Theory of photosynthesis

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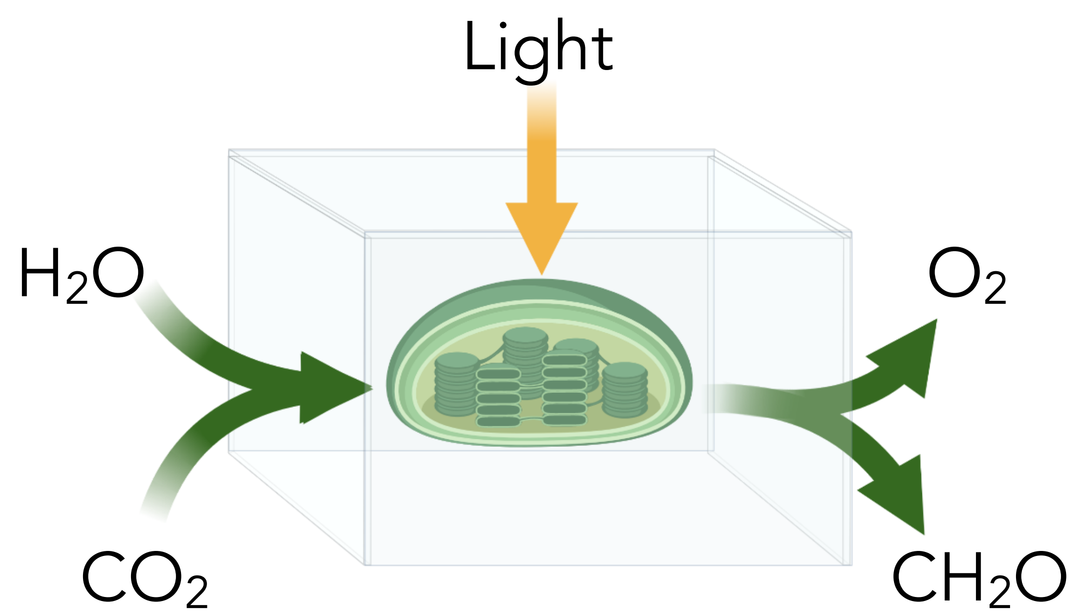
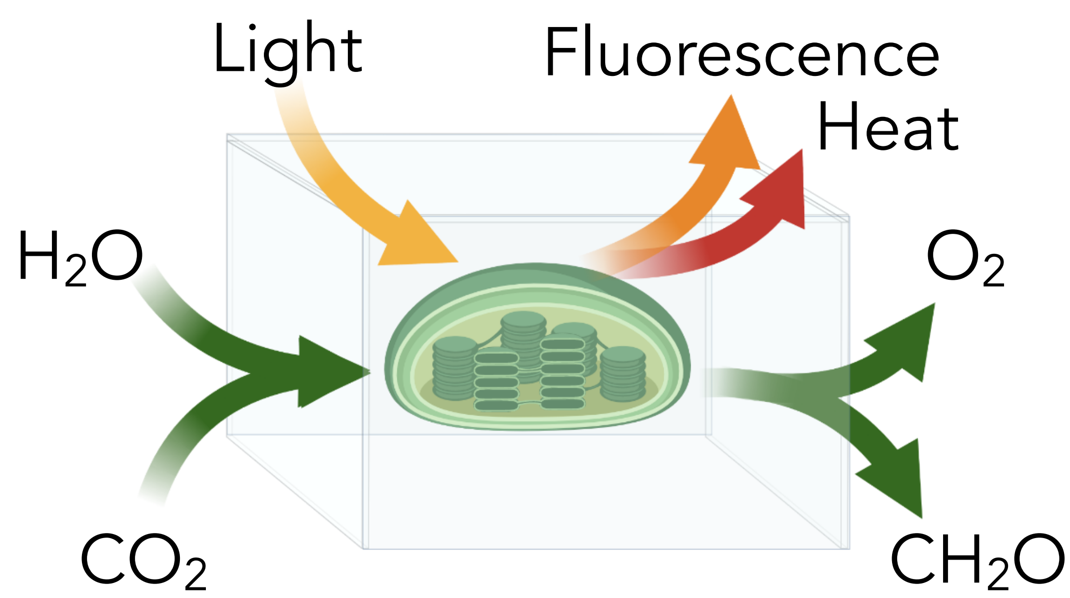
The traditional ecological perspective on photosynthesis:



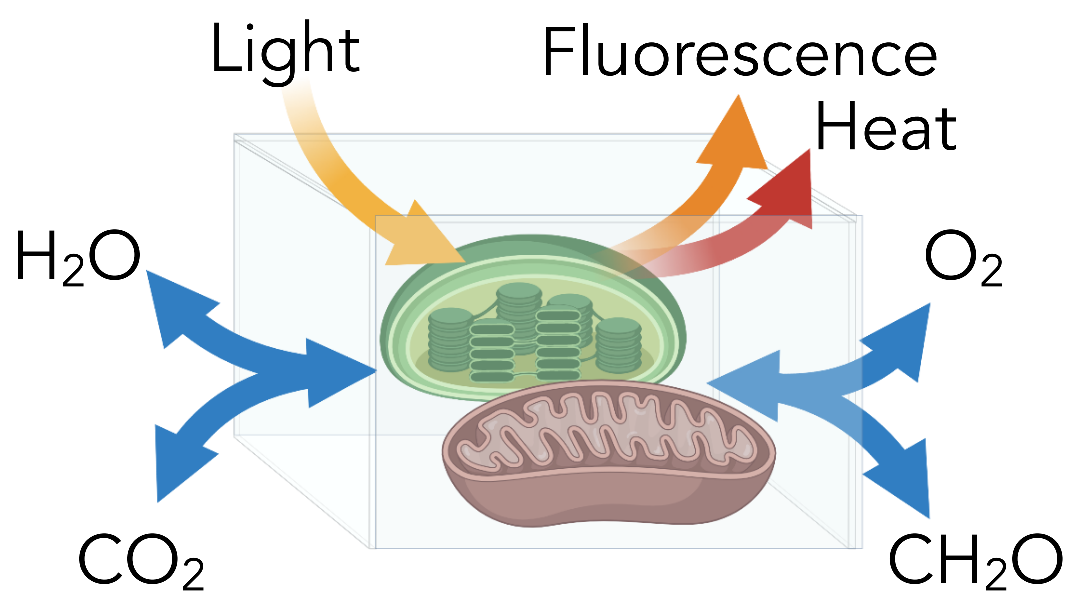
- Light capture splits water, generating chemical energy and releasing oxygen
- Chemical energy drives fixation of carbon dioxide into a stable organic form

The emerging ecological perspective on photosynthesis:



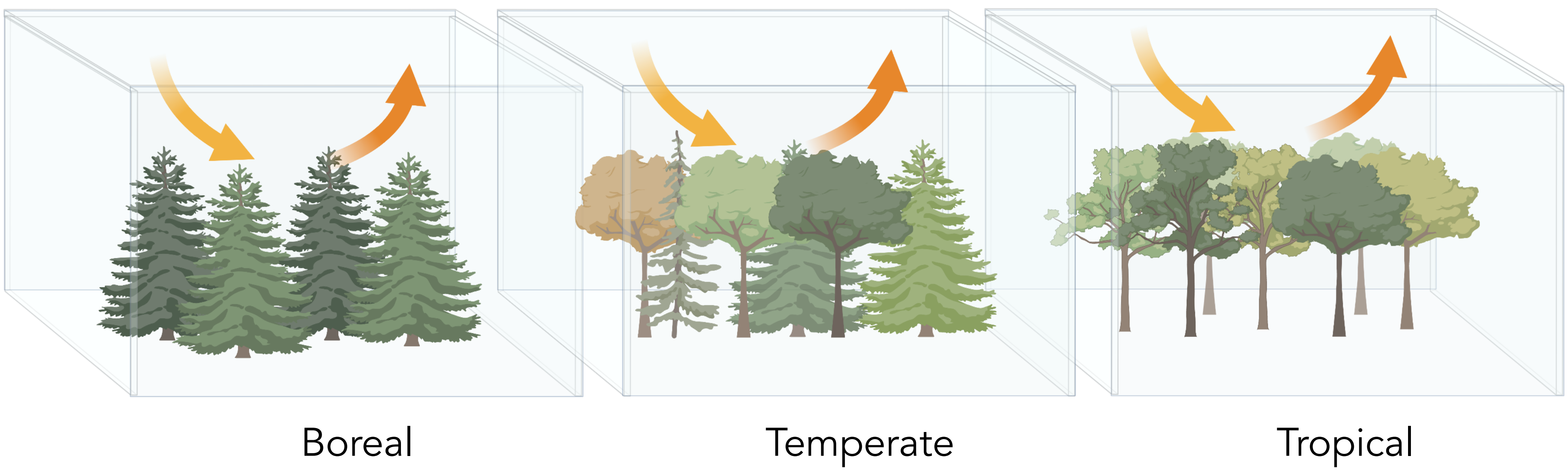
- Absorbed light is partitioned between photochemistry, heat, and fluorescence
- Shift driven by advances in proximal and remote sensing over past decade

Why this matters for ecologists:



- At scales for ecological analysis, there are mitochondria as well as chloroplasts
- Mitochondrial respiration reverses the photosynthetic trace gas fluxes

Why this matters for Fluxcourse:



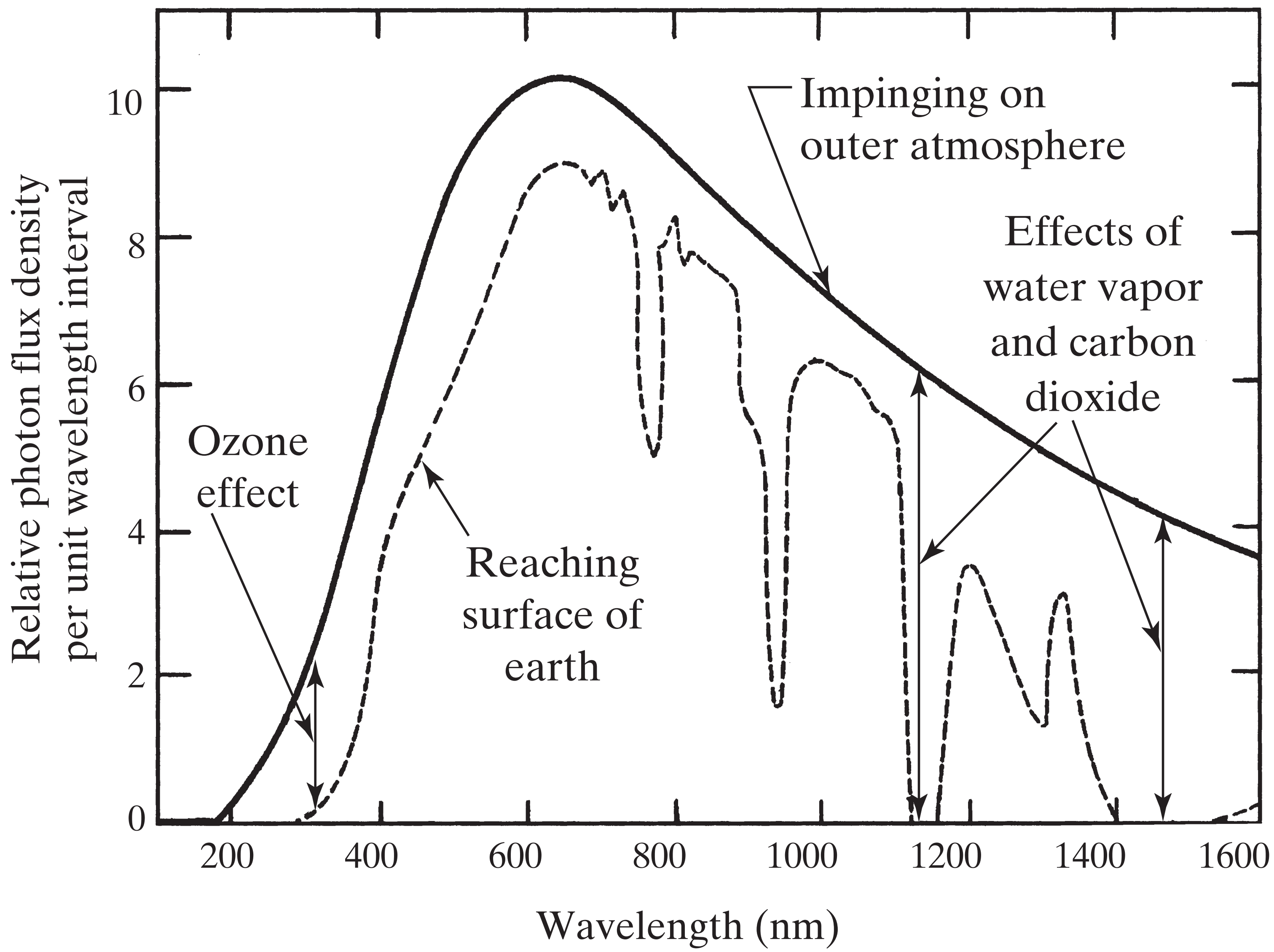
- We measure net fluxes of trace gases - then use theory to partition gross fluxes
- The absorption of light and release of fluorescence are unique to photosynthesis

