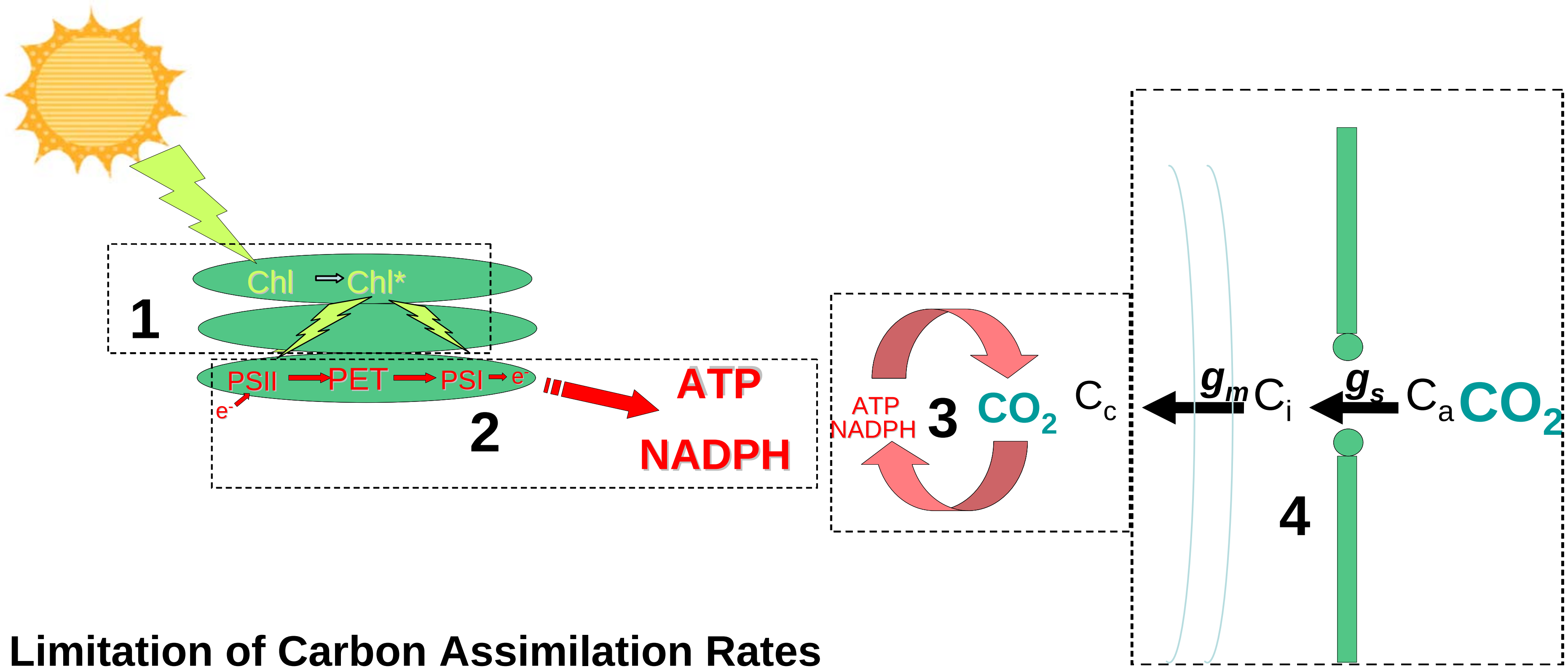
Ecophysiology

Please Note: Some of the slides are Animated and are best viewed as a Slide Show; some slides have attached notes below the slides and these are best viewed in Normal (editing) view.

Part 1
Photosynthesis
Light

What Limits C3 Photosynthesis?



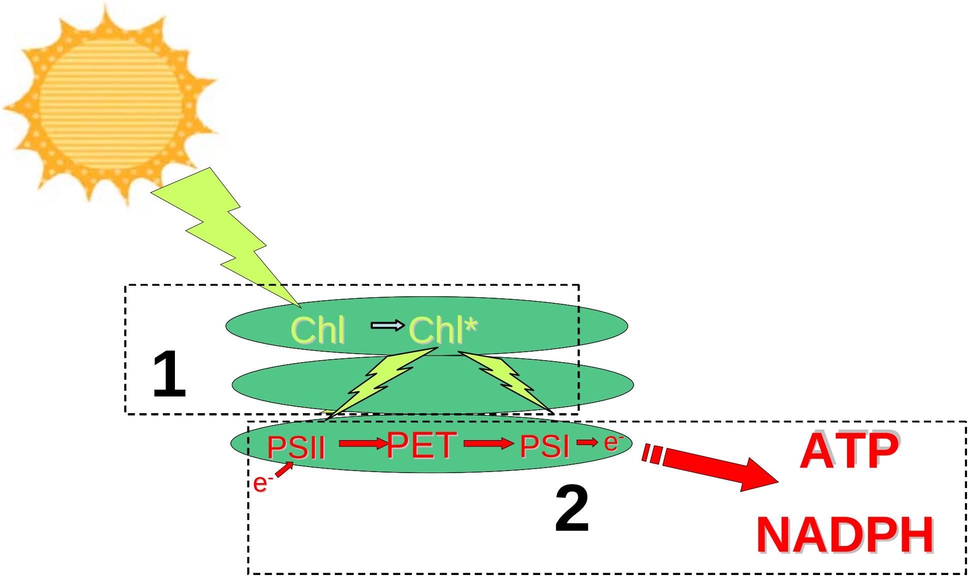
Limitation of Carbon Assimilation Rates

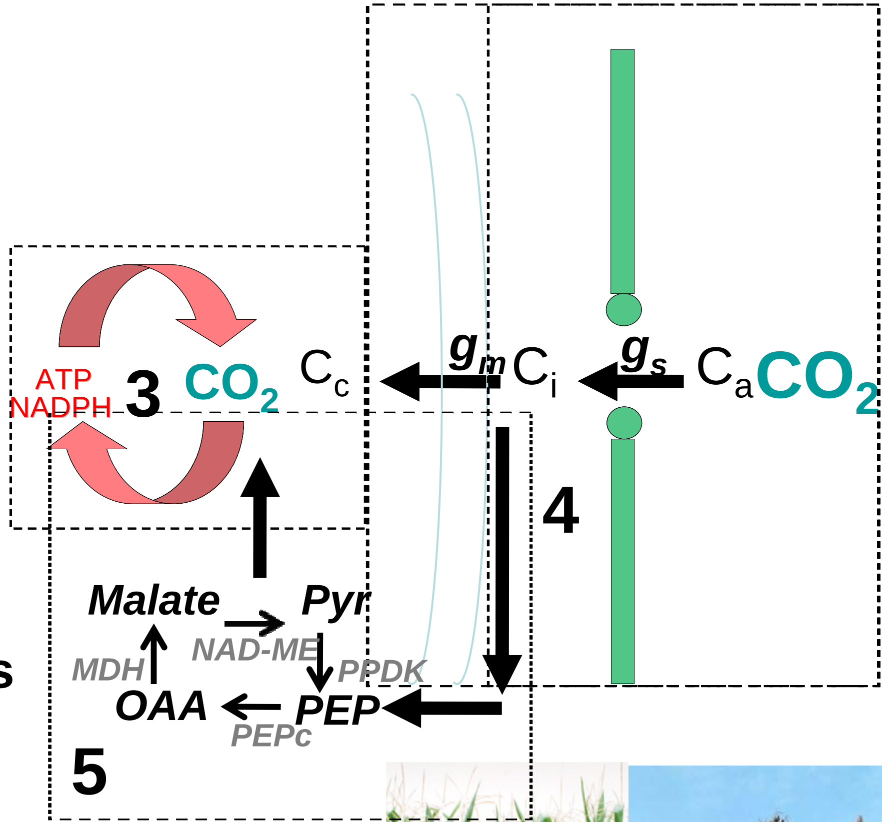
1. Light Harvesting Capacity
2. Photosynthetic Electron Transport / Chemiosmosis
3. C3 Cycle Kinetics (RuBisCO Activase?)
4. CO_2 Supply / g_s / g_m

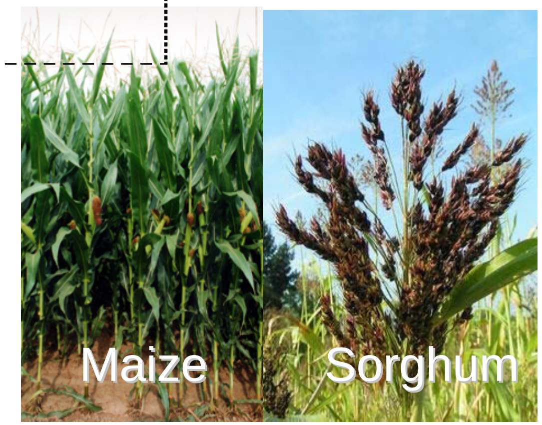
Ca, Ci, Cc ~ CO_2 Levels in Air, Intercellular Space, Chloroplast

gs & *gm* ~ Stomatal Conductance & Mesophyll Conductance

What Limits C4 Photosynthesis?







Limitation of Carbon Assimilation Rates

1. Light Harvesting Capacity
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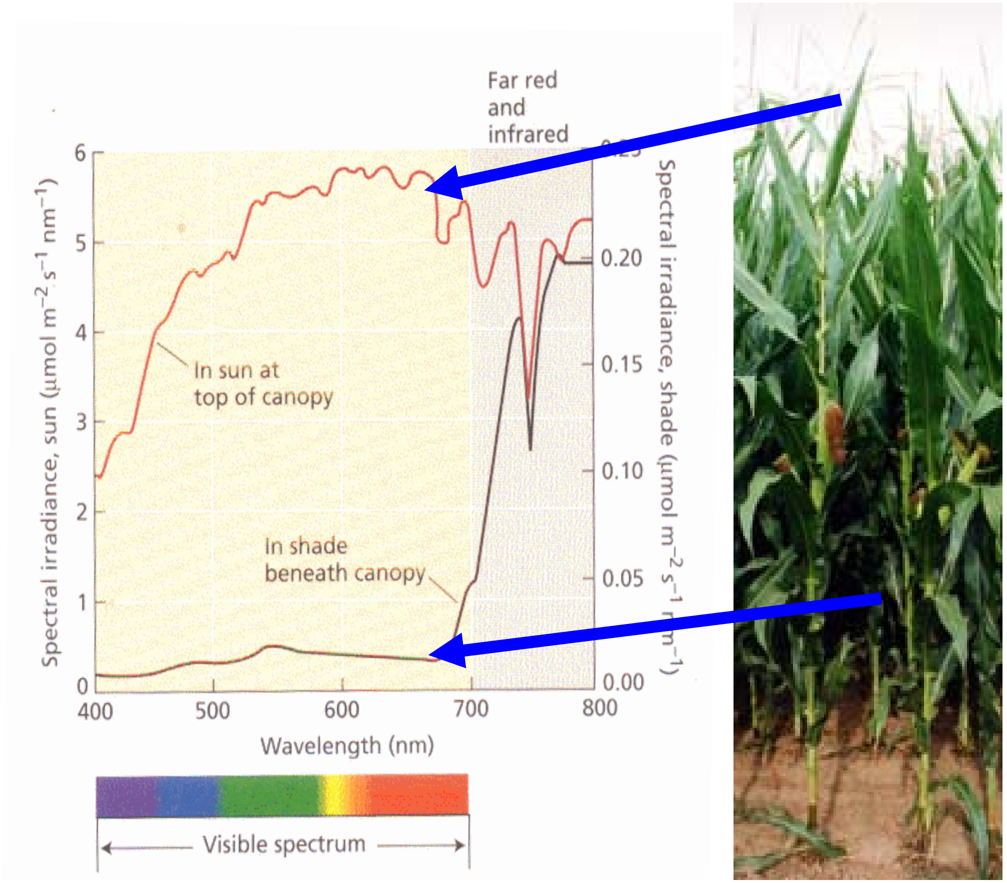
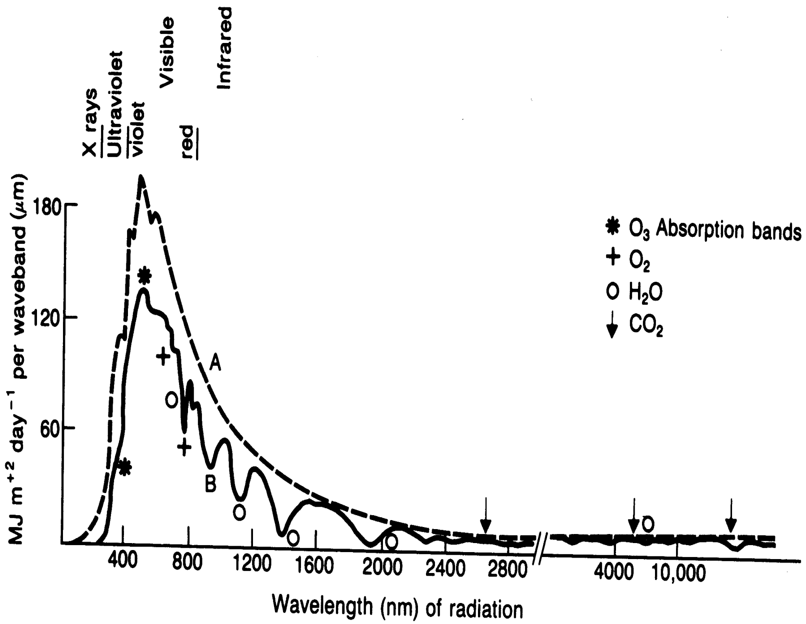
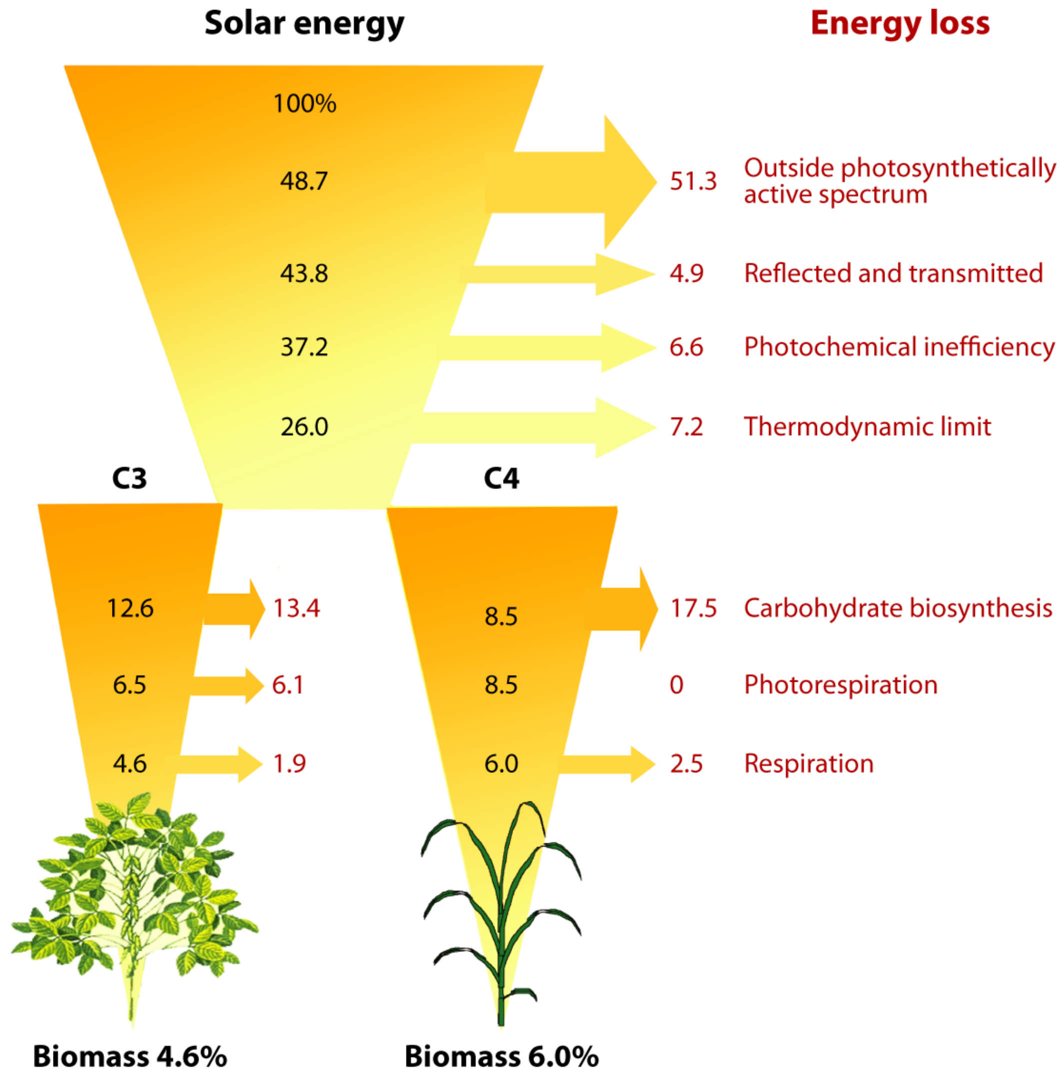
How Efficient is Light Utilization?

