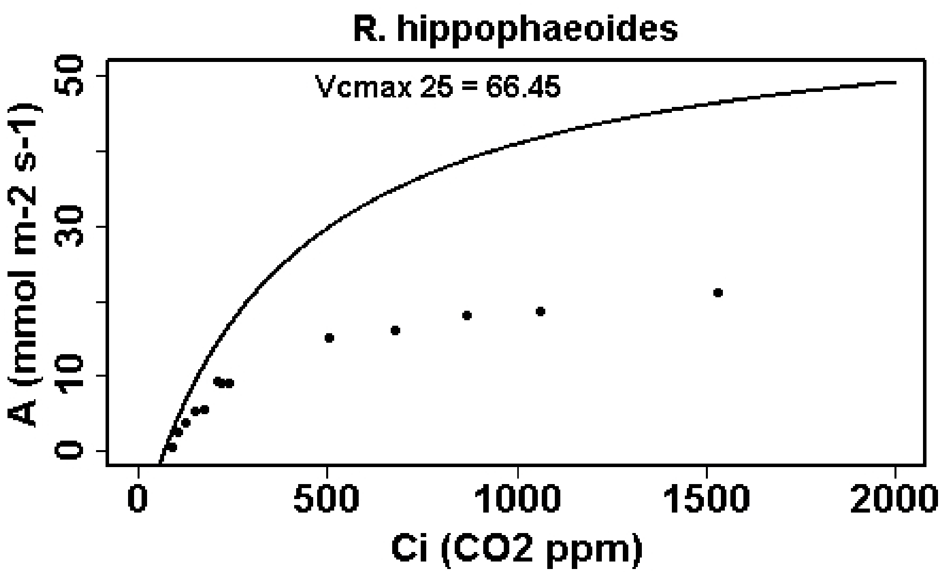
Biochemical model response curves



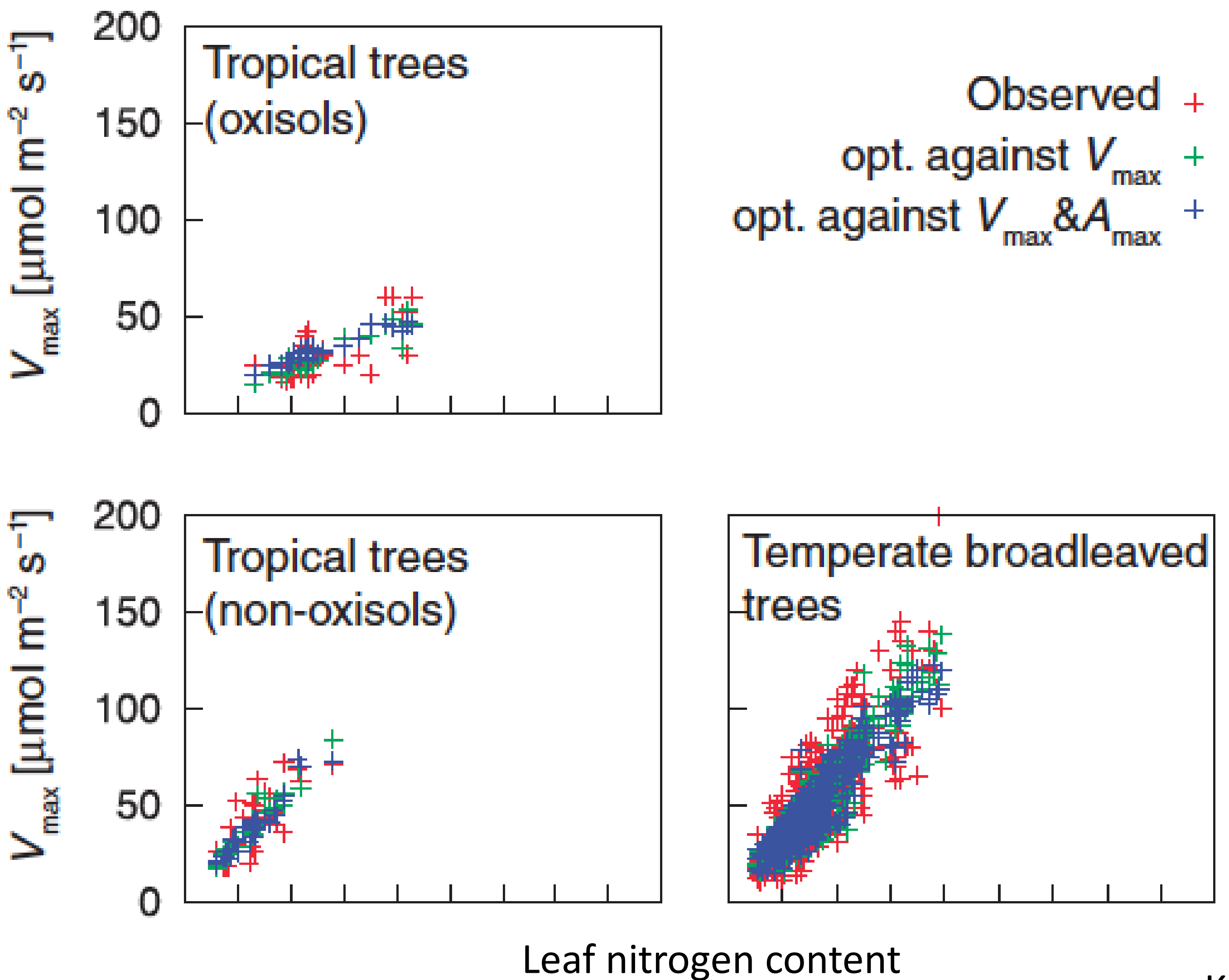
Vcmax

- Vcmax and Ci are needed
- Vcmax: Maximum rate of carboxylation
- Measure with:
  - Field measurements

$$J_C = \frac{V_m(C_{ci} - \Gamma^*)}{C_{ci} + K_c(1 + C_{oa} / K_o)}$$



Carbon and water cycling



Kattge 2009

Vcmax

- Vcmax and Ci are needed
- Vcmax: Maximum rate of carboxylation
- Measure with:
  - Field measurements
  - Modeled (Haxeltine and Prentice 1996)
    - Optimization algorithm based on evidence that N content and Rubisco activity vary vertically within the canopy and seasonally
    - Takes form of light-use efficiency model

$$J_C = \frac{V_m(C_{ci} - \Gamma^*)}{C_{ci} + K_c(1 + C_{oa} / K_o)}$$