Outline for today:

- Part 1: Environmental control of photosynthesis
  —Light: photons, photochemistry, and Cytochrome b6f
  —Carbon dioxide: diffusion, biochemistry, and Rubisco
  —Other resources and stressors

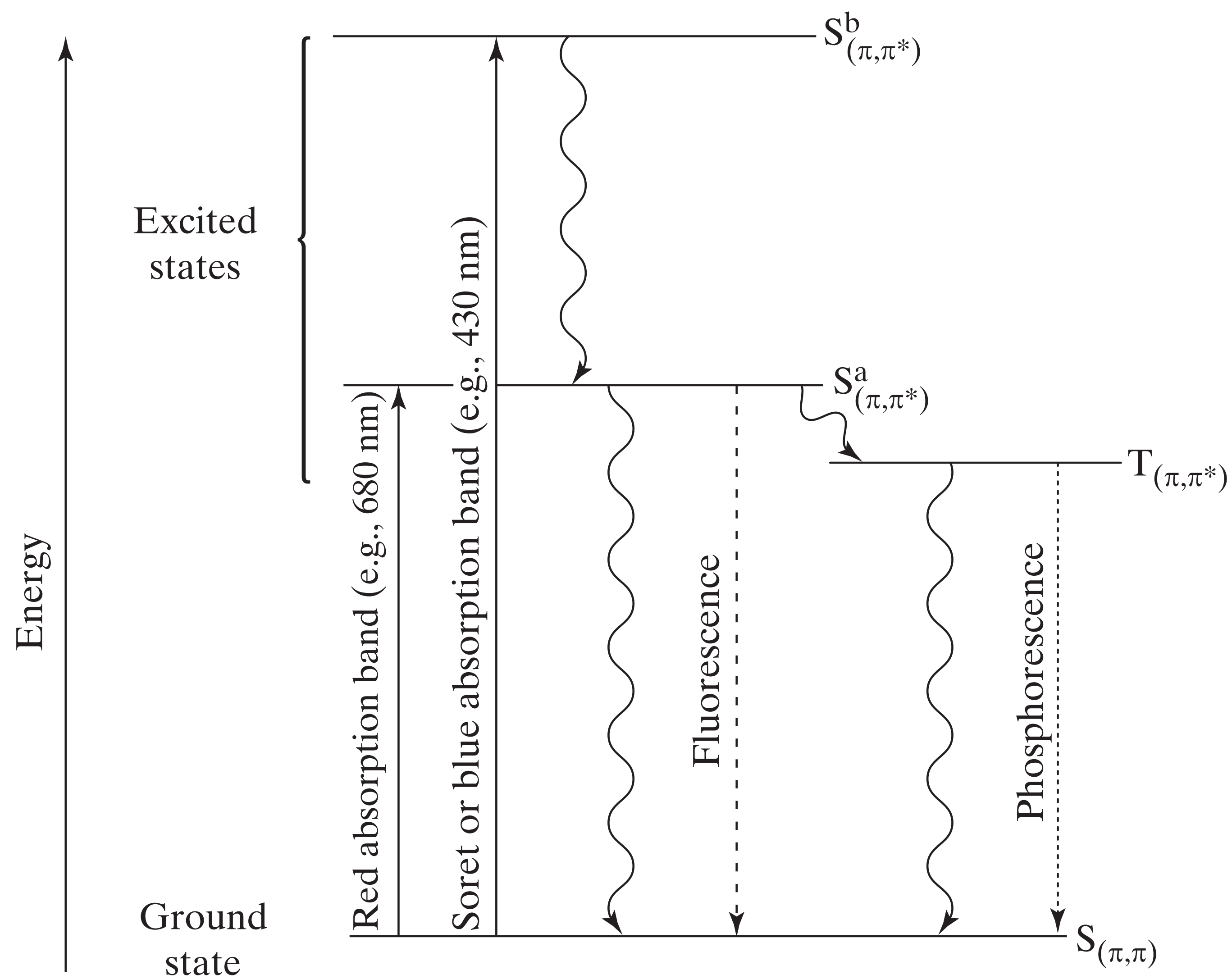
- Part 2: Quantitative expressions for photosynthesis
  —Top down: Monteith
  —Bottom up: Farquhar, von Caemmerer, and Berry
  —Connecting top down to bottom up: Johnson and Berry

The part of the solar spectrum that drives photosynthesis is called photosynthetically active radiation



- This is abbreviated "PAR", and includes wavelengths in the 400-700 nm range

Once photons are absorbed by chlorophyll, they have several potential fates



- For chlorophyll that is **isolated**:

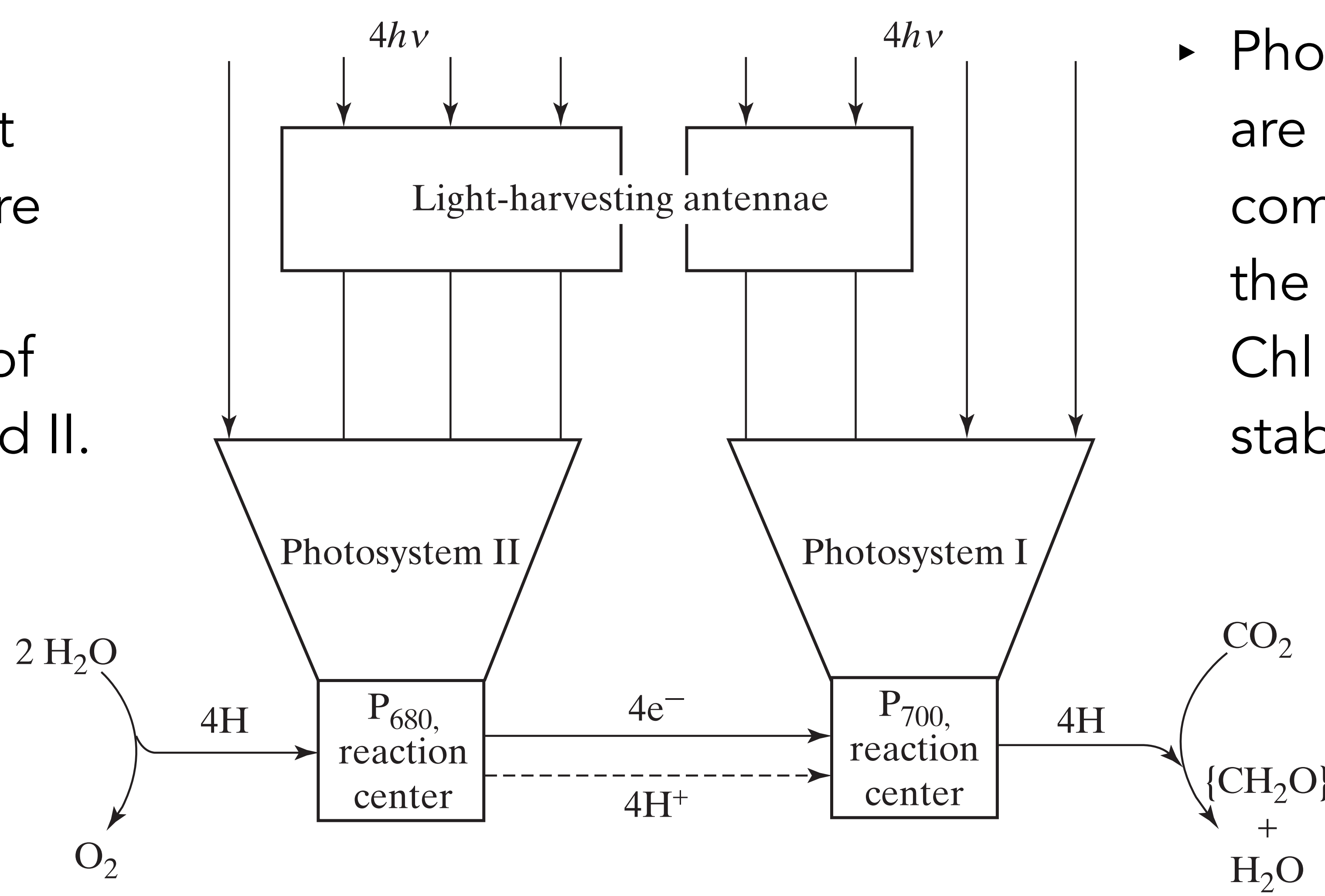
  Energy in from absorption
  is either lost as heat
  or lost as fluorescence.

- For chlorophyll in a **leaf**:

  Energy in from absorption
  either drives photochemistry
  or it escapes as heat
  or as fluorescence.

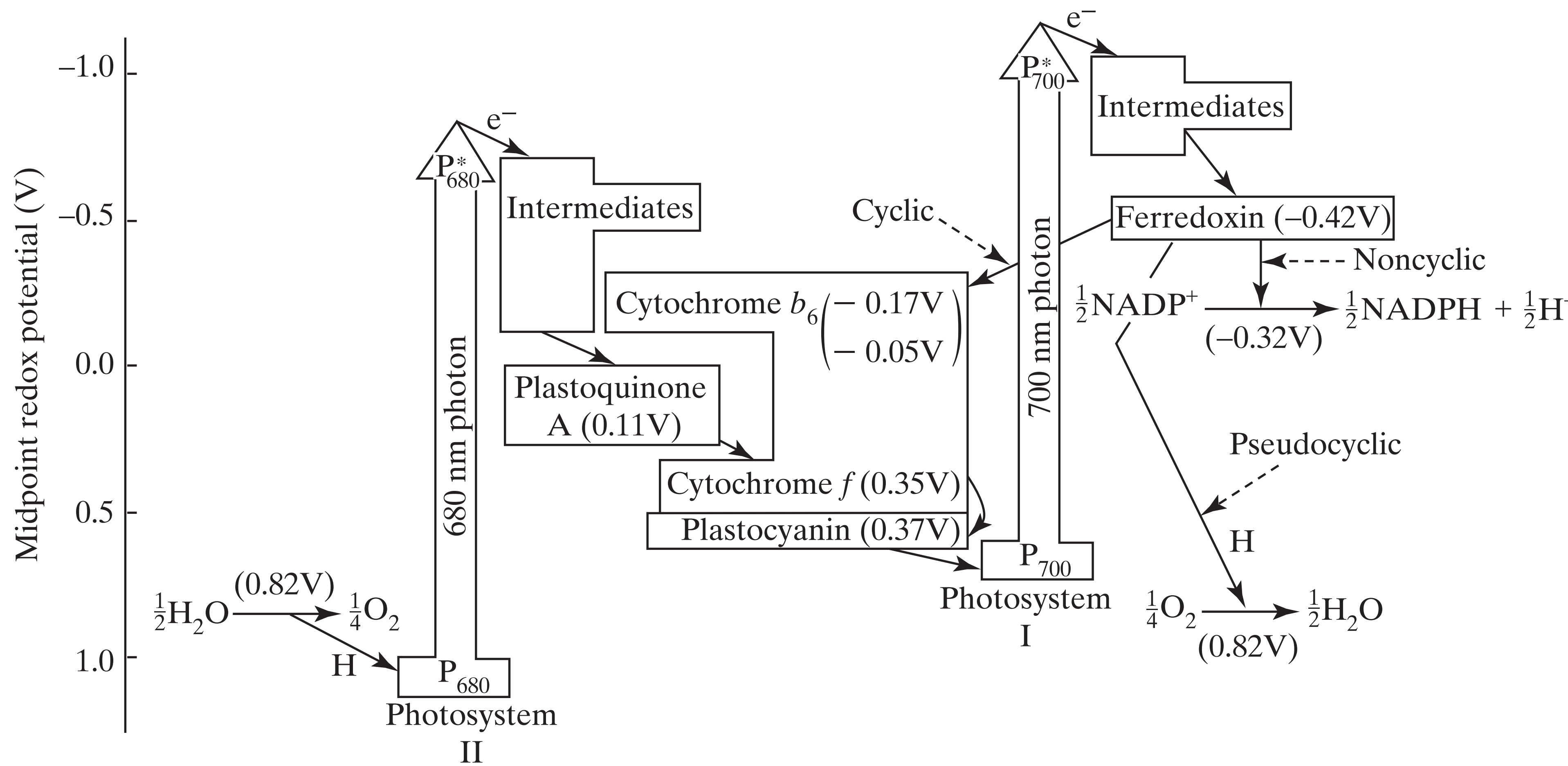
Photochemistry occurs when excitation from antennae pigments is trapped by the photosynthetic reaction centers

- Excitons circulate between pigment molecules, and are funneled to the reaction centers of Photosystem I and II.



