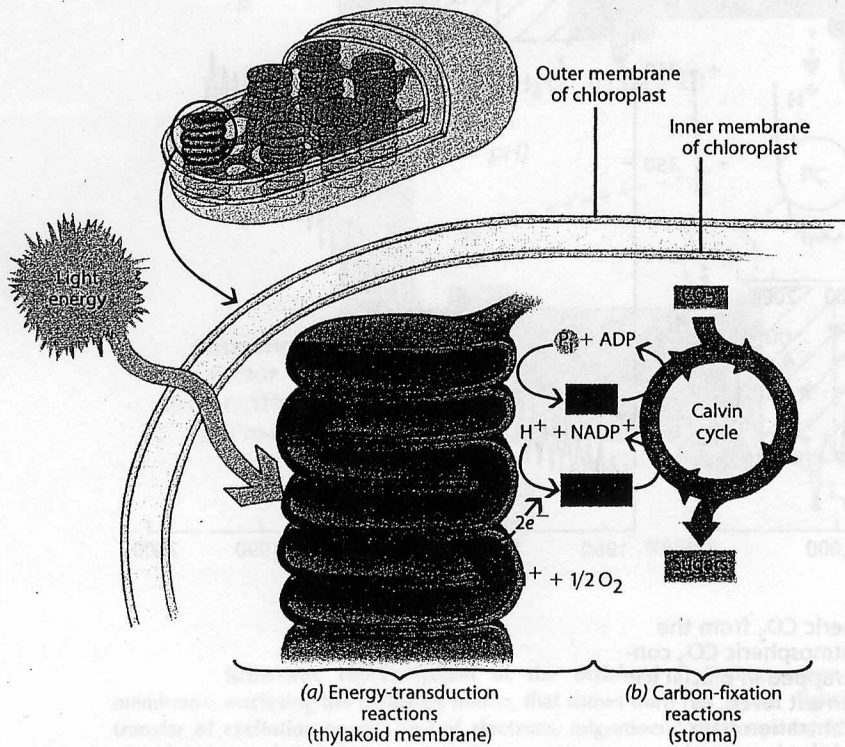


Photosynthesis: an overview of limitations

I. *Photosynthesis* - is a process which is dependent and limited by multiple resources

A. Fundamental process distinguishing plants from animals and a central process relating directly or indirectly to almost all adaptations seen in plants

B. Two aboveground resources are necessary for photosynthesis: light (driving force, varies in space and time) and CO₂ (essentially constant, but increasing with time; see Figure)



An overview of photosynthesis. Photosynthesis takes place in two stages: the energy-transduction reactions and the carbon-fixation reactions. (a) In the energy-transduction reactions, light energy absorbed by chlorophyll a molecules in the thylakoid membrane is used indirectly to power the synthesis of ATP. Simultaneously, in the interior of the thylakoid, water is split into oxygen gas and hydrogen atoms (electrons and protons). The electrons are ultimately accepted by NADP⁺ and H⁺, producing NADPH. (b) In the carbon-fixation reactions, which occur in the stroma of the chloroplast, sugars are synthesized from carbon dioxide and the hydrogen carried by NADPH. This process is powered by the ATP and NADPH produced in the energy-transduction reactions. As we shall see, it involves a series of reactions, known as the Calvin cycle, that are repeated over and over.

1. Light capture depends upon,

- a. light availability (time, orientation, canopy position)
- b. efficiency of light capture apparatus (absorbance, chlorophyll content)

2. CO₂ capture depends upon,

- a. atmospheric CO₂ concentration (1996: 357.4 ppm, increasing 1.7 to 2.1 ppm per year with odd fluctuations since mid-1980's)
- b. diffusional gradients/barriers - stomata, mesophyll, ...
- c. diffusion constant (mm s⁻¹) at 25° C is dependent on medium

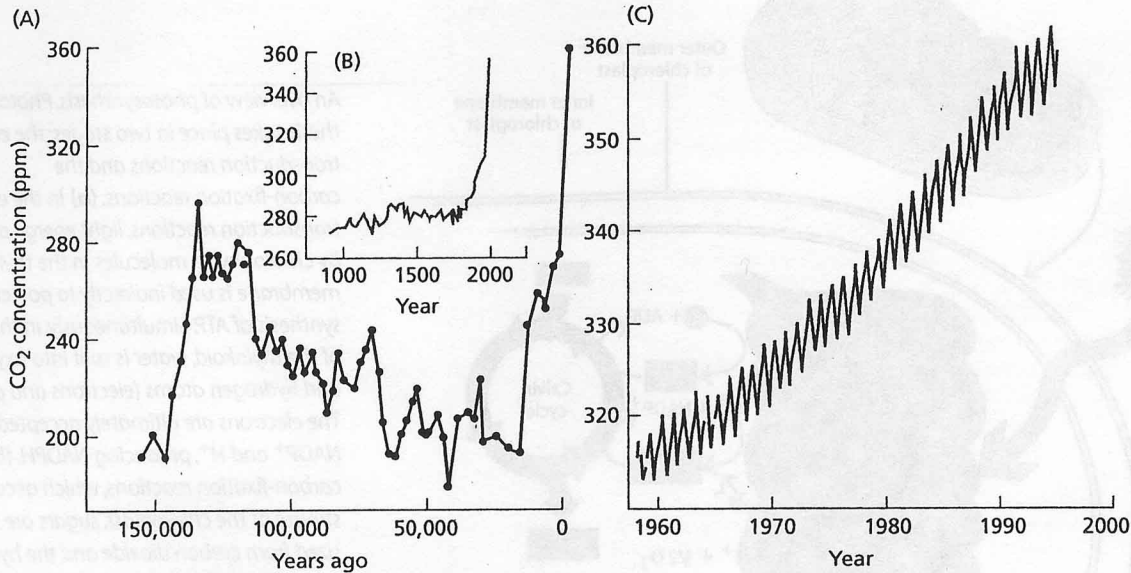
(see figure next page)

CO ₂ in air	15.1	
CO ₂ in water	0.0016	
HCO ₃ ⁻ in water	0.0014	
H ₂ O in air	24.9	(note: water diffuses 1.65 times faster in air than CO ₂)
H ₂ O in H ₂ O	0.0025	

- d. surface to volume ratio for cells - much of the surface area surrounding
- e. solubility of CO₂ (m³ m⁻³) in water is low and temperature dependent

10° C	1.194
20° C	0.878
30° C	0.665

C. Overall rate of net CO₂ uptake depends on the balance between the rates of individual resource capture processes; these are coupled processes and both must be working.