$$V_m = (1 / b_{C3})\,(C1_{C3} / C2_{C3})\,[(2\theta - 1)s - (2\theta s - C2_{C3})\sigma]\ \mathrm{APAR}$$

Vcmax

- Vcmax and Ci are needed
- Vcmax: Maximum rate of carboxylation
- Measure with:
  - Field measurements
  - Modeled (Haxeltine and Prentice 1996)
  - Estimate from leaf nitrogen (Cox 1998)

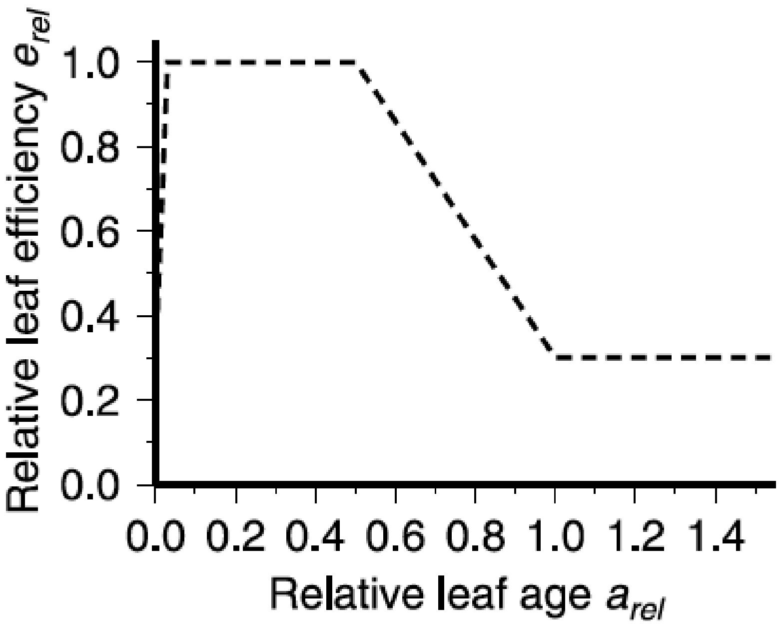
$$J_C = \frac{V_m(C_{ci} - \Gamma^*)}{C_{ci} + K_c(1 + C_{oa} / K_o)}$$

$$V_{c,\max} = n_2 N$$

Vcmax

- Vcmax and Ci are needed
- Vcmax: Maximum rate of carboxylation
- Measure with:
  - Field measurements
  - Modeled (Haxeltine and Prentice 1996)
  - Estimate from leaf nitrogen (Cox 1998)
  - Prescribe from observation (Viovy 1996)
    - Modify for leaf age
    - Soil moisture
    - Canopy position (follow light extinction)