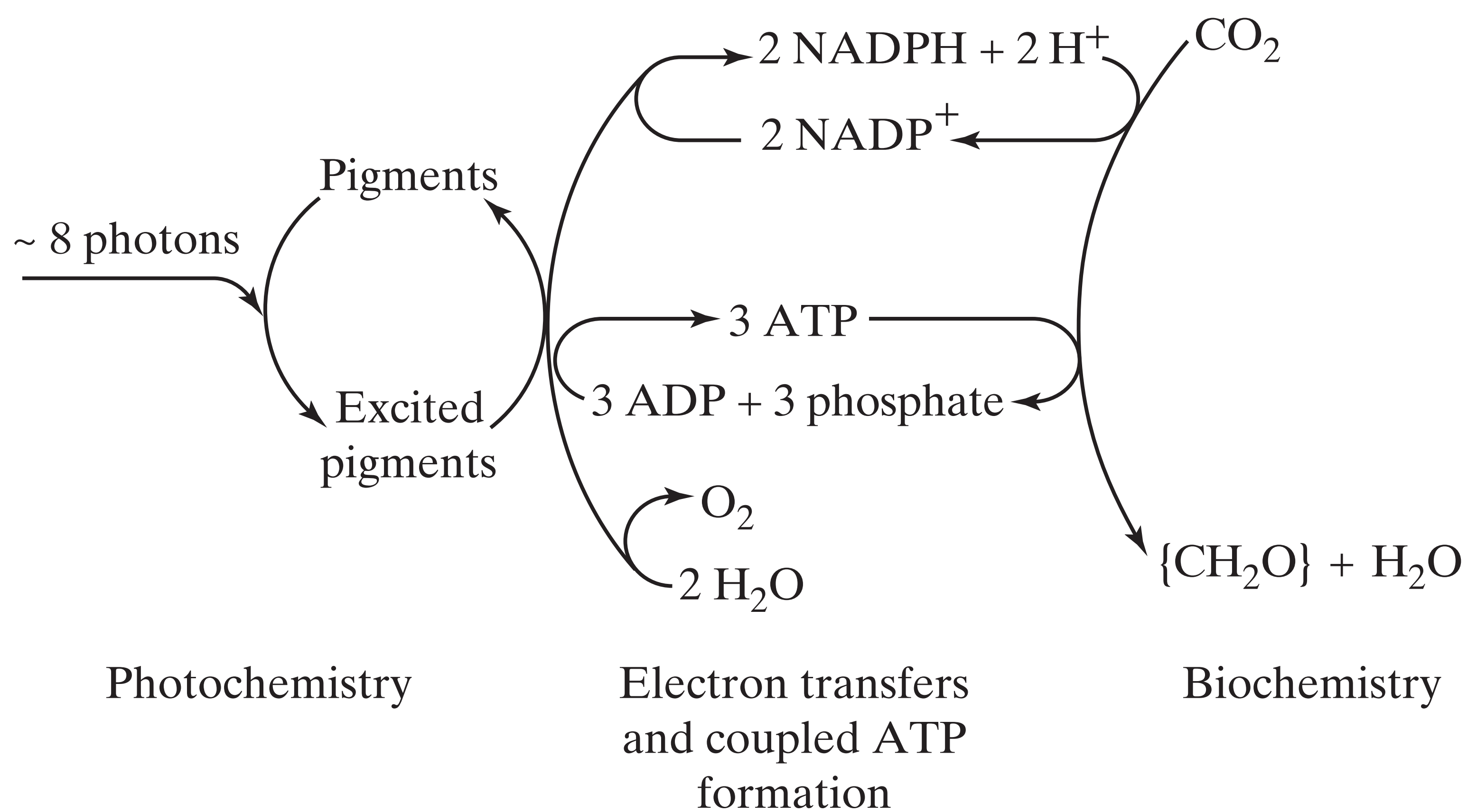
- Photosystem I and II are pigment-protein complexes that trap the energy from the Chl excited state in a stable chemical form.

Steady-state electron flow through Photosystems II and I is limited by an enzyme called the Cytochrome b_6f complex



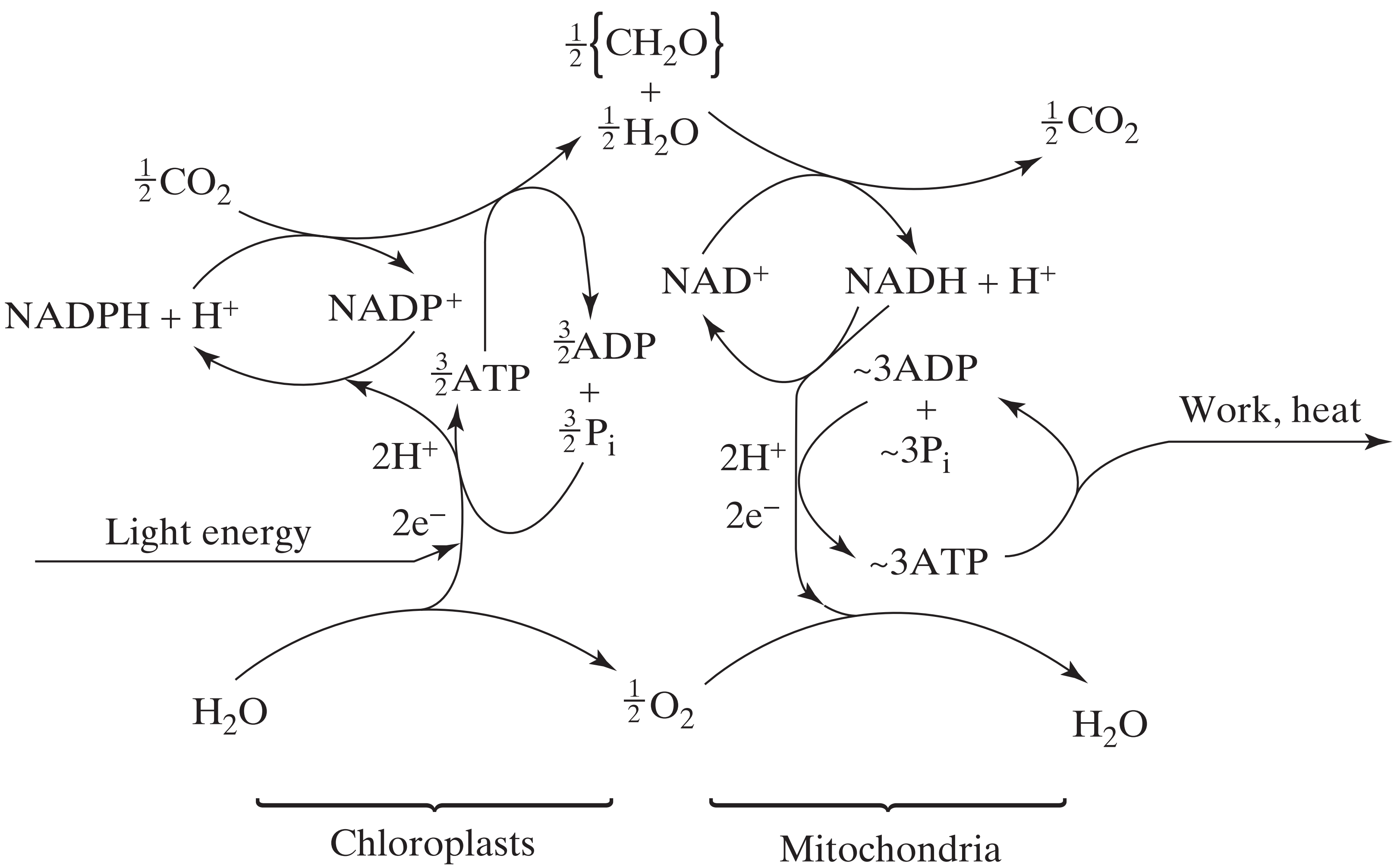
- Cyt b_6f has a dual role: it is both rate-limiting, and subject to feedback regulation

The energy supply through the electron transport system is regulated to satisfy the energy demands of carbon metabolism



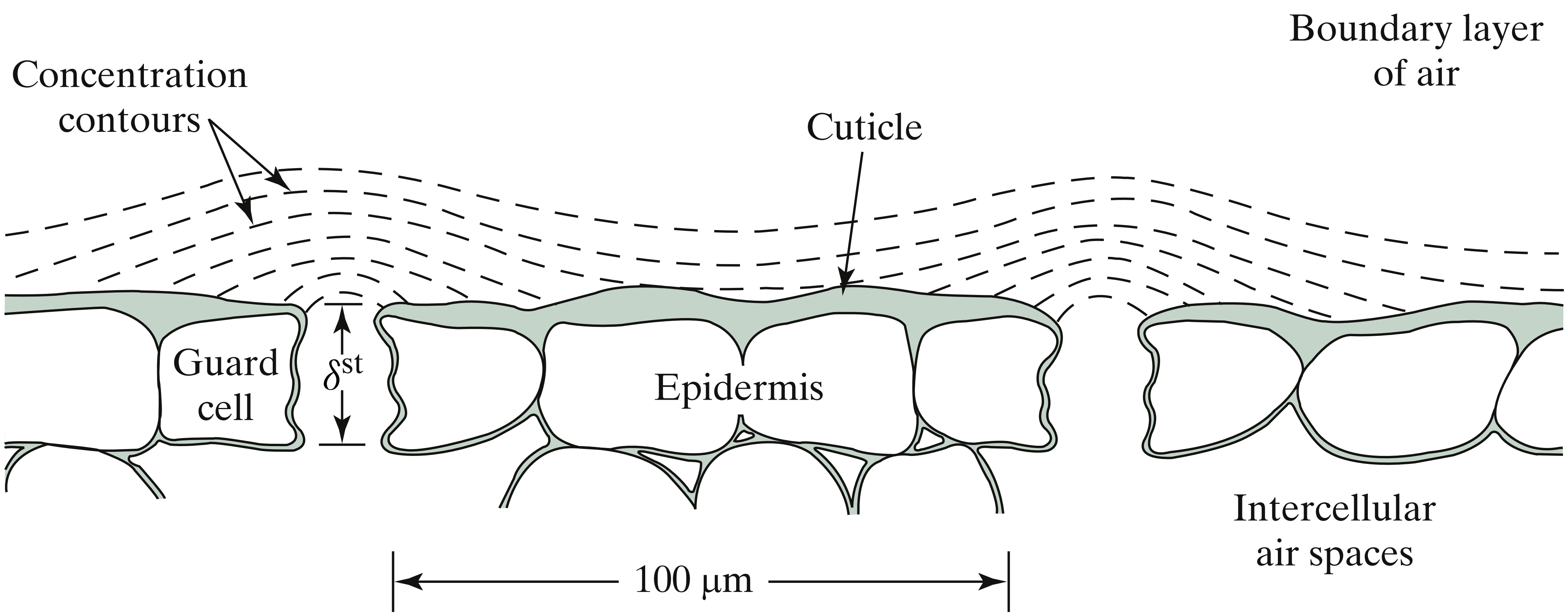
- The pools of the energetic intermediates are small, and they turn over rapidly
- The supply and demand for energy come into balance in the steady-state

Photosynthesis is subject to regulation on both physiological and ecological timescales