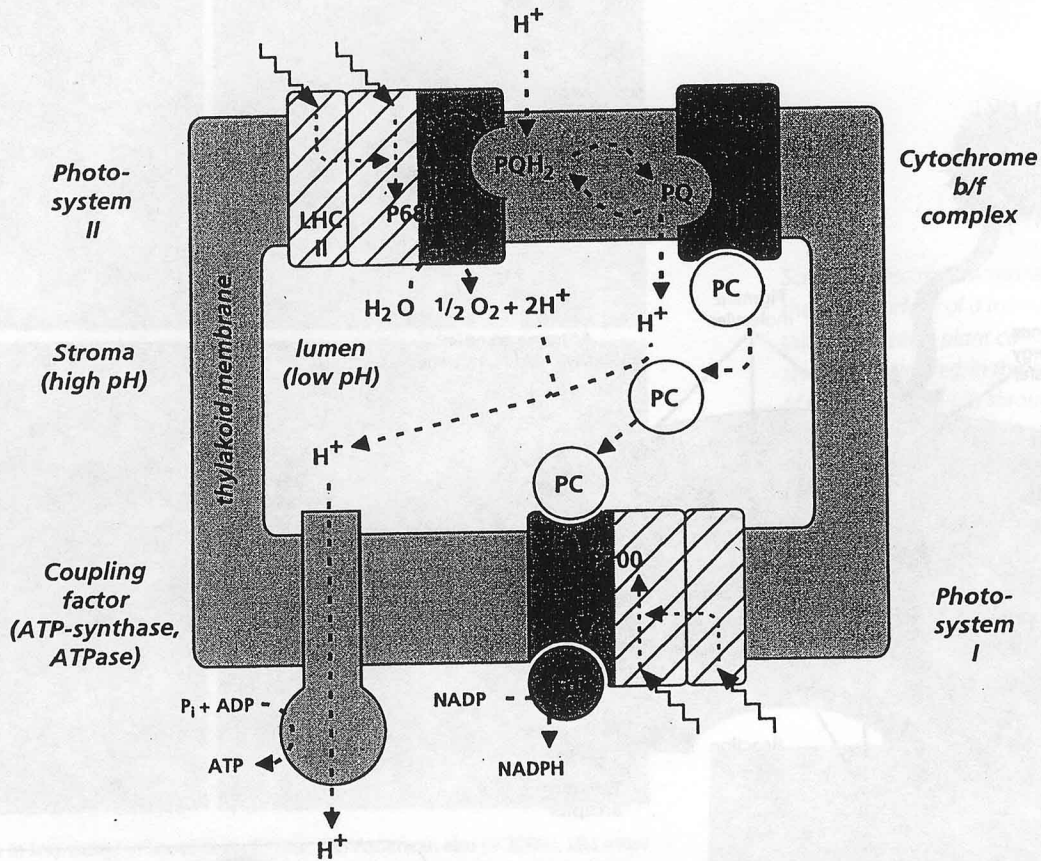


Concentration of atmospheric CO₂ from the present to 160,000 years ago. (A) Past atmospheric CO₂ concentrations, determined from bubbles trapped in glacial ice in Antarctica, were much lower than current levels. (B) In the last 1000 years, the rise in CO₂ concentration has coincided with the Industrial Revolution and the increased burning of fossil fuels. (C) Current atmospheric concentrations of CO₂ measured at Mauna Loa, Hawaii, continue to rise. Each year, the highest concentration is observed in May, just before the Northern Hemisphere growing season, and the lowest concentration is observed in October. (After Barnola et al. 1994, Keeling and Whorf 1994, Neftel et al. 1994, and Keeling et al. 1995.)

II. Light capture

A. Two photosystems arranged in linear sequence with electron transport components between them (Figures)

1. In both systems, an antenna pigment system transfers an electron to a central chlorophyll unit (reaction center) that passes electron onto electron transport system,
2. Photosystem I - high chlorophyll a/b ratio and reaction center is P700 (receives its electrons
3. Photosystem II - low chlorophyll a/b ratio and reaction center is P680 (processes photons
4. ATP and NADPH are generated (Figure) - the KEY products,
5. Initial capture and transfer (PSII/P680 ----> PQ and PSI/P700 ----> X) is temperature independent and fast (10⁻¹² s); electron transport is temperature sensitive

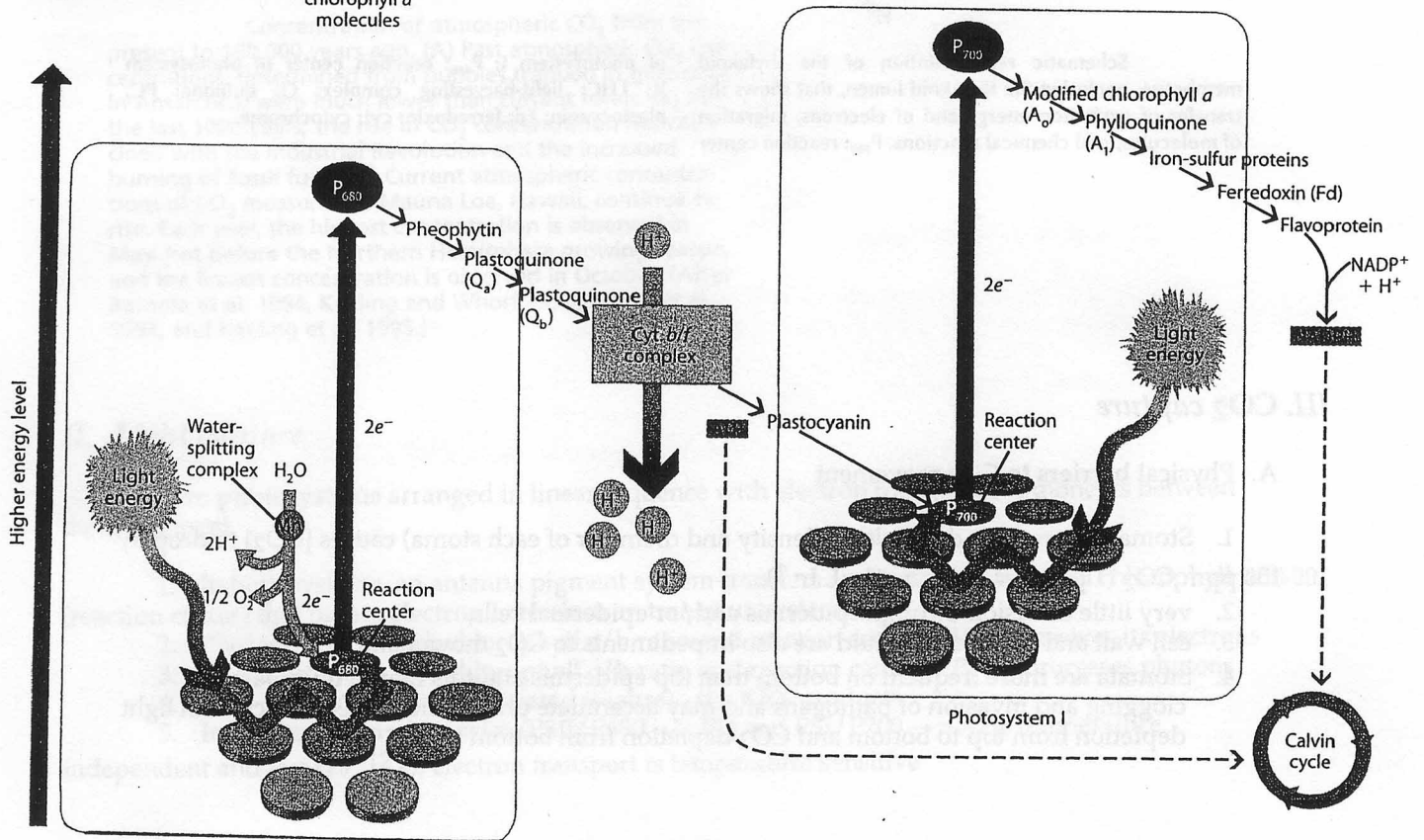
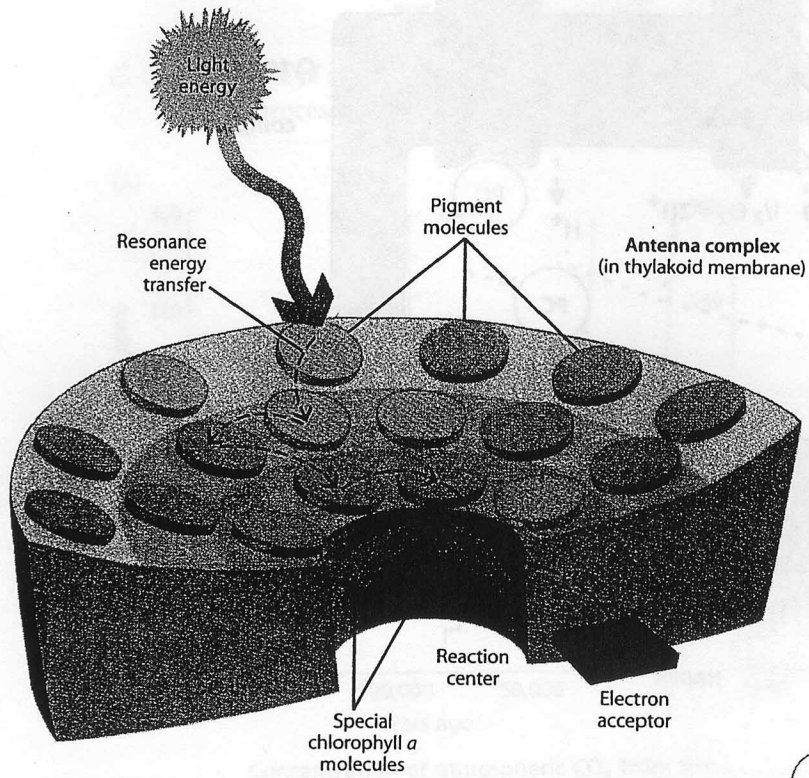