$$J_C = \frac{V_m(C_{ci} - \Gamma^*)}{C_{ci} + K_c(1 + C_{oa} / K_o)}$$

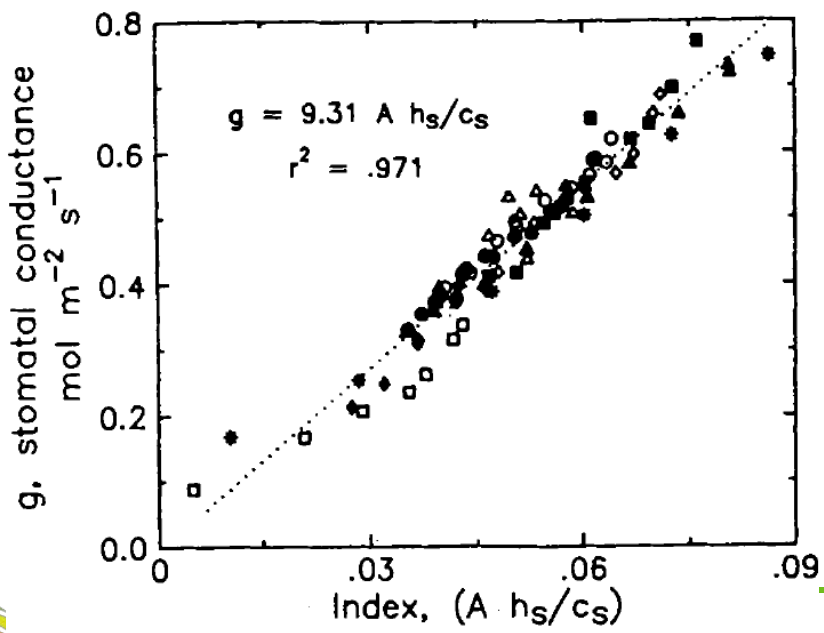


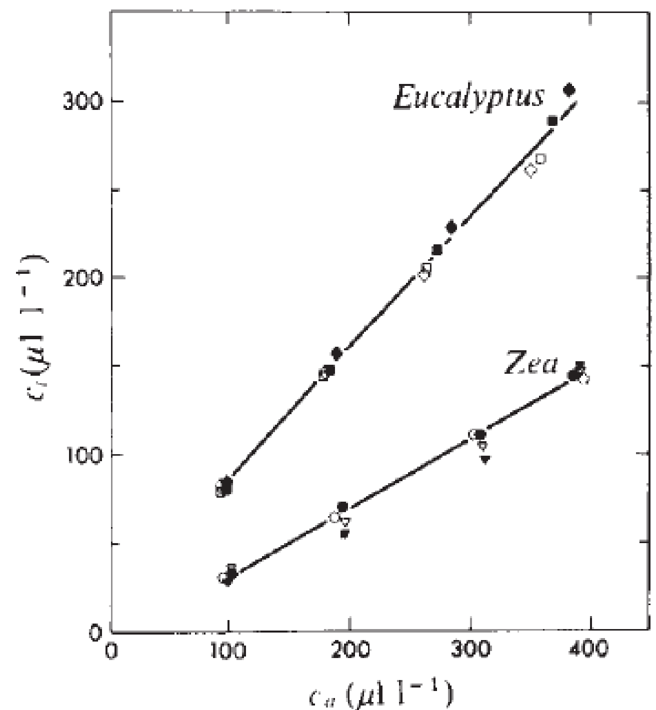
Internal leaf CO_2 concentration

- Still need Ci
- Depends on stomata and rate of photosynthesis
- Constant Ci/Ca (Wong 1979
  - Suggests stomates optimize A / T

$$J_C = \frac{V_m(C_{ci} - \Gamma^*)}{C_{ci} + K_c(1 + C_{oa} / K_o)}$$

$$g_c = \frac{A_{n,leaf}}{(C_{ca} - C_{ci})}$$





Internal leaf CO_2 concentration

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  - Suggests stomates optimize A / T

$$J_C = \frac{V_m (C_{ci} - \Gamma^*)}{C_{ci} + K_c (1 + C_{oa} / K_o)}$$

$$A_{n,leaf} = g_c (C_{ca} - C_{ci}) \quad \rightarrow \quad C_{ci} = \frac{A_{n,leaf}}{g_c} + C_{ca}$$