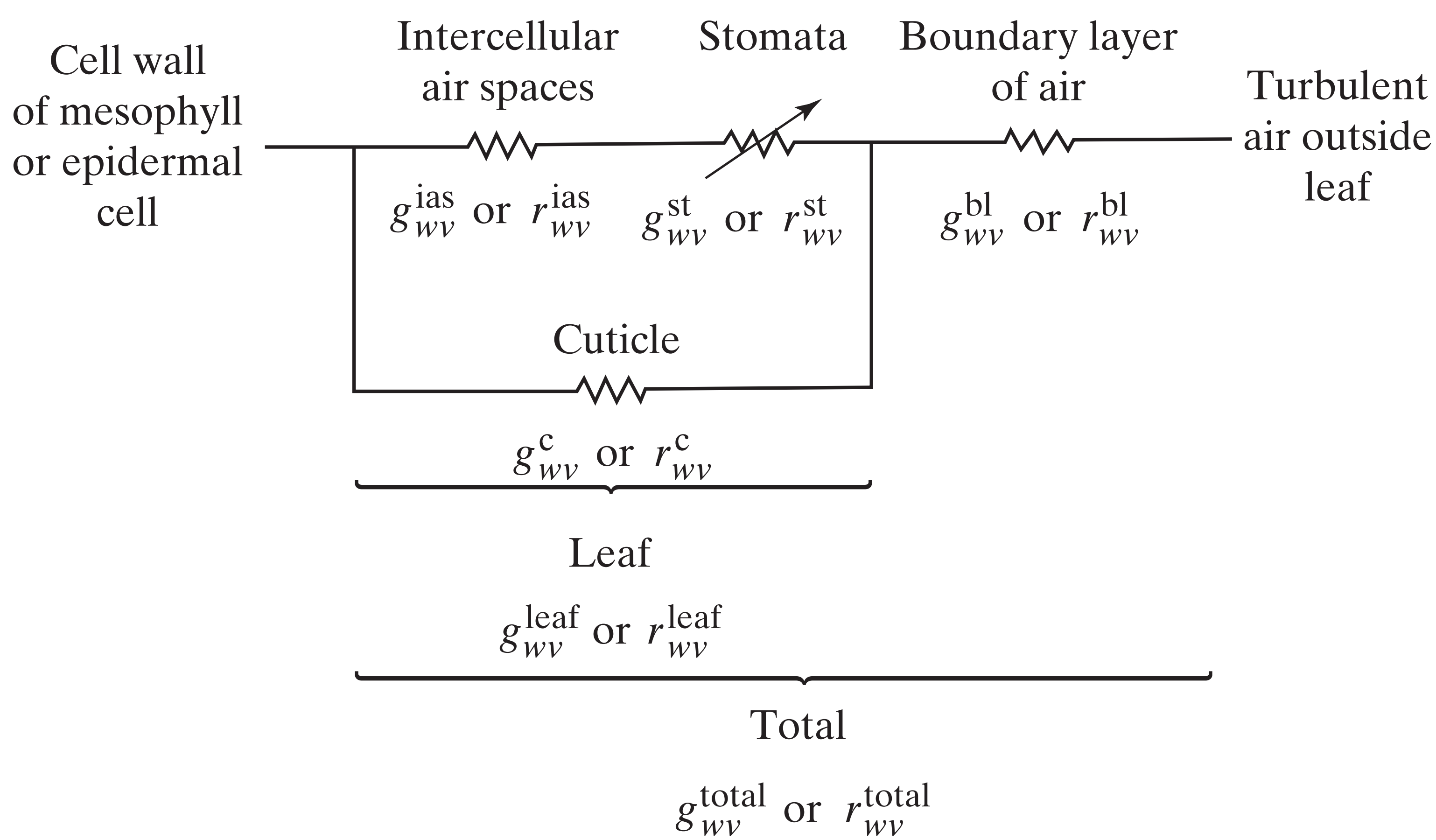
- Regulation functions to manage energy flow in a way that is safe and efficient

Carbon dioxide diffuses from the atmosphere down a concentration gradient into the chloroplasts



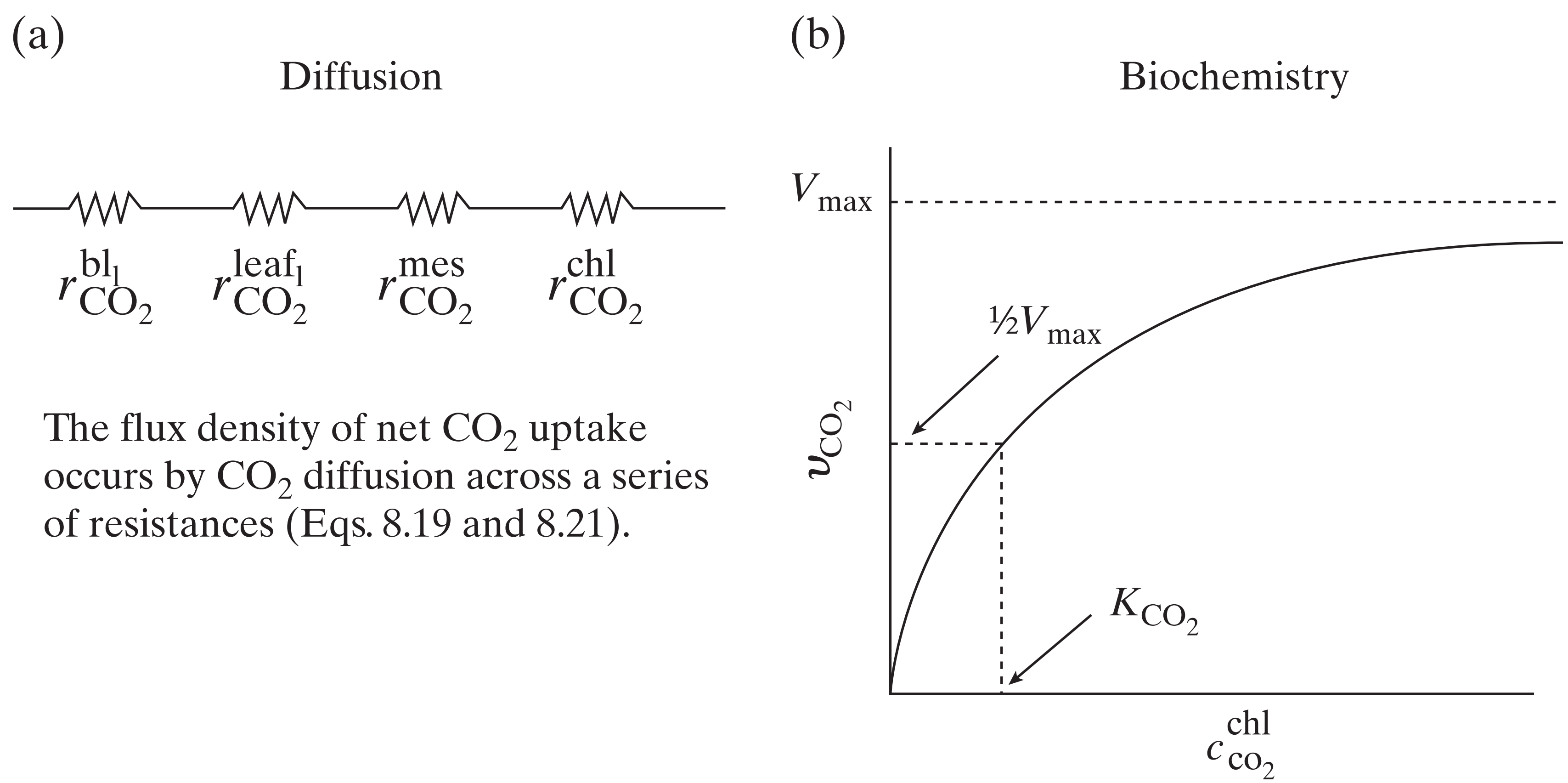
- Transport is via turbulent diffusion in moving air, and molecular diffusion in still air

Diffusive transport is often conceptualized with analogies to electrical circuits



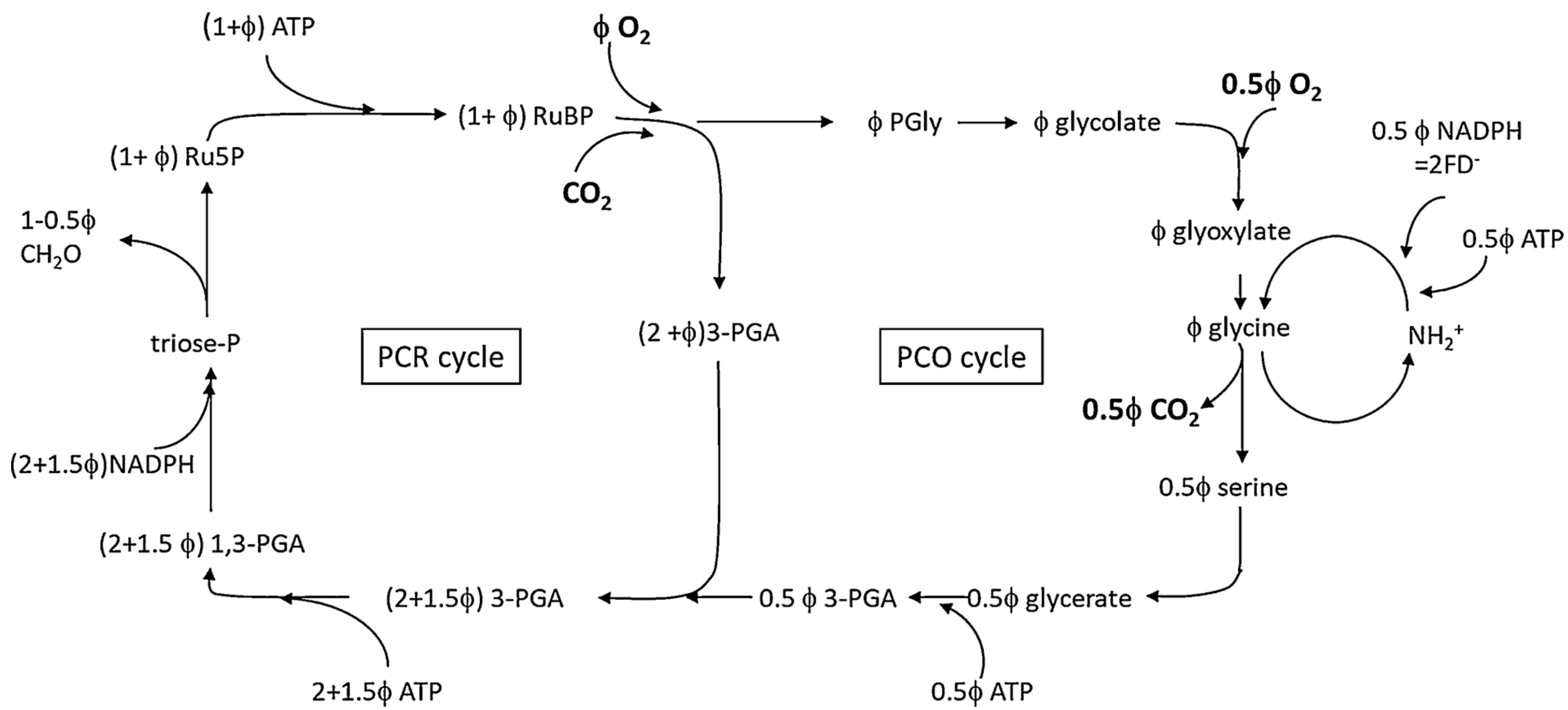
- Ohm's law: flux is proportional to product of driving gradient and conductance
- NB, gradients are bidirectional & conductance is inverse of resistance (g = 1/r)

Net diffusive transport of CO_2 is coordinated with net CO_2 exchange of carbon metabolism



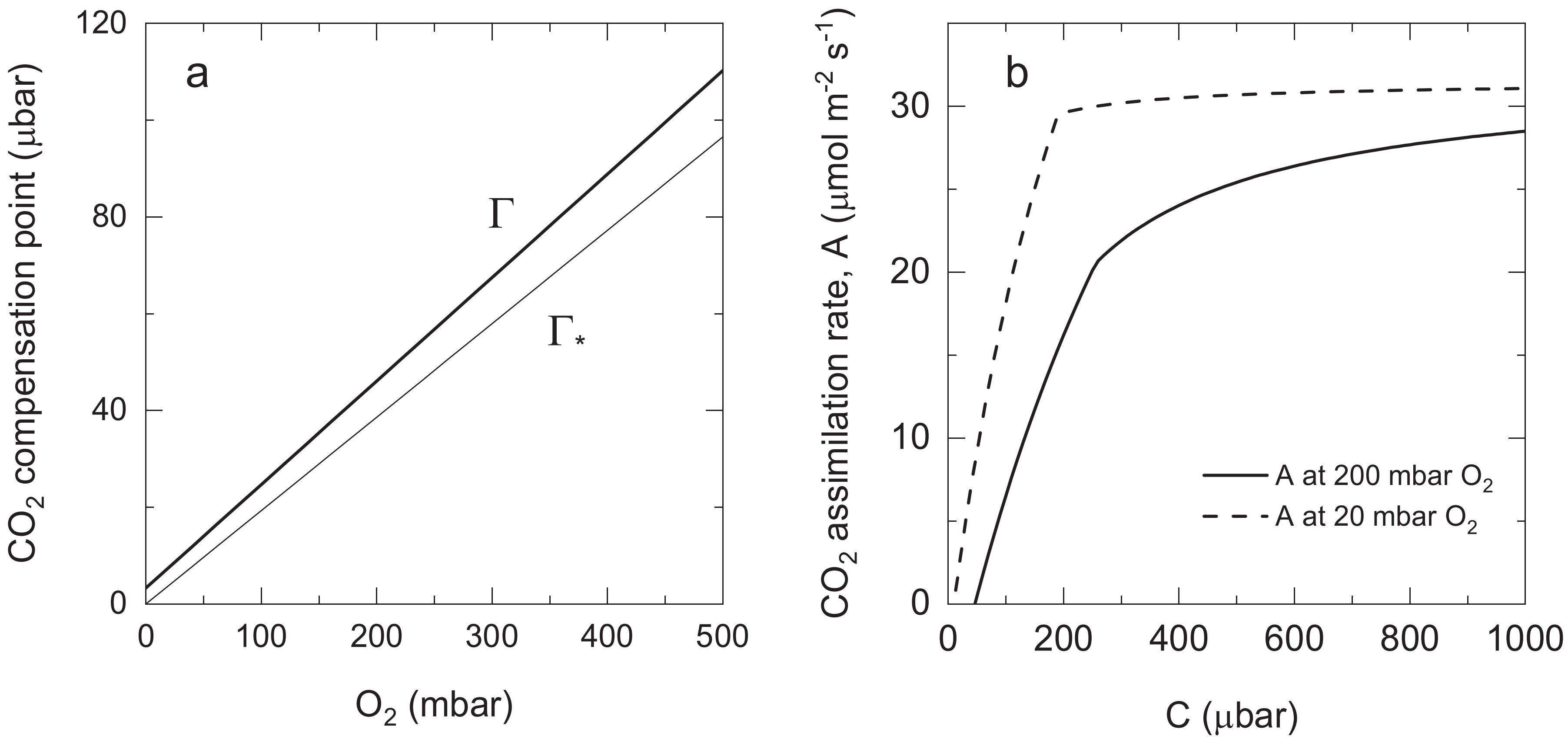
- Ultimately, the biochemical reactions can only go as fast as diffusion allows

