40 Years of Excellence

Theory of Leaf-Level Gas Exchange Measurements

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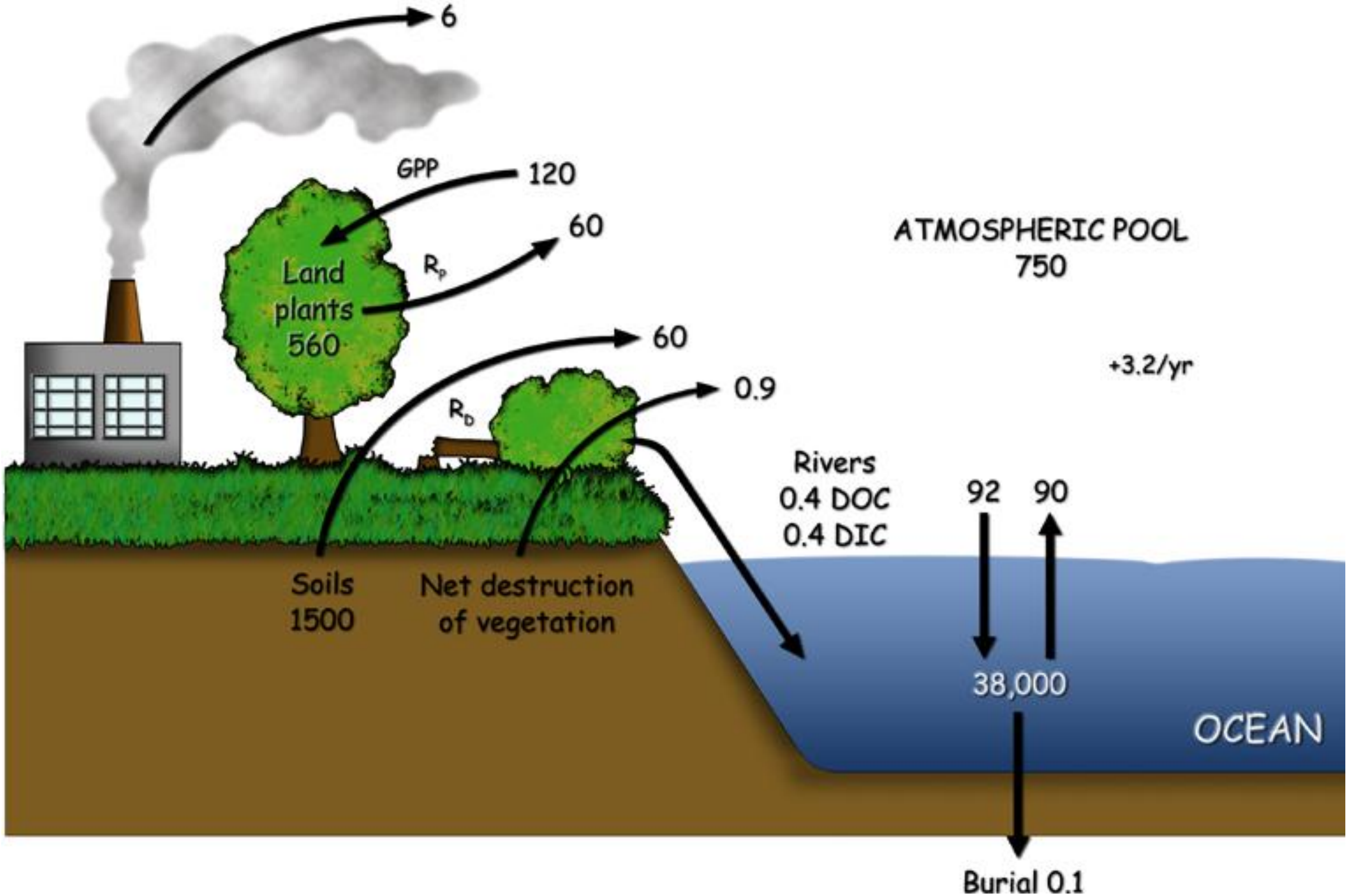
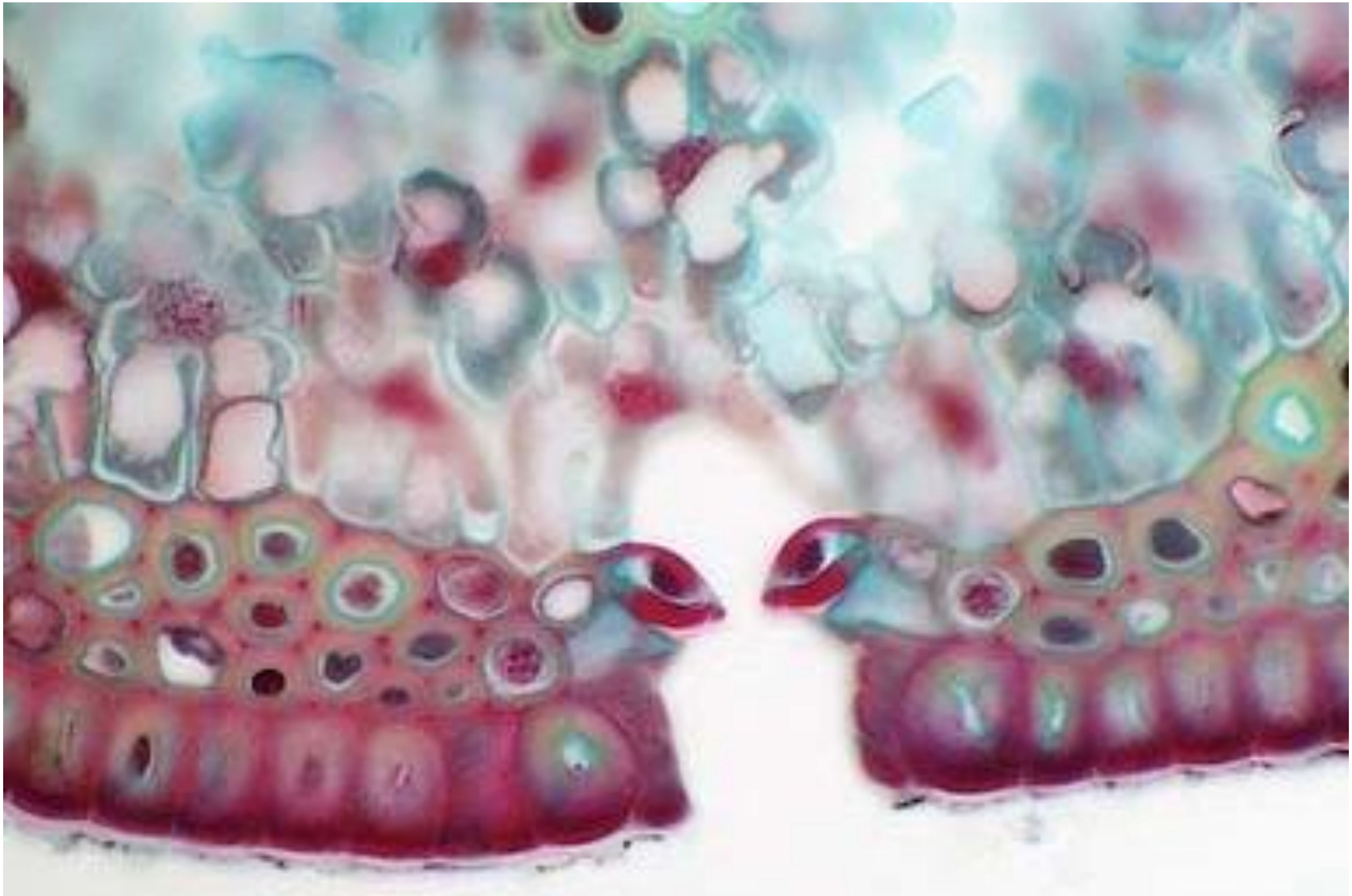
Global Carbon cycle ($x10^{15}$ gC)



How is Vegetation Measured?