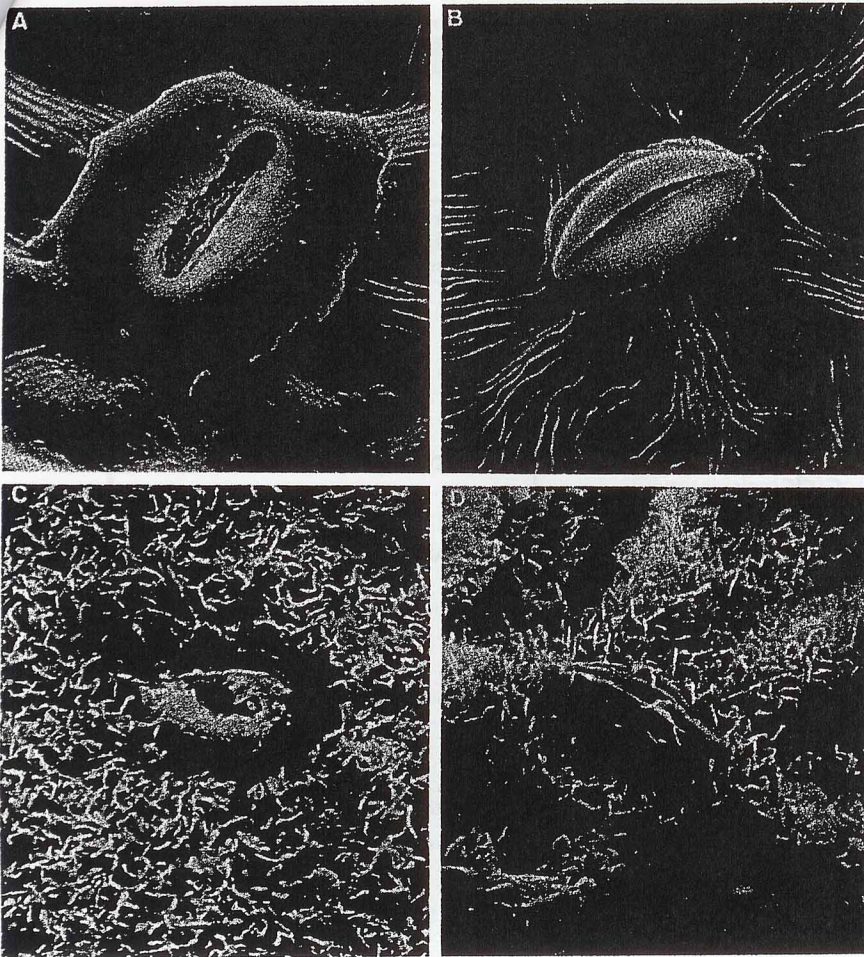
Schematic representation of the thylakoid membrane, enclosing the thylakoid lumen, that shows the transfer of excitation energy and of electrons, migration of molecules, and chemical reactions. P₇₀₀: reaction center of photosystem I; P₆₈₀: reaction center of photosystem II; LHC: light-harvesting complex; Q: quinone; PC, plastocyanin; Fd: ferredoxin; cyt: cytochrome.

III. CO₂ capture

A. Physical barriers to CO₂ movement

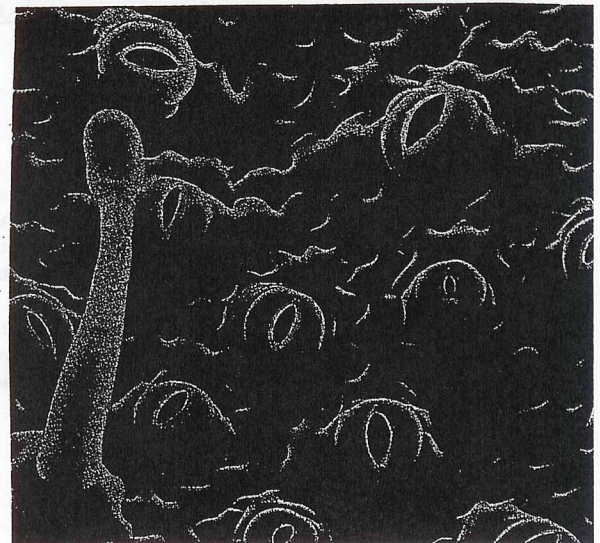
1. Stomatal pore (size depends on density and diameter of each stoma) causes [CO₂] to drop by 100-150 ppm CO₂ (1 part per million = 1 μL L⁻¹),
2. very little diffusion through epidermis and/or epidermal cells,
3. cell wall and cytoplasmic fluid are also impediments to CO₂ movement
4. Stomata are more frequent on bottom than top epidermis and this may reduce particle clogging and invasion of pathogens and may accentuate photosynthetic efficiency with light depletion from top to bottom and CO₂ depletion from bottom to top





Variations in leaf waxes of broad-leaved trees: (A) American elm (×2000), (B) white ash (×2000), (C) sugar maple (×2000), and (D) eastern redbud (×2000). Photos by W. J. Davies.