- Insolation ~1.3kW m^{-2}



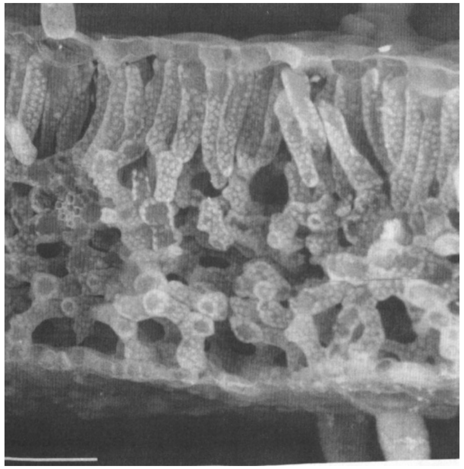


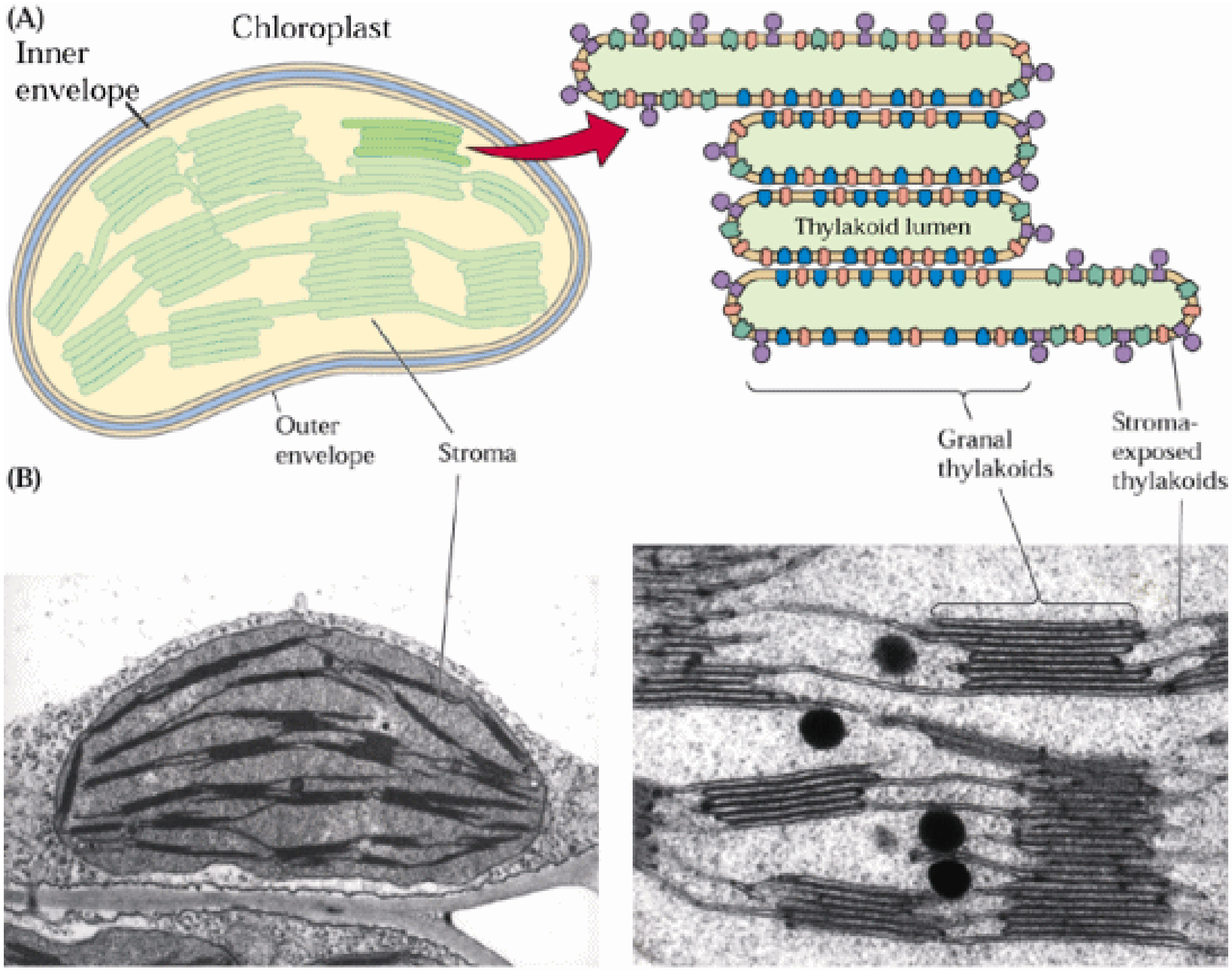
How Efficient is Light Utilization?



Zhu X-G, et al. 2010.
Annu. Rev. Plant. Biol. 61:235–61

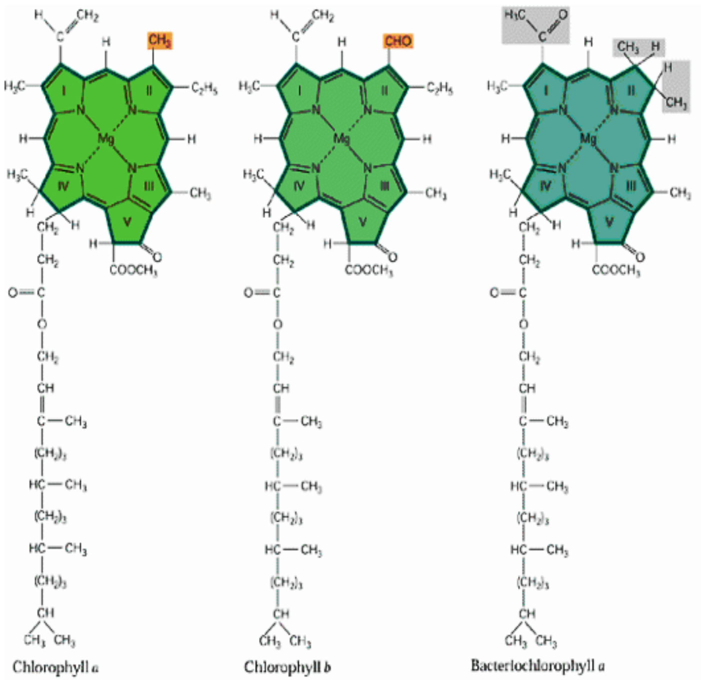
Photosynthesis

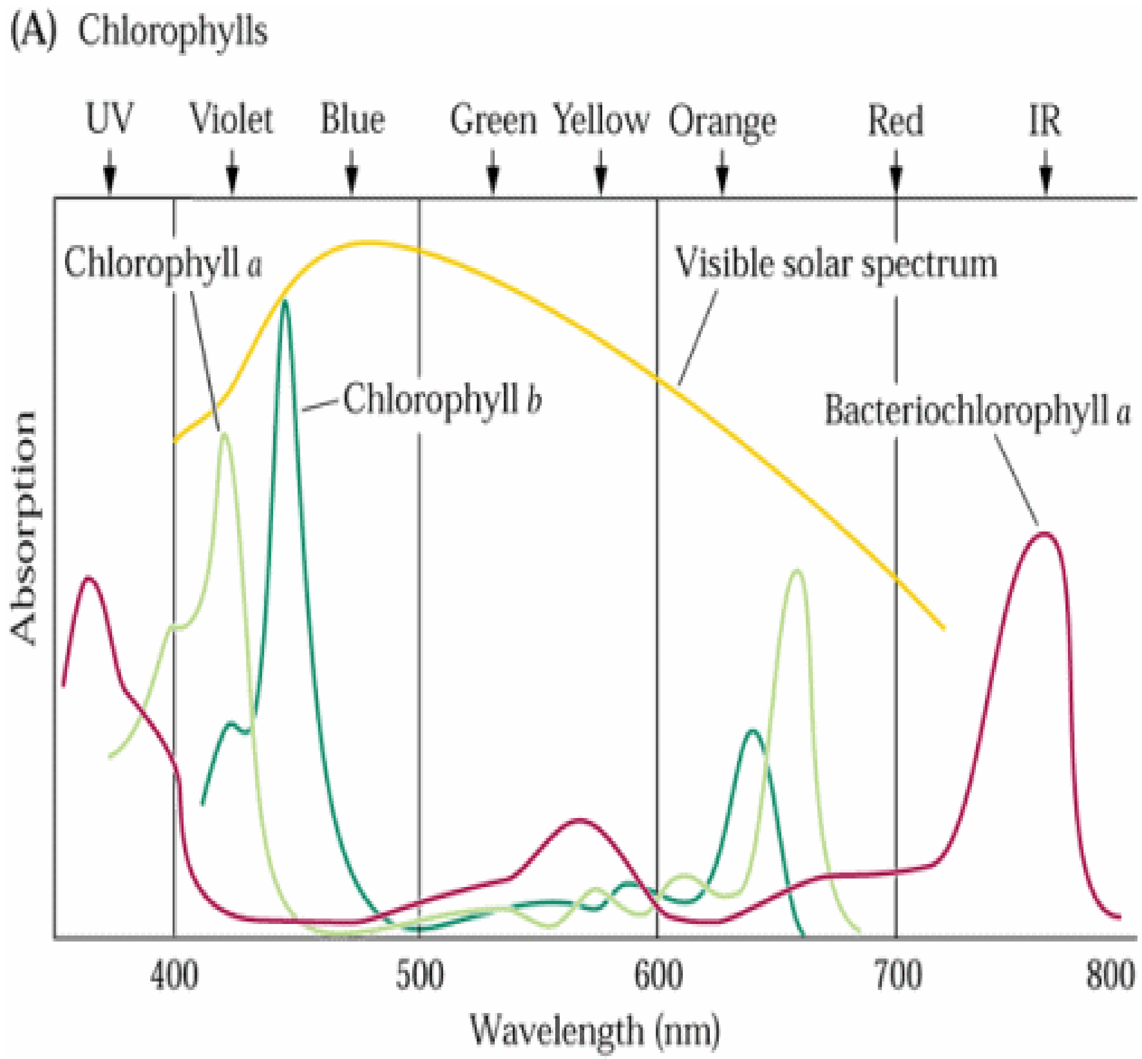




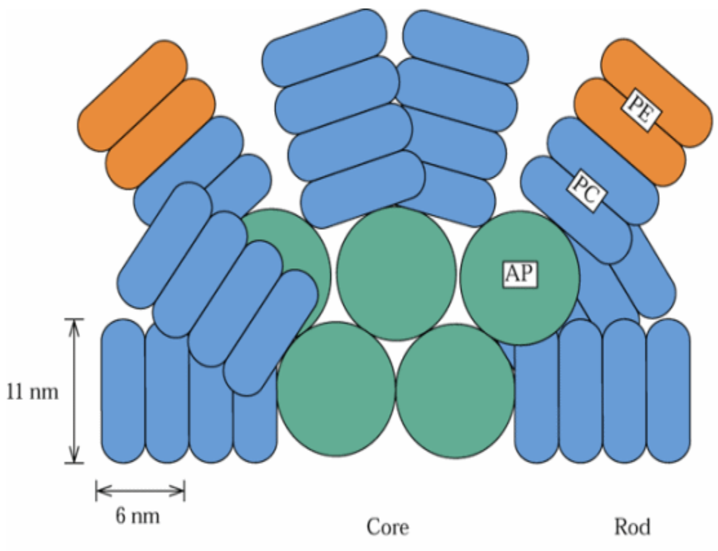
See Lambers *et al.* Fig 2.1

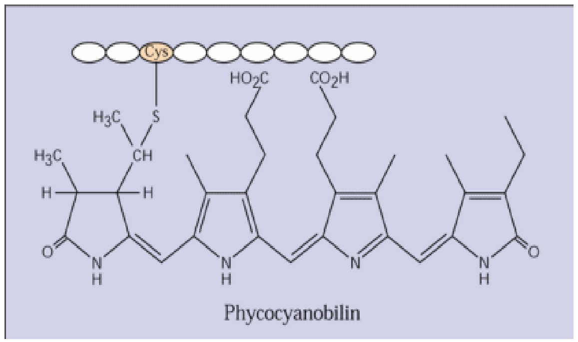
Light Harvesting Capacity: Pigments I

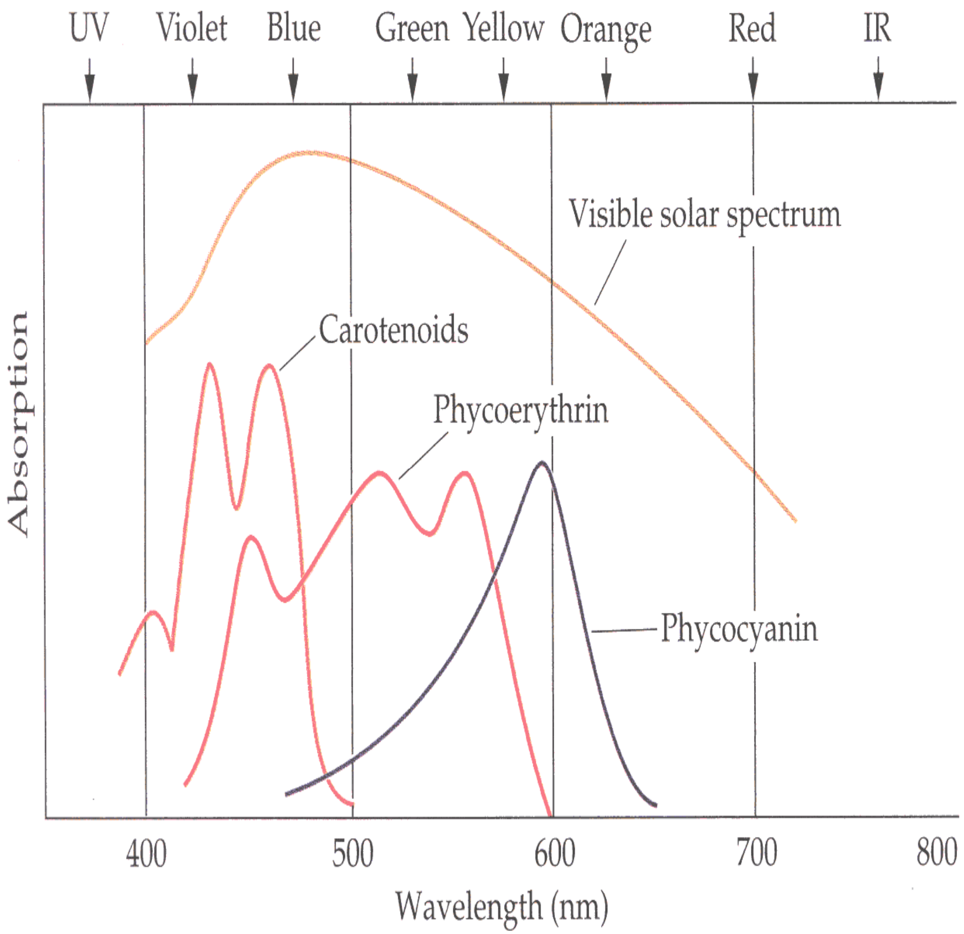




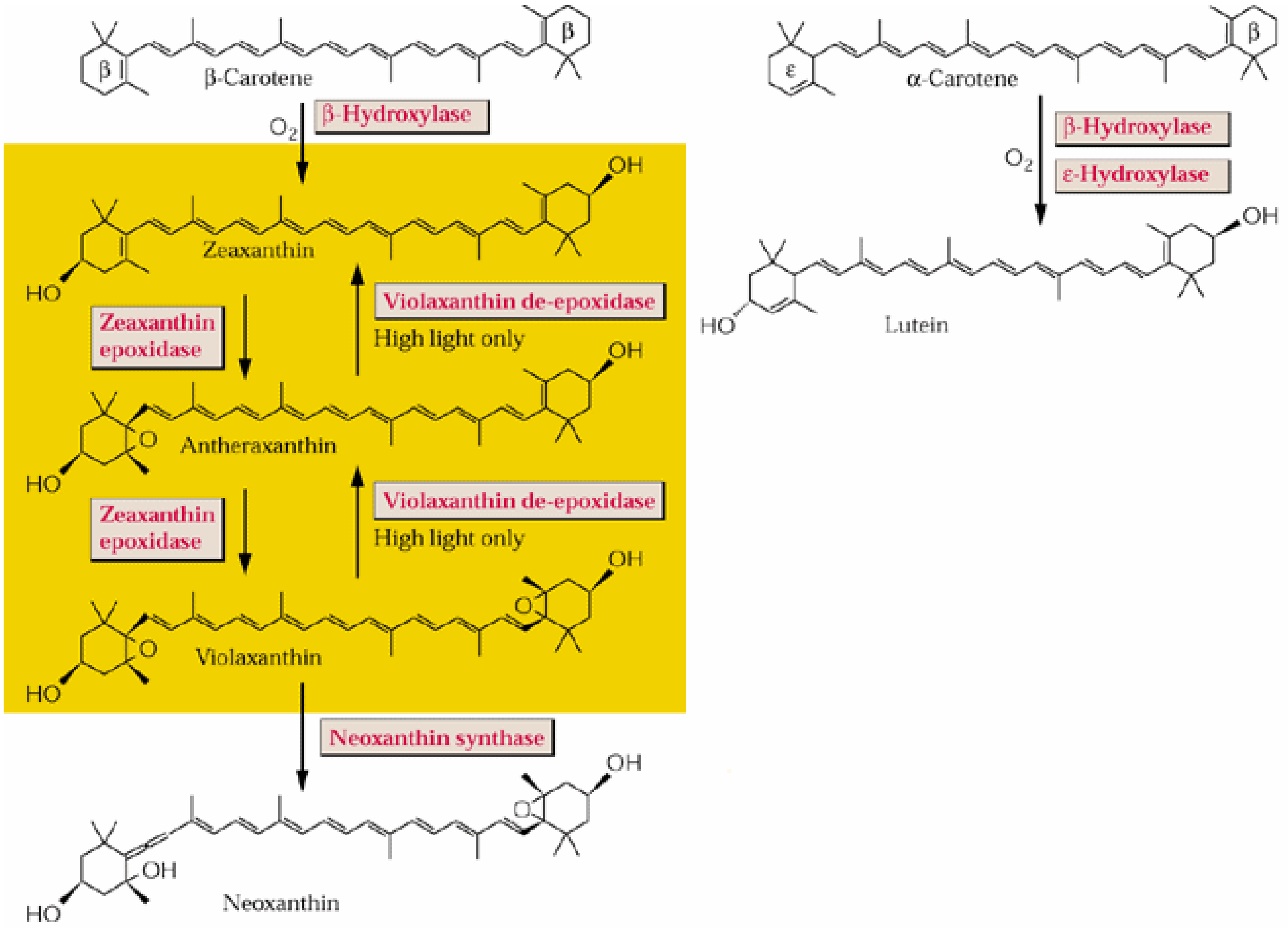
Novel Pigment - Protein Complexes: Phycobilisomes