Steady-state dynamics of carbon metabolism are limited by CO_2, O_2, and the enzyme Rubisco



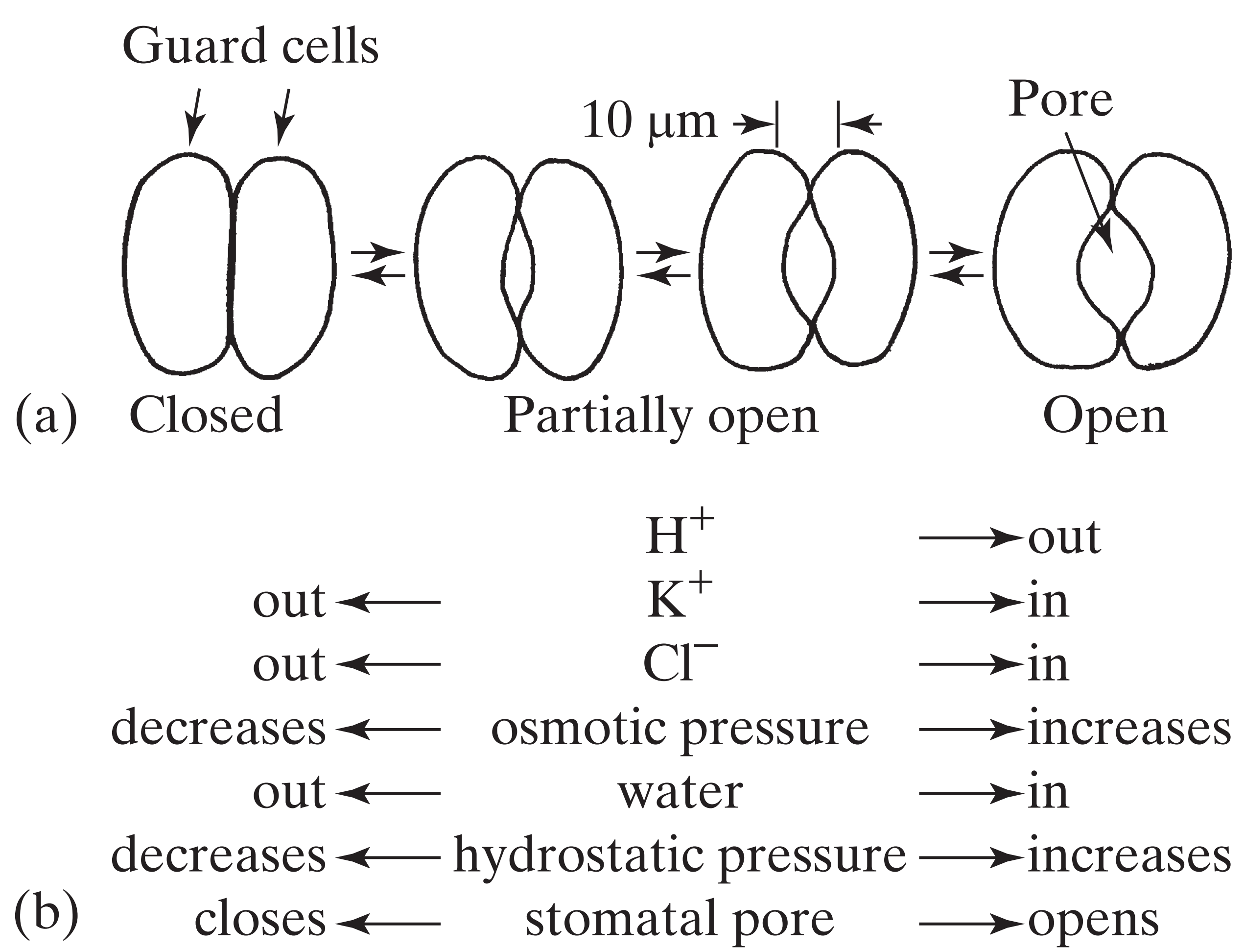
- PCR cycle: photosynthetic carbon reduction cycle (Calvin cycle)
- PCO cycle: photosynthetic carbon oxidation cycle (photorespiration)

Relative abundance of CO_2 and O_2 at Rubisco determines PCR and PCO cycle activity



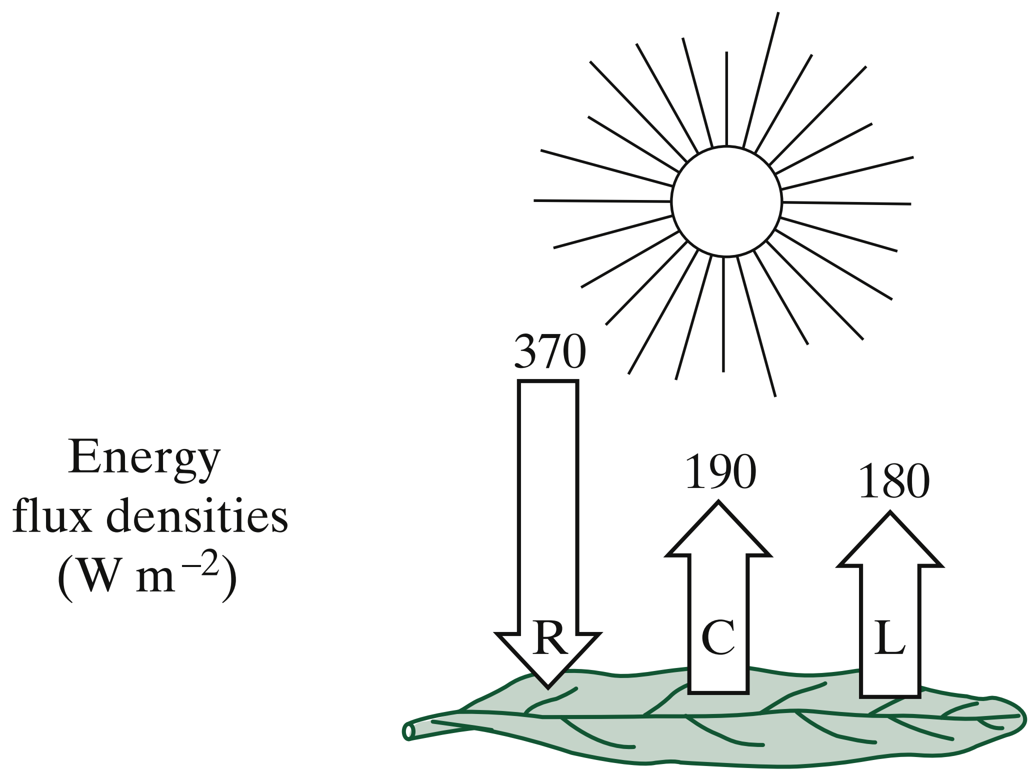
- **Γ** (Gamma): the CO_2 compensation point, where PCR and PCO activity balance

Diffusive uptake of CO_2 coupled to loss of H_2O because both move through stomatal pores



- Stomatal conductance controls water loss through transpiration

Due to the high heat capacity of water, transpiration is a key control on leaf temperature



Leaf temperature	25°C
Air temperature	20°C
Relative humidity	50%
Wind speed	0.8 m s^{-1}
Water flux density	4 mmol m^{-2} s^{-1} transpired

- Photosynthesis is controlled by the interaction of multiple resources and stressors

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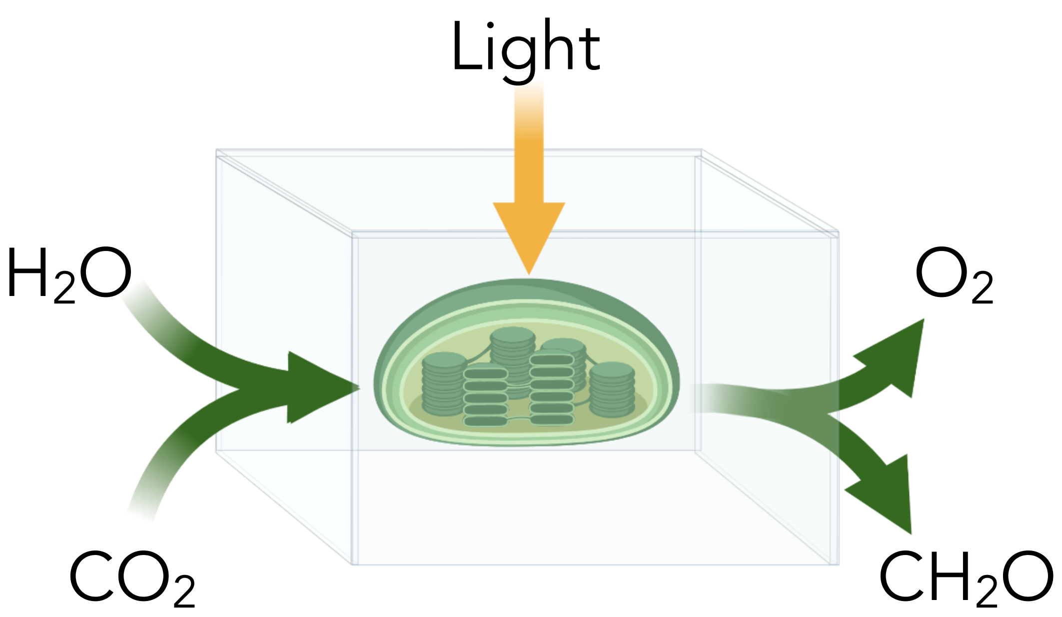
  - —Top down: Monteith
  - —Bottom up: Farquhar, von Caemmerer, and Berry
  - —Connecting top down to bottom up: Johnson and Berry

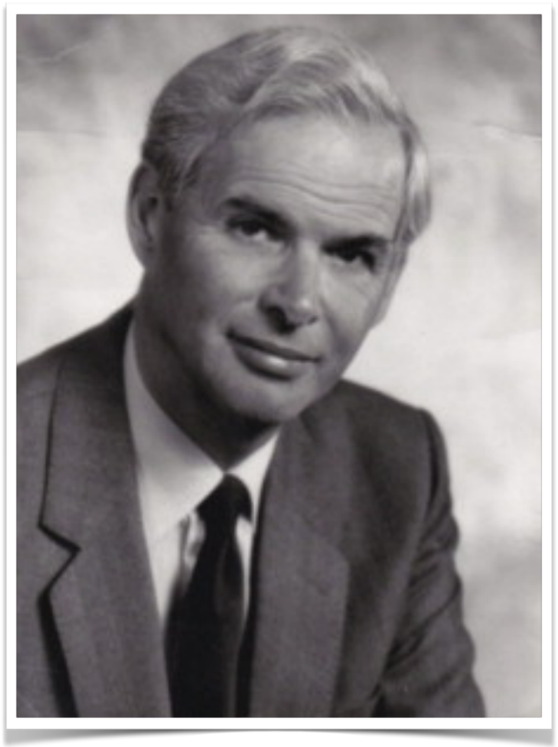
The traditional ecological perspective on photosynthesis:



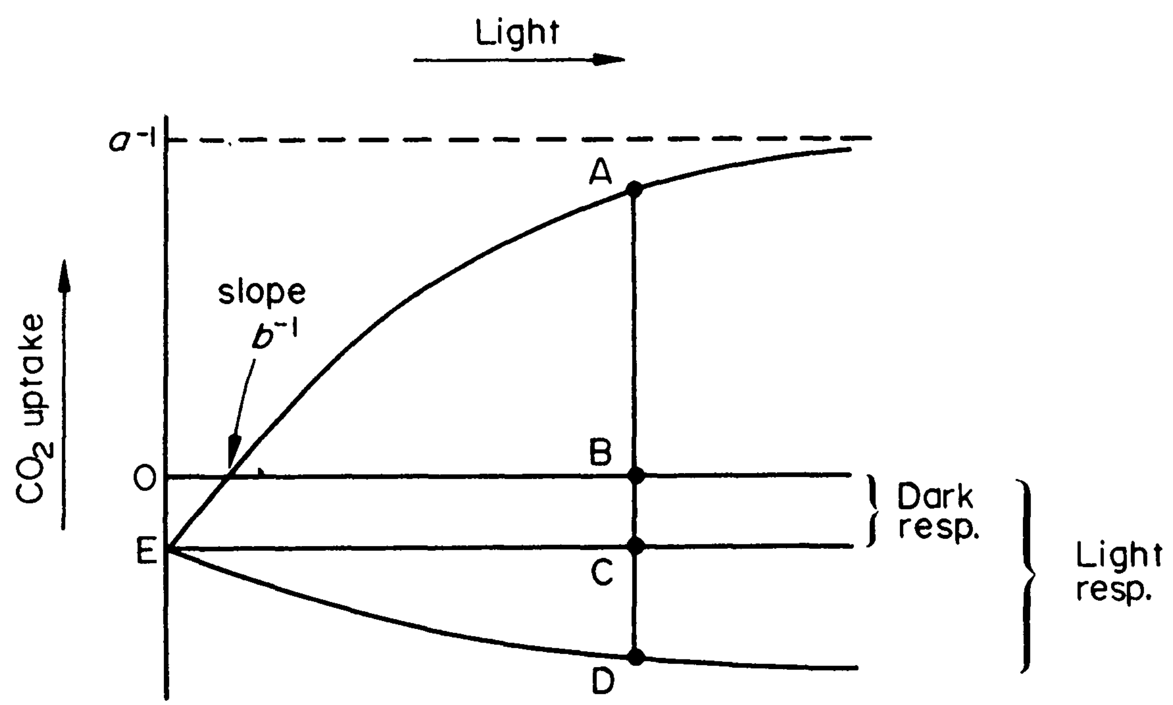
- Top down model was formulated by Monteith (1972)
- Bottom up model was formulated by Farquhar, von Caemmerer, and Berry (1980)
- Incomplete separation of environmental versus physiological controls

The Monteith model: GPP = APAR x LUE

- GPP: gross primary production (photosynthesis)
- APAR: absorbed photosynthetically active radiation
- LUE: the light-use efficiency of photosynthesis

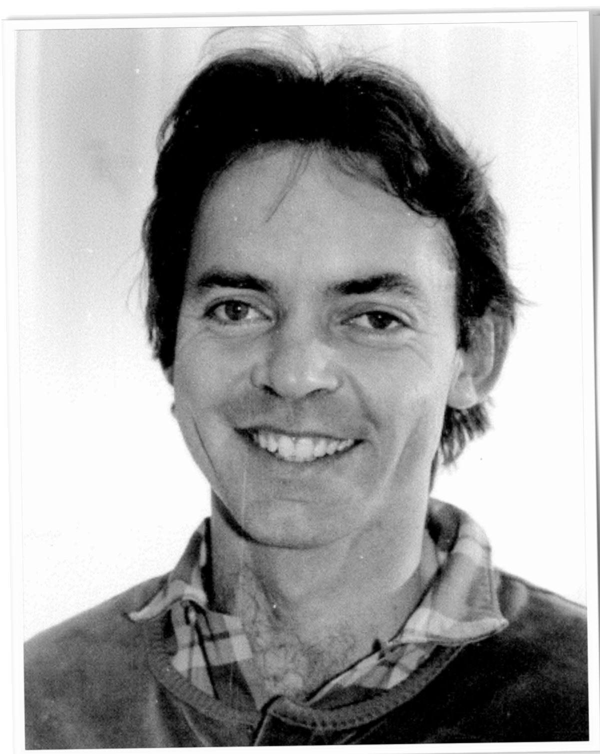


J. Monteith



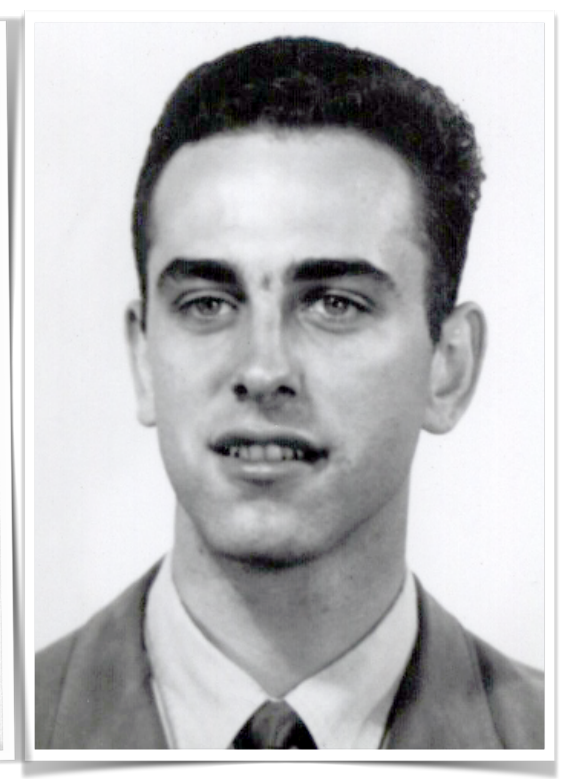
The Farquhar, von Caemmerer, Berry model: A = min of {Aj, Ac}

- Aj: potential light-limited rate of photosynthesis
- Ac: potential light-saturated rate of photosynthesis



G. Farquhar

S. von Caemmerer

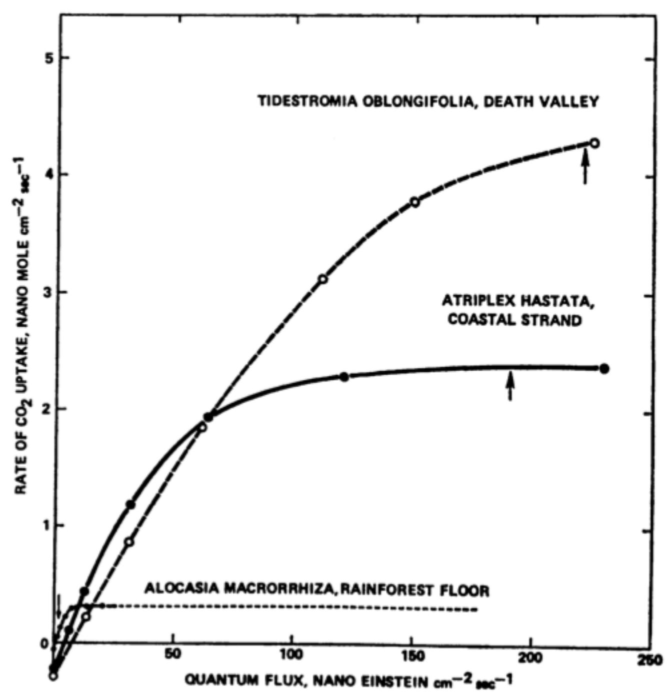


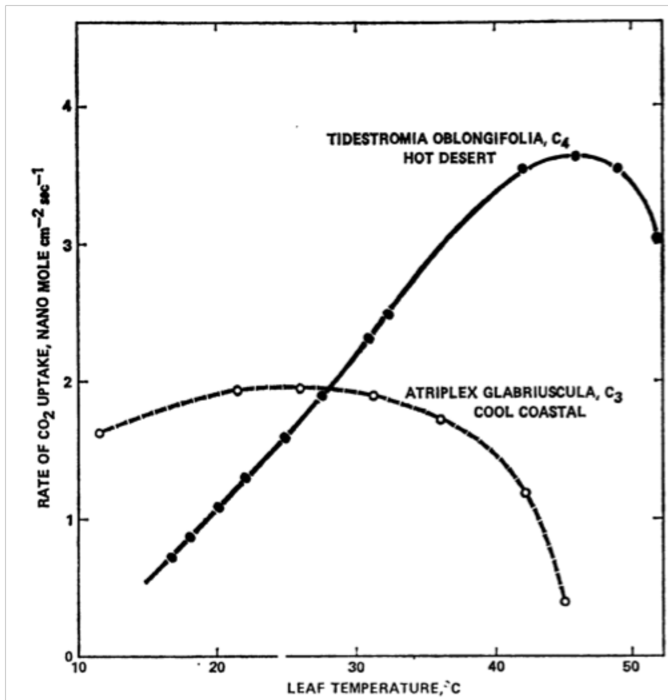
J. Berry

FvCB: motivating observations

- Photosynthetic responses to light, temperature, and CO_2 are non-linear and interact with one another

Fig. 1. Light dependence of net CO_2 uptake by single attached leaves, grown under the contrasting light intensity regimes of their natural habitats. Rates were determined at near-optimum temperature for each species, a CO_2 partial pressure of 320 μbar, and an O_2 concentration of 21 percent by volume. The arrows indicate the average maximum light intensities to which the plants were exposed during growth. [Source: (7)]





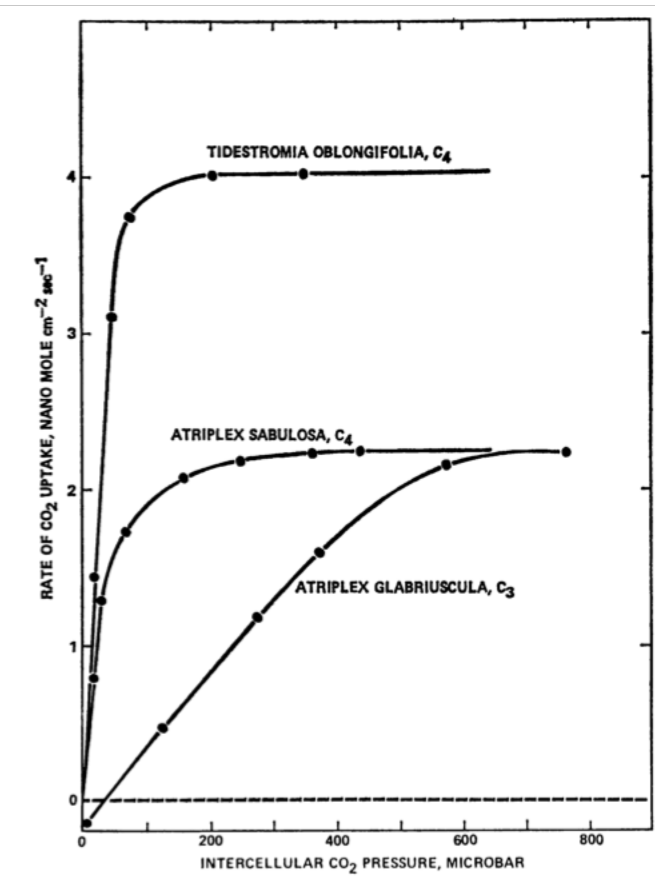


Fig. 3 (left). Temperature dependence of photosynthesis in *Tidestromia oblongifolia* and *Atriplex glabriuscula* at high light intensity of 160 nanoeinstein cm^{-2} sec^{-1}, a CO_2 partial pressure of 320 μbar, and an O_2 concentration of 20 percent by volume. Stomatal conductances were almost identical in the two species. The plants were grown under the light and temperature regimes of their respective habitats. [Source: (7)]

Fig. 4 (right). Photosynthesis as a function of the CO_2 concentration in the intercellular spaces in C_3 and C_4 species, grown under a temperature regime of 40°C by day and 30°C by night. Measurements were made at a leaf temperature of 40°C, a light intensity of 160 nanoeinstein cm^{-2} sec^{-1}, and an O_2 concentration of 21 percent by volume. [Source: (7)]

FvCB: key insight

- The steady-state fluxes are under the kinetic control of the rate-limiting step in electron transport or carbon metabolism, and the system switches efficiently as the environment varies.