Plant and Atmosphere Interface



Stomata regulate H_2O loss from and CO_2 entry into leaf

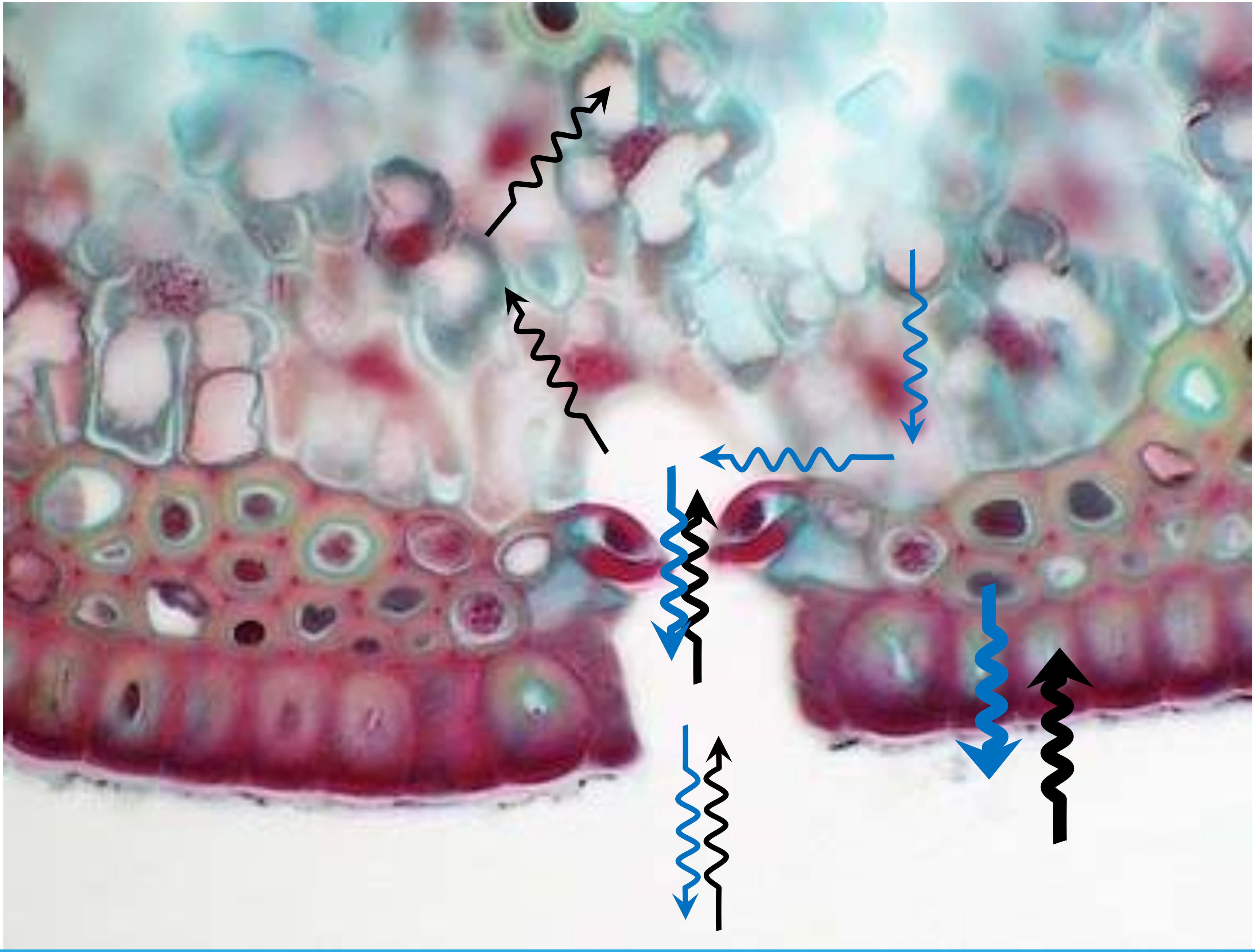
Ohm's Law

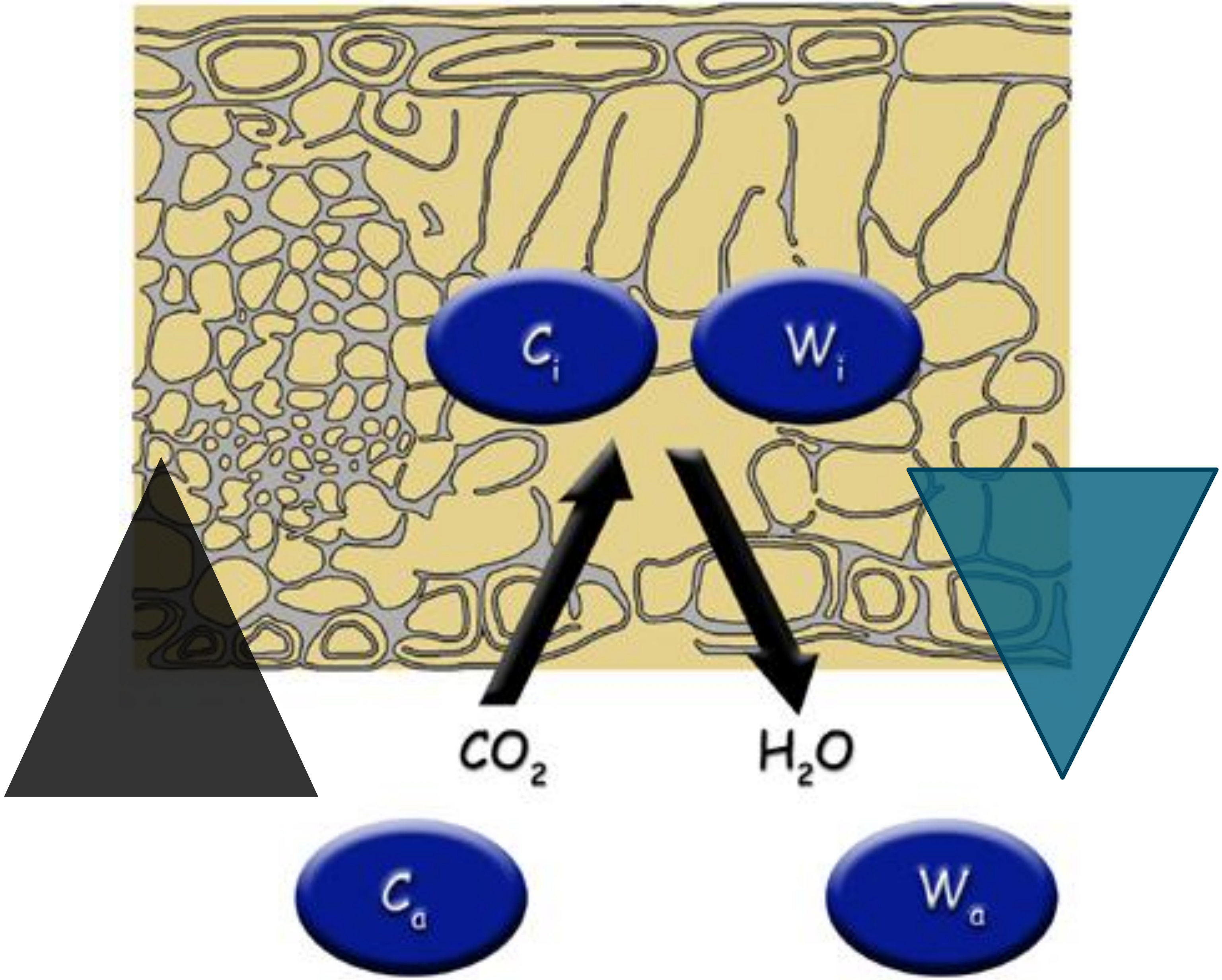
$$\boxed{\begin{array}{l} \Delta E = IR \\ I = \Delta E / R \end{array}}$$

ΔE = driving force
(electric potential difference)
R = resistance

conductance = 1/R

I = current





C_i
W_i
CO_2
H_2O
C_a
W_a

Fick's First Law

$$J_j = -D_j \frac{\partial c_j}{\partial x}$$

$$= g_j^{\mathrm{bl}} \Delta c_j^{\mathrm{bl}}$$

Δc_j = concentration gradient

g_j = conductance

J_j = flux

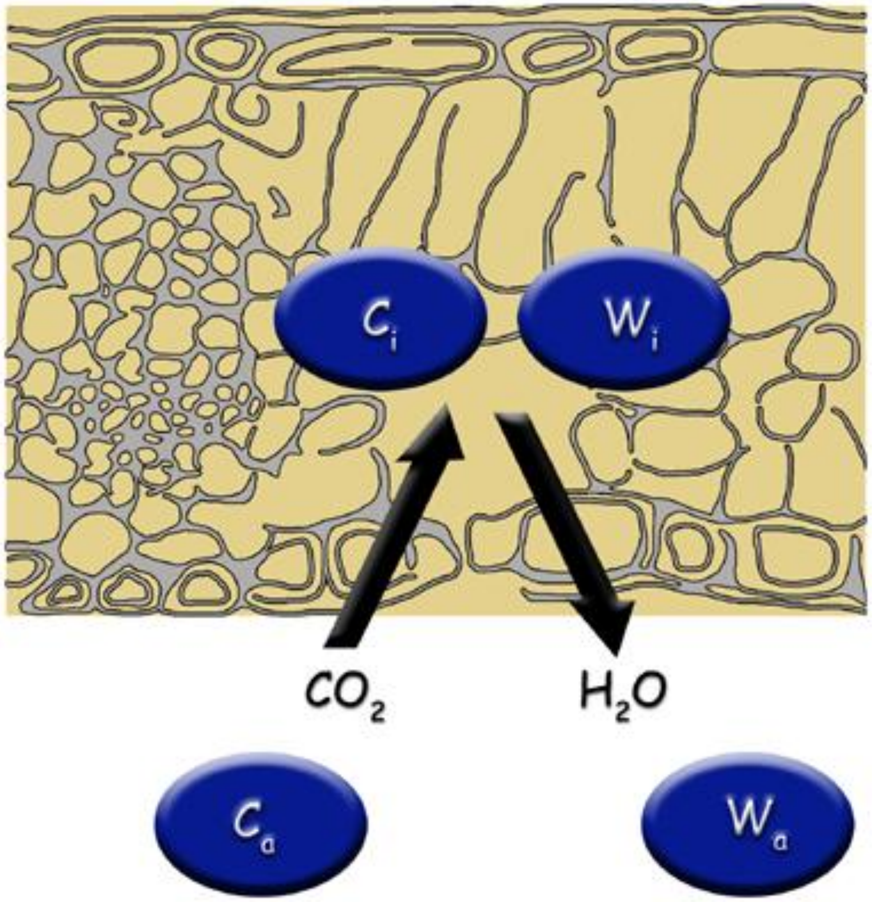
H_2O and CO_2 Flux

- Photosynthesis

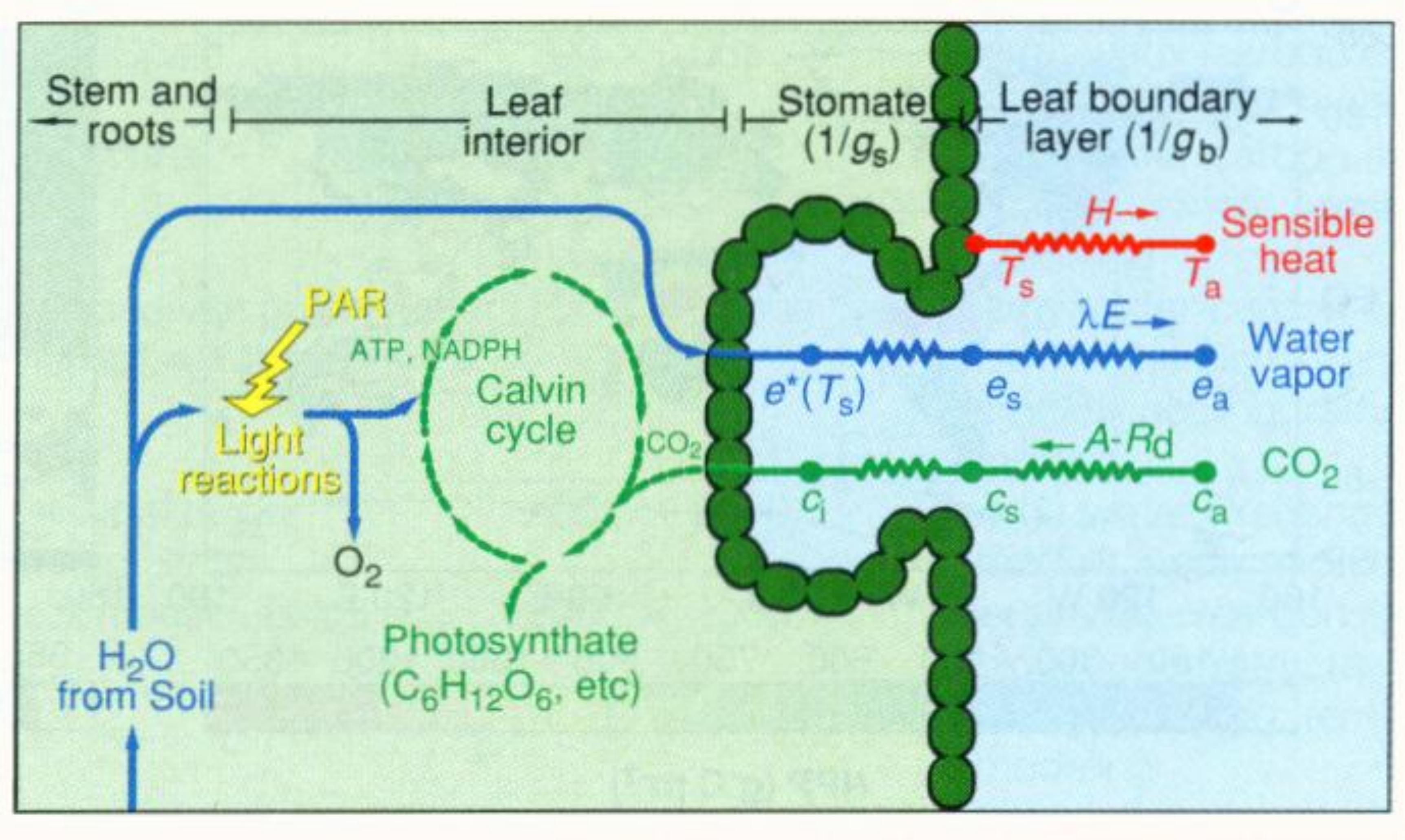
  $A = (c_a - c_i)g_{CO2}$

- Transpiration

  $E = (w_i - w_a)g_{H2O}$

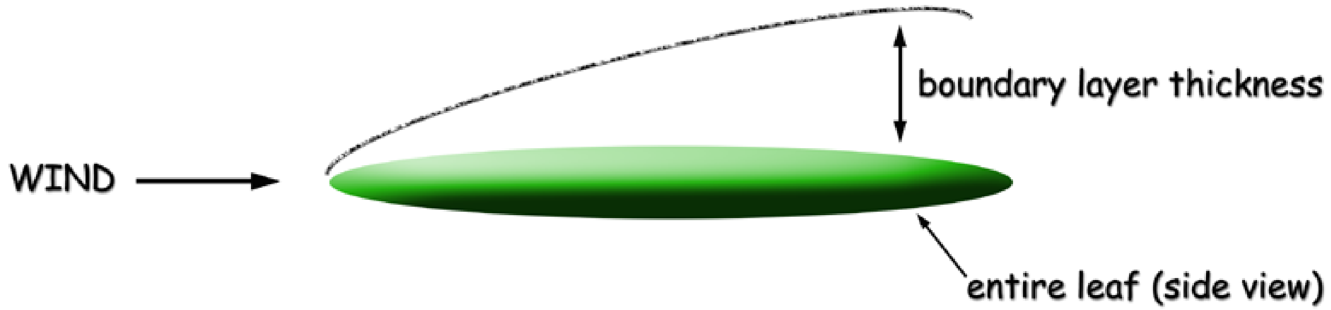


Leaf Conductance



$r_t = r_{bl} + r_s + r_c + r_m$

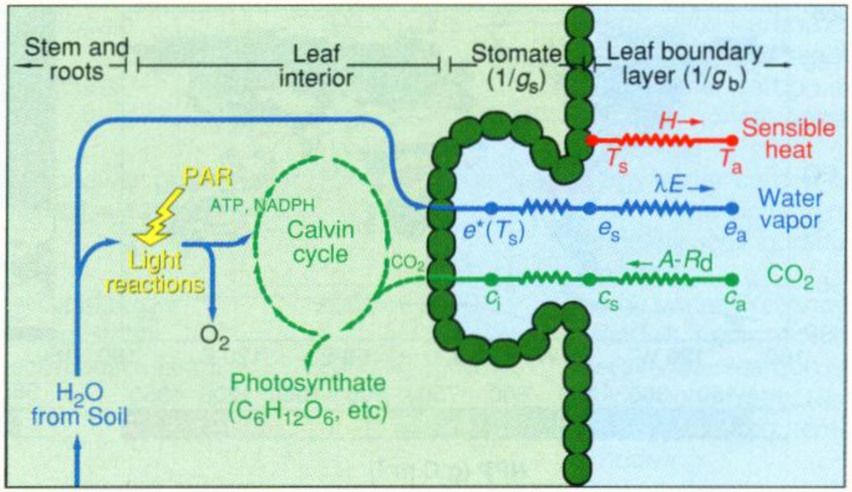
Boundary Layer



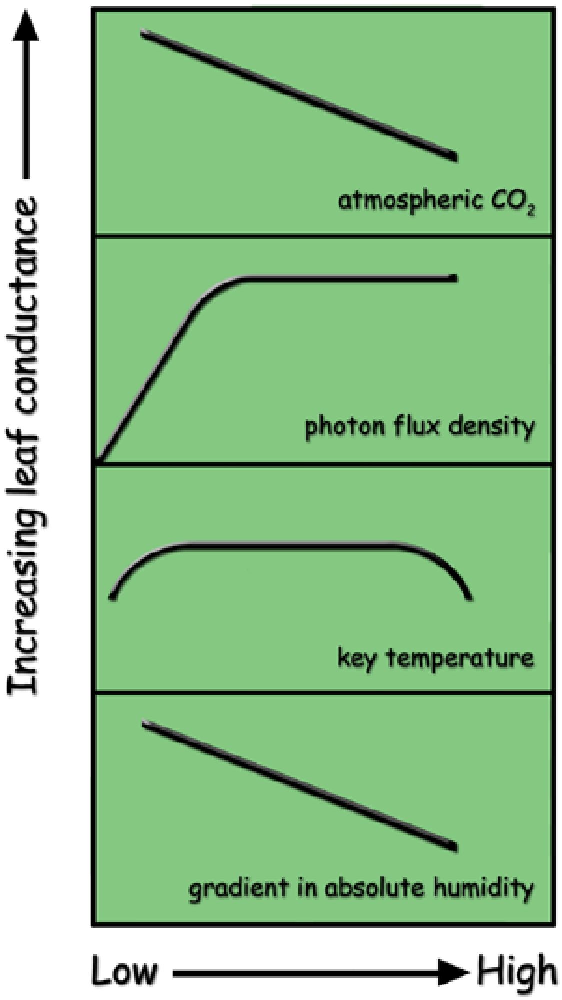
$$\delta^{\mathrm{bl}}_{(mm)} = 4.0\sqrt{\frac{l_{(m)}}{v_{(m\,s^{-1})}}}$$