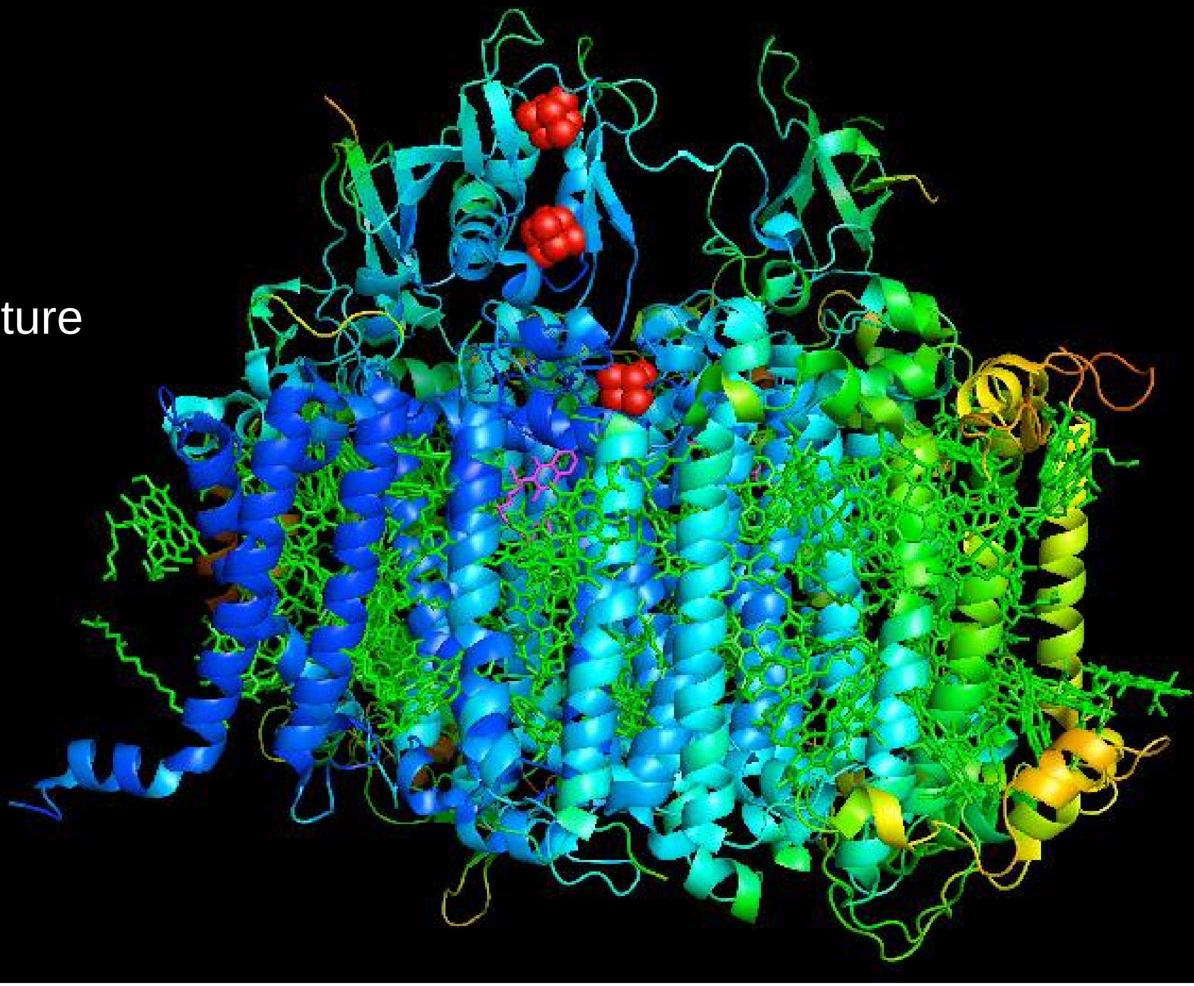
Carotenoids Harvest Light & Protect Against $^1O^*_2$



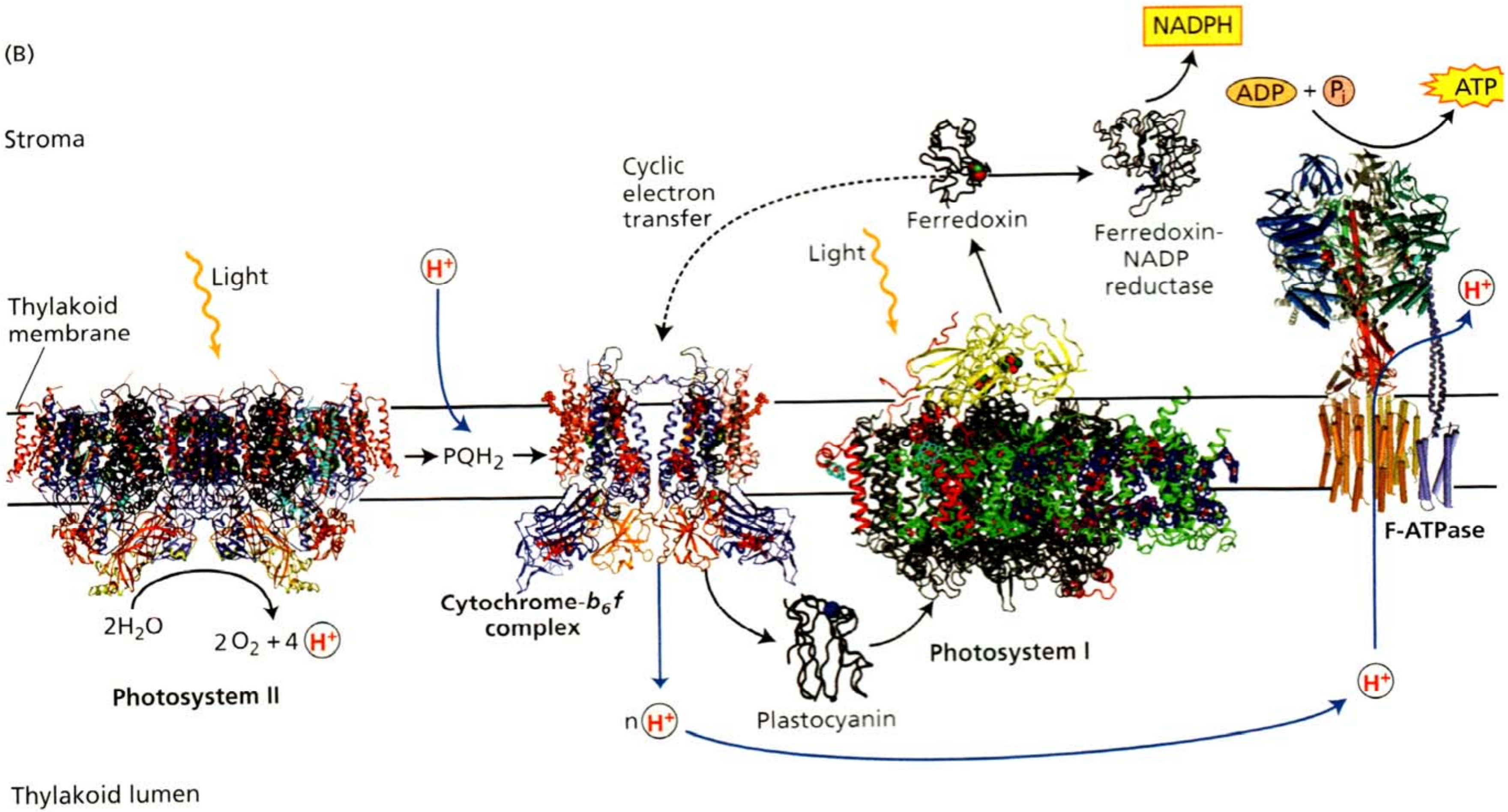
How Efficient are the Components of the Photosynthetic Apparatus?

The Structure of The Components of the ‘Light Reactions’ is known to Very High Resolution

PSI Structure

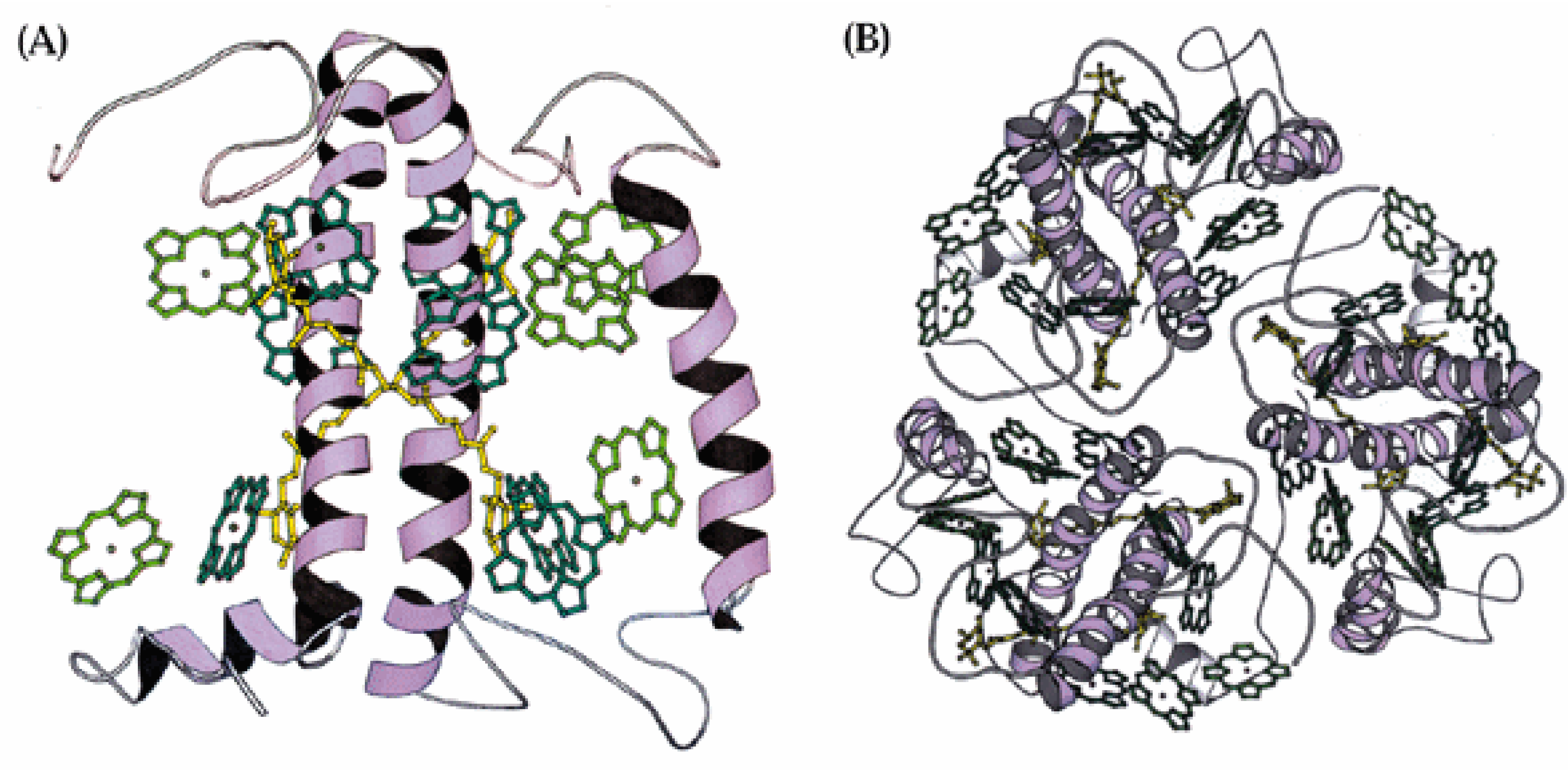


The Structure of the Components of the Thylakoid Membrane



See Lambers et al. Fig 2.3

LHCII From Higher Plants



The C_3 (Calvin) Cycle.