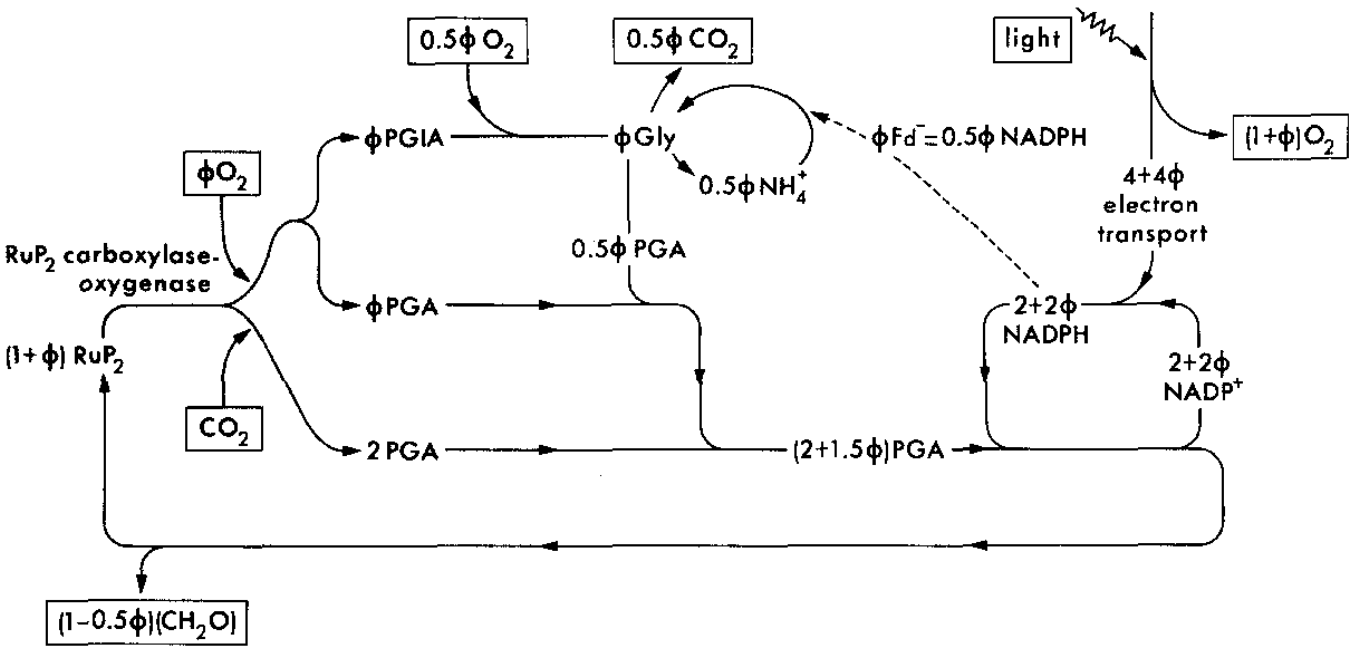


Fig. 1. Simplified photosynthetic carbon reduction (PCR) and photorespiratory carbon oxidation (PCO) cycles, with cycle for regeneration of NADPH linked to light driven electron transport. For each carboxylation, ϕ oxygenations occur. Gly denotes glycine, Fd^- denotes reduced ferredoxin (assumed equivalent to 1/2 NADPH), PGA denotes 3-phosphoglycerate, PGlA phosphoglycolate. At the compensation point $\phi = 2$

FvCB: terminology

$$A = min\{A_j, A_c\}$$

$A,$ observed rate of net CO_2 assimilation

$min\{\},$ minimum of the terms in following brackets

$A_j,$ potential rate of net CO_2 assimilation under light limitation

$A_c,$ potential rate of net CO_2 assimilation under light saturation

FvCB: A_c based on Michaelis-Menten kinetics

$$[E] + [S] \rightleftharpoons [ES] \rightarrow [E] + [P]$$

$$v_0 = \frac{k_3 \cdot E \cdot S}{(k_2 + k_3)/k_1 + S}$$

$$v_0 = \frac{V_{max} \cdot S}{K_m + S}$$

E, enzyme

S, substrate

ES, enzyme-substrate complex

P, product

k_1, rate constant for ES formation

k_2, rate constant for ES dissociation

k_3, rate constant for P formation

FvCB: A_c accounts for competition between CO_2 and O_2

$$A_c = \frac{V_{max\ (RUBC)} \cdot C}{K_c \cdot (1 + O/K_o) + C} \cdot (1 - \Gamma_*/C) - R_d \qquad \Gamma_* = \frac{1}{2} \cdot \frac{O}{S} = \frac{k_c}{K_c} \cdot \frac{K_o}{k_o}$$

A_c, Potential rate of net CO_2 assimilation under light saturation

$V_{max\ (RUBC)}$, Maximum carboxylase activity of Rubisco

k_c, k_o, Catalytic constants of Rubisco for CO_2 and O_2

K_c, K_o, Michaelis constants of Rubisco for CO_2 and O_2

S, Specificity of Rubisco for CO_2 versus O_2

Γ_*, CO_2 compensation point in absence of Rd

R_d, Mitochondrial/dark respiration

C, O, Partial pressure of CO_2 and O_2 in the chloroplast

FvCB: simulations of the responses to CO_2 and O_2

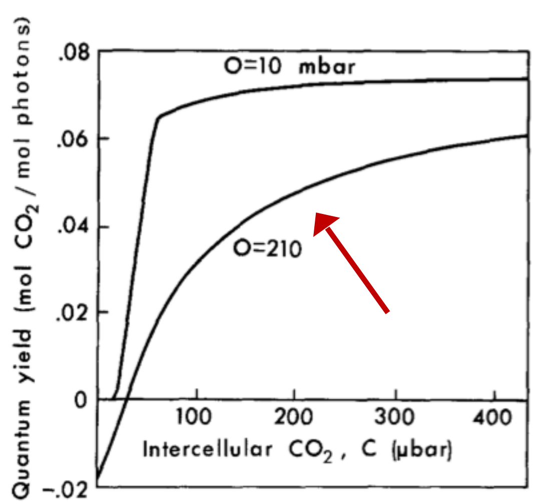


Fig. 4. Quantum yield versus intercellular $p(CO_2)$, C. The quantum yield is determined as the slope of the curve relating CO_2 assimilation rate, A, to absorbed irradiance, I, in the range 50–150 µmol photons $m^{-2} s^{-1}$ at 25 C. The responses are plotted for two intercellular partial pressures of O_2, 10 and 210 nbar

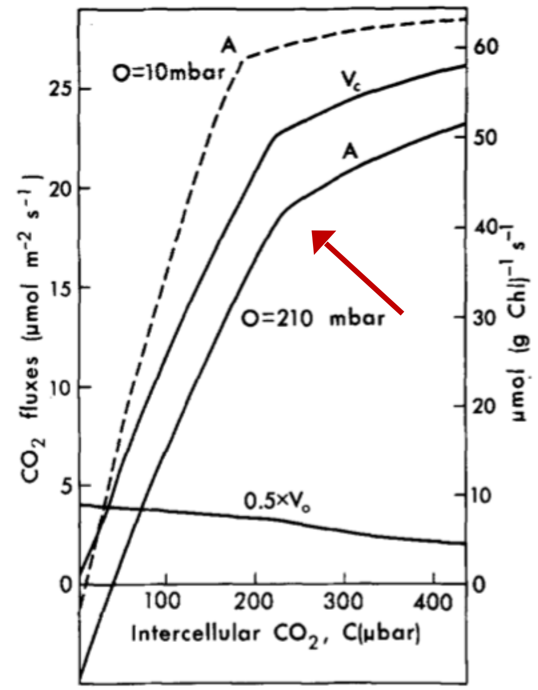


Fig. 7. CO_2 fluxes versus intercellular $p(CO_2)$, C(µbar). The solid lines at 25C and 1000 µmol photons $m^{-2} s^{-1}$ represent the situation in ambient (210 mbar) $p(O_2)$, with V_c, A and $0.5 \cdot V_o$ denoting the rates of carboxylation, the net rate of assimilation of CO_2 and the rate of release of photorespired CO_2. The dashed line represents the rate of CO_2 assimilation in 10 mbar $p(O_2)$)

FvCB: terminology

$A = min\{A_j, A_c\}$

$A,$ observed rate of net CO_2 assimilation
$min\{\},$ minimum of the terms in following brackets
$A_j,$ potential rate of net CO_2 assimilation under light limitation
$A_c,$ potential rate of net CO_2 assimilation under light saturation

FvCB: A_j also accounts for competition between CO_2 and O_2

$$A_j = \frac{J'_{P680}}{4 + 8 \cdot \Gamma_* / C} \cdot (1 - \Gamma_* / C) - R_d$$

A_j, Potential rate of net CO_2 assimilation under light limitation

J'_{P680}, Potential rate of linear electron transport

Γ_*, CO_2 compensation point in absence of Rd

R_d, Mitochondrial/dark respiration

C, Partial pressure of CO_2 in the chloroplast

FvCB: A_j expression for electron transport is empirical

$$J'_{P680} = \begin{cases} a = \dfrac{b + J_{max} - \sqrt{(b + J_{max})^2 - 4 \cdot \theta \cdot b \cdot J_{max}}}{2 \cdot \theta} \\ \\ b = Q \cdot \alpha_2 \cdot \Phi_{P2(max)} \end{cases}$$

J'_{P680}, Potential rate of linear electron transport

J_{max}, Observed maximum rate of linear electron transport

θ, An empirical curvature parameter

Q, Photosynthetically active radiation (PAR) incident on the leaf

α_2, Fraction of incident PAR absorbed by Photosystem II

$\Phi_{P2(max)}$, Maximum photochemical yield of Photosystem II

FvCB: simulation of the light response

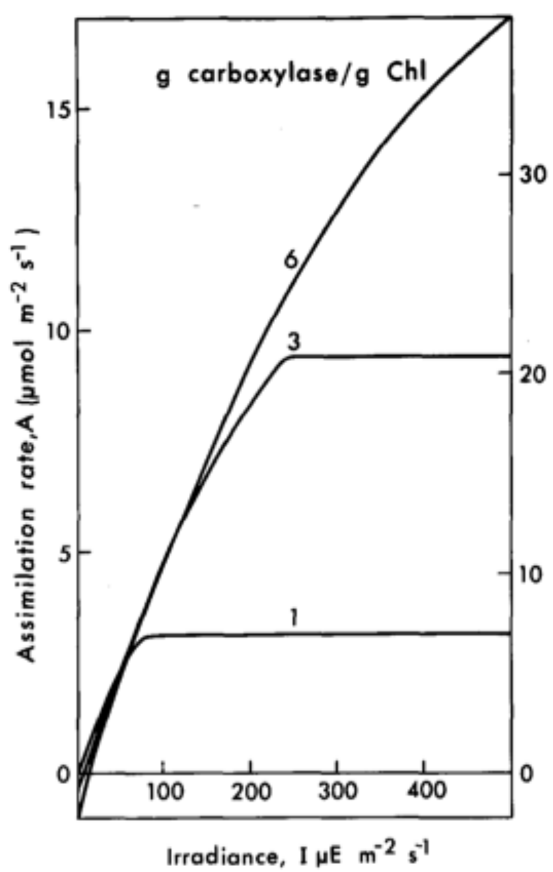


Fig. 10. Rate of assimilation of CO_2, *A*, versus absorbed irradiance, *I*, at three levels of carboxylase – 6, 3 and 1 g carboxylase/g chlorophyll. Rates of "dark respiration" are scaled accordingly

FvCB: temperature-dependent parameters

Saturating-type light dependence function:	Unsaturating-type light dependence function:
J_{max}, Activation and deactivation	
$V_{max\ (RUBC)}$, Activation only	$V_{max\ (RUBC)}$, Activation and deactivation
K_c, Activation only	K_c, Activation only
K_o, Activation only	K_o, Activation only
$1/S$, Activation only	$1/S$, Activation only
R_d, Activation only	R_d, Activation only

FvCB: temperature-dependence based on Arrhenius function

$$k = k_{ref} \cdot exp\left(\frac{E_a}{R} \cdot \left[\frac{1}{T_{ref}} - \frac{1}{T_{leaf}}\right]\right) \cdot \frac{\left[1 + exp\left(\frac{T_{ref} \cdot \Delta S - H_d}{T_{ref} \cdot R}\right)\right]}{\left[1 + exp\left(\frac{T_{leaf} \cdot \Delta S - H_d}{T_{leaf} \cdot R}\right)\right]}$$

k, Parameter value at T_{leaf}

k_{ref}, Parameter value at T_{ref}

E_a, Enthalpy of activation (kJ mol^{-1})

ΔS, Entropy factor (kJ mol^{-1} K^{-1})

H_d, Enthalpy of deactivation (kJ mol^{-1})

R, Universal gas constant (0.008314 kJ mol^{-1} K^{-1})

T_{ref}, Reference temperature (25°C = 298 K)

T_{leaf}, Leaf temperature (K)

FvCB: temperature-dependence based on Q_{10} function

$$k = k_{ref} \cdot \frac{exp\left(ln(Q_{10}) \cdot \left[T_{leaf} - T_{ref}\right]/10\right)}{1 + exp(c \cdot [T_{leaf} - T_{limit}])}$$

k, Parameter value at leaf temperature of interest

k_{ref}, Parameter value at reference temperature (25°C = 298 K)

T_{ref}, Reference temperature (25°C = 298 K)

T_{leaf}, Leaf temperature (°C or K)

Q_{10}, Upward scaling parameter quantifying change per 10°C

T_{limit}, Limiting temperature above which to scale downward (°C or K)

c, Downward scaling parameter applied above T_{limit}

FvCB: simulations of photosynthetic temperature-dependence

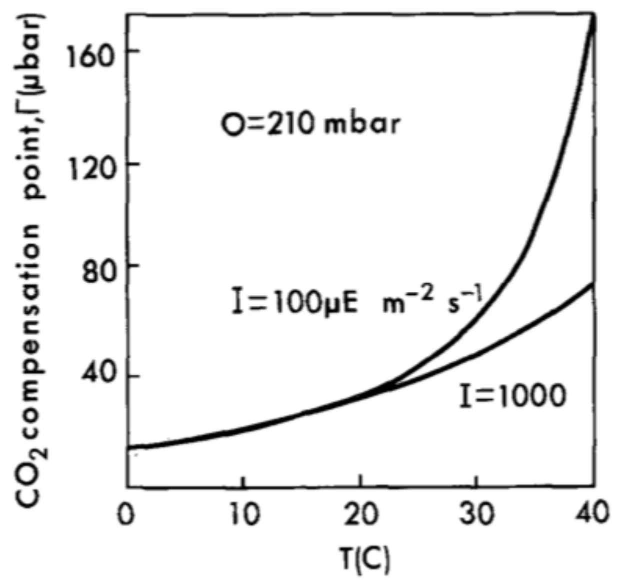


Fig. 6. CO_2 compensation point, Γ (μbar) versus temperature, at two absorbed irradiances (100 and 1,000 μmol photons $m^{-2}s^{-1}$) and an intercellular $p(O_2)$ of 210 mbar