The boundary layer retards the transfer of heat, CO_2, and H_2O from the leaf to the bulk air.

Stomatal Conductance (g_s)

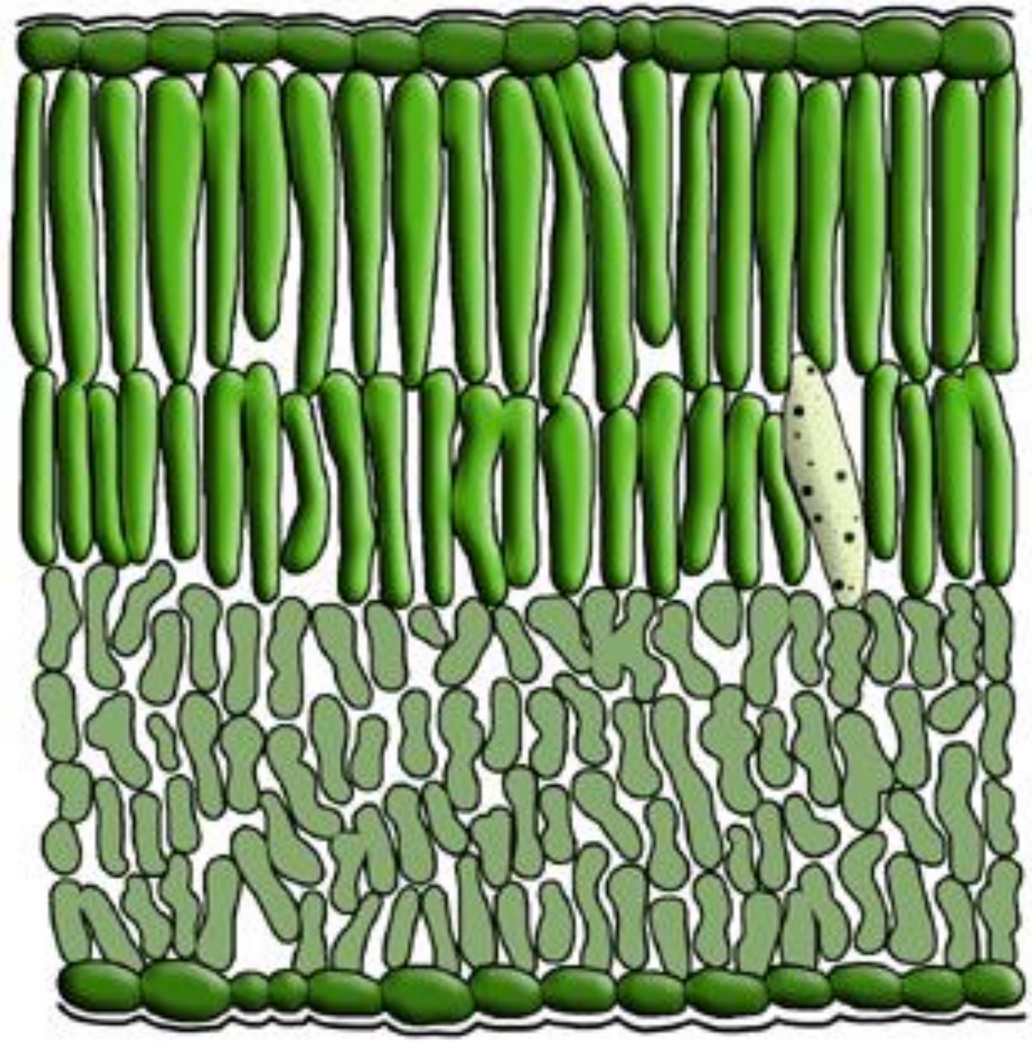


- Major resistance in leaf
  - Regulated to prevent H_2O loss while maximizing CO_2 influx

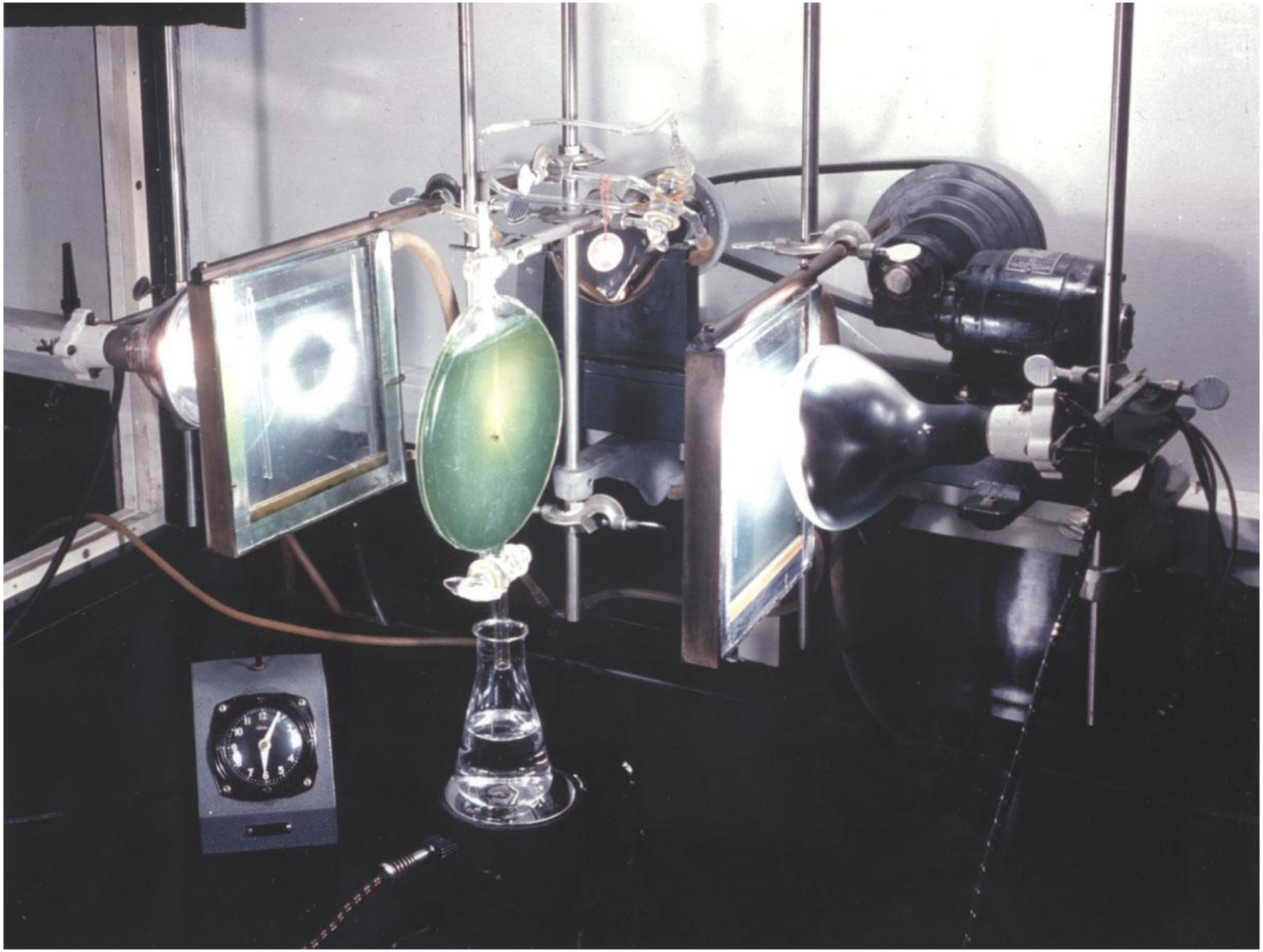


Resistance within Apoplast and Cell

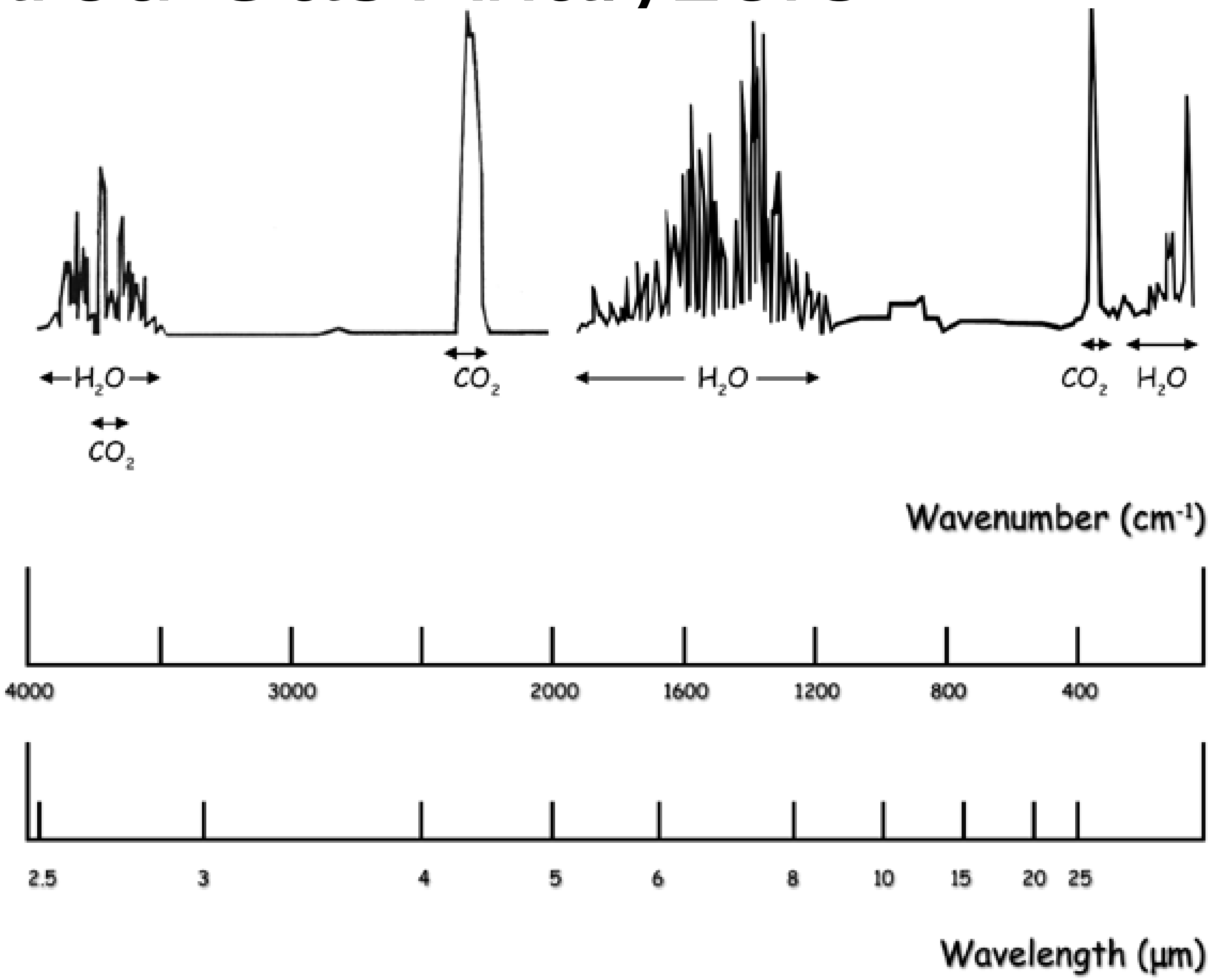
- Apoplastic resistance due to diffusion