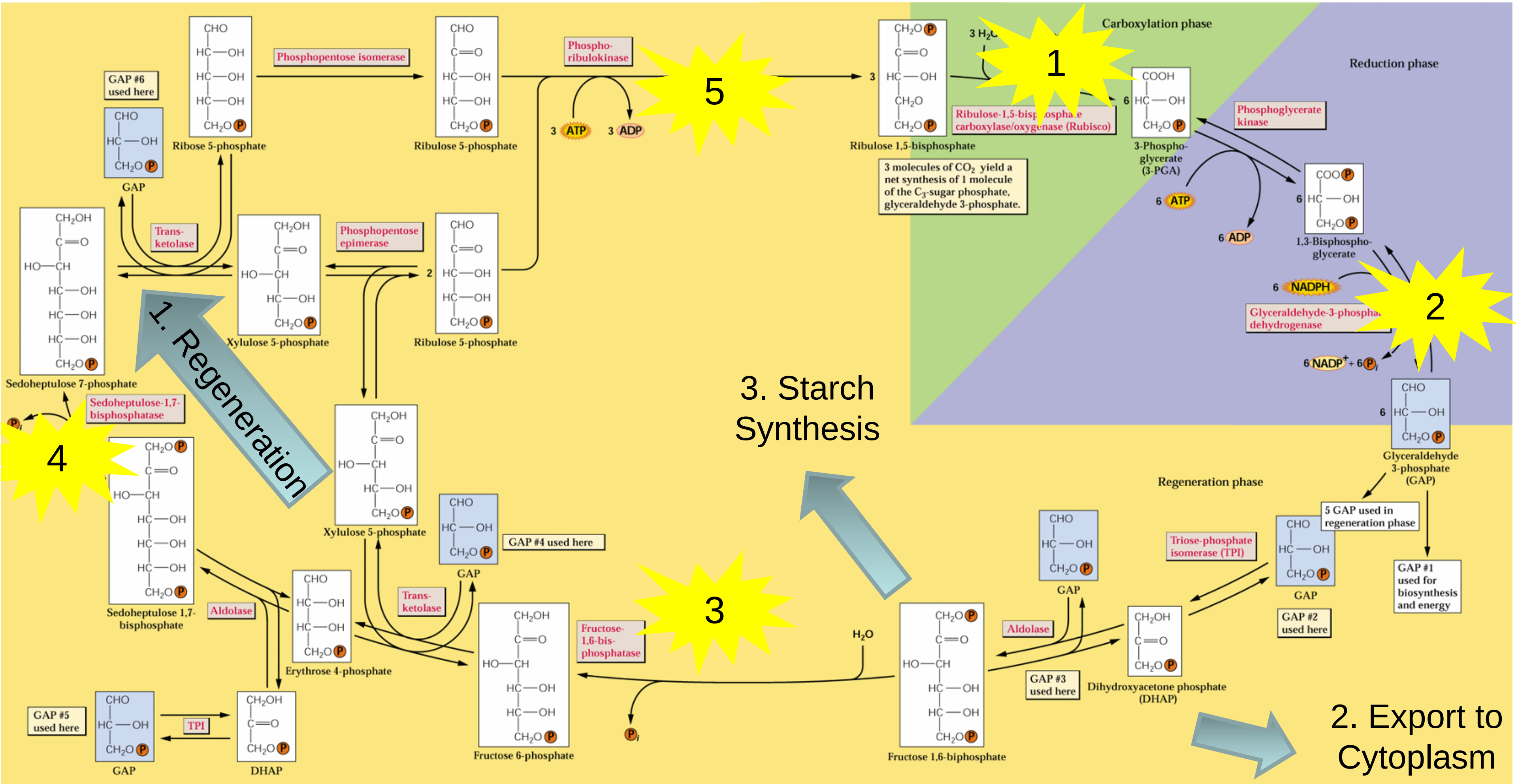
3 Fructose-1,6-bis-phosphatase

1 Rubisco

5 Ribulose-5 phosphate kinase

4 Sedoheptulose-1,7 bis-phosphatase

2 NADPH G3P dehydrogenase

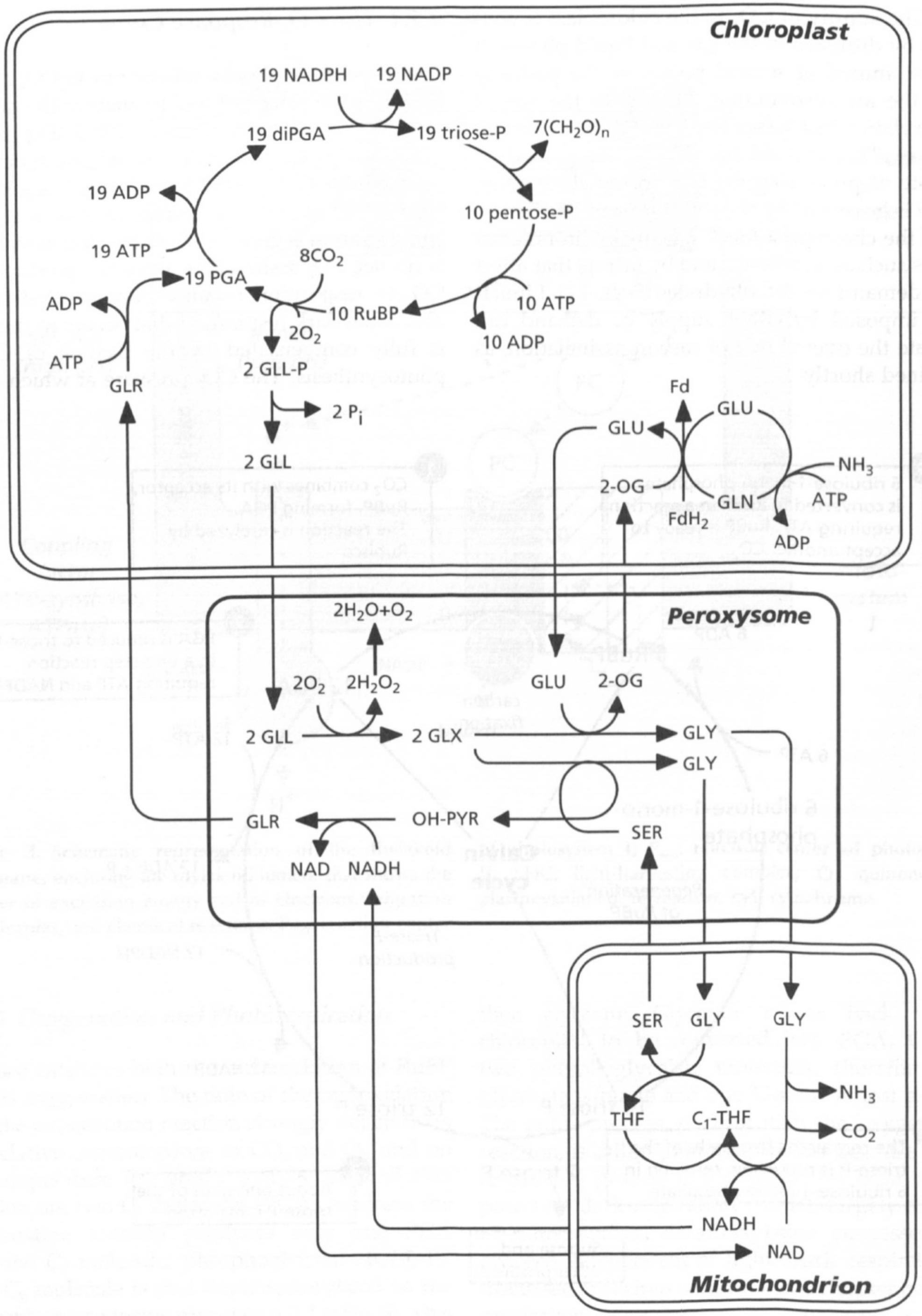


The Photorespiratory Pathway

Loss of Fixed Carbon

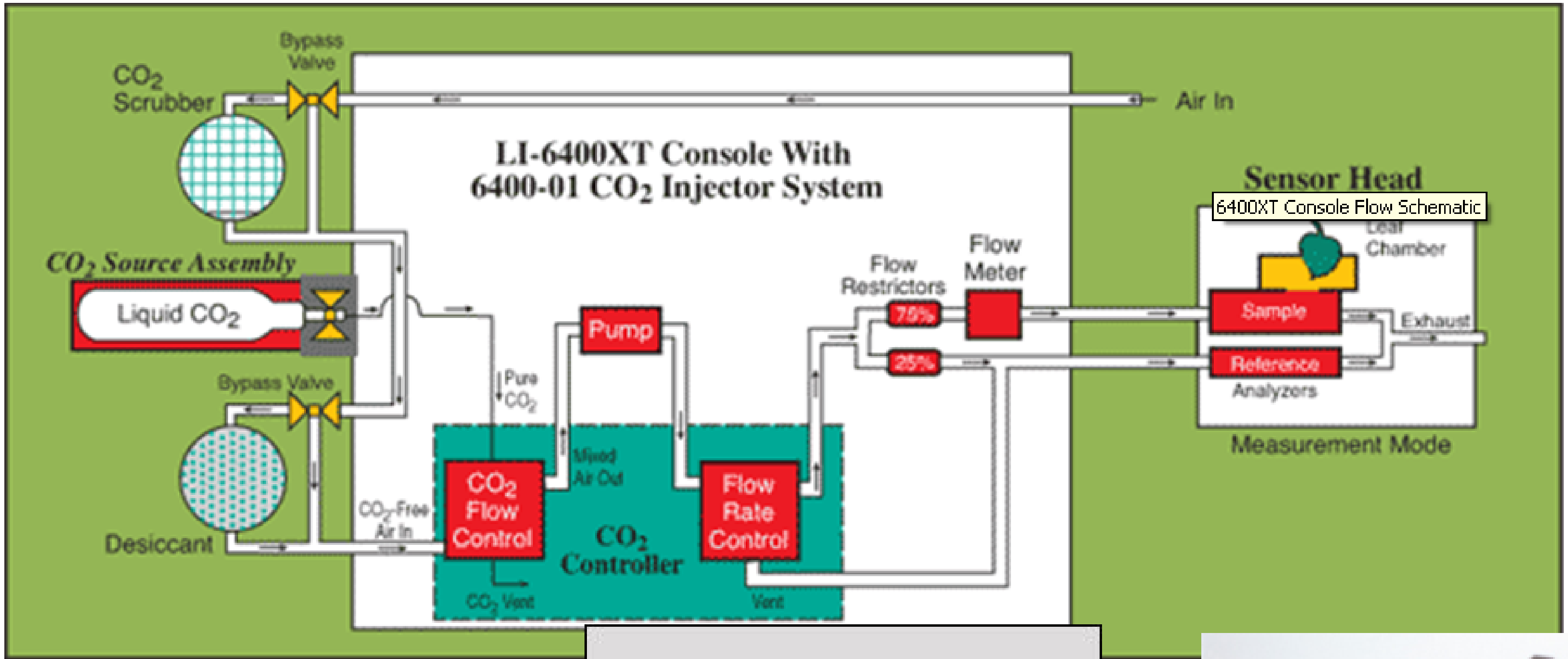
~ 20% in non-stressed C3 plants

> 50% in stressed C3 Plants



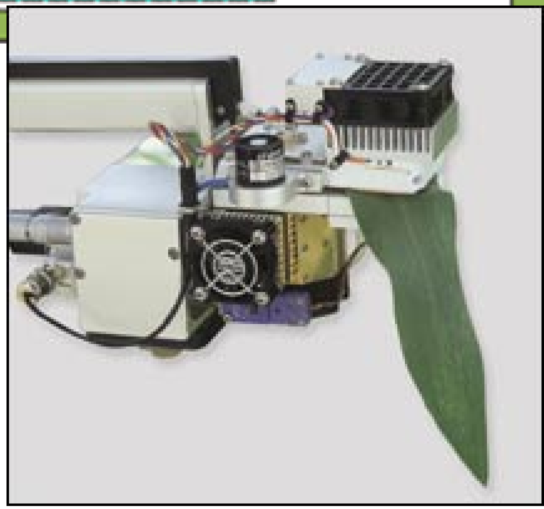
See Lambers et al. Fig 2.5

Measuring Photosynthetic Response to Light–
Light Response Curves

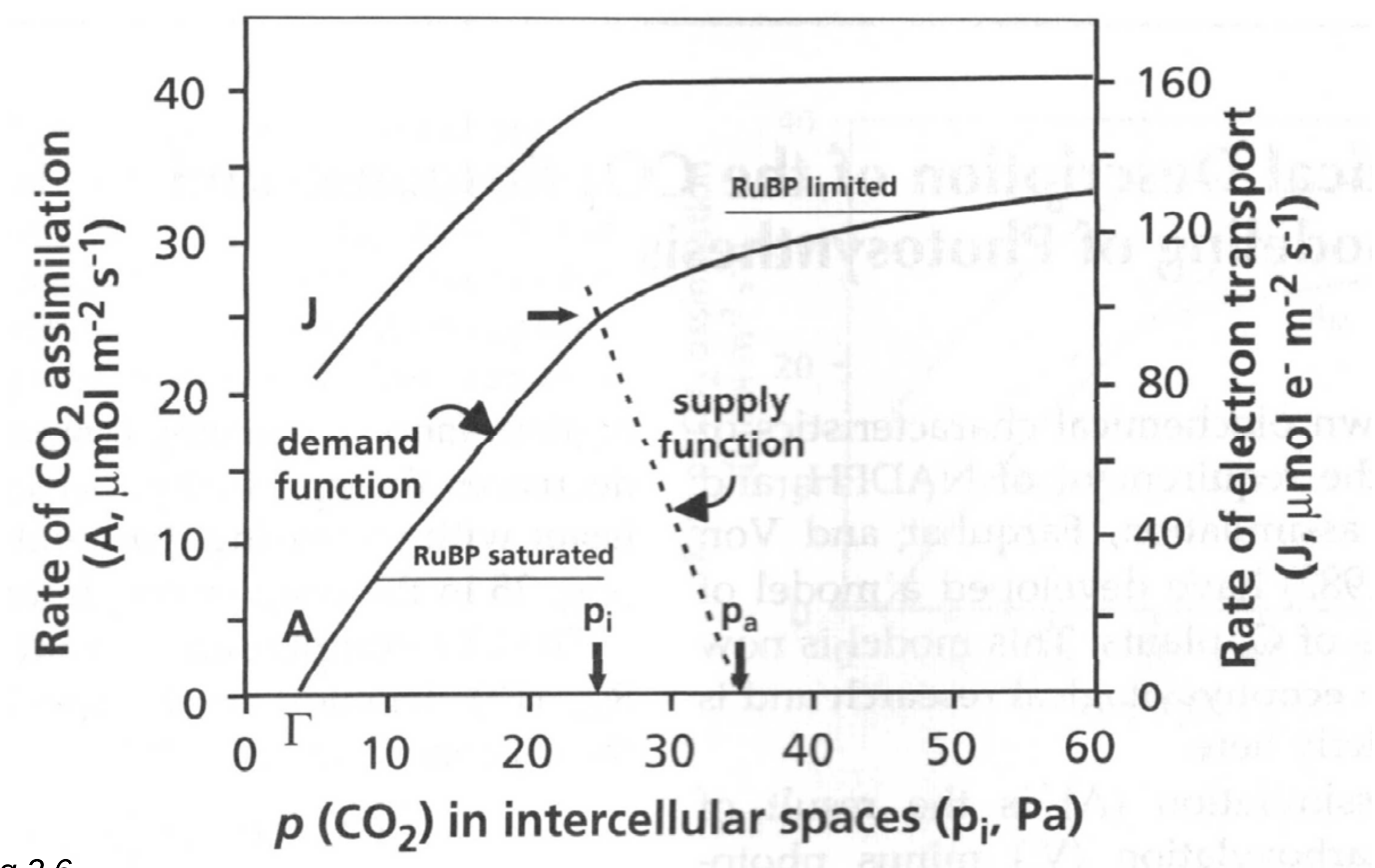


Infra Red Gas Analysers

IRGAs



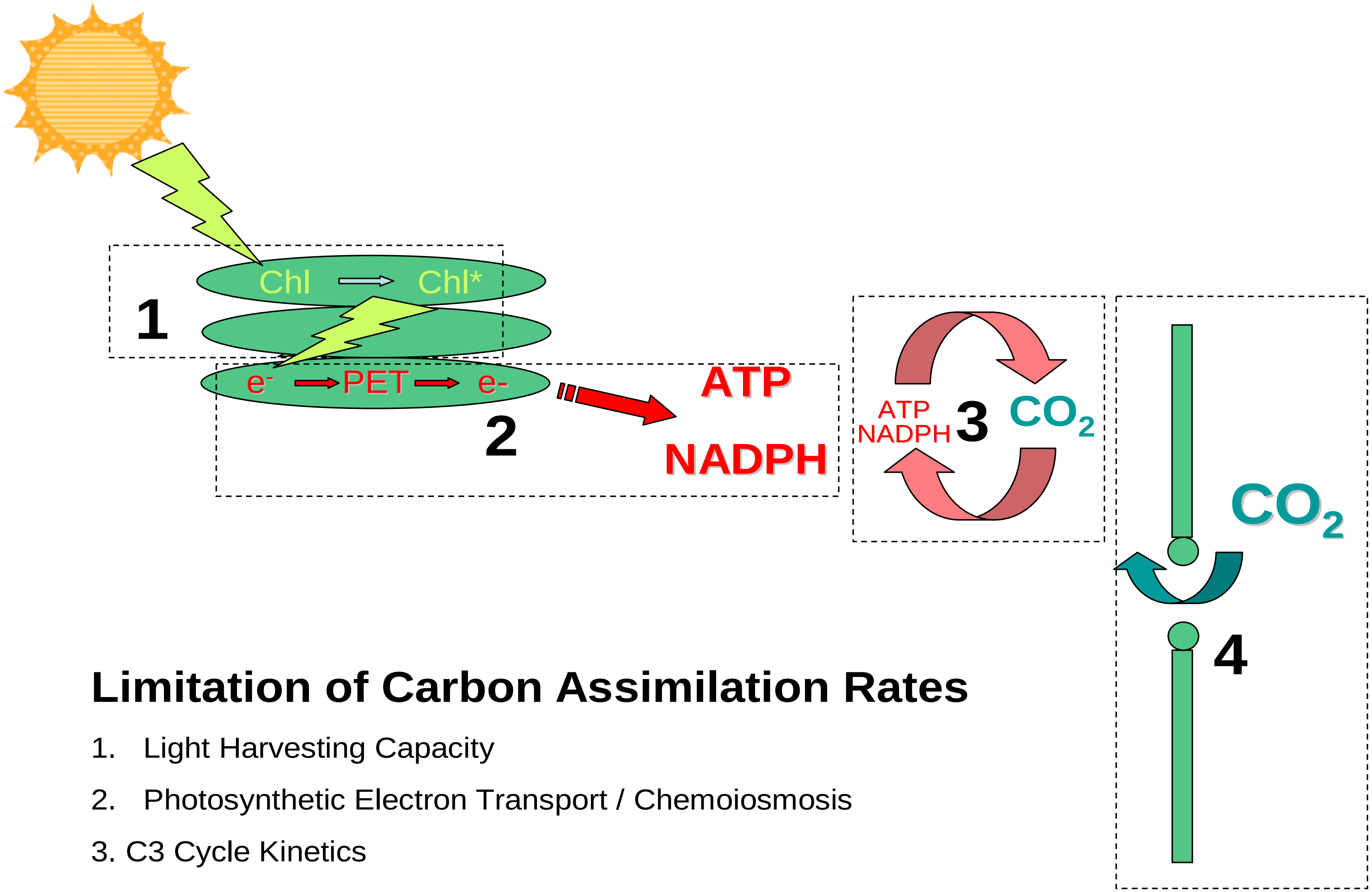
CO_2 Assimilation and Internal CO_2 Concentration