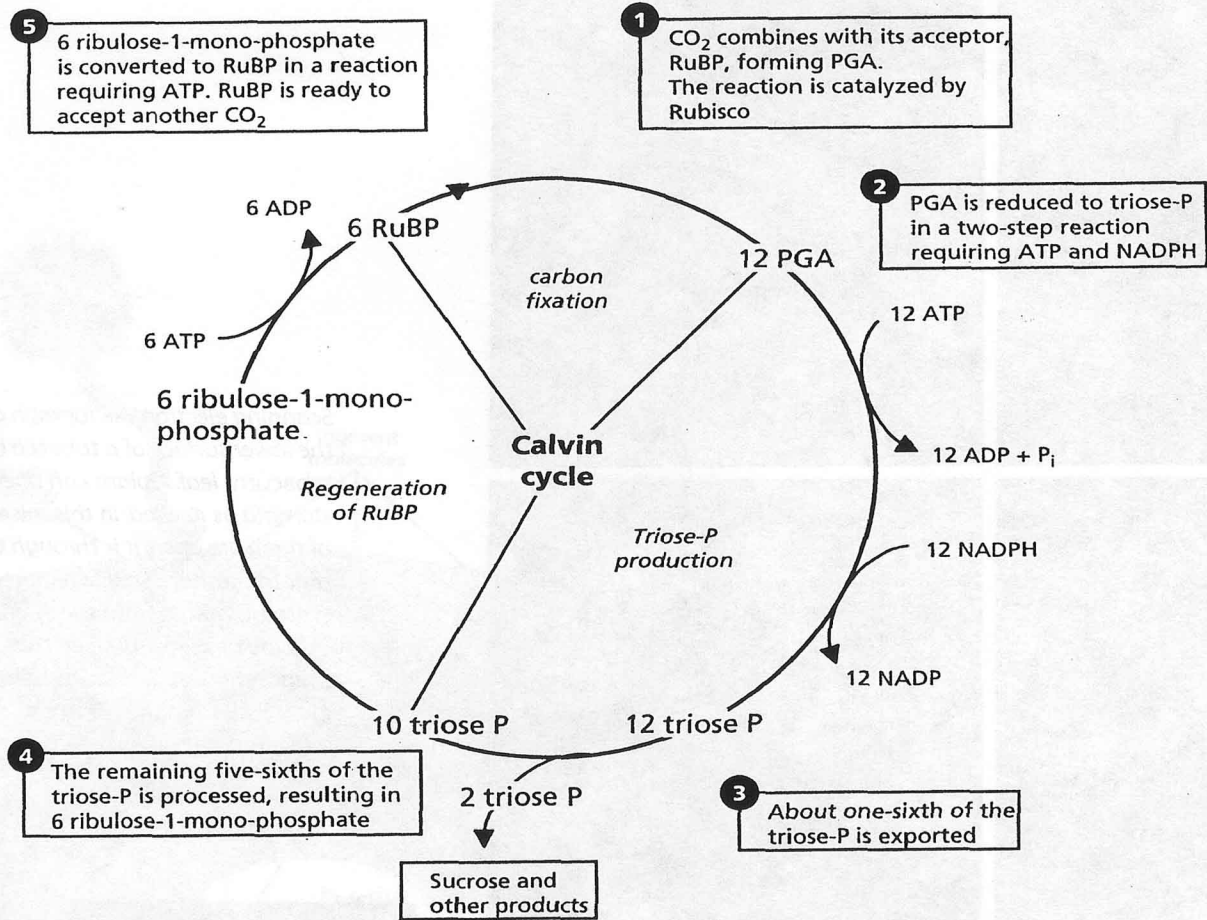
Scanning electron micrograph of stomata on the surface of a tobacco (*Nicotiana tabacum*) leaf. A plant can open or close its stomata as needed; in this micrograph, most of them are open. It is through the stomata that the carbon dioxide required for photosynthesis diffuses into the interior of the leaf and the oxygen produced as a by-product of photosynthesis diffuses out. The structure extending from the surface at the lower left is a leaf hair.



60 μm

B. Photosynthetic carbon reduction (PCR) cycle (Figure next page) + p. 5b

1. $\text{CO}_2 + \text{RuBP} \rightarrow 2 \text{PGA} + \text{NADPH} + \text{ATP} \rightarrow \text{RuBP} + (\text{CH}_2\text{O})_n$,
2. under sufficient light levels, the initial carboxylation step by RuBP carboxylase is usually the rate-limiting step in net CO_2 fixation,
3. RuBP carboxylase is a large protein (m.w. 500,000) consisting of 8 large, identical subunits (chloroplast genome) and 8 small, identical subunits (nuclear genome),



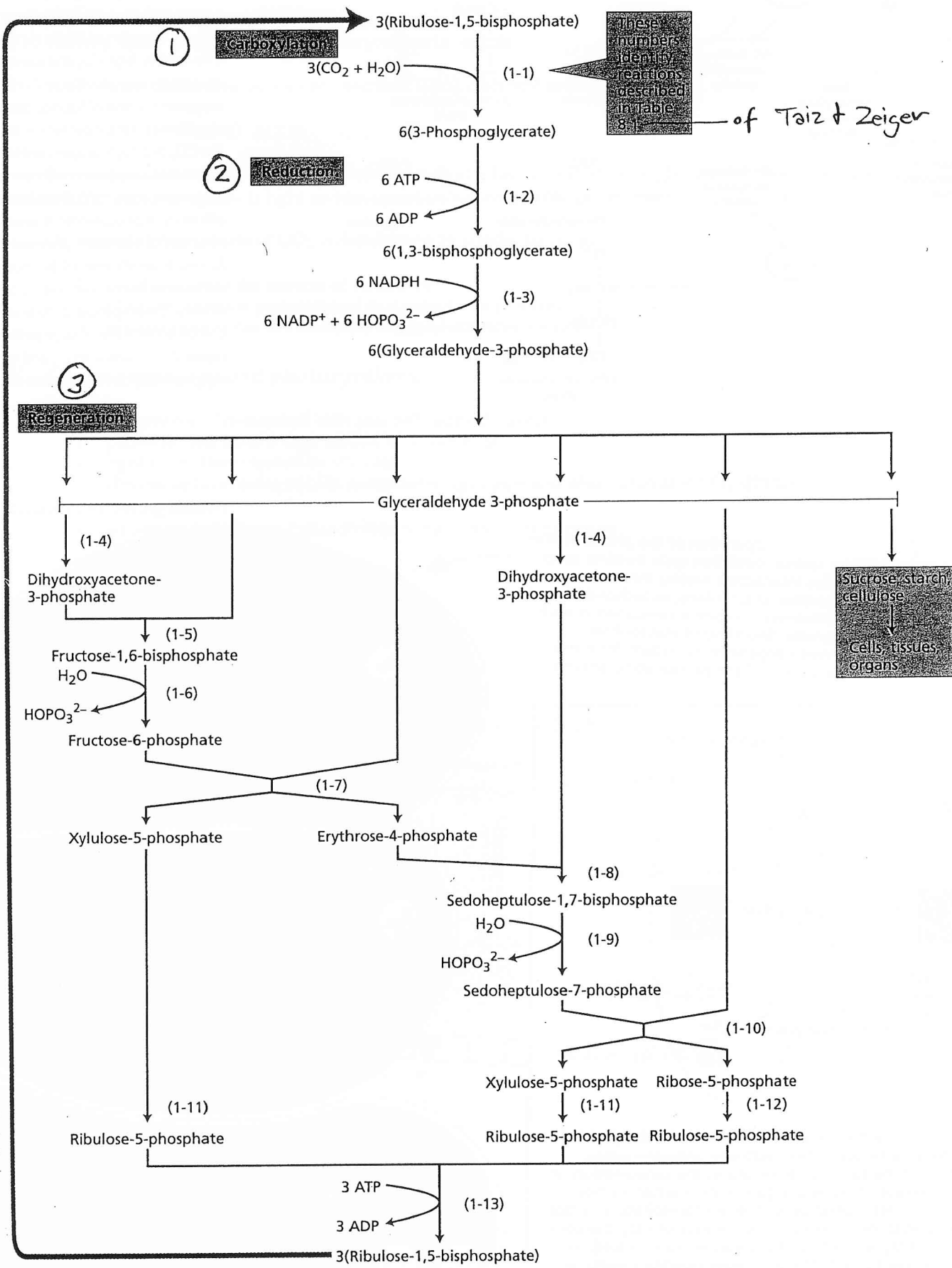
Schematic representation of the photosynthetic carbon reduction cycle (Calvin cycle) that shows major steps: carbon fixation, triose-P production, and regeneration of RuBP. 1: CO_2 combines with its substrate, ribulose-1,5-bisphosphate (RuBP), catalyzed by ribulose biphosphate carboxylase/oxygenase (Rubisco), producing phosphoglyceric acid (PGA). 2: PGA is reduced to triose-phosphate (triose-P), in a two-step reaction; the reaction

for which ATP is required is the conversion of PGA to 1,3-bisphosphoglycerate, catalyzed by phosphoglycerate kinase. 3 & 4: Part of the triose-P is exported to the cytosol, in exchange for P_i ; the remainder is used to regenerate ribulose-1-monophosphate. 5: ribulose-1-monophosphate is phosphorylated, catalyzed by ribulose-5-phosphate kinase, producing RuBP.