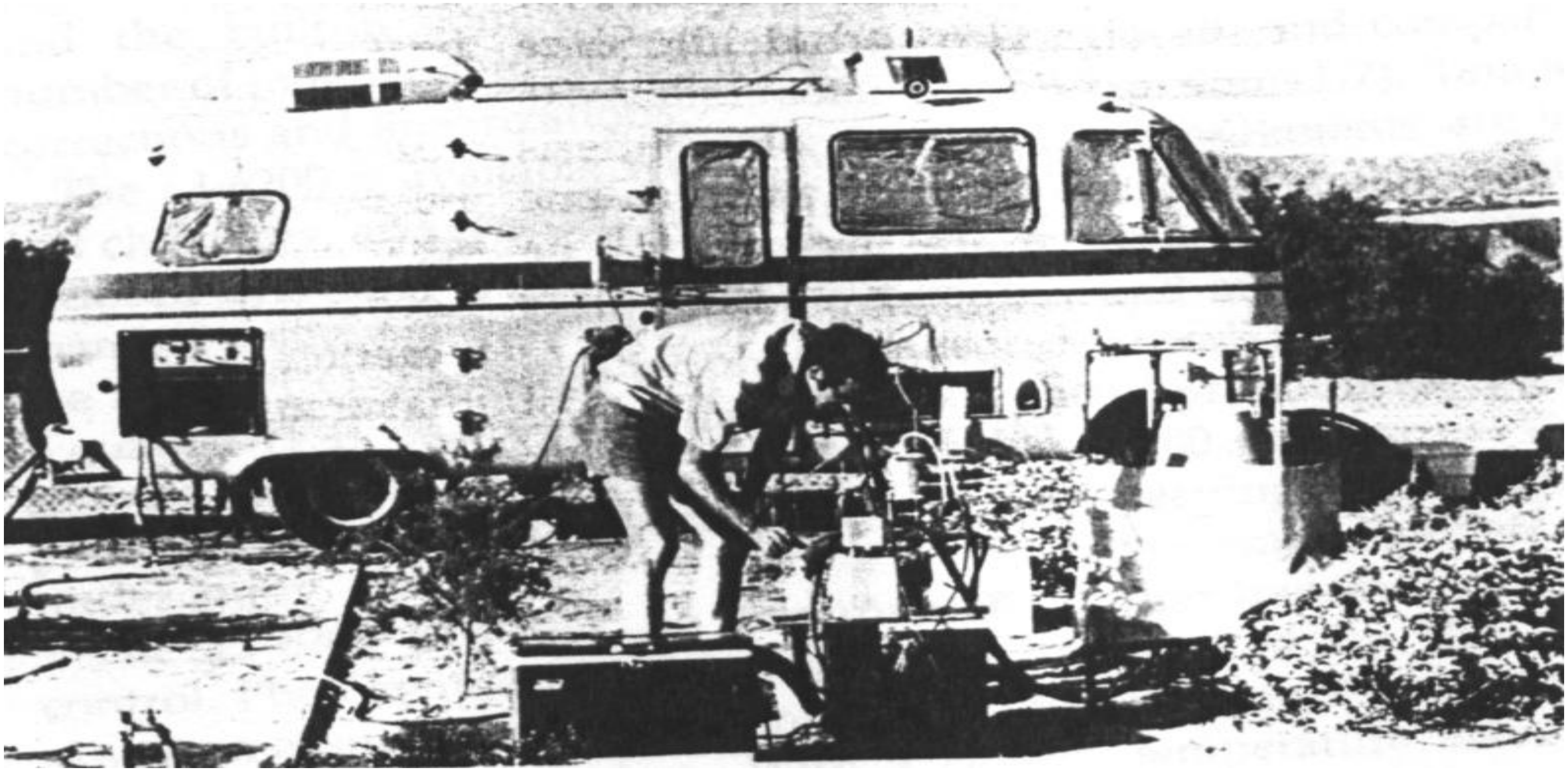


How Are Conductance and Concentrations Measured to Calculate Photosynthesis and Transpiration Fluxes?



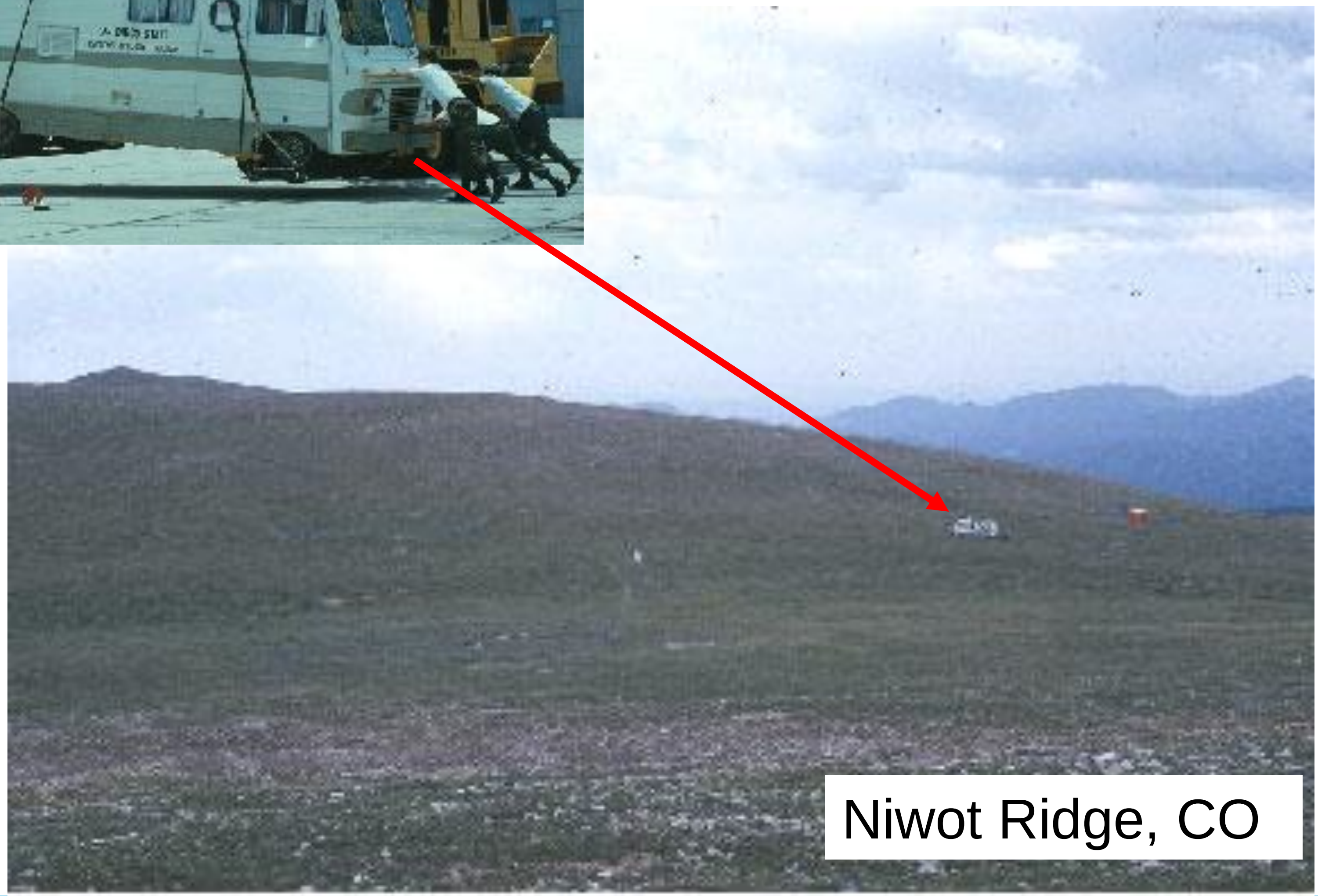
Infrared Gas Analyzers





Mooney, H.A., et al. 1971. A mobile laboratory for gas exchange measurements. Photosynthetica, 5, 128-32.

Field measurements, then …



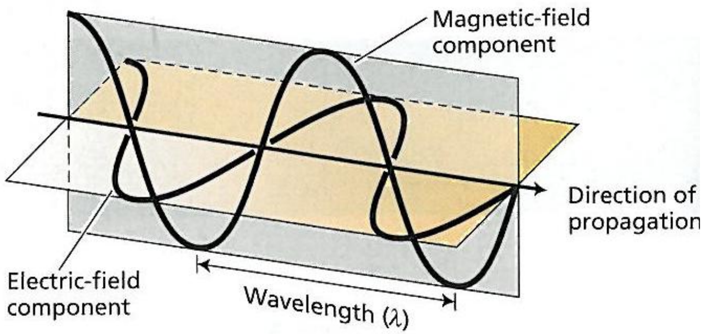
Infrared Gas Analyzers

Mooney, H.A., et al. 1971. A mobile laboratory for gas exchange measurements. Photosynthetica, 5, 128-32.

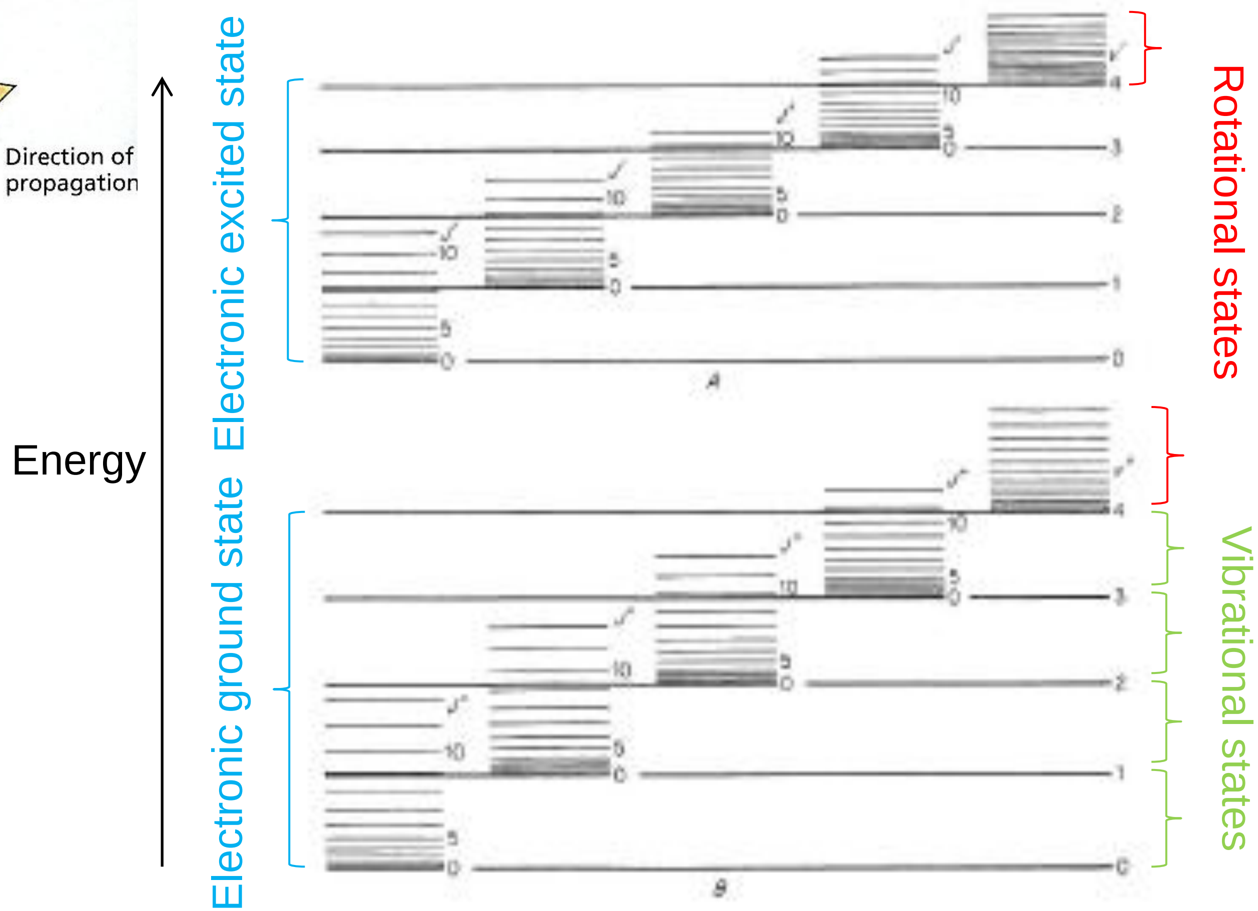
Then

Now

Absorption of light by molecules



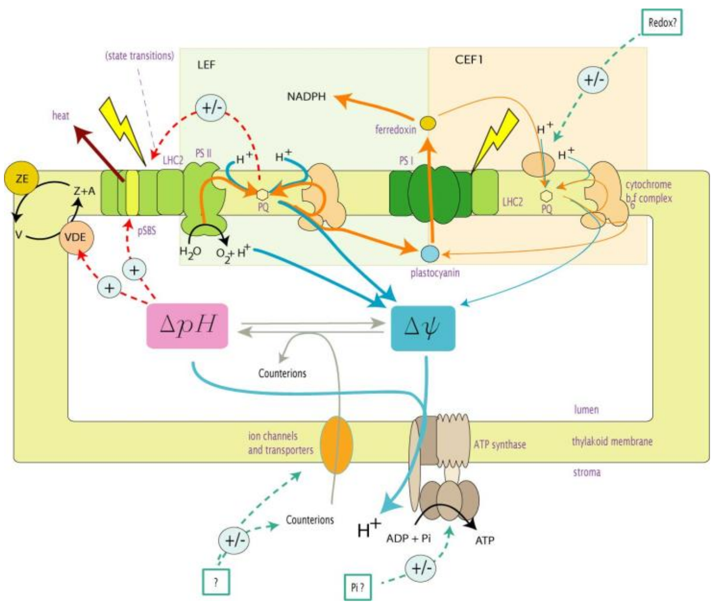
The energy of a molecule is the sum of electronic, vibrational, and rotational contributions.