Internal leaf CO_2 concentration

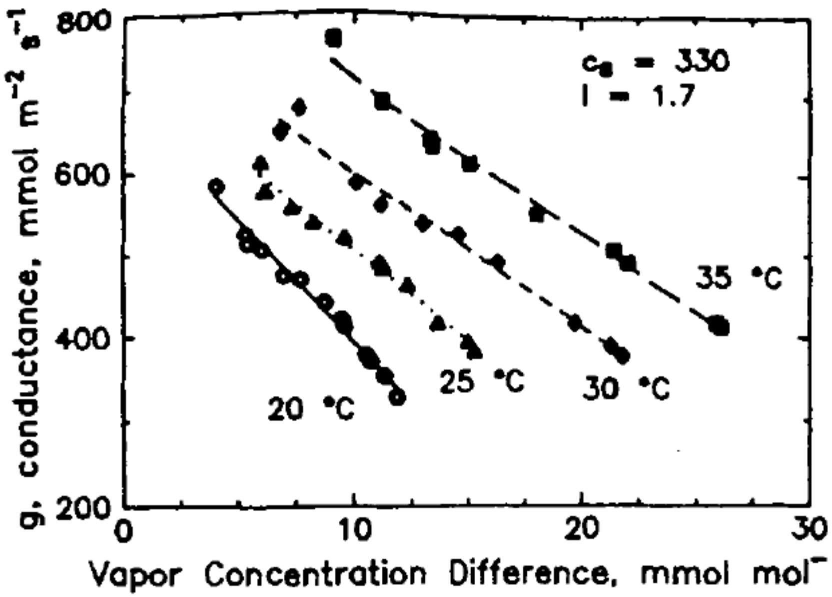
- Conductance model is required to relate assimilation and stomatal conductance to the gradient of CO_2 between the atmosphere and Rubisco

$$J_C = \frac{V_m(C_{ci} - \Gamma^*)}{C_{ci} + K_c(1 + C_{oa}/K_o)}$$

- Stomata respond to:
  - Light
  - CO2
  - Humidity
  - VPD
  - Soil moisture

- Ball-Berry model:

$$g_{cs} = m\frac{A_n h_s}{C_{cs}} + b$$



Ball et al. 1987

Internal leaf CO_2 concentration

- Conductance model is required to relate assimilation and stomatal conductance to the gradient of CO_2 between the atmosphere and Rubisco

$$J_C = \frac{V_m(C_{ci} - \Gamma^*)}{C_{ci} + K_c(1 + C_{oa} / K_o)}$$

- Stomata respond to:
  - Light
  - CO2
  - Humidity
  - VPD
  - Soil moisture

- Simultaneous solution for A, Ci, and Gc

$$g_{cs} = m\frac{A_n h_s}{C_{cs}} + b \qquad A_{n,leaf} = g_c(C_{ca} - C_{ci}) \qquad A_{net} = A - R_d$$

Model application

- ORCHIDEE
  - Farquhar photosynthesis
    - Vmax – age and soil moisture limited
  - Ball-Berry conductance model
    - No direct soil moisture limitation

Table 1. PFTs and PFT-Specific Parameters in ORCHIDEE[a]

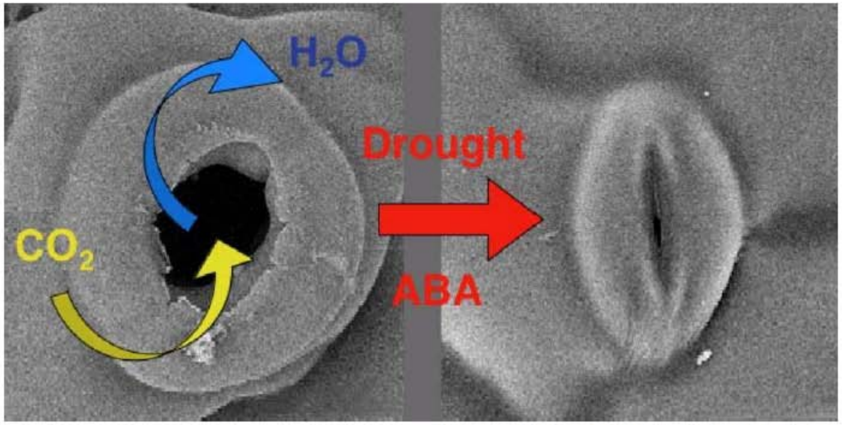
PFT	$V_{cmax,opt}$	T_{opt}	λ_{max}	z_{root}	α_{leaf}	h	A_c	T_s	H_s
TrBE	50	37	10	1.25	0.12	25	910	-	0.3
TrBR	60	37	10	1.25	0.14	25	180	-	0.3
TeNE	37.5	27	5	1.	0.14	15	910	-	-
TeBE	37.5	32	5	1.25	0.14	15	730	-	-
TeBS	37.5	28	5	1.25	0.14	15	180	12.5	-
BoNE	37.5	25	4.5	1.	0.14	10	910	-	-
BoBS	37.5	25	4.5	1.	0.14	10	180	5	-
BoNS	35	25	4	1.25	0.14	10	180	7	-
NC3	70	$27.5 + 0.25T_l$	2.5	0.25	0.20	0.2	120	4	0.2
NC4	70	36	2.5	0.25	0.20	0.2	120	5	0.2
AC3	90	$27.5 + 0.25T_l$	6	0.25	0.18	0.4	150	10	0.2
AC4	90	36	3	0.25	0.18	0.4	120	10	0.2