4. RuBP carboxylase can catalyze two reactions (Figure below) - p. 5c

- a. $RuBP + CO_2 \rightarrow 2\text{ PGA}$ (PCR cycle)
- b. $RuBP + O_2 \rightarrow \text{PGA} + \text{p-glycolate}$ (PCO cycle)

the PCO cycle is known as photorespiration as it involves the consumption of O_2 and the evolution of CO_2 ; it is temperature dependent and light independent



IV. Ohm's Law analogy for photosynthesis

A. Photosynthetic rate (A) can be described using electrical analog

$$A = (c_a - c_i) \cdot g_{CO_2}$$

B. compensation point is the CO₂ concentration at which A = R under high light (no net carbon gain or loss); compensation point is light and temperature dependent (R = respiration)

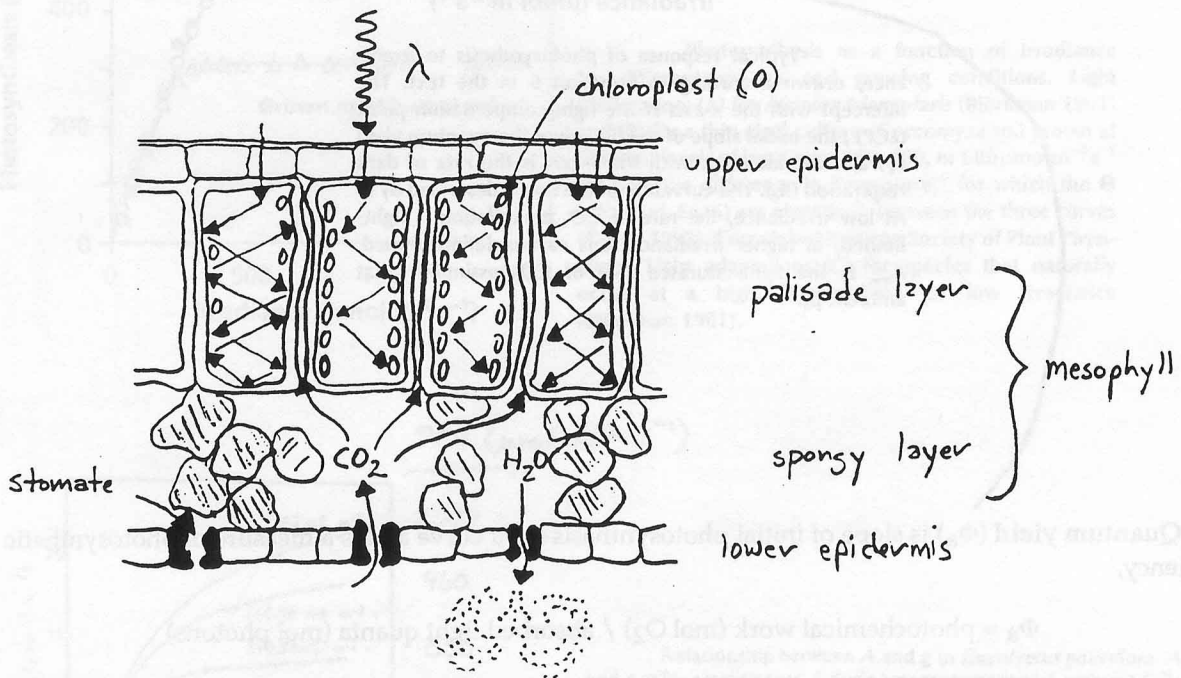
C. overall diffusion rate of CO₂ is determined by conductance (g)

1. conductance is the inverse of resistance
2. photosynthesis is proportional to conductance (Figure)
3. resistance in series are additive, but conductances are not

V. Leaf morphology and photosynthesis

A. Arrangement of mesophyll cells into palisade cell layers

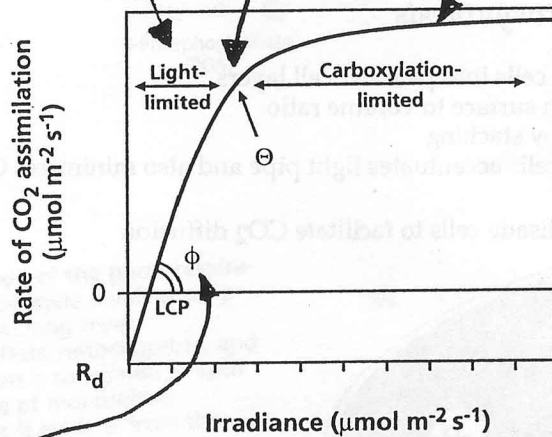
1. palisade cells have a high surface to volume ratio
2. light pipe effect created by stacking
3. chloroplasts on sides of cells accentuates light pipe and also minimizes CO₂ diffusion distances (drawing below)
4. air spaces in between palisade cells to facilitate CO₂ diffusion



VI. Pattern of photosynthesis versus light intensity

A. General response curve shows three distinct zones (Figure)

1. low light - limited by capacity of light harvesting pigments and photochemical conversion of light,
2. high light - limited by capacity of biochemical processes and by physical barriers to CO₂ diffusion,
3. intermediate light - rate governed by both
4. decreasing stomatal conductance results in photosynthetic saturation at lower light levels (Figure)



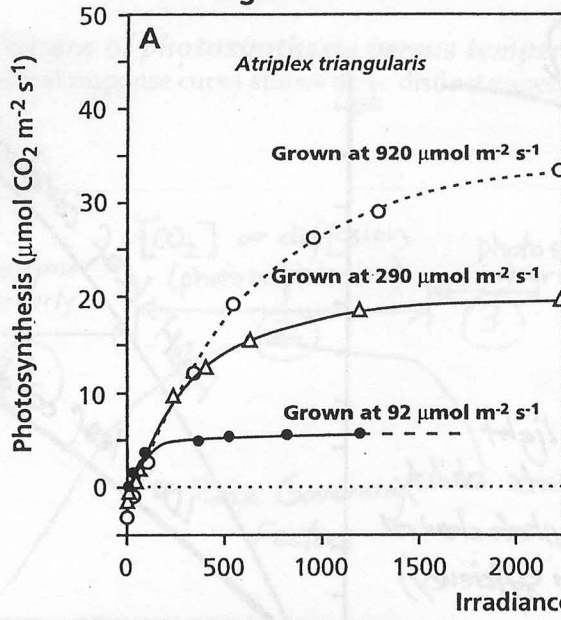
Typical response of photosynthesis to irradiance, drawn according to Equation 6 in the text. The intercept with the x-axis is the light-compensation point (LCP), the initial slope of the line gives the quantum yield (ϕ) and the intercept with the y-axis is the rate of dark respiration (R_d). The curvature of the line is described by θ . At low irradiance, the rate of CO₂ assimilation is light-limited; at higher irradiance A is carboxylation limited. A_{max} is the light-saturated rate of CO₂ assimilation at ambient p_a .