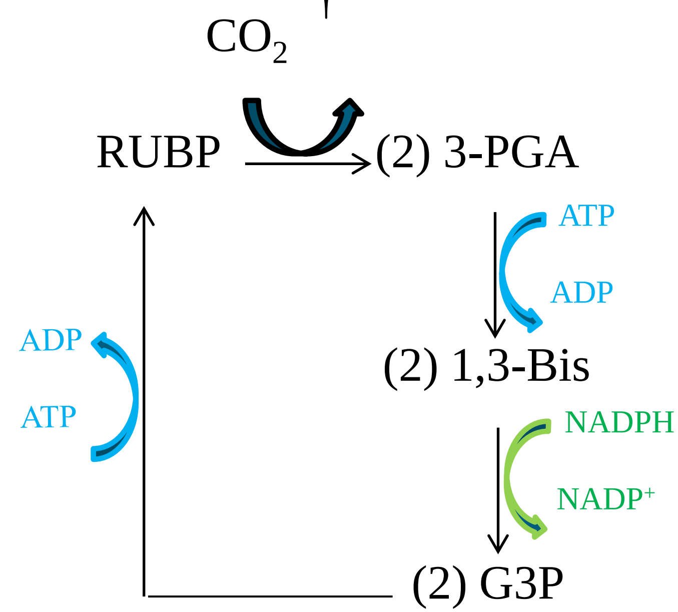


More, W.J. 1962

Using light to study photosynthesis

http://cmb.physics.wisc.edu/tutorial/spectrum.htm



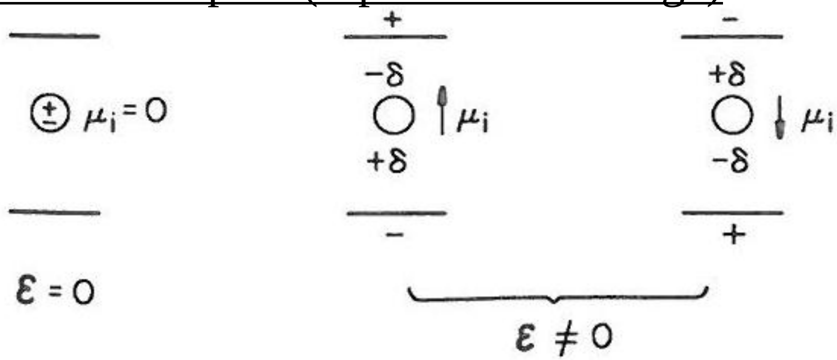


H_2O and CO_2 Absorption in the IR region involves rotations and vibrations

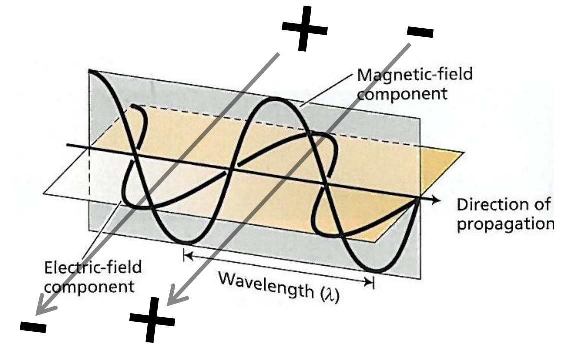
Induction of a dipole (separation of charge)

(μ_i = dipole)

(ε = electric field)



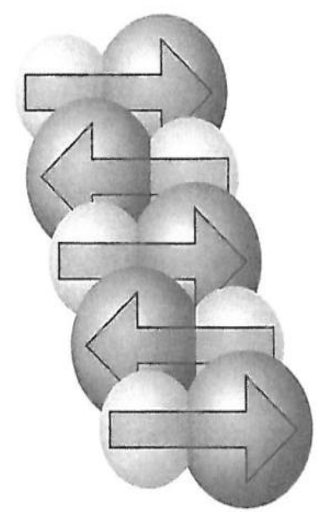
dipole

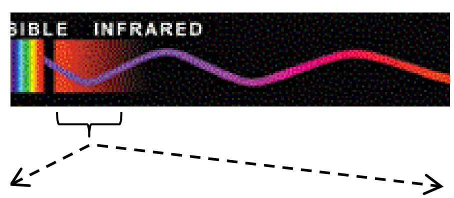


Oscillating dipole of a rotating polar molecule

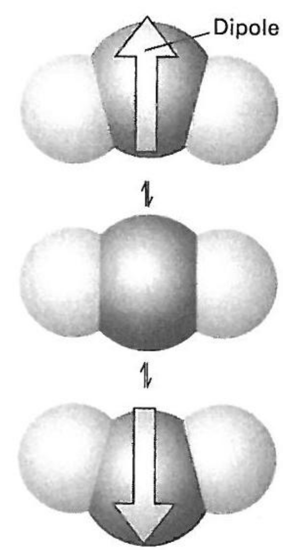
dipole

+ → −





Oscillating dipole of a vibrating non-polar molecule



dipole

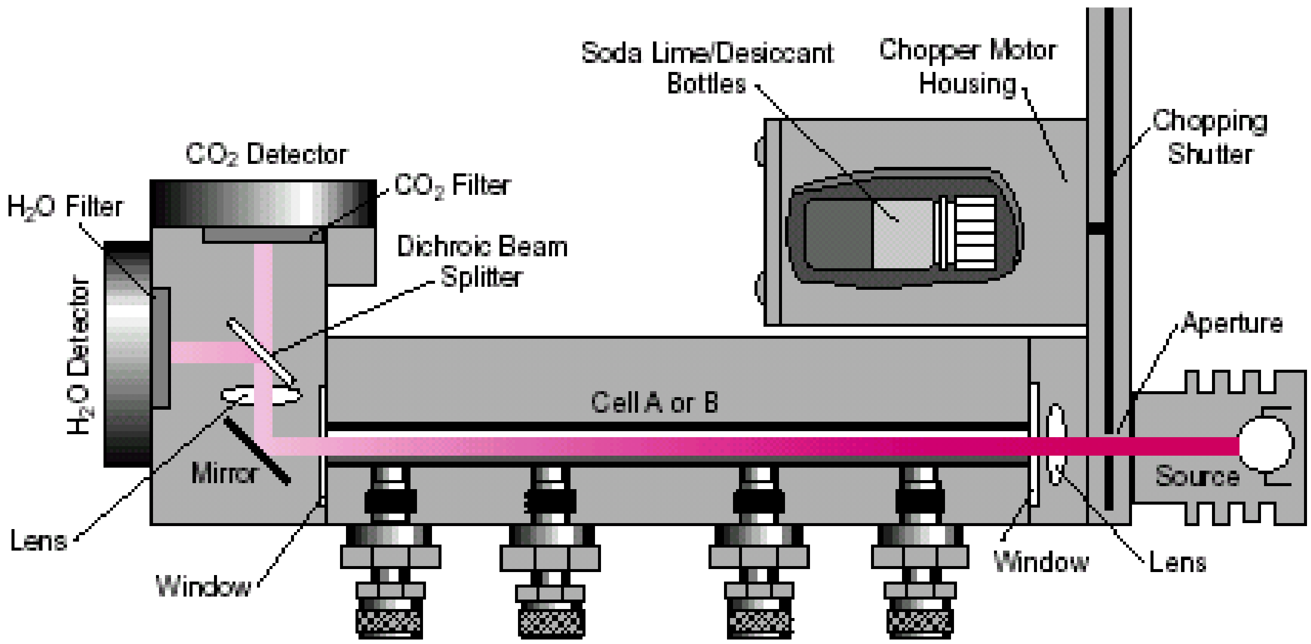
−

↑

+

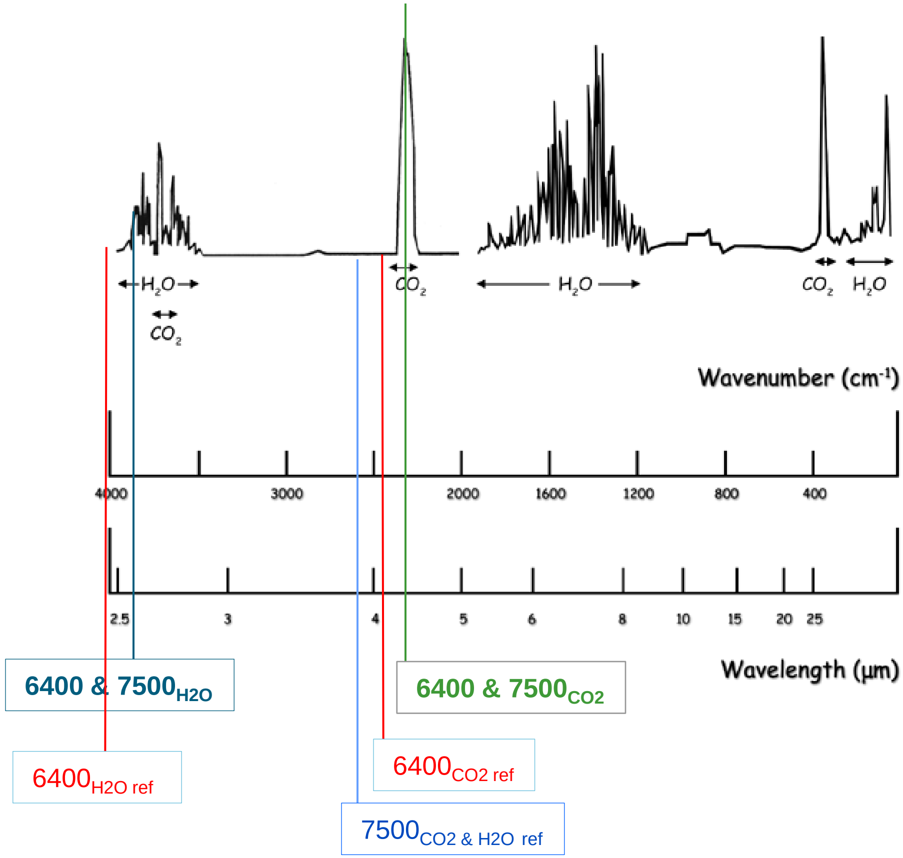
H_2O

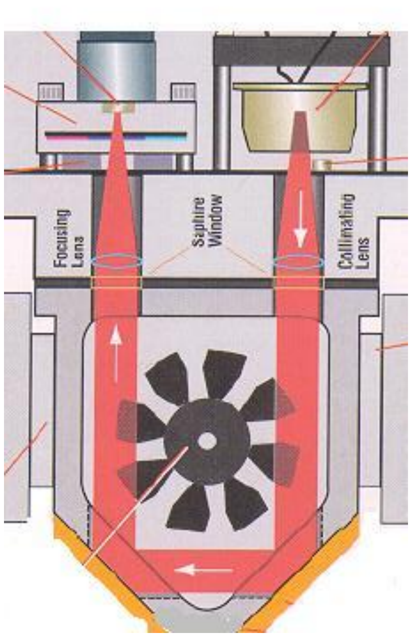
- H_2O absorbs infrared light about 2.4 μm