Model application

Symbol	Value	Units	Q_{10}	Description
K_c	30[a]	Pa	2.1	Michaelis constant for CO_2
K_o	30[a]	kPa	1.2	Michaelis constant for O_2
τ	2600[b]		0.57	CO_2/O_2 specificity ratio
α_{C3}	0.08[a]			C_3 quantum efficiency
b_{C3}	0.015[c]			R_d/V_m ratio for C_3 plants
λ_{mC3}	0.7[d]			optimal c_i/c_a for C_3 plants
α_{C4}	0.053[e]			C_4 quantum efficiency
b_{C4}	0.035			R_d/V_m ratio for C_4 plants
λ_{mC4}	0.4			optimal c_i/c_a for C_4 plants
α_a	0.5			scaling parameter for α
c_a	340	$\mu mol\ mol^{-1}$		ambient mole fraction CO_2
P	100	kPa		atmospheric pressure
O_2	20.9	kPa		partial pressure O_2
C_{mass}	12	$g\ mol^{-1}$		molar mass of carbon
k	0.5[f]			extinction coefficient
θ	0.7[g]			co-limitation parameter

Model application

- LPJ
  - Farquhar photosynthesis
    - No soil moisture limitation
  - Haxeltine conductance model
    - If not enough soil moisture to sustain potential conductance, Gc is reduced, and Ci is reduced



Stomata in plant leaves

www.isv.cnrs-gif.fr/jg/images/stomata.jpg

Scaling from leaves to canopies

- Real canopies
  - LAI gradients
  - Leaf angle
  - Shade/sun
  - N gradients
  - Light gradients
  - …

$$\mathrm{FPAR} = 1 - \exp(-k\,\mathrm{LAI})$$

$$N_0 = N_{can} k / f_{PAR}$$

$$A_{can} = A_0 f_{PAR} / k$$

- Big leaf: assumes that canopy carbon fluxes have the same relative responses to the environment as any single leaf, and that the scaling from leaf to canopy is therefore linear.
  - Beer's Law
    - Integrate over vertical canopy layers

- Two-layer:
  - Sun – shade division
  - Diffuse vs direct light

Take home message

- Coupled approach must be used to model photosynthesis (Anet)
  - Gc
  - Ci

- Leaf to canopy scaling requires integration over non-linear processes

- Move beyond semi-empirical approaches
  - Medlyn 2011

$$E - \lambda A$$

- Plenty of uncertainties to explore
  - Temperature sensitivities
  - Light sensitivities
  - CO_2 sensitivities
  - Nutrient sensitivities
  - Vcmax
  - Vertical canopy gradients

Recommended reading

- Books
  - An introduction to environmental biophysics (Campbell and Norman 1998)
  - Physicochemical and Environmental Plant Physiology (Nobel 1999)

- Some papers

  - Wong, S. and I. F. Cowan, G. (1979). "Stomatal conductance correlates with photosynthetic capacity." Nature **282**: 424-426.
  - Farquhar, G. D., S. von Caemmerer, et al. (1980). "A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species." Planta **149**: 78-90.
  - Collatz, G. J., J. T. Ball, et al. (1991). "Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: A model that includes a laminar boundary layer." Agricultural and Forest Meteorology **54**: 107-136.
  - Sellers, P. J., J. A. Berry, et al. (1992). "Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme." Remote Sensing of Environment **42**: 187-216. Friend, A. D. (2001). "Modelling canopy CO2 fluxes: Are 'Big-Leaf' simplifications justified?" Global Ecology and Biogeography **10**(6): 603-619.
  - Damour, G., T. Simonneau, et al. (2010). "An overview of models of stomatal conductance at the leaf level." Plant, Cell and Environment **33**: 1419-1438.
  - Medlyn, B. E., R. A. Duursma, et al. (2011). "Reconciling the optimal and empirical approaches to modelling stomatal conductance." Global Change Biology: doi: 10.1111/j.1365-2486.2010.02375.x.