B. Quantum yield (Φ_a) is slope of initial photosynthesis-light curve and is a measure of photosynthetic efficiency,

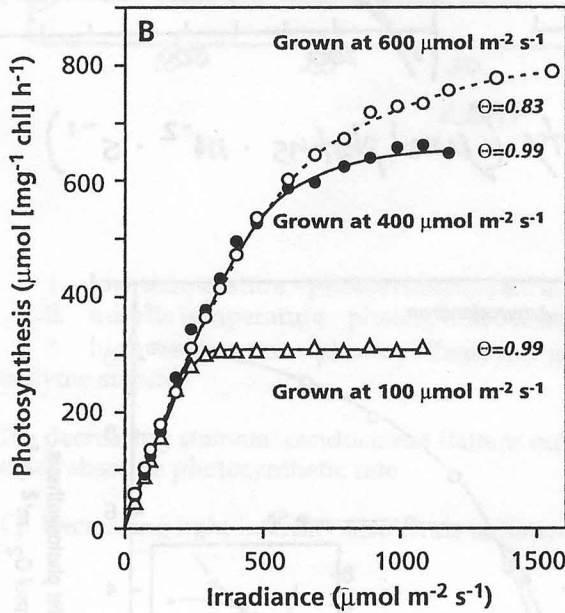
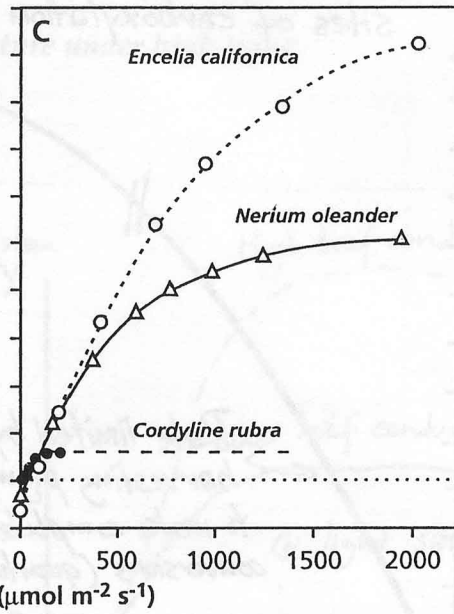
$$\Phi_a = \text{photochemical work (mol O}_2\text{)} / \text{absorbed light quanta (mol photons)}$$

1. under natural conditions, quantum yield is about 0.05-0.12 (5-12%) mol O₂ per mol photons absorbed or 20-48 photons to reduce 1 molecule CO₂,
2. quantum yield is dependent on leaf temperature, CO₂, and O₂ - for low light plants can be an important adaptation

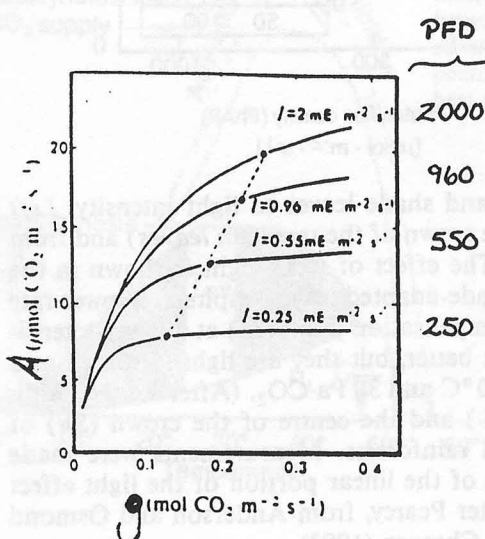
Light acclimation



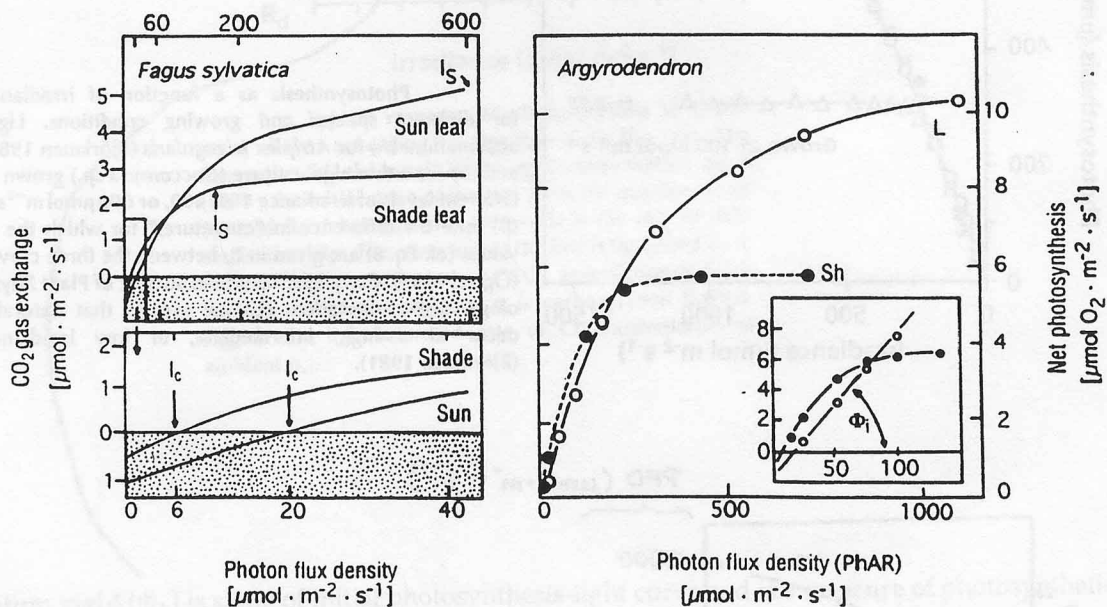
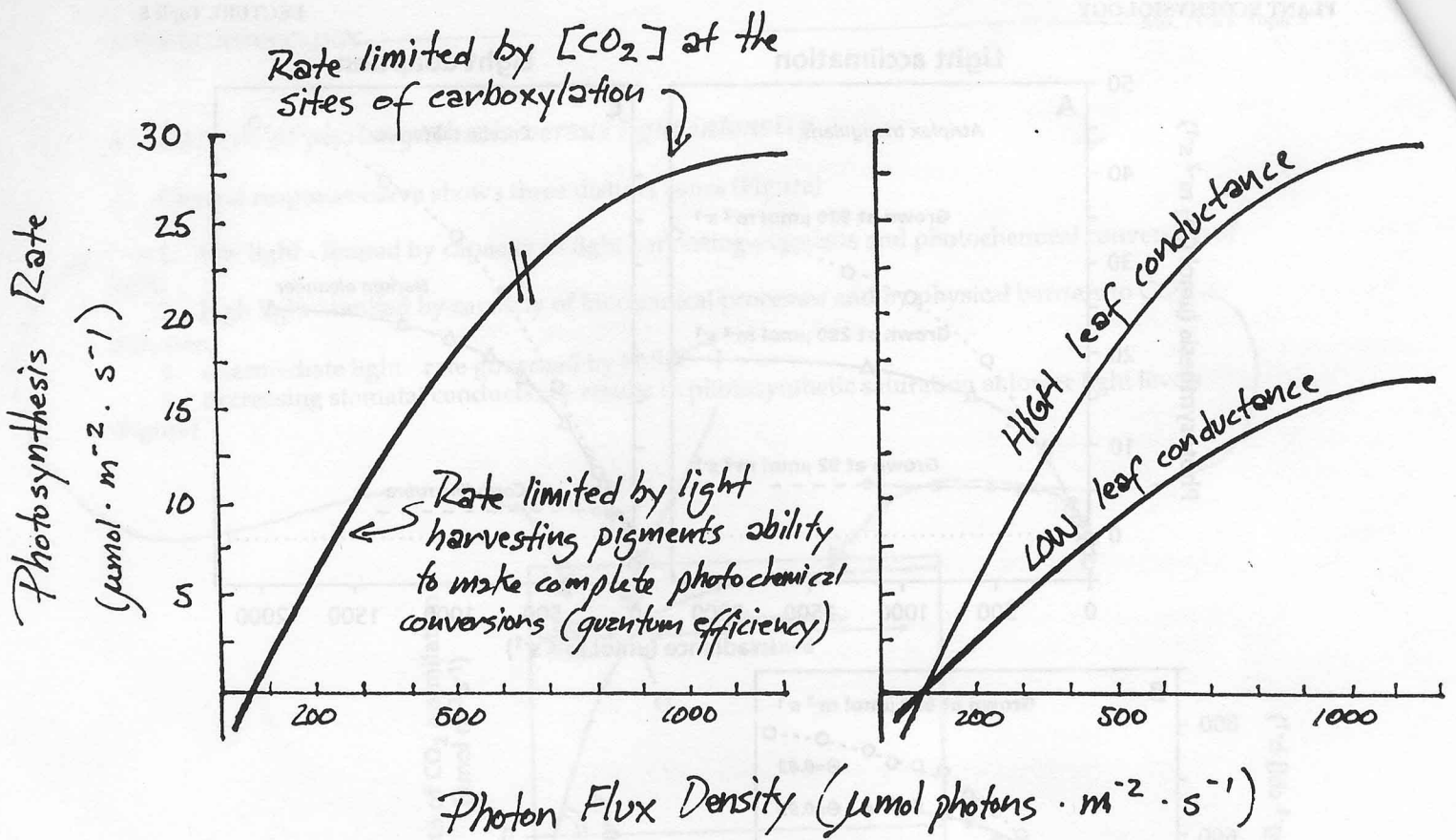
Light adaption