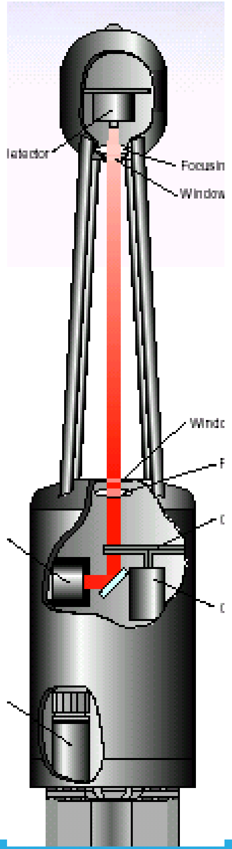


CO_2

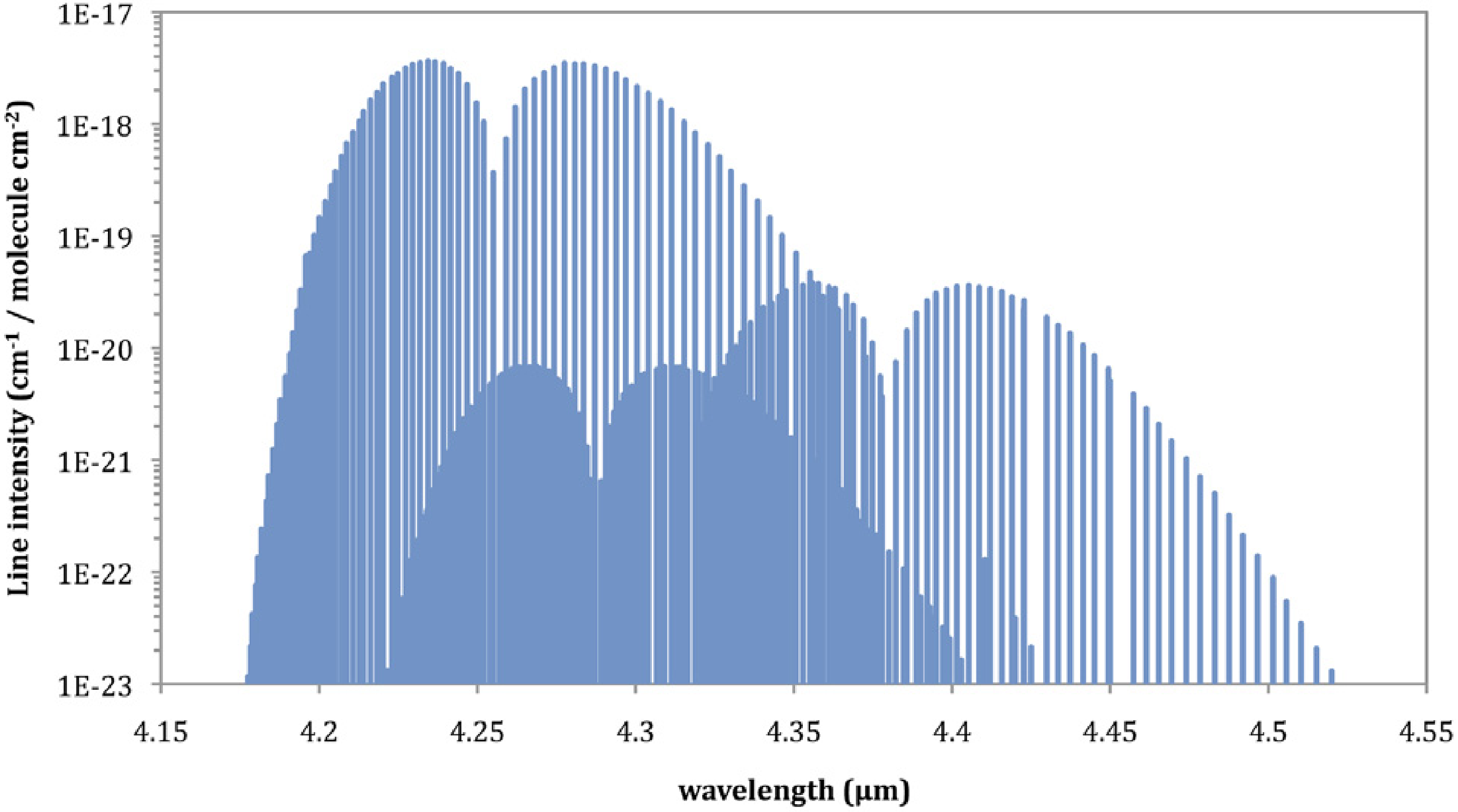
- CO_2 absorbs infrared light about 4.2 µm







CO_2 Absorption Spectrum



Band Broadening Corrections

- Intermolecular collisions with other gases in mixtures affect the IR absorption lines of CO_2.
  - Increasing collisions increases the total absorption without corresponding increase in concentration.

$$C = f\left(V\frac{P_o}{P}\right)\frac{T}{T_o}$$

- C is CO_2 in μmol mol^{-1}, f(x) is the fundamental LI-COR gas analyzer calibration function, P & T are the total pressure (kPa) and temperature (K), P_o = 101.3 kPa, T_o = 273K.

Effective Pressure Broadening

- Not all gases equally effective in causing pressure broadening of absorption lines.

$$P_e = P_{N_2} + \sum \alpha_i P_i + b_{CO_2}$$

- For example water and CO_2 in air would be:

$$P_e = P_{N_2}\alpha_{N_2} + P_{O_2}\alpha_{O_2} + P_w\alpha_w + b_{CO_2}$$

Pressure Broadening Cont.

- Substituting P_e for P in the CO_2 calculation gives the calibration equation that includes the pressure broadening effects of variable water vapor and oxygen:

$$C = c(w, x_o)F\left[\frac{VP_o}{P_c(w, x_o)}\right]\frac{T}{T_o}$$

Gas Exchange Techniques

- Enclosure Methods
  - Disturbs plants to some degree
  - Possibility for controlled experiments
  - Can measure individual components:
    - Different leaves
    - Roots
    - Soil
- Micrometerological Methods
  - Minimum disturbance
  - Summary of large areas
  - Difficult to do controlled experiments or isolate individual components

How Are Photosynthesis & Transpiration Measured in an Enclosure?

- Closed System

  $A = \Delta CO_2\, V\, (\Delta t\, S)^{-1}$

- No air enters or leaves the system

  Leaks can cause large errors

- Transient measurement

  CO_2, H_2O, T & P changes

- Open System

  $A = (u_e c_e - u_o c_o)\, S^{-1}$

- Flow of air must be constant & known (accurate flow meter)

- Steady-state measurement

  controlling environmental variables

LI-6250 Flow Schematic

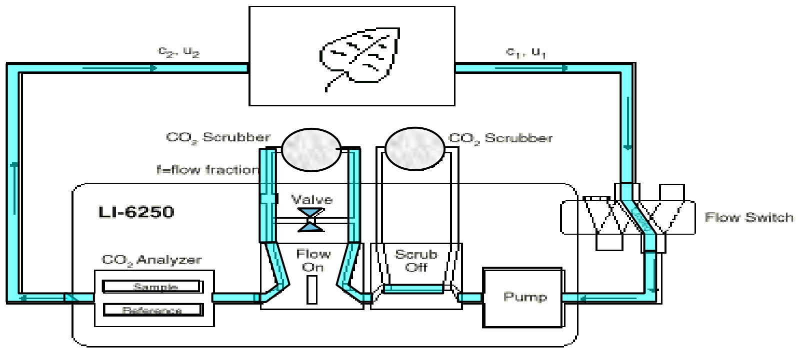
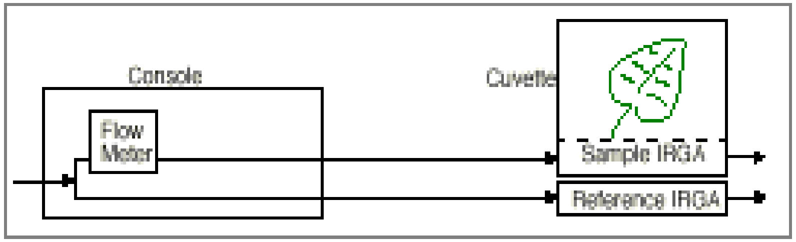


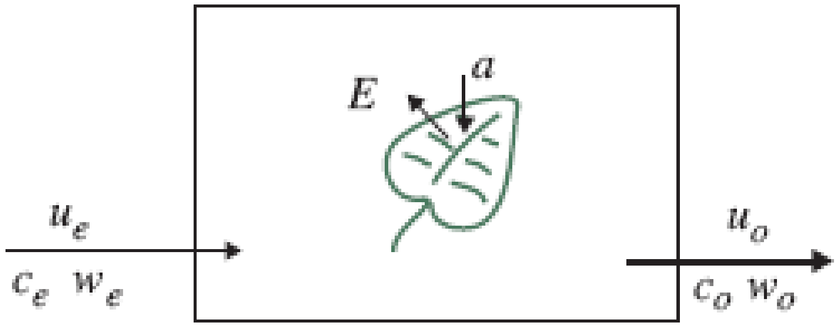
Figure 1. Schematic diagram of flow circuit.

LI-6400



Measured Variables

- CO_2
- H_2O
- Flow rate
- Light
- Temperature
  - Air and Leaf



Assumptions

- Flow rate into chamber equals flow rate out
- Leaf interior saturated $e(t_s)$
- g_c is negligible
- g_{bl} is known
- Diffusion difference between CO_2 and H_2O is 1.6

Leaf Transpiration

$$sE = (\mu_i + sE)w_o - \mu_e w_e$$

$$E = \frac{\mu_e(w_o - w_e)}{s(1 - w_o)}$$

- Transpiration (E) calculated from entering and exiting H_2O concentrations and flow rates.
- Normalized to leaf area (*s*).

Stomatal Conductance (gsw)

$$g_{sw} = \frac{1}{\frac{1}{g_{tw}} - \frac{k_f}{g_{bw}}}$$

$$g_{tw} = \frac{E\left(1 - \frac{w_l - w_e}{2}\right)}{w_l - w_e}$$

$$k_f = \frac{k^2 + 1}{(k+1)^2}$$

- $\mathbf{g_{tw}}$ is calculated from the E, the measured H_2O in chamber (w_e) and assumed H_2O inside leaf (w_l)
- $\mathbf{g_{sw}}$ (mol H_2O m^{-2} s^{-1}) is calculated from total conductance
  - Boundary layer known
- $\boldsymbol{k_f}$ is a factor based on the estimate ***k***
  - ***k*** = fraction of stomatal conductance of one side of the leaf to the other (*stomatal ratio*).