See Lambers et al. Fig 2.6

BOX 1 Mathematical Description of CO_2 Response

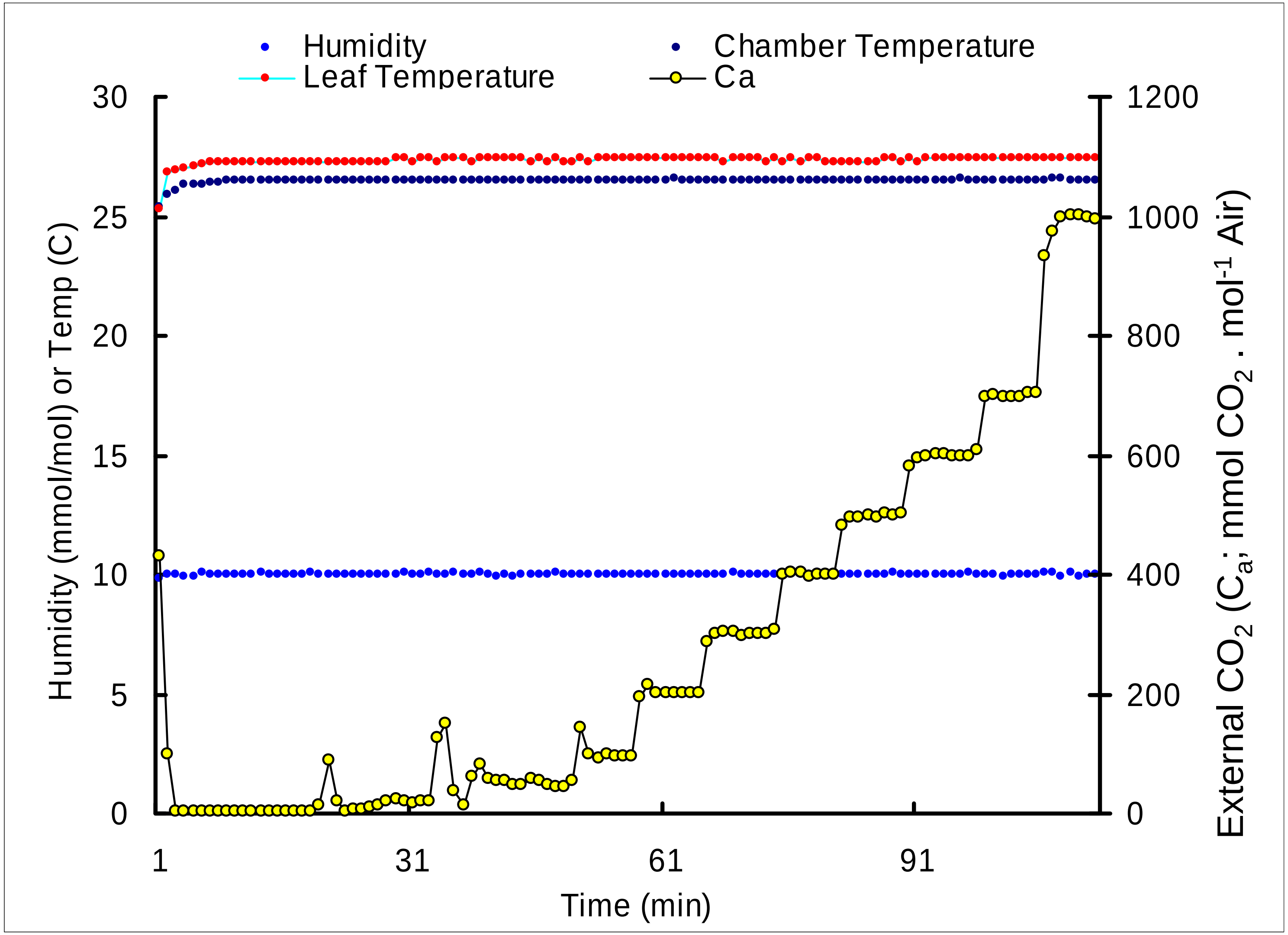
Photosynthesis - The Physiologist's View - Can Be Limited at 4 Stages



Limitation of Carbon Assimilation Rates

1. Light Harvesting Capacity
2. Photosynthetic Electron Transport / Chemoiosmosis
3. C3 Cycle Kinetics
4. CO_2 Supply / g_s

Typical IRGA Program for Collecting a CO_2 Response Curve



CO_2 Diffusion into Leaves is Limited Mainly by the Stomatal Conductance (g_s) (see Lambers *et al.*) – but recent evidence suggests Mesophyll Conductance (g_m) May also be Important

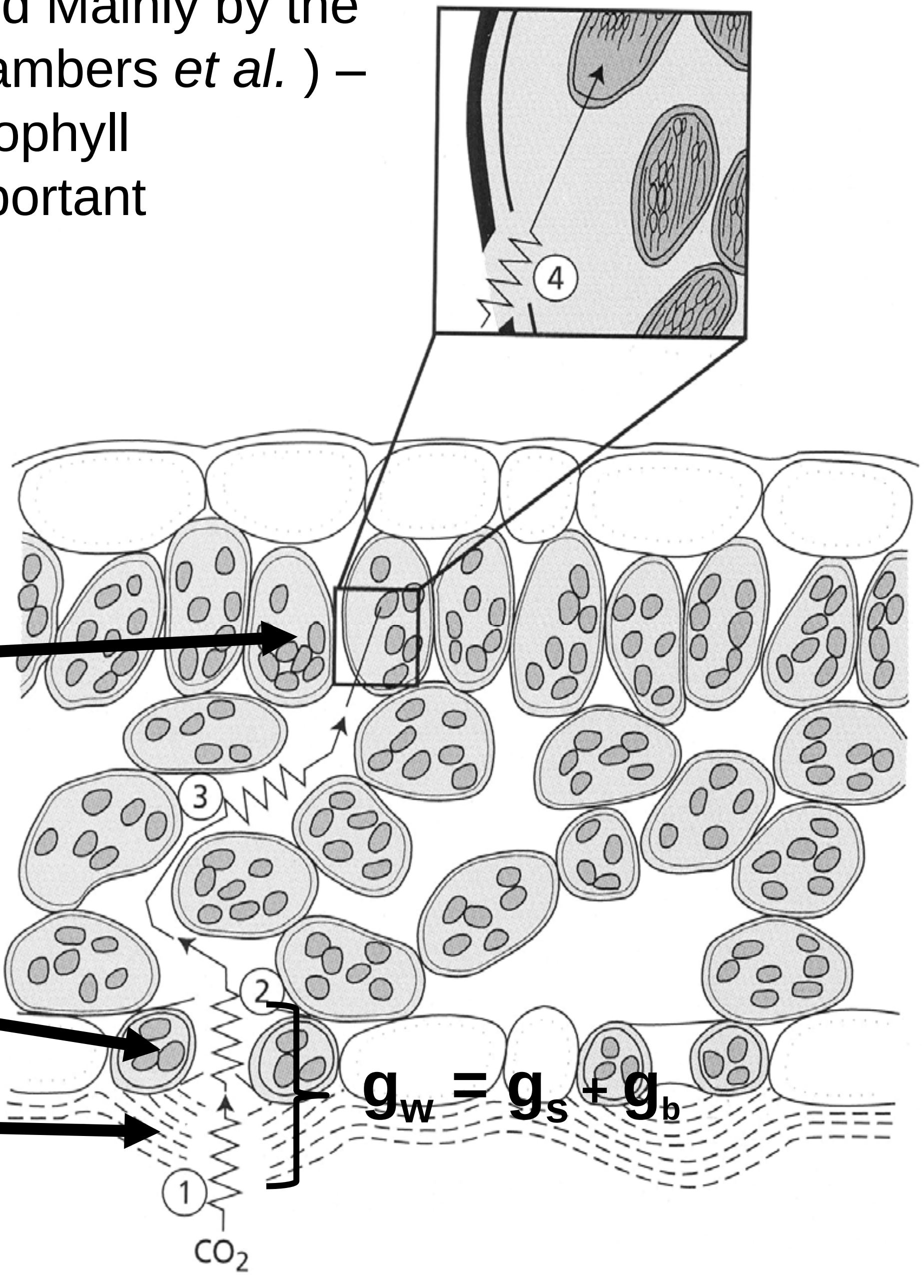
m^2–s . mol^{-1} | $mol\ m^{-2}\ s^{-1}$

r_m Mesophyll (4) g_m (0.5-5)

(3) – diffusion, insignificant

r_s Stomatal (2) g_s (0-1)

r_b Boundary (1) g_b (2-10)



Stomatal Conductance Can Be Measured From The Transpiration Rate

In rapidly moving air, $g_b \Rightarrow 10$ then,

$$E = g_w \frac{(e_i - e_a)}{P}$$

$$g_s = \frac{EP}{(e_i - e_a)}$$

E	Transpiration Rate (mmol m^{-2} s^{-1})
g_s	Stomatal Conductance (mol m^{-2} s^{-1})
e_i e_a	Humidity of inside & outside the leaf (e_i = saturated, mmol m^{-3})
P	Atmospheric pressure

If g_s is known for a leaf, g_b can be measured by turning off the mixing fan and measuring the new *E*

$$g_s + g_b = \frac{EP}{(e_i - e_a)}$$

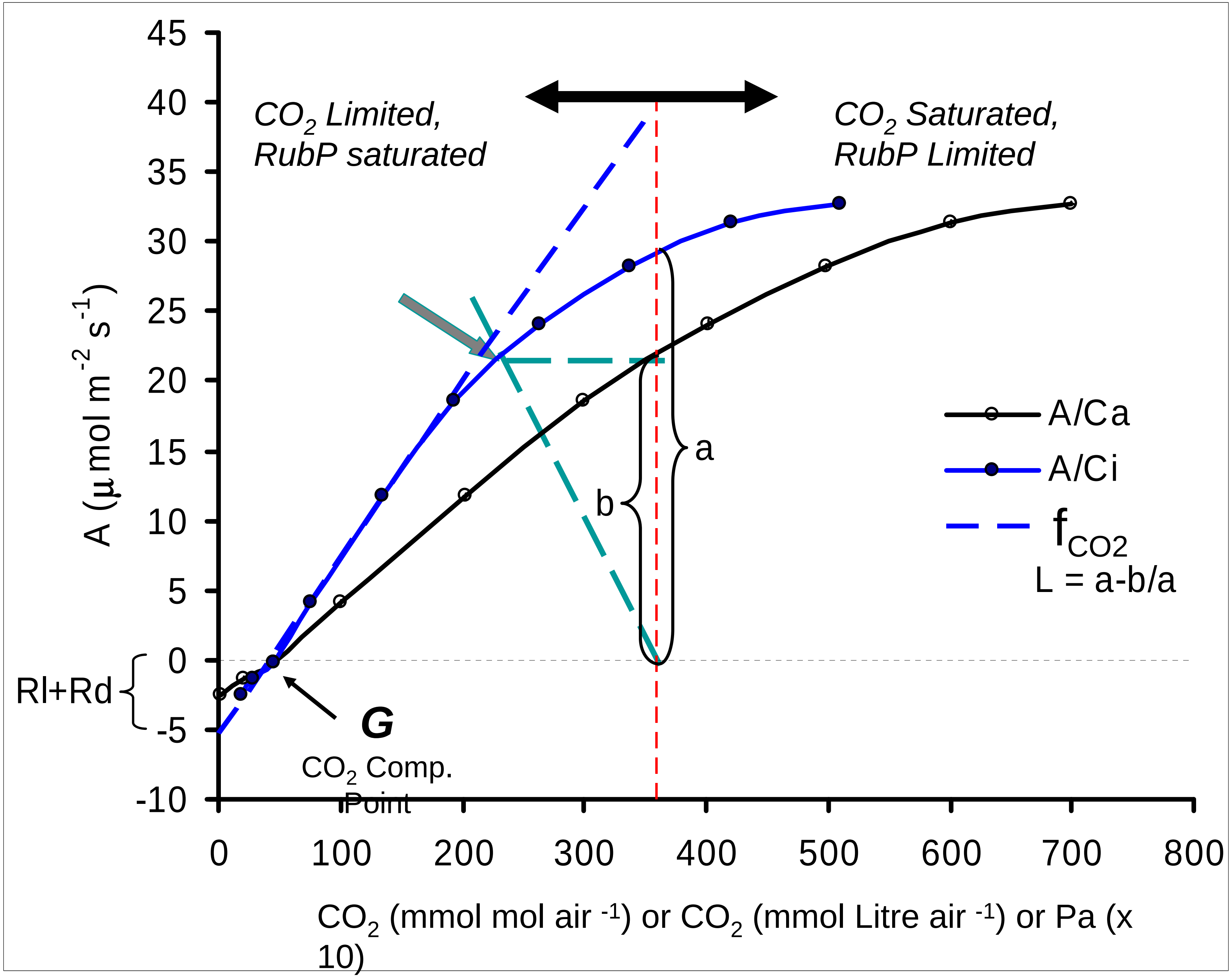
Internal CO_2 Levels, Ci, can be Calculated if g_s is Known

$$A = \frac{(C_a - C_i)}{1.6P} g_s$$

$$C_i = C_a - \left(\frac{1.6PA}{g_s}\right)$$

A	Assimilation Rate (mmol CO_2 m^{-2} s^{-1})
g_s	Stomatal Conductance (mol m^{-2} s^{-1})
C_i C_a	CO_2 concentration inside & outside the leaf (mol mol_{air} or Pa)
P	Atmospheric pressure (value of 1.6 is included to account for the different diffusion rates of CO_2 & H_2O

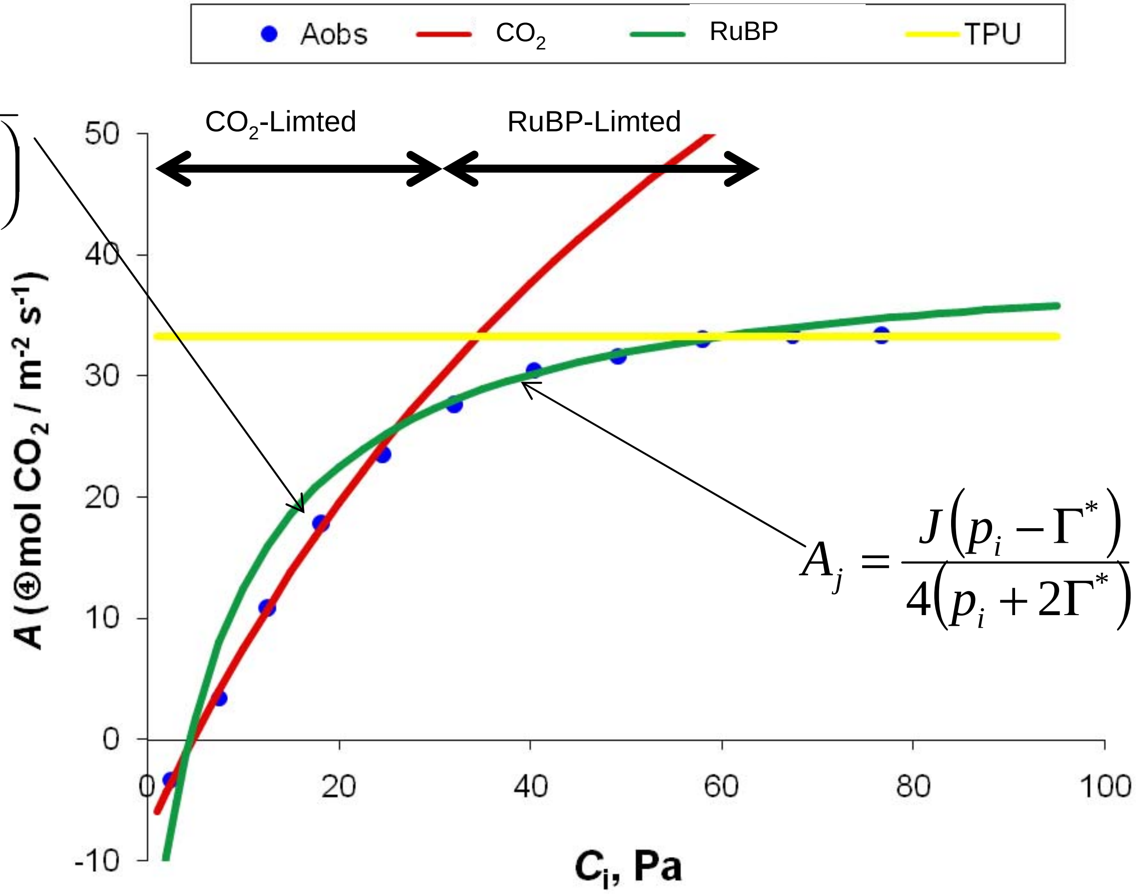
C_i, is an important parameter that reveals a great deal about the physiological state of the leaf



CO2 Limited,
RubP saturated
CO2 Saturated,
RubP Limited
A/Ca
A/Ci
fCO2
L = a-b/a
a
b
Rl+Rd
G
CO2 Comp. Point
A (µmol m-2 s-1)
45
40
35
30
25
20
15
10
5
0
-5
-10
0
100
200
300
400
500
600
700
800
CO2 (mmol mol air -1) or CO2 (mmol Litre air -1) or Pa (x 10)

The A / Ci Curve has to be Modelled in 2 or 3 Bits

$$A_c = \frac{V_{c\max}\left(p_i - \Gamma^*\right)}{p_i + K_c\left(1 + O/K_o\right)}$$



$$A_j = \frac{J\left(p_i - \Gamma^*\right)}{4\left(p_i + 2\Gamma^*\right)} - R_{day}$$

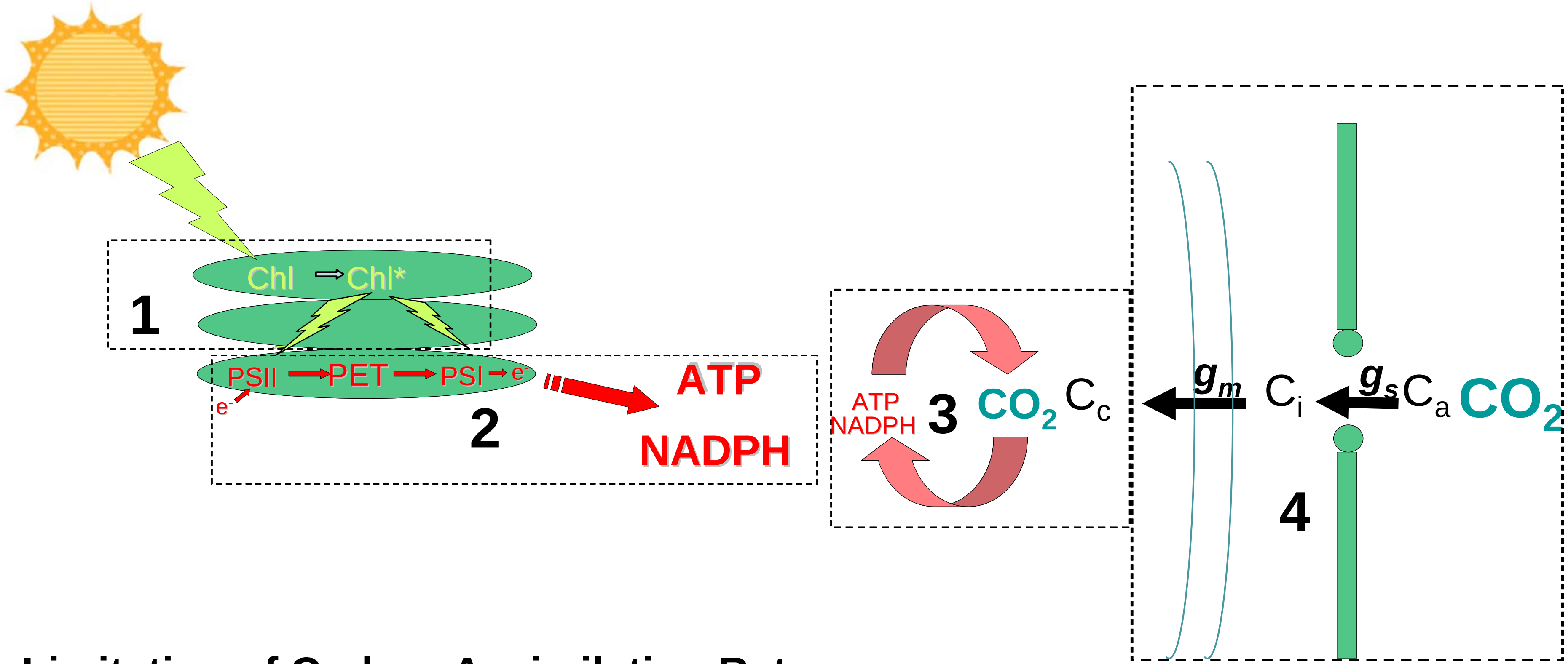
Kinetic Properties of Rubisco

K_c	~ 40.4 Pa (~ 18 mM),
K_o	~ 24, 800 Pa (~ 1.1 mM)
V_{cMax}	~5 – 25 mmol CO_2 m^{-2} s^{-1}
V_{oMax}	~1 – 6 mmol O_2 m^{-2} s^{-1}
$[CO_2]$	C_a, 38 Pa (~ 17 mM), but C_i less
$[O_2]$	21,000 Pa (210 mM) = O_i

K_c & K_o , and V_{cMax} & V_{oMax}, do not Change much for most Higher Plants in Most Environmental Conditions,

But C_i Does (& O_i)

What Limits C3 Photosynthesis?