Photosynthesis as a function of irradiance for different species and growing conditions. Light acclimation: (A) for *Atriplex triangularis* (Björkman 1981) and (B) for a thin algal culture (*Coccomyxa* sp.) grown at different levels of irradiance 100, 400, or 600 μmol m⁻² s⁻¹ (B) note the difference in "curvature," for which the Θ values (cf. Eq. 6) are given in B, between the three curves (Ögren 1993). Copyright American Society of Plant Physiology. Light adaptation: (C) for species that naturally occur at a high, intermediate, or low irradiance (Björkman 1981).



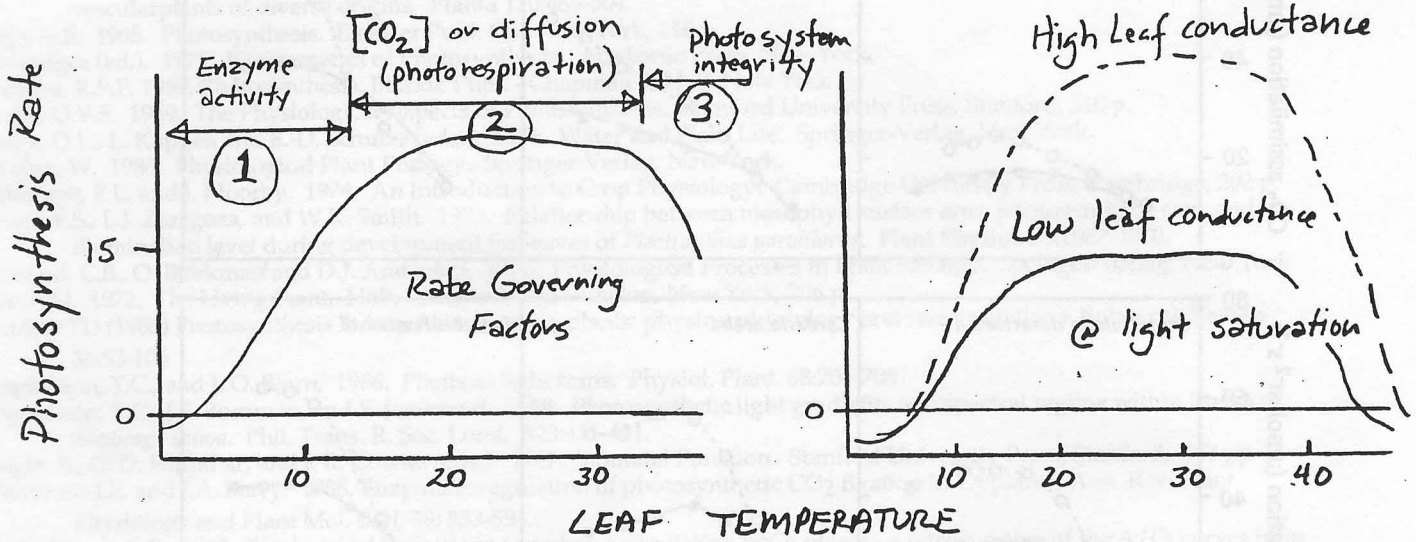
Relationship between A and g in *Eucalyptus pauciflora*. A and g at four irradiances, I , during measurement with ambient CO₂ concentration = 320 μl l⁻¹, leaf temperature = 25 °C, leaf to air vapour pressure difference = 18 mbar. Curves represent the variation of A that would occur if g were independently perturbed; they are computed from measurements of the responses of A to changes in intercellular CO₂ concentration.



Response of CO_2 gas exchange of sun and shade leaves to light intensity. *Left* Leaves of *Fagus sylvatica* from the periphery of the crown of the tree (*sun leaves*) and from the shaded interior of the crown (*shade leaves*). The effect of weak light is shown in the *lower left diagram*, with the abscissa expanded. Shade-adapted leaves respire at a lower rate than those adapted to light; they reach the light compensation point (I_c) at a lower intensity, and also after this point they utilize weak light better, but they are light-saturated at a lower intensity (I_s). Measurements were made at 30°C and $30\text{ Pa } CO_2$. (After Retter 1965). *Right* Leaves from the periphery of the crown (*L*) and the centre of the crown (*Sh*) of *Argyrodendron*, a shade-tolerant tree of tropical rainforests. Measurements were made under conditions of CO_2 saturation. The slope ϕ_i of the linear portion of the light effect curve corresponds to the light quantum yield. (After Pearcy, from Anderson and Osmond 1987). For light response of photorespiration, see Chmora (1993)

VII. Pattern of photosynthesis versus temperature under high light

A. General response curve shows three distinct zones:



1. low temperature - photosynthetic rate is limited by enzyme activity,
2. middle temperature - photosynthetic rate is limited by CO₂ diffusion and photorespiration,
3. high temperature - photosynthetic rate is unstable and is limited by photosystem integrity and enzyme stability

B. decreasing stomatal conductance flattens out the photosynthesis-temperature response curve and decreases absolute photosynthetic rate