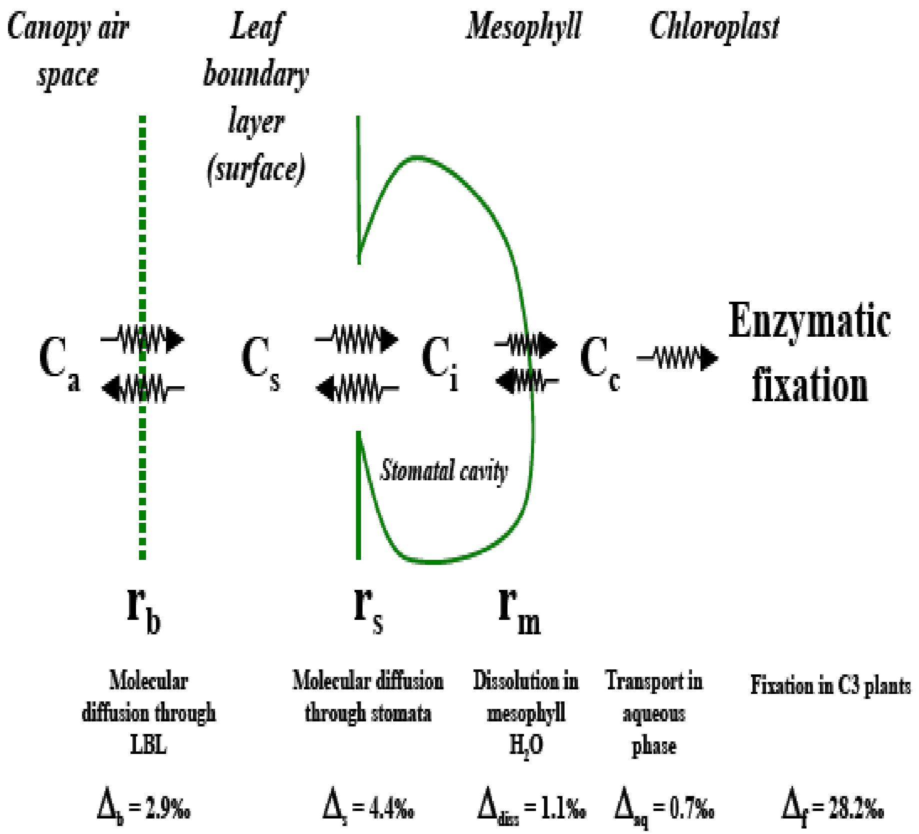
Photosynthesis

- $u_o = u_e + sE$
- $sA = u_e c_e - (u_e + sE) c_o$

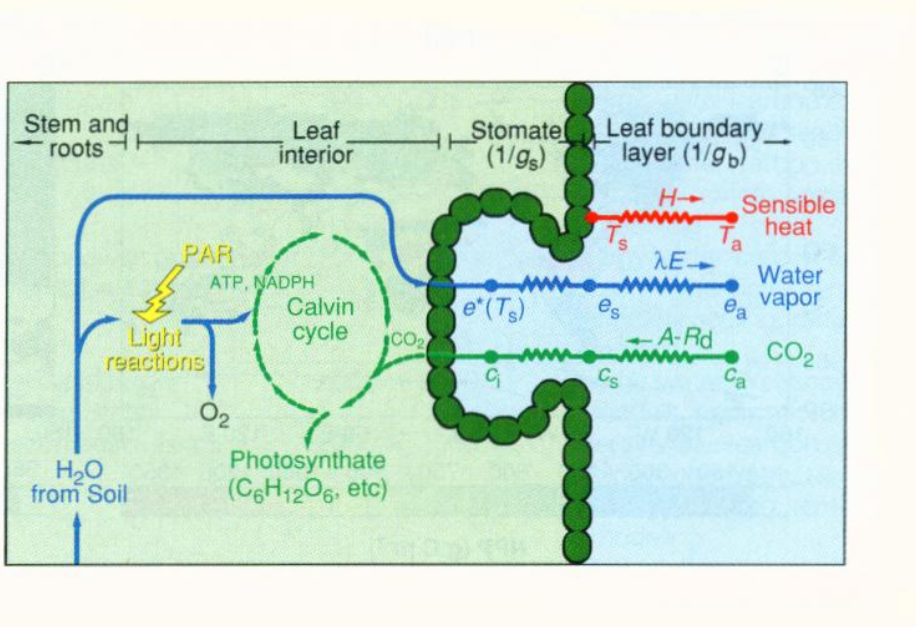
$$A = \frac{u(C_r - C_s)}{100S} - C_s E$$

- **μ** is flow rate (μmol mol^{-1}), ***Cr*** and ***Cs*** are reference and sample CO_2 concentrations (μmol mol^{-1}), ***S*** is leaf area (m^2), and ***E*** is transpiration (mol m^{-2} s^{-1})
- Dilution due to H_2O vapor

C_i



- $g_{sc} = 1.6\ g_{sw}$
- $r_{sc} = 1 / g_{sc}$
- Fick Law
  - $A = (c_a - c_i) / r_{sc}$



C_i cont'd.

$$g_{tc} = \frac{1}{\frac{1.6}{g_{sw}} + \frac{1.37k_f}{g_{bw}}}$$

$$C_i = \frac{(g_{tc} - \frac{E}{2})C_s - A}{g_{tc} + \frac{E}{2}}$$

- The ratio between the diffusivities of CO_2 and water in the boundary layer is 1.37, compared to 1.6 in air

Some Uses of Leaf-level Measures

- Plant growth models
- GCMs
  - Canopy A, E and g_s validation and modeling
- Eddy Covariance
  - Scale-up validation

What parameters do researchers want to measure?

- Net flux of CO_2 (photosynthesis or respiration)
- Transpiration (E) & Stomatal Conductance (g_s)
- Leaf internal CO_2 concentration (C_i) and CO_2 concentration inside the chloroplast (C_c)
- Electron Transport Rate (J)
- Velocity of Carboxylation (V_c)

Exploring limitations to photosynthesis

Journal of Experimental Botany, Vol. 54, No. 392, pp. 2393–2401, November 2003
DOI: 10.1093/jxb/erg262

Journal of Experimental Botany

REVIEW ARTICLE: FIELD TECHNIQUES

Gas exchange measurements, what can they tell us about the underlying limitations to photosynthesis? Procedures and sources of error

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[2] USI

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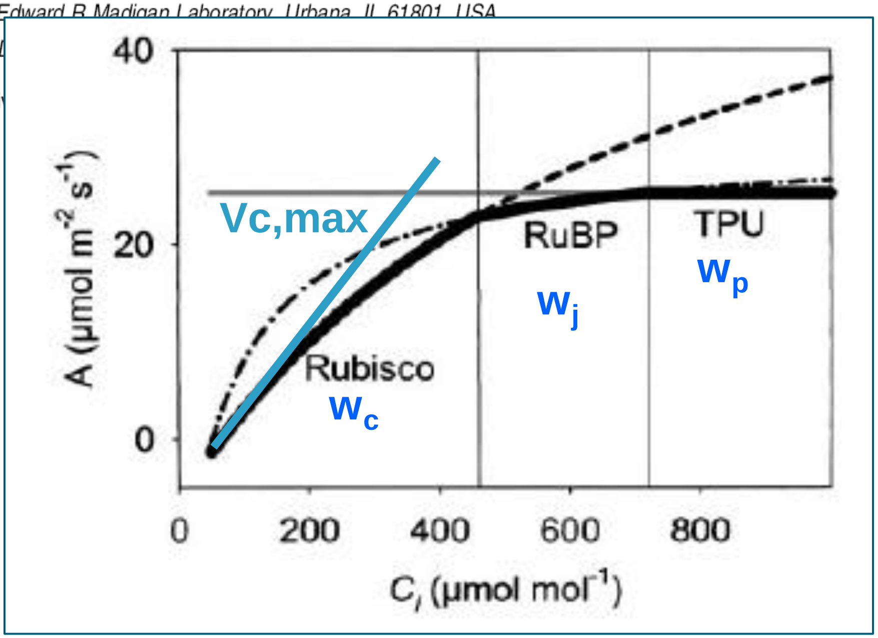


A-C_i Curves

Farquhar, von Caemmerer & Berry analysis:

$$A = \min\{w_c, w_j, w_p\}\left(1 - \frac{\Gamma*}{C_i}\right) - R_d$$

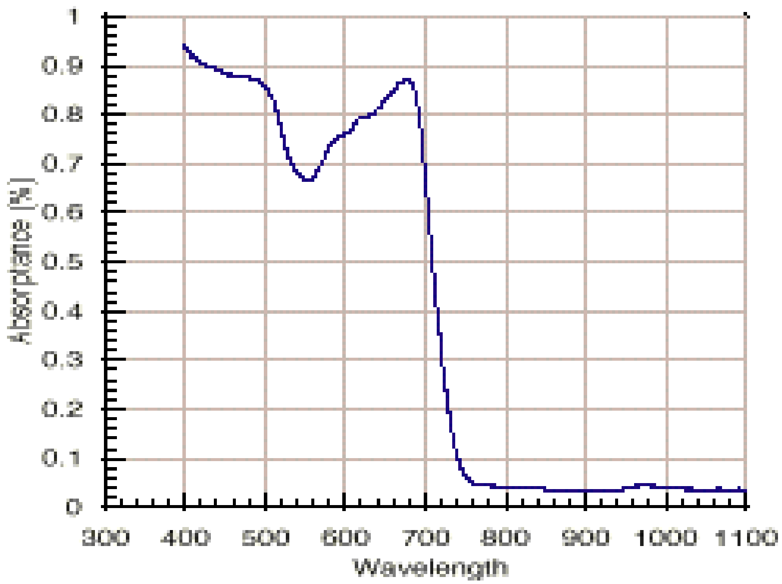
where:

$$w_c = \frac{V_{c,\max} C_i}{C_i + K_c(1 + O/K_o)}$$

$$w_j = \frac{J C_i}{4.5 C_i + 10.5\Gamma^*}$$

$$w_p = \frac{3 V_{tpu}}{\left(1 - \frac{\Gamma*}{C_i}\right)}$$

Exploring limitations to photosynthesis

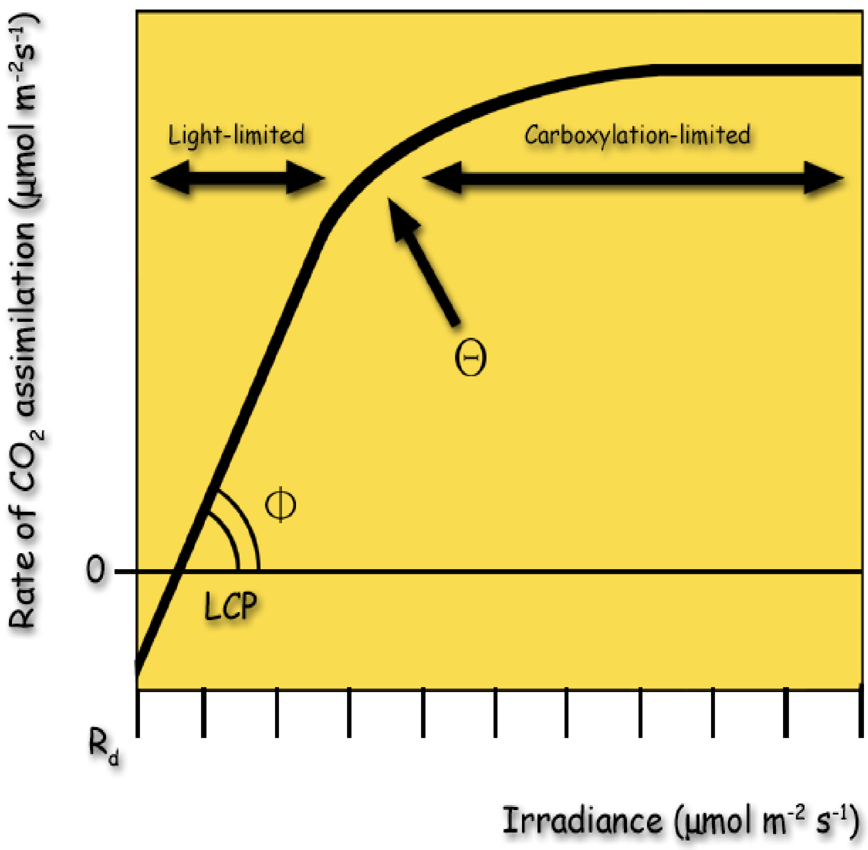


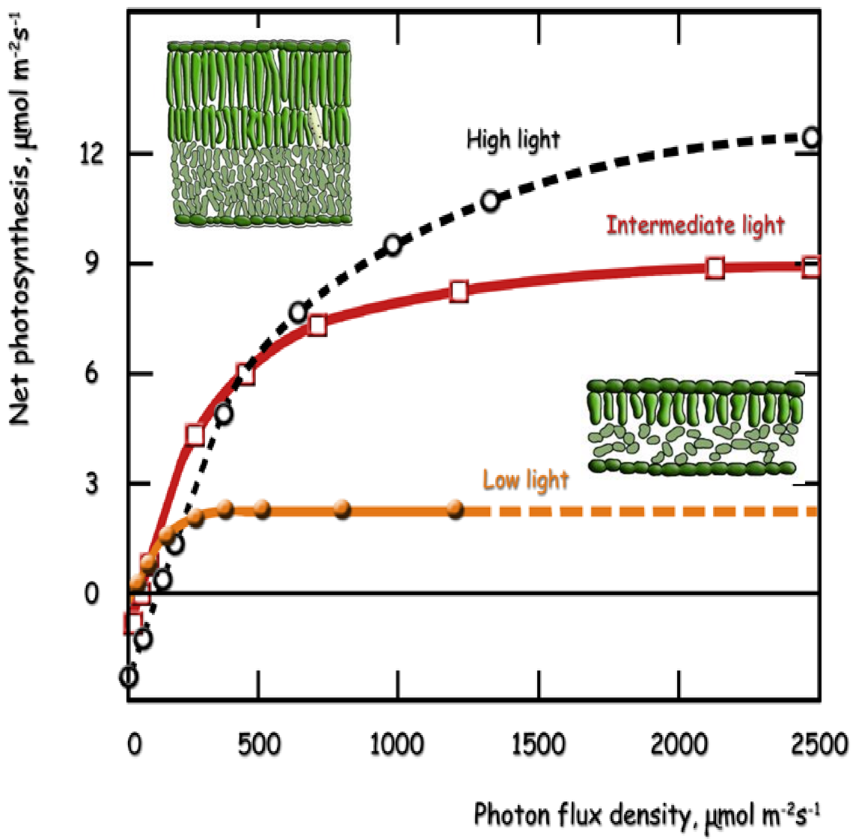
Photosynthesis depends more on the number of photons, rather than the amount of energy of the photons

- Irradiance: Radiant flux incident on a surface (W m^{-2})
- Photosynthetically Active Radiation (PAR): Radiation 400 to 700 nm (W m^{-2}), about 50% of total radiation
- Photosynthetic Photon Flux Density (PPFD): Number of photons (400-700 nm) incident per unit time and area (µmol m^{-2} s^{-1})