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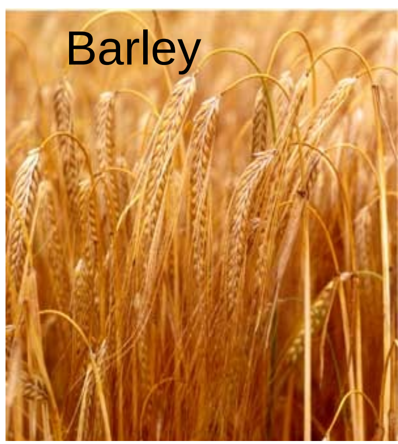
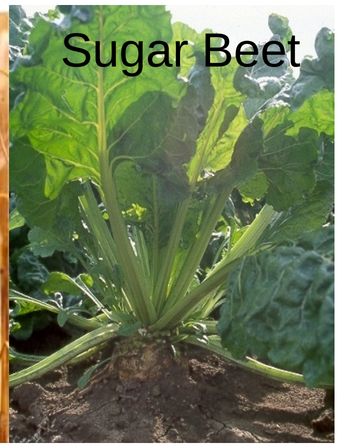
Ca, Ci, Cc ~ CO2 Levels in Air, Intercellular Space, Chloroplast

gs & *gm* ~ Stomatal Conductance & Mesophyll Conductance





BOX 2 Discrimination of Carbon Isotopes

d ^{13}C Ratios Differs in C3 and C4 Plants

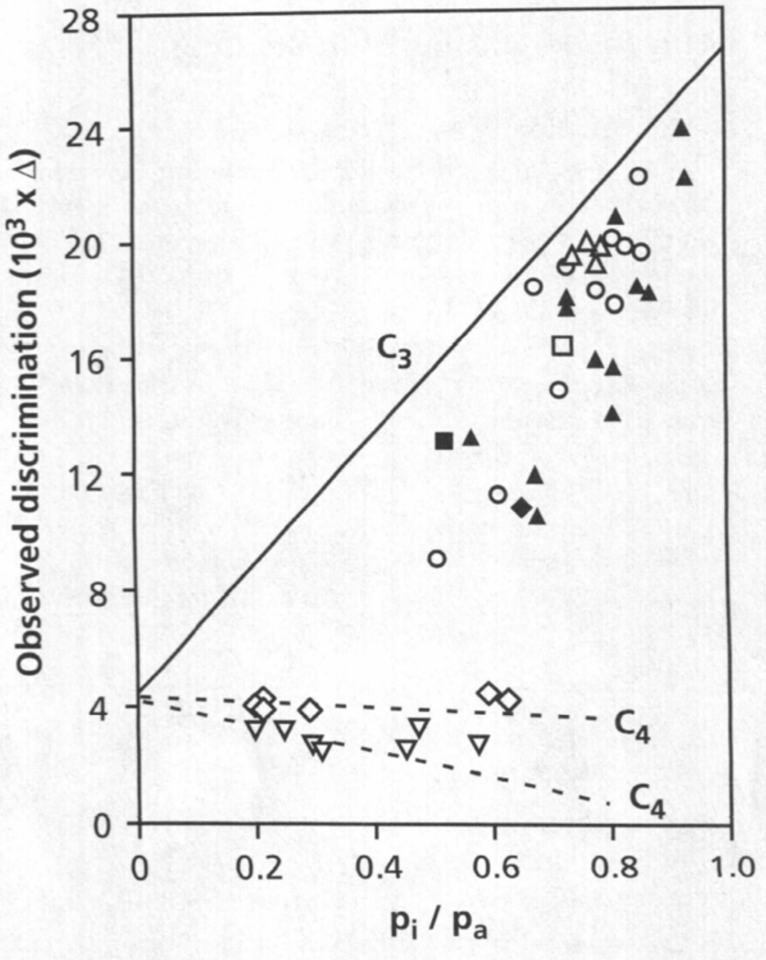
Box 2. *Continued*

TABLE 1. The magnitude of the fractionation during CO_2 uptake.

Process or enzyme	Fractionation (‰)
Diffusion in air	4.4
Diffusion through the boundary layer	2.9
Dissolution of CO_2	1.1
Diffusion of aqueous CO_2	0.7
CO_2 and HCO^-_3 in equilibrium	−8.5 at 30°C −9.0 at 25°C
CO_2 − HCO^-_3 catalyzed by carbonic anhydrase	1.1 at 25°C
HCO^-_3 − CO_2 in water, catalyzed by carbonic anhydrase	10.1 at 25°C
PEP carboxylase	2.2
Combined process	−5.2 at 30°C −5.7 at 25°C
Rubisco	30 at 25°C

Source: Henderson et al. 1992.

Ca = 34 Pa



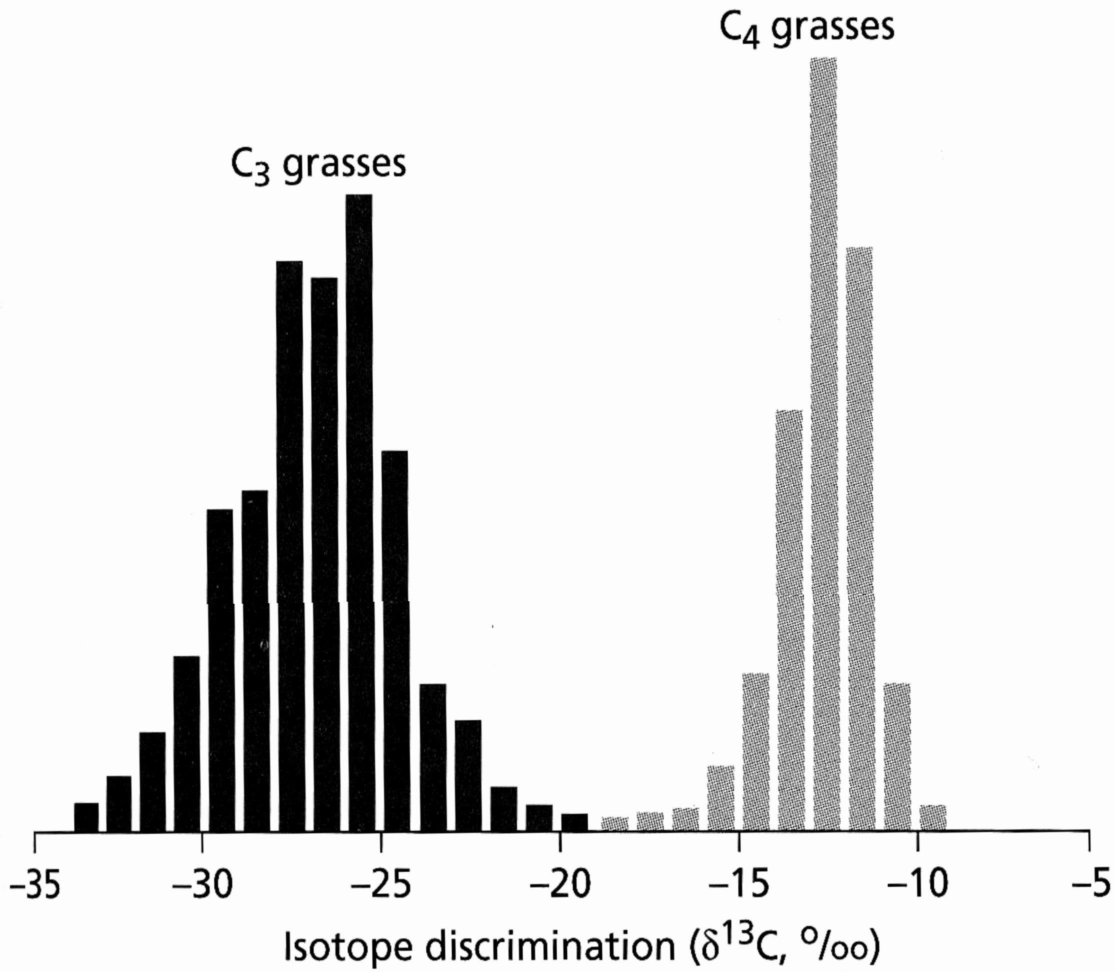
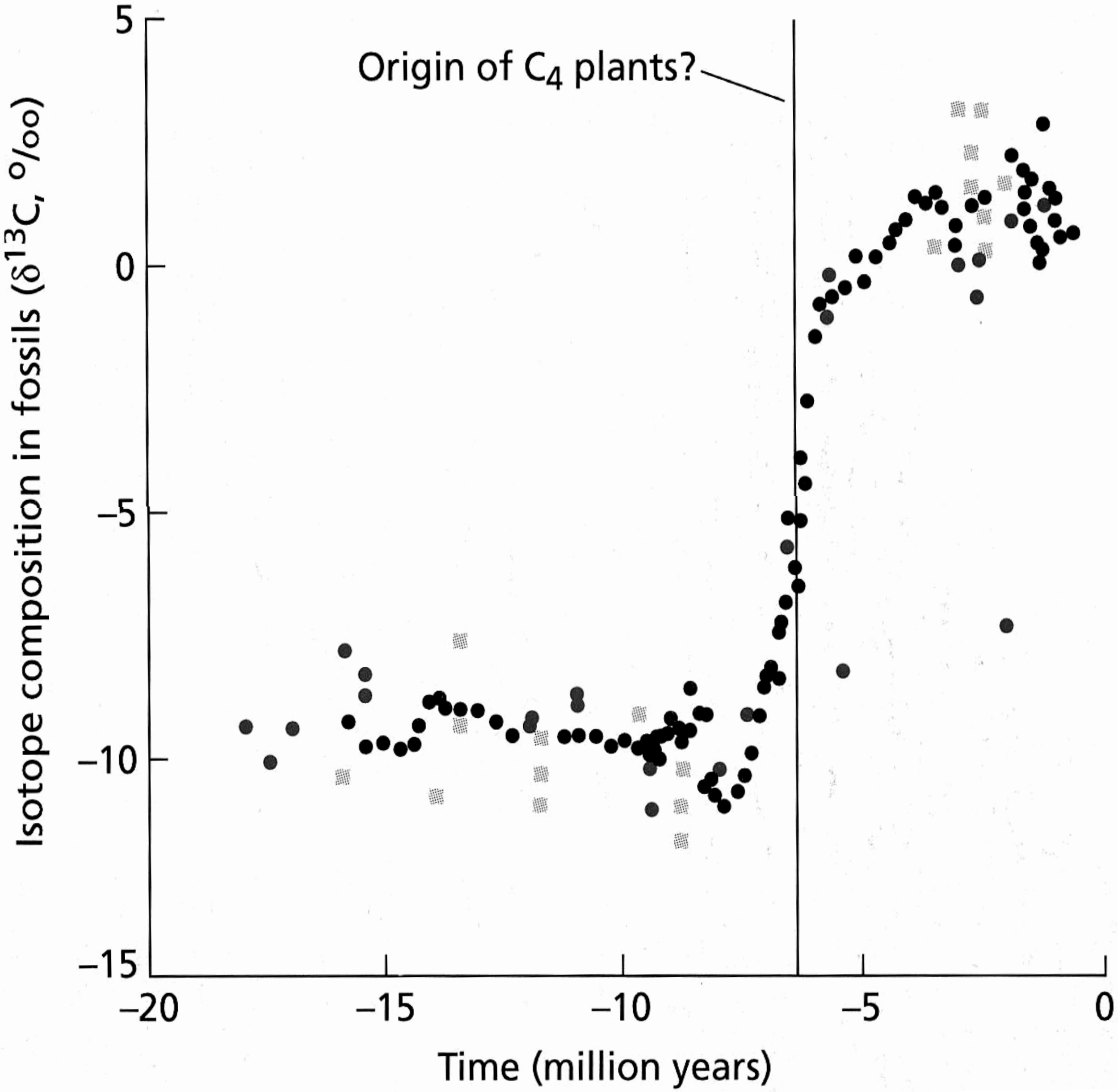


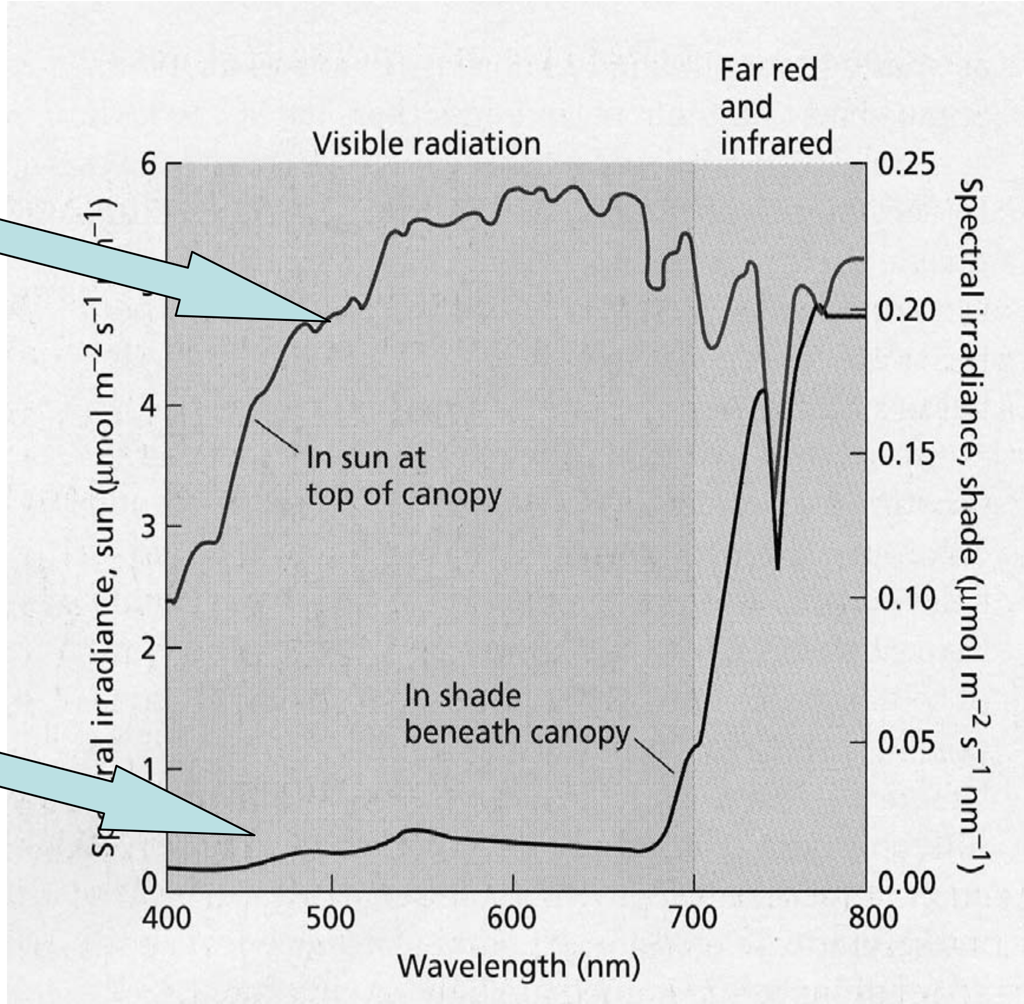
Figure 9.20 Carbon isotope discrimination in plants. C_3 plants discriminate against and take up less ^{13}C than C_4 plants do. Consequently, C_3 and C_4 grasses have distinct isotope compositions. (From Čerling et al. 1997.)