C. decreasing light intensity also tends to flatten out the photosynthesis-temperature response curve

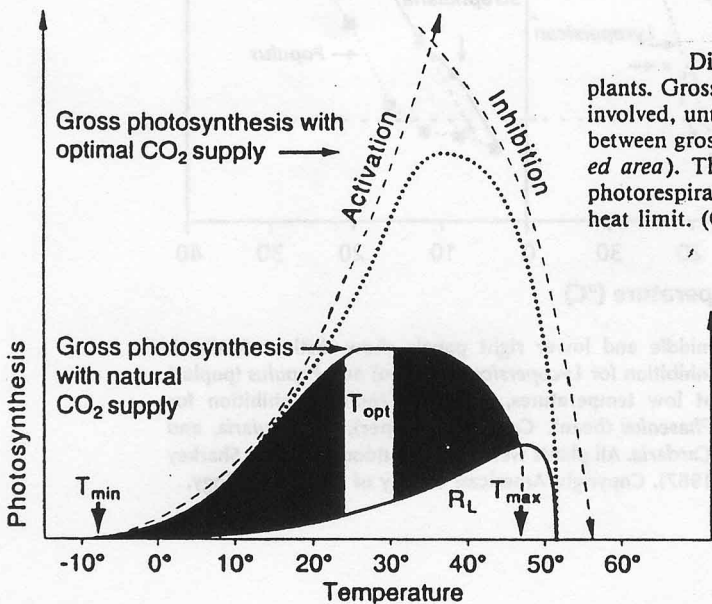
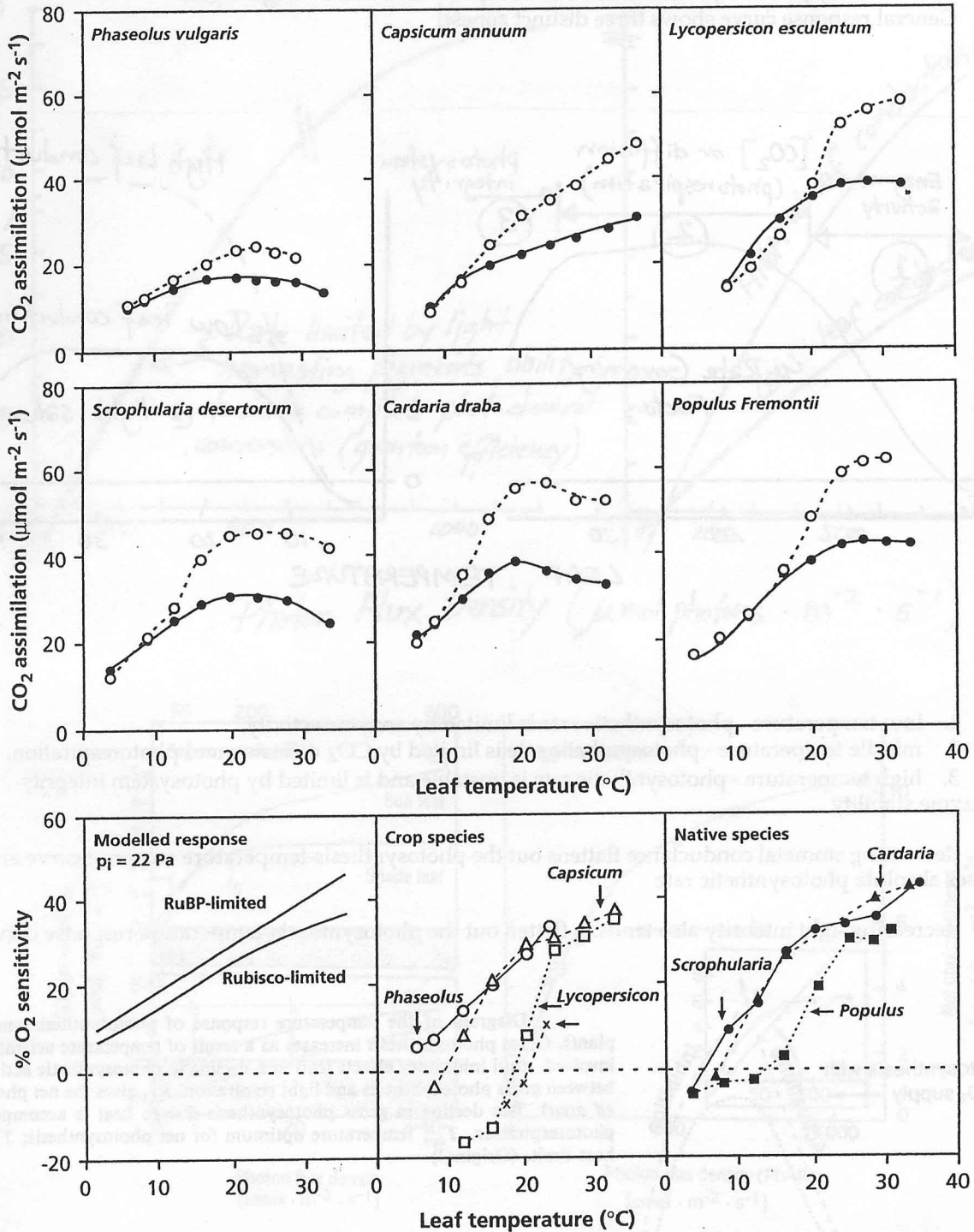


Diagram of the temperature response of photosynthesis and respiration in C₃ plants. Gross photosynthesis increases as a result of temperature activation of the enzymes involved, until inhibitory effects lead to a decline in photosynthetic activity. The difference between gross photosynthesis and light respiration, R_L, gives the net photosynthesis (hatched area). The decline in gross photosynthesis due to heat is accompanied by decreased photorespiration. T_{opt} Temperature optimum for net photosynthesis; T_{min} cold limit; T_{max} heat limit. (Original)



The effect of temperature on the net rate of CO₂ assimilation at 18 (filled symbols) and 3 (open symbols) kPa O₂ (top, middle), and the oxygen sensitivity of photosynthesis (bottom) for a number of species. The model (lower left panel) simulated oxygen sensitivity in the absence of feedback inhibition of CO₂ assimilation. The

middle and lower right panels show distinct feedback inhibition for *Lycopersicon* (tomato) and *Populus* (poplar) at low temperatures, and less feedback inhibition for *Phaseolus* (bean), *Capsicum* (pepper), *Scrophularia*, and *Cardaria*. All plants were grown outdoors (Sage & Sharkey 1987). Copyright American Society of Plant Physiology.

Some important literature:

- Baker, N. R., and S. P. Long (eds.). 1986. Photosynthesis in Contrasting Environments. Elsevier, Amsterdam. 423 pp.
- Berry, J.A. 1975. Adaptation of photosynthetic processes to stress. *Science* 180:644-650.
- Björkman, O. and J.A. Berry. 1973. High efficiency photosynthesis. *Scientific American* 229:80-93.
- Björkman, O. and B. Demmig. 1987. A survey of photon yield of O₂ evolution and chlorophyll 77 K fluorescence among vascular plants of diverse origins. *Planta* 170:489-504.
- Fogg, G.E. 1968. Photosynthesis. Elsevier Publ. Co., New York, 116 p.
- Govindjee (ed.). 1975. Bioenergetics of Photosynthesis. Academic Press, New York.
- Gregory, R.P.F. 1989. Photosynthesis. Blackie Publ. - Chapman & Hall, New York.
- Heath, O.V.S. 1969. The Physiological Aspects of Photosynthesis. Stanford University Press, Stanford, 310 p.
- Lange, O.L., L. Kappen and E.-D. Schulze (eds.). 1976. Water and Plant Life. Springer-Verlag, New York.
- Larcher, W. 1980. Physiological Plant Ecology. Springer-Verlag, New York.
- Milthorpe, F.L. and J. Moorby. 1974. An Introduction to Crop Physiology. Cambridge University Press, Cambridge, 202 p.
- Nobel, P.S., L.J. Zaragoza, and W.K. Smith. 1975. Relationship between mesophyll surface area, photosynthetic rate, and illumination level during development for leaves of *Plectranthus parviflorus*. *Plant Physiol.* 55:1067-1070.
- Osmond, C.B., O. Björkman and D.J. Anderson. 1980. Physiological Processes in Plant Ecology. Springer-Verlag, New York.
- Ray, P.M. 1972. The Living Plant. Holt, Rinehard, and Winston, New York, 206 p.
- Sharkey TD (1985) Photosynthesis in intact leaves of C₃ plants: physics, physiology and rate limitations. *Botanical Review* 51:53-106
- Vogelmann, T.C., and L.O. Bjorn. 1986. Plants as light traps. *Physiol. Plant.* 68:704-708.
- Vogelmann, T.C., J.F. Bornman, and S. Jossierand. 1989. Photosynthetic light gradients and spectral regime within leaves of *Medicago sativa*. *Phil. Trans. R. Soc. Lond.* 323:411-421.
- Zeiger, E., G. D. Farquhar, and I. R. Cowan (eds.). 1987. Stomatal Function. Stanford University Press, Stanford. 503 pp.
- Woodrow, I.E. and J.A. Berry. 1988. Enzymatic regulation of photosynthetic CO₂ fixation in C₃ plants. *Ann. Rev. Plant Physiology and Plant Mol. Biol.* 39: 533-594.
- Wullschleger, S.D. 1993. Biochemical limitations to carbon assimilation in C₃ plants - a retrospective of the A/C_i curves from 109 species.