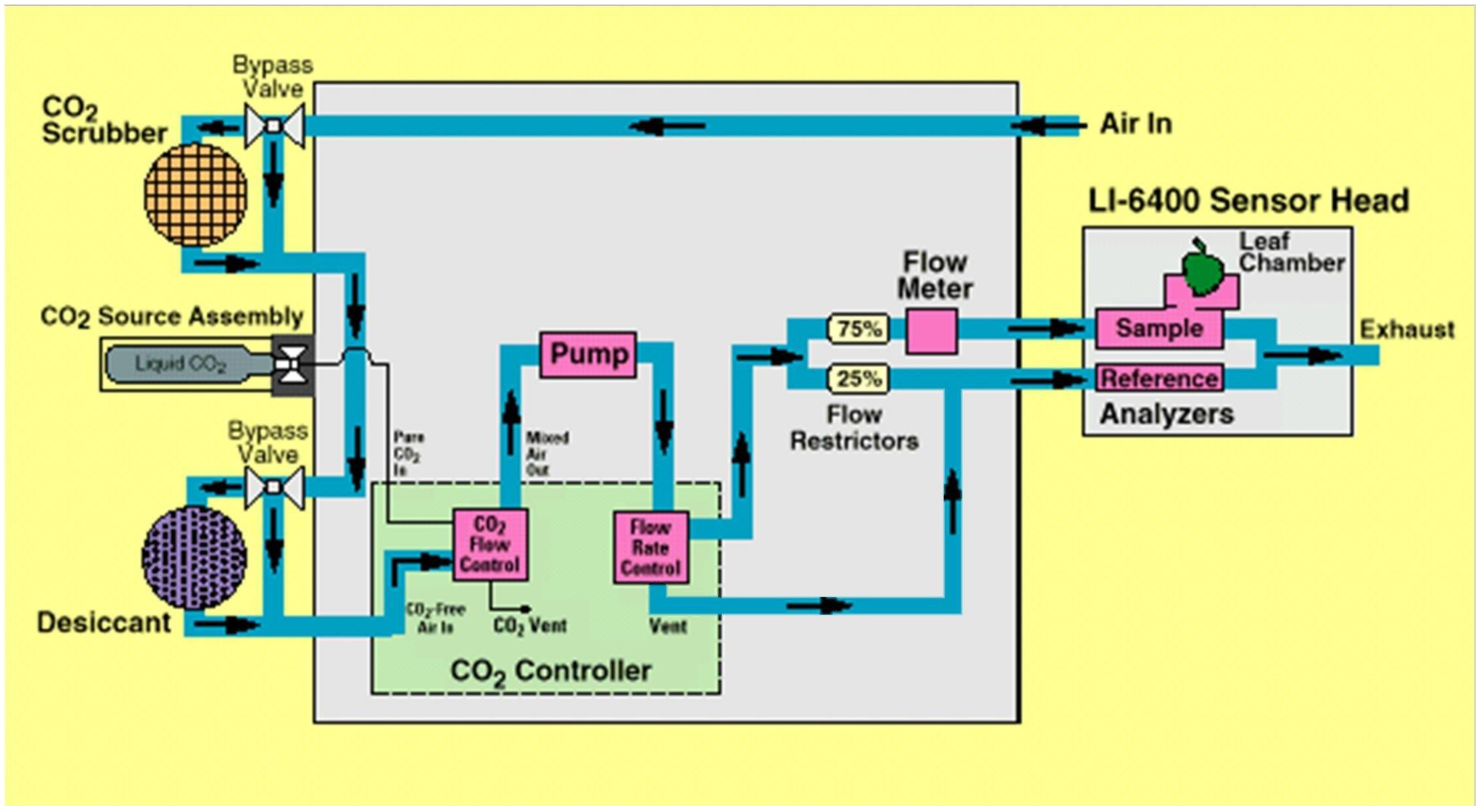
Exploring limitations to photosynthesis

Light Curves



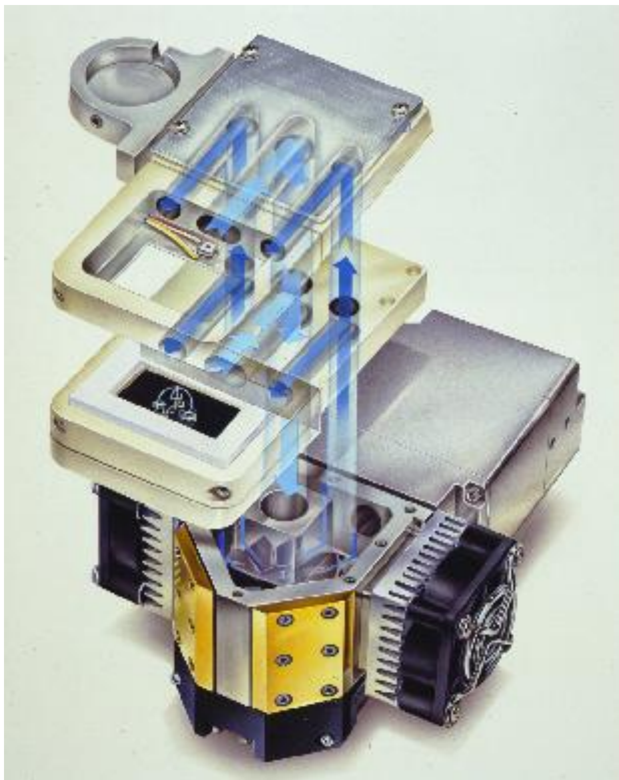


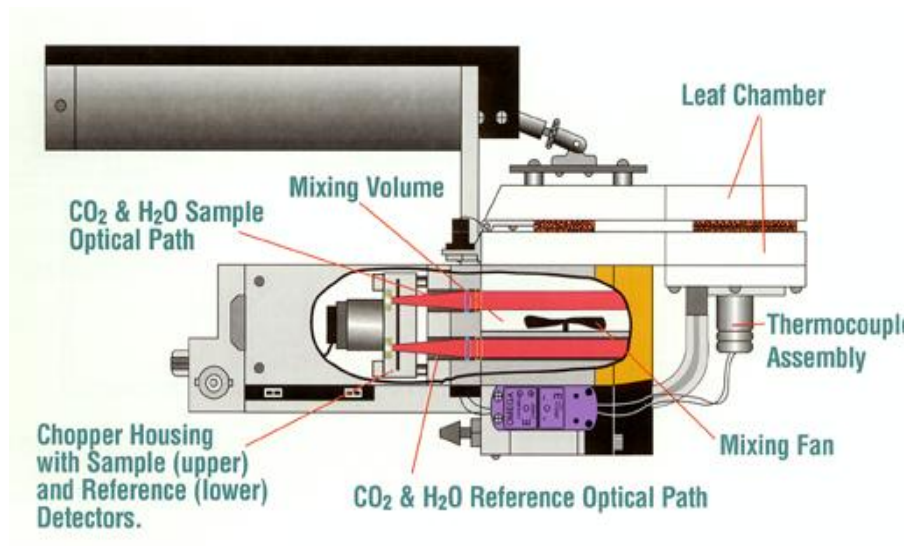
Flow Path

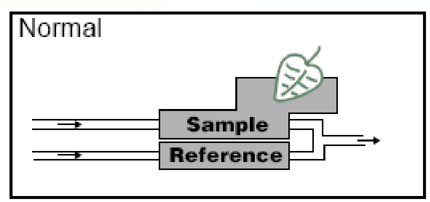


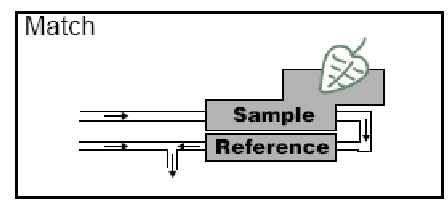
Bypass Valve
CO_2 Scrubber
Air In
LI-6400 Sensor Head
Leaf Chamber
Flow Meter
CO_2 Source Assembly
Liquid CO_2
Pump
75%
25%
Sample
Reference
Exhaust
Analyzers
Flow Restrictors
Bypass Valve
Pure CO_2 In
Mixed Air Out
CO_2 Flow Control
Flow Rate Control
Desiccant
CO_2-Free Air In
CO_2 Vent
Vent
CO_2 Controller

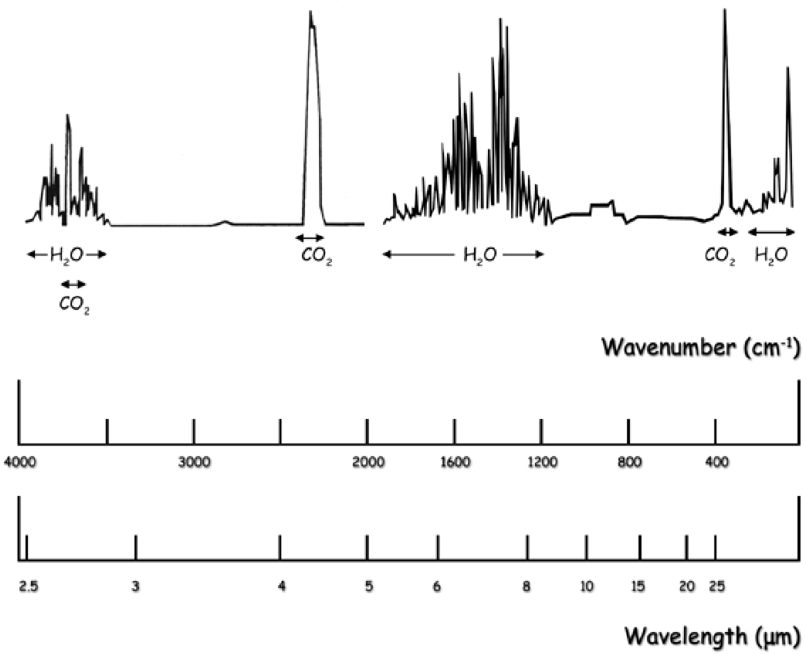
Mixing and Analyzers



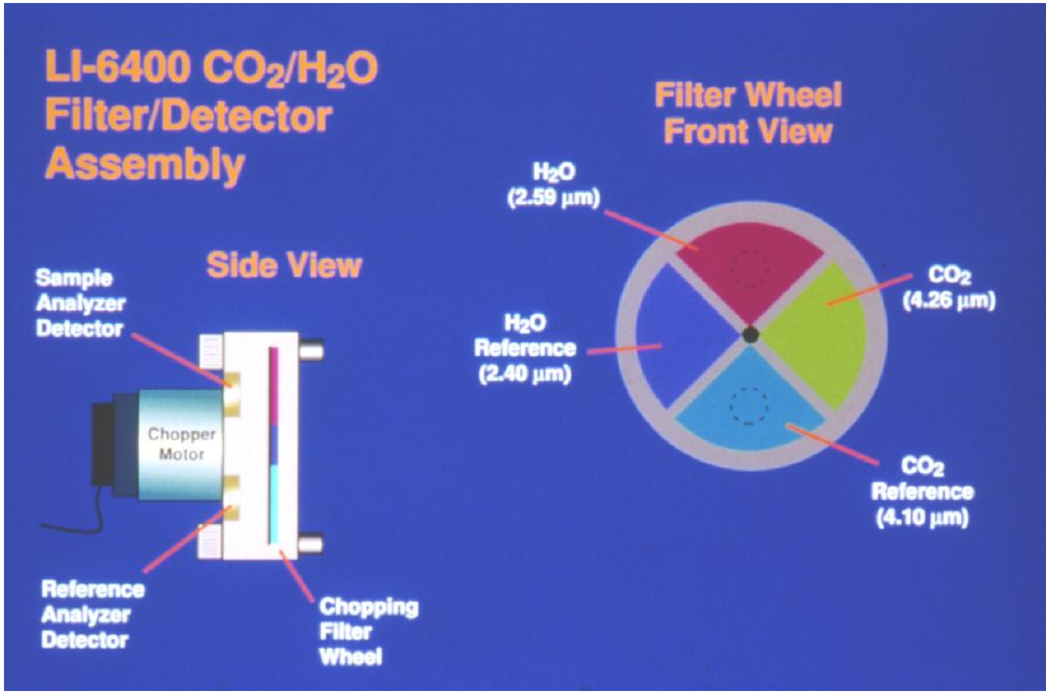








H2O
CO2
CO2
H2O
CO2
H2O
Wavenumber (cm-1)
4000
3000
2000
1600
1200
800
400
2.5
3
4
5
6
8
10
15
20
25
Wavelength (µm)



LI-6400 CO2/H2O Filter/Detector Assembly
Side View
Sample Analyzer Detector
Chopper Motor
Reference Analyzer Detector
Chopping Filter Wheel
Filter Wheel Front View
H2O (2.59 µm)
CO2 (4.26 µm)
H2O Reference (2.40 µm)
CO2 Reference (4.10 µm)