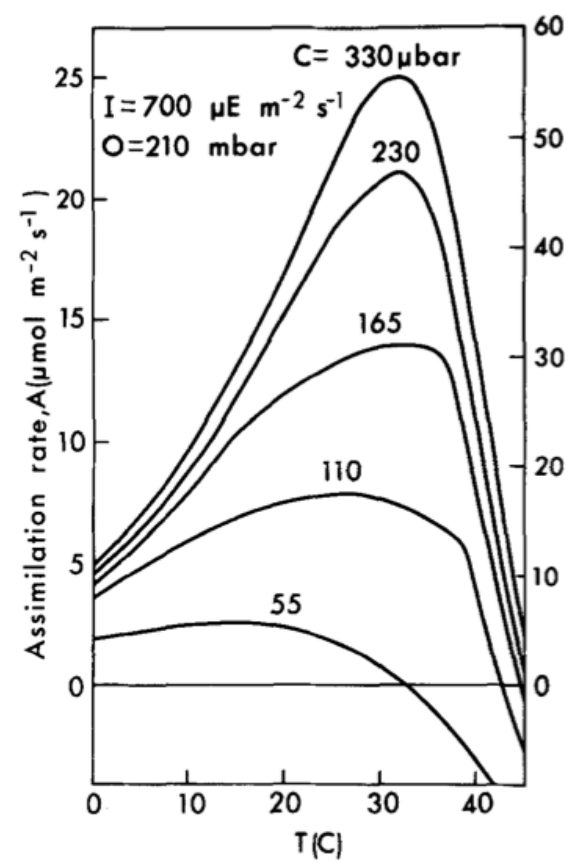


Fig. 8. Effect of intercellular $p(CO_2)$, C(μbar), on the temperature response of net CO_2 assimilation rate. The absorbed irradiance is 700 μmol photons $m^{-2}s^{-1}$ and the $p(O_2)$ is 210 mbar

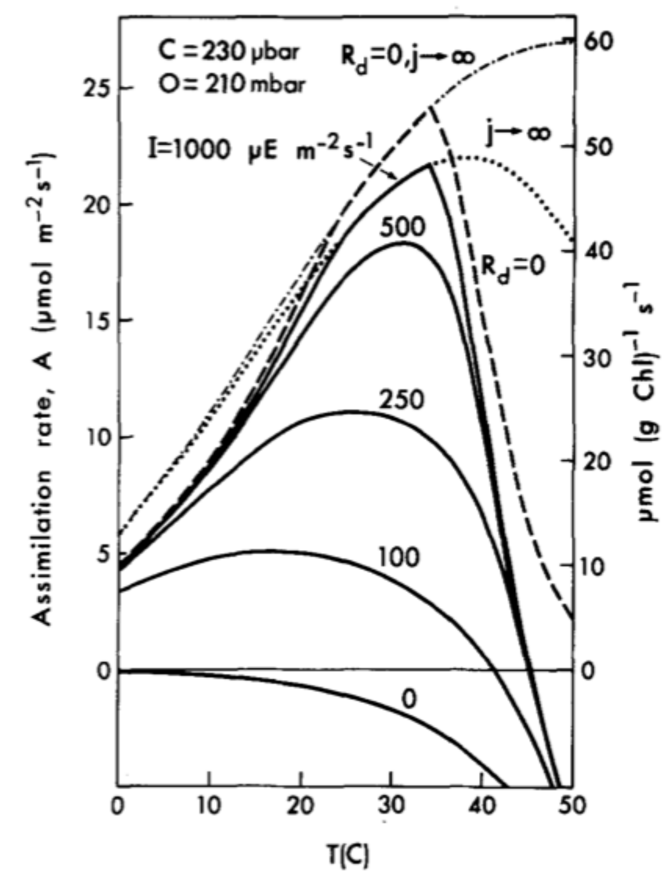
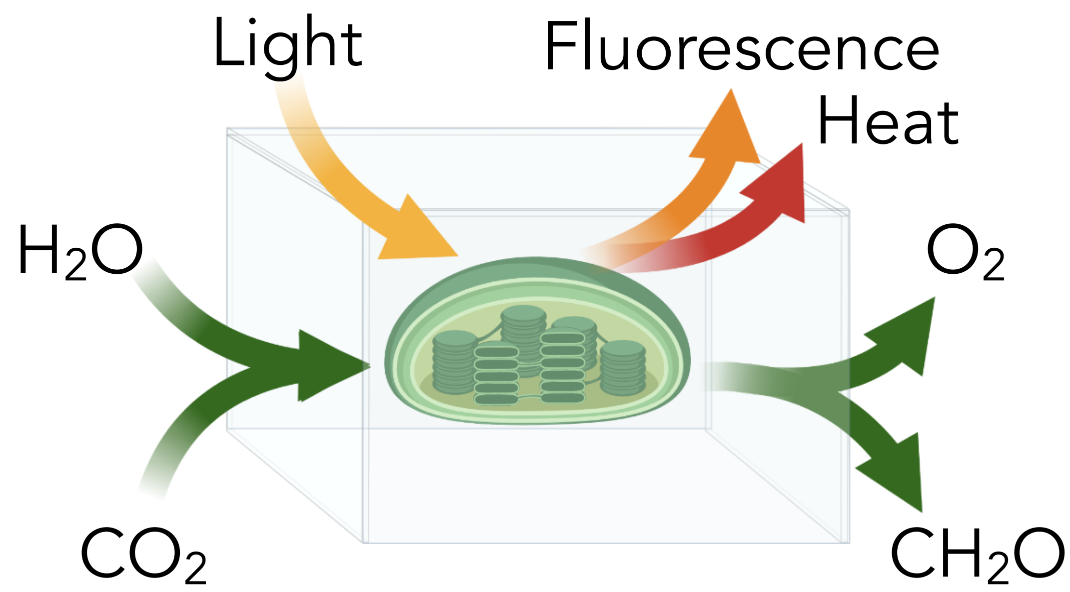


Fig. 9. Effect of absorbed irradiance, I, on the temperature dependence of net CO_2 assimilation rate. The effect of removal of "dark respiration," R_d, is shown as the dashed line and the effect of removal of electron transport limitations (potential electron transport, $j \rightarrow \infty$) is shown as the dotted line. The simultaneous removal of both $R_d=0, j \rightarrow \infty$) is shown as (· — · —)

The emerging ecological perspective on photosynthesis:



- How exactly is absorbed light used to drive the fixation of carbon dioxide?
- Johnson and Berry (2021) separate the environmental vs. physiological controls

JB: mechanistic expression for the potential rate of electron flow

$$J'_{P700} = \frac{V_{max\ (CB6F)} \cdot Q}{\frac{V_{max\ (CB6F)}}{\alpha_1 \cdot \Phi_{P1\ (max)}} + Q}$$

Symbol	Defintion
J'_{P700}	Potential rate of electron transport through Photosystem I
Q	Photosynthetically active radiation incident on leaf
α_1	Absorption cross-section of Photosystem I
$\Phi_{P1\ (max)}$	Maximum photochemical yield of Photosystem I
$V_{max\ (CB6F)}$	Maximum activity of Cytochrome b_6f complex

Light-limited (Cyt b6f-limited) state:

$$A_j = \frac{J'_{P680}}{4 + 8 \cdot \Gamma_*/C} \cdot (1 - \Gamma_*/C) - R_d$$

Light-saturated (Rubisco-limited) state:

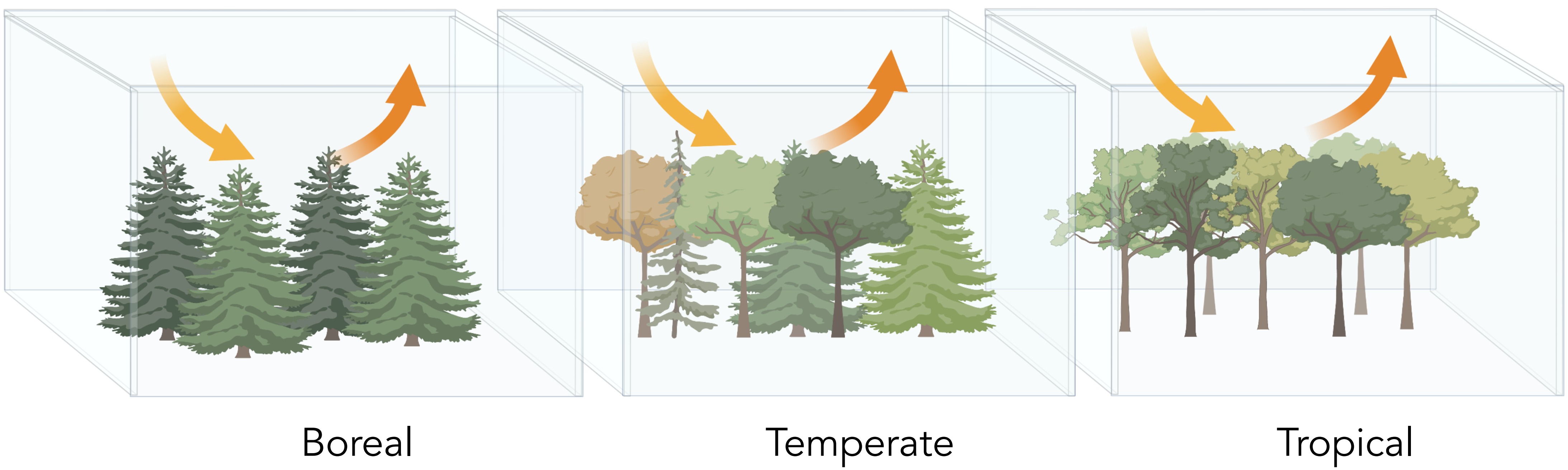
$$A_c = \frac{V_{max\ (RUBC)} \cdot C}{K_c \cdot (1 + O/K_o) + C} \cdot (1 - \Gamma_*/C) - R_d$$

Actual state:

$$A = min\{A_j, A_c\}$$

Symbol	Definition
A_j	Potential rate of net carbon dioxide assimilation under Cyt b_6f limitation
A_c	Potential rate of net carbon dioxide assimilation under Rubisco limitation
C, O	Partial pressures of carbon dioxide and oxygen in the chloroplast
J'_{P680}	Potential rate of linear electron transport
K_c, K_o	Michaelis-Menten constants of Rubisco for carbon dioxide and oxygen
R_d	Rate of dark respiration (mitochondrial respiration)
$V_{max\ (RUBC)}$	Maximum carboxylase activity of Rubisco
Γ_*	Carbon dioxide compensation point in the absence of dark respiration

JB: new tool for understanding and simulating photosynthesis



- Diagnostic applications: interpret experimental measurements of leaves & canopies
- Prognostic applications: simulate leaf-level photosynthesis in land surface models

References

- Slides 2-5: diagrams made with biorender.com
- Slides 7-15 & 18-19: Nobel, P. 2020. Phys. and Env. Plant Physiology, 5th Ed. Acad. Press
- Slides 16-17: von Caemmerer. 2020. J Plant Phys 252: 153240
- Slide 22: Monteith, J. 1972. J. Applied Ecology 9: 747-766
- Slide 22: portrait from: https://en.wikipedia.org/wiki/John_Monteith
- Slides 23, 25-26, 28-31, 33, 35, 37: Farquhar, von Caemmerer, Berry. 1980. Planta 149: 78-90
- Slide 24: Berry. 1975. Science 188: 644-650
- Slide 27: Cornish-Bowden. 2012. Fundamentals of Enzyme Kinetics. Wiley Blackwell
- Slide 32: version (a) Farquhar and Wong. 1984. Aust J Plant Physiol 11: 191-210
- Slide 32: version (b) Collatz et al. 1991. Agric Forest Meteorol 54: 107-136
- Slide 34: Sat.-type - Farquhar, von Caemmerer, Berry. 1980. Planta 149: 78-90
- Slide 34: Unsat.-type - Collatz et al. 1991. Agric Forest Meteorol 54: 107-136
- Slides 38-40: Johnson and Berry. 2021. Photosynthesis Research 148: 101–136

Questions?

- Part 1: Environmental control of photosynthesis
  - —Light: photons, photochemistry, and Cytochrome b6f
  - —Carbon dioxide: diffusion, biochemistry, and Rubisco
  - —Other resources and stressors

- Part 2: Quantitative expressions for photosynthesis
  - —Top down: Monteith
  - —Bottom up: Farquhar, von Caemmerer, and Berry
  - —Connecting top down to bottom up: Johnson and Berry