Carbon Isotope & Taxonomic Evidence Suggests the C4 Mechanism Arose Independently About 25 million Years Ago, but did Not Become Significant until ~ 7 million years ago.



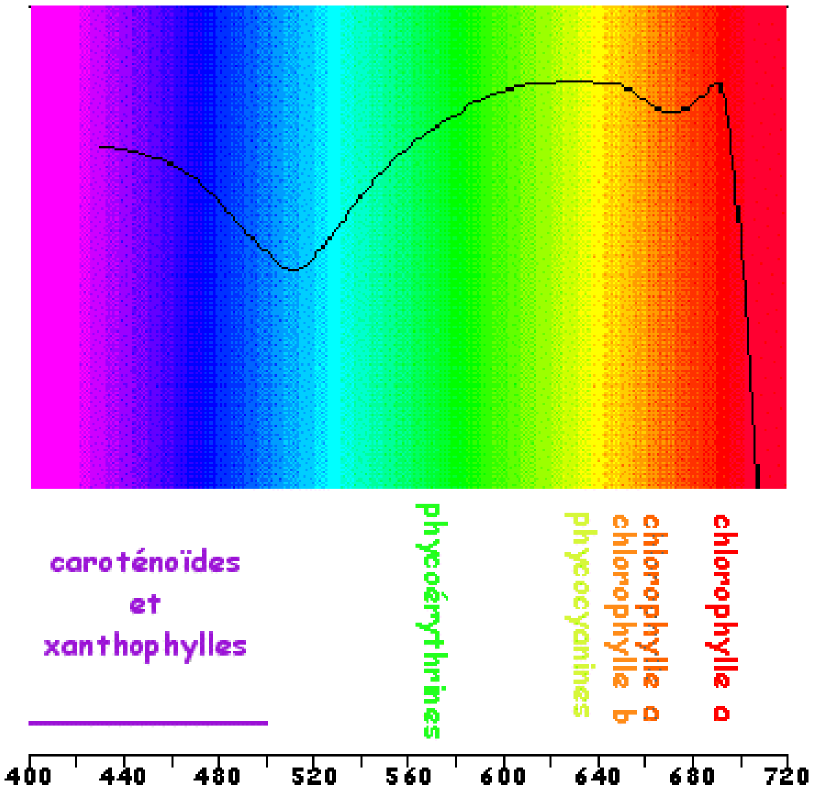
Response of Photosynthesis to Light
Maximizing Light Capture & Photosynthetic Efficiency

The Photosynthetic Apparatus has to Cope with Major Changes in Irradiance

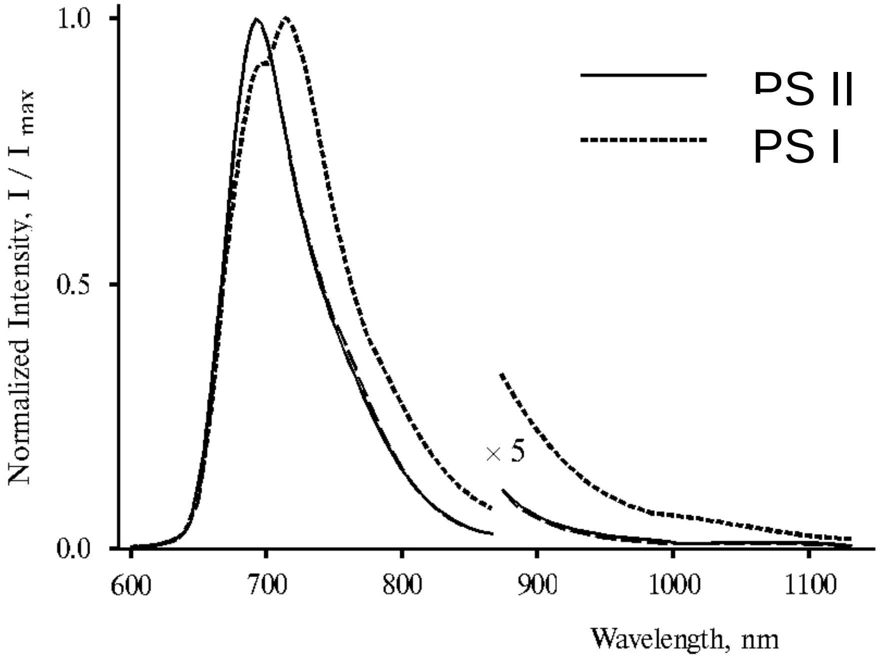


…and Spectral Composition…

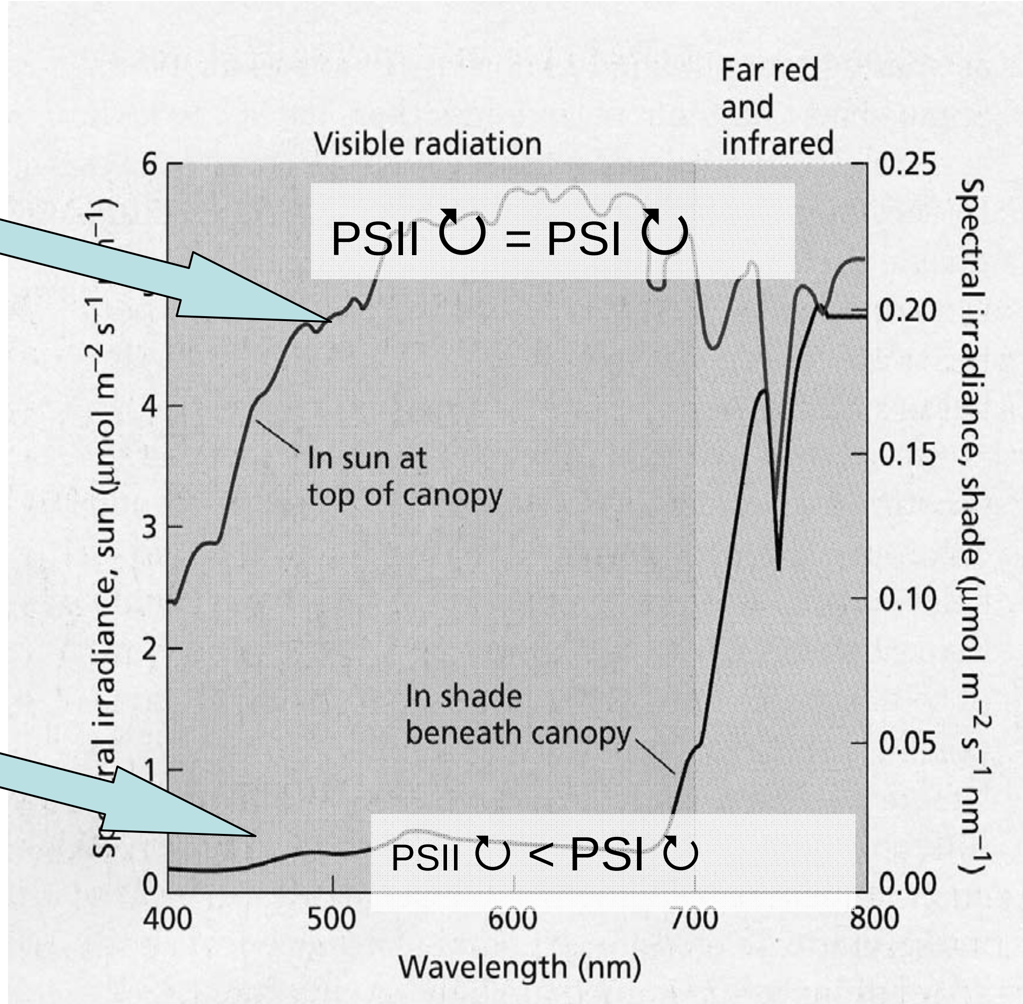
Emerson’s Red Drop / Enhancement



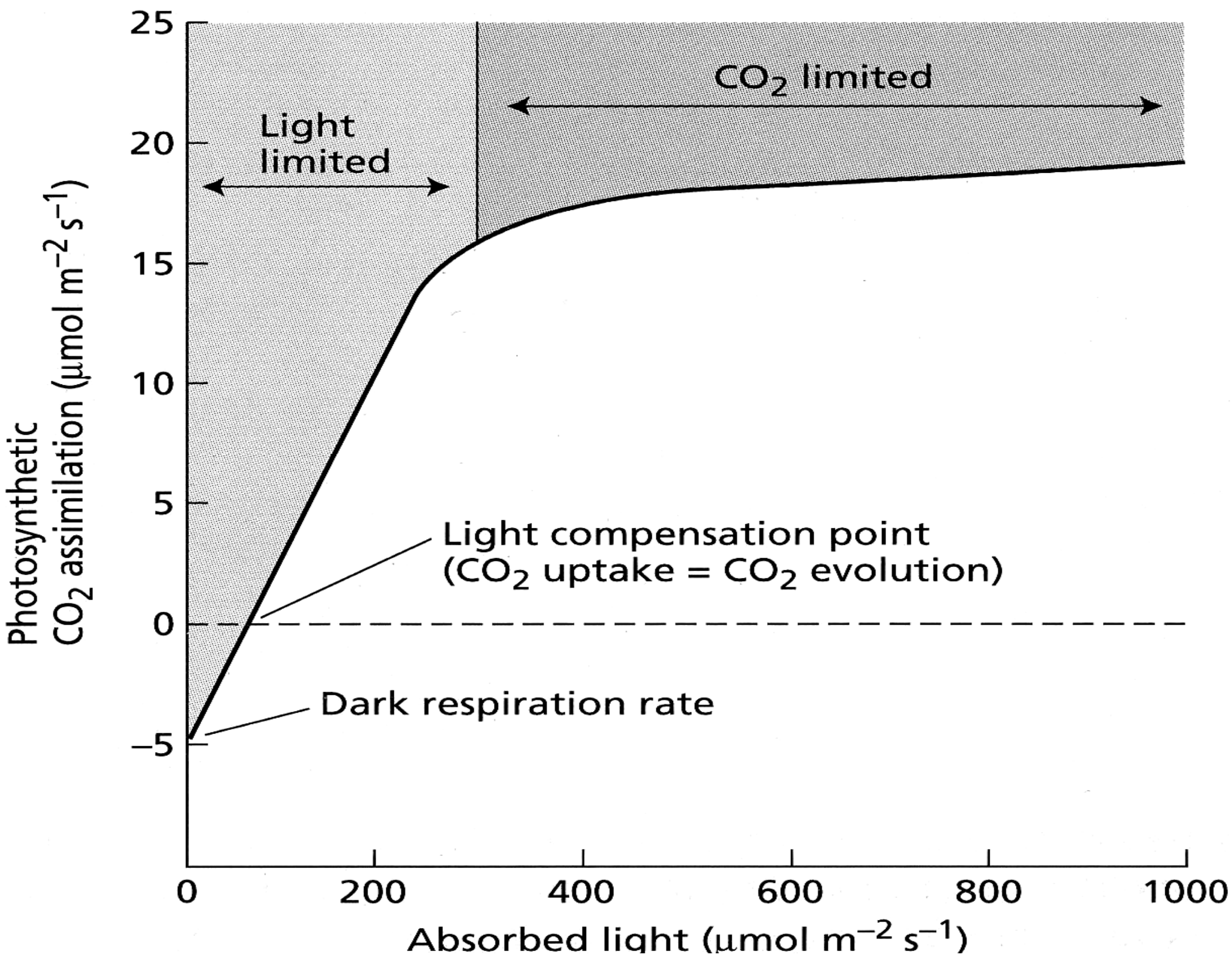
Wavelength (nm)



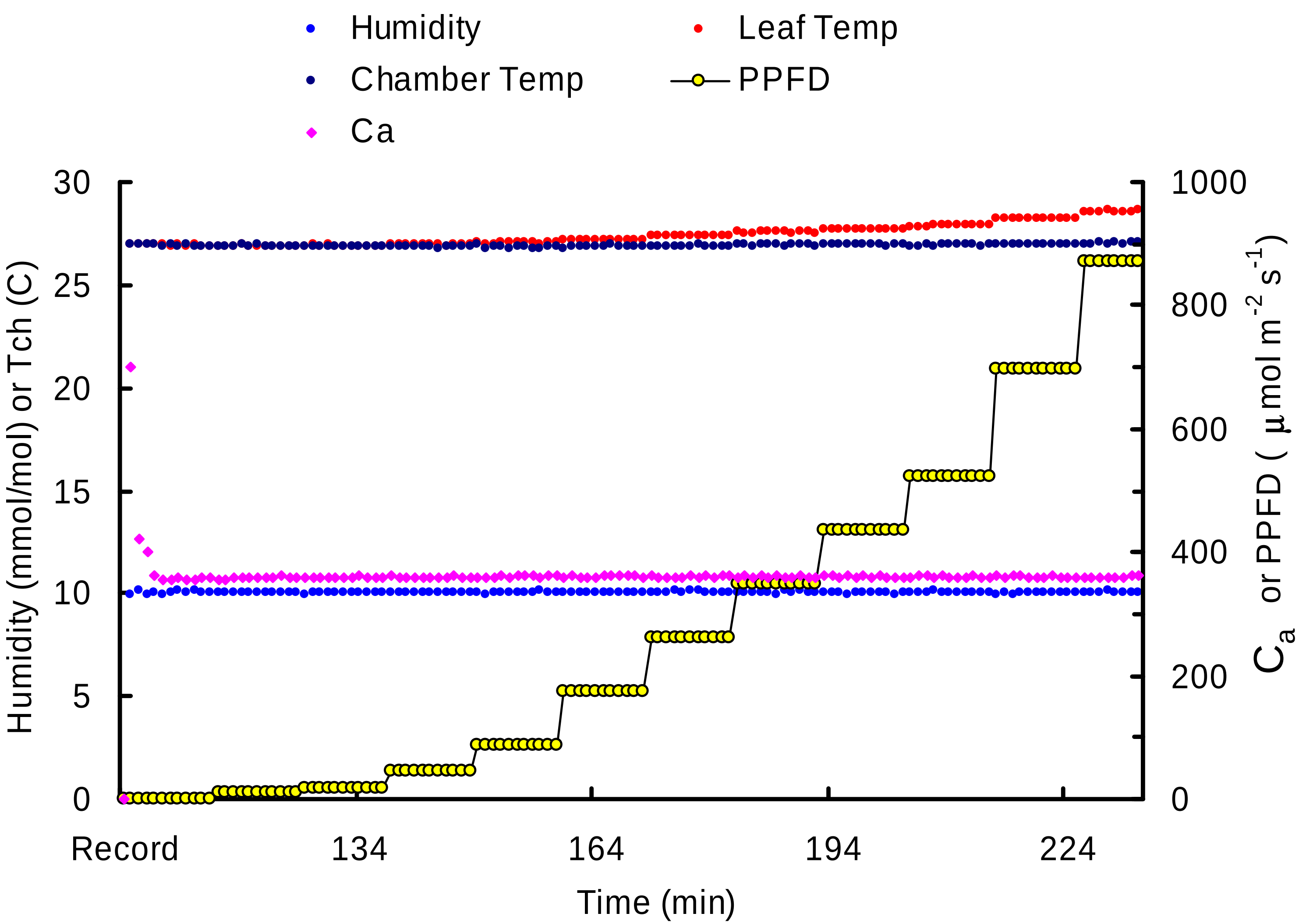
…so Turnover of PS II & PSI has to be Balanced



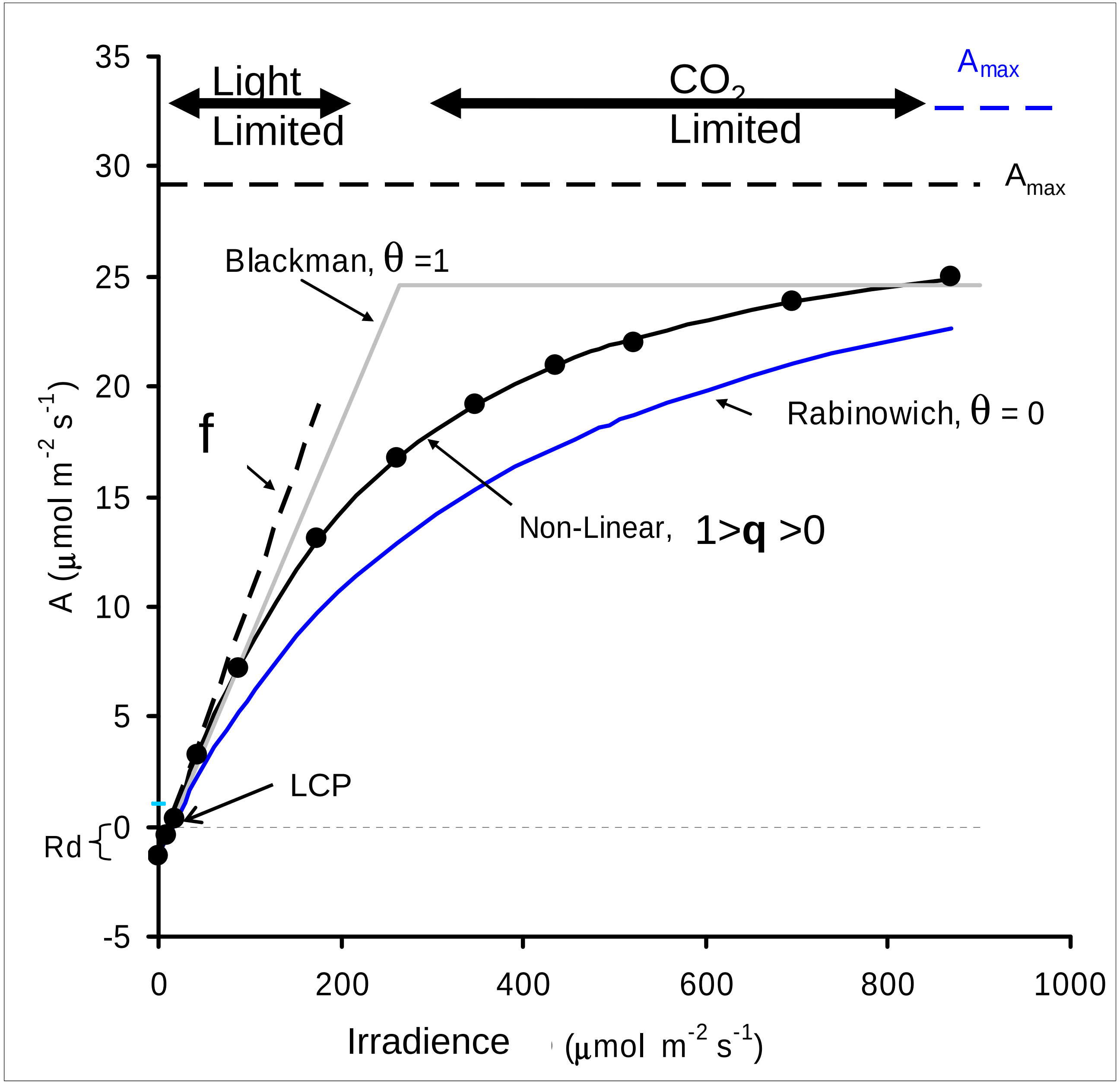
Changes in Irradiance Levels



Measuring Photosynthetic Response to Light – Light Response Curves



Barley Light Response Curve



See Lambers et al. Fig 2.8

Three Models Fit Most LRCs

- Blackman Model

$$A = A_{\max}\frac{I}{I_s}$$ when *I* < *Is*, and when *I* > *Is*. $$A = A_{\max}$$

- Rabinowich

(Rectangular Hyperbola or 'Linear')

$$A = \frac{A_{\max}\alpha I}{A_{\max} + \alpha I}$$

- 'Non-Linear'

(Thornley; Marshall & Biscoe ~ 'Quadratic')

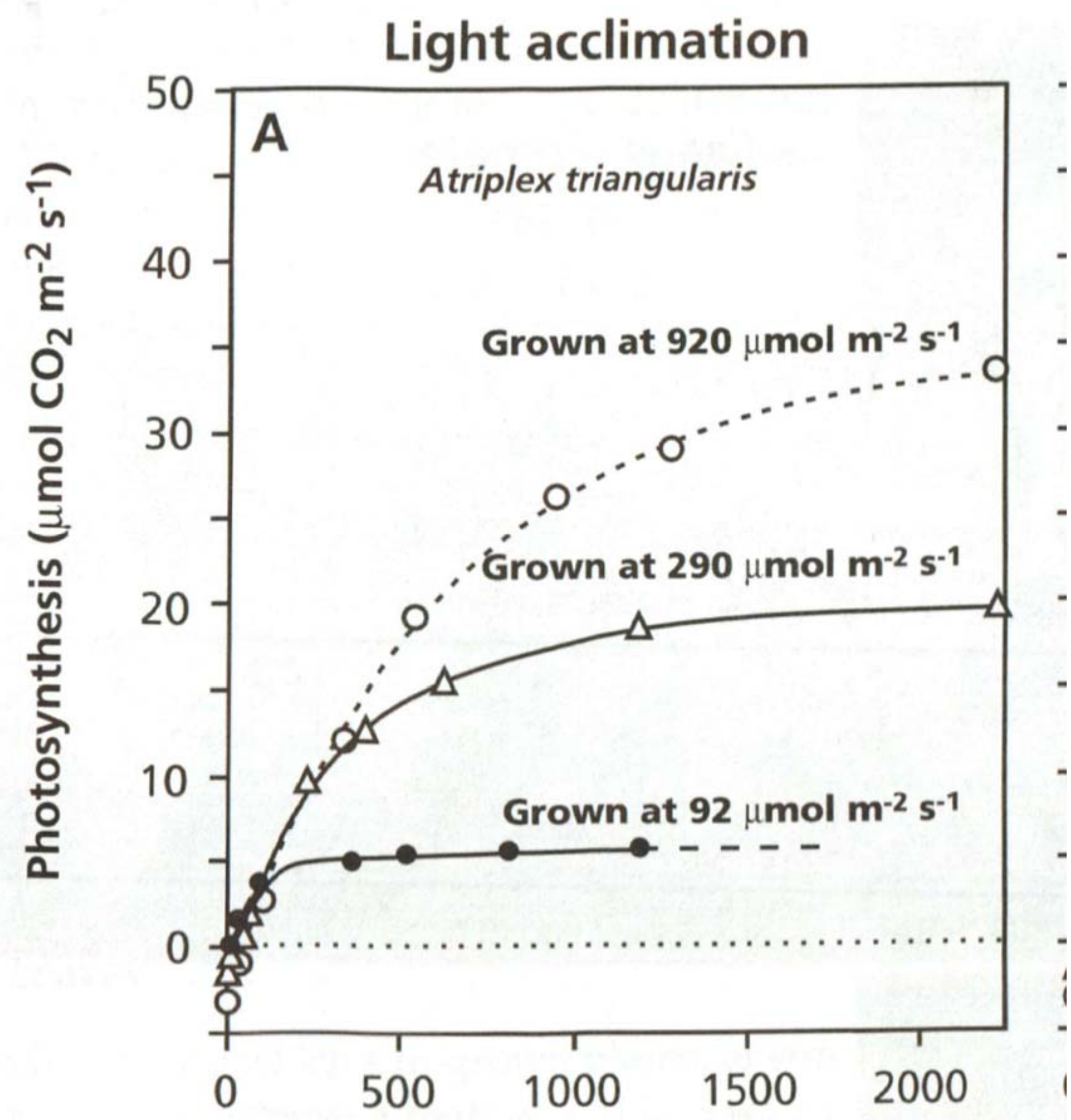
$$0 = \left(A_{\max}\alpha I\right) - \left(A_{\max} + \alpha I\right)A + \theta A^2$$

Solved by

$$A = \frac{\phi\, I + A_{max} - \sqrt{\left(\phi\, I + A_{max}\right)^2 - 4\theta\left(\phi\, I\ A_{max}\right)}}{2\theta}$$

$$A = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

Light Acclimation



Irradiance (mmol m^{-2} s^{-1})

Controlled At The **Developmental** Level

High Light Acclimation

- Less Chlorophyll
- Lower Quantum Efficiency

Low Light Acclimation

- Often Dark Green
- Higher Quantum Efficiency

See Lambers *et al.* Fig 2.9A

Light Acclimation

Light Acclimation of Green Alga *Coccomyxa sp.*

Controlled At The **Developmenta** Level

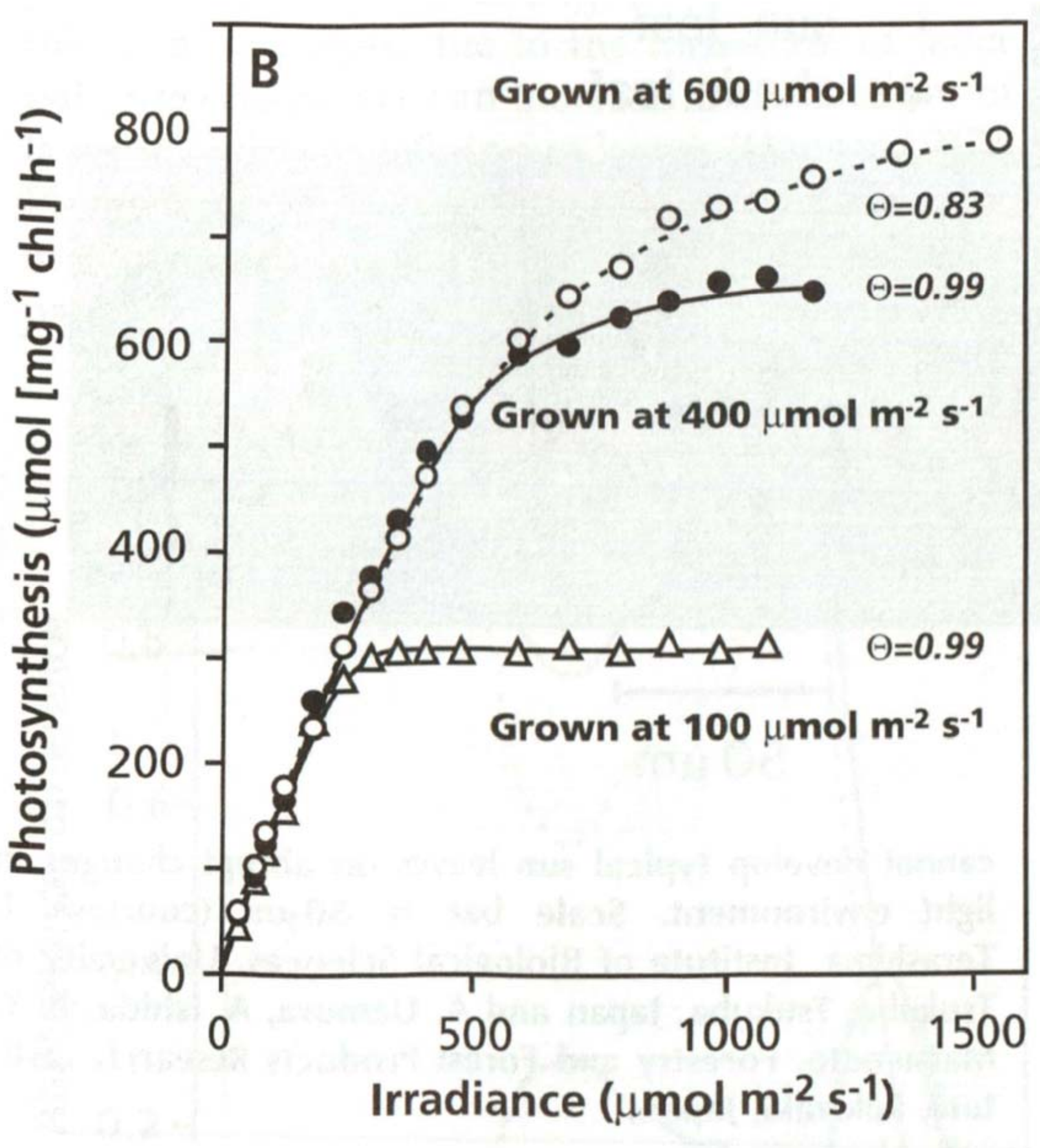
High Light Acclimation

- Less Chlorophyll
- Lower Quantum Efficiency

Low Light Acclimation

- Often Dark Green
- Higher Quantum Efficiency

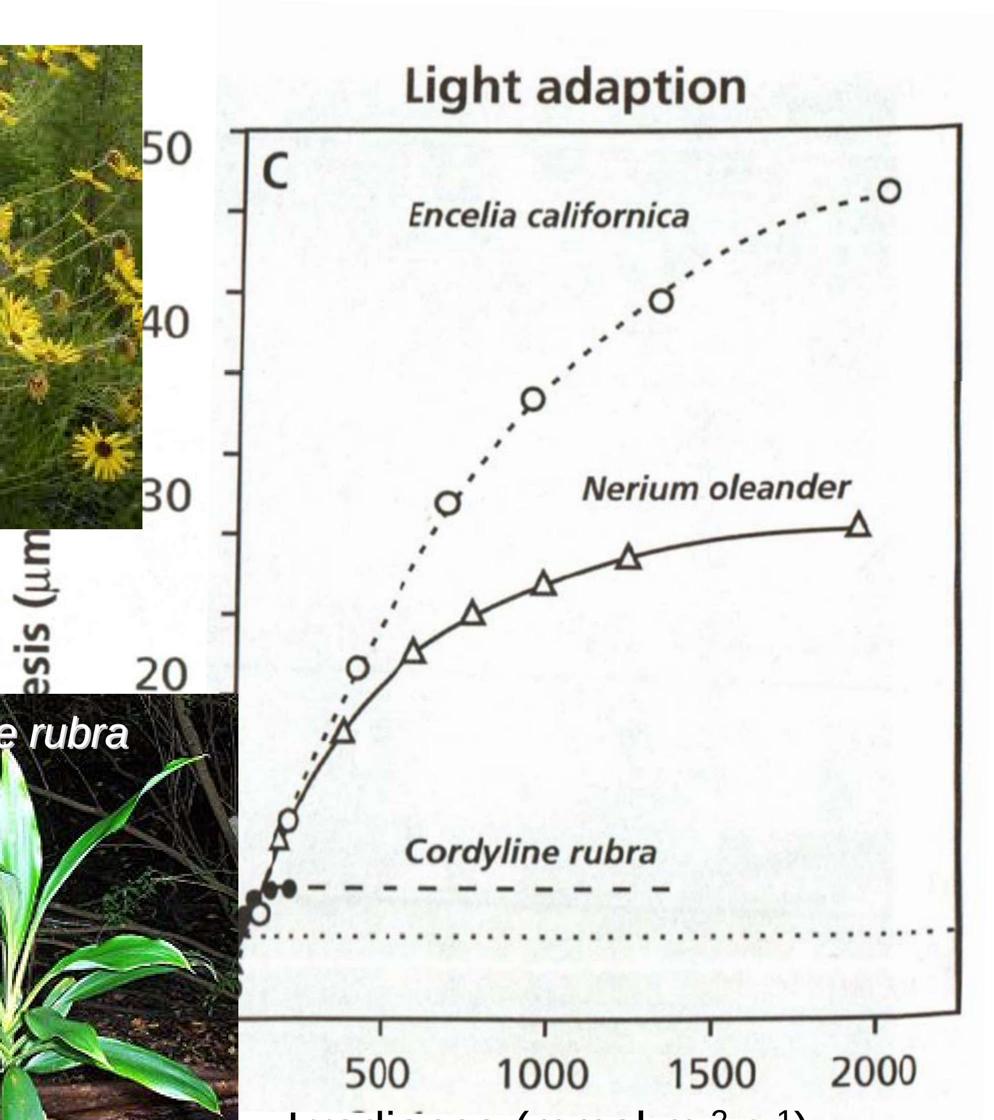
See Lambers et al. Fig 2.9B



Light Adaptation

Controlled At

Sun Plants



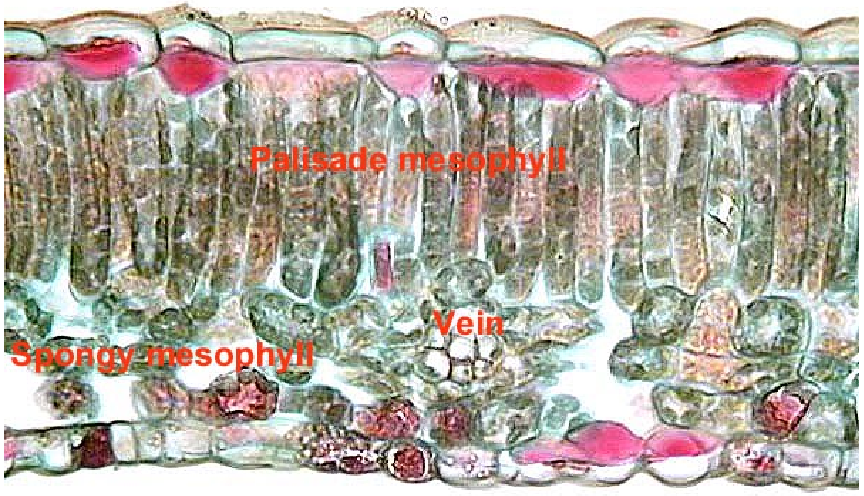
Irradiance (mmol m^{-2} s^{-1})

Photoinhibit Or Photobleach
High Irradiance

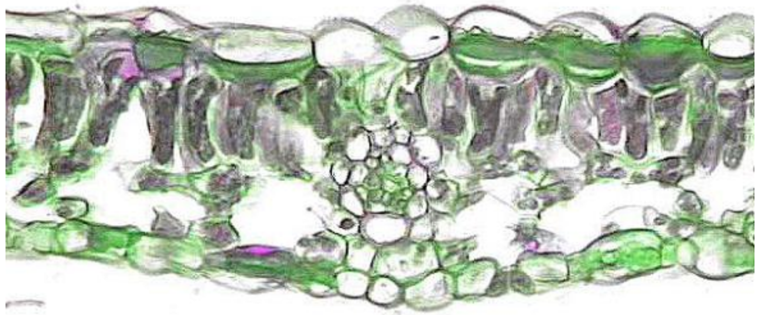
See Lambers et al. Fig 2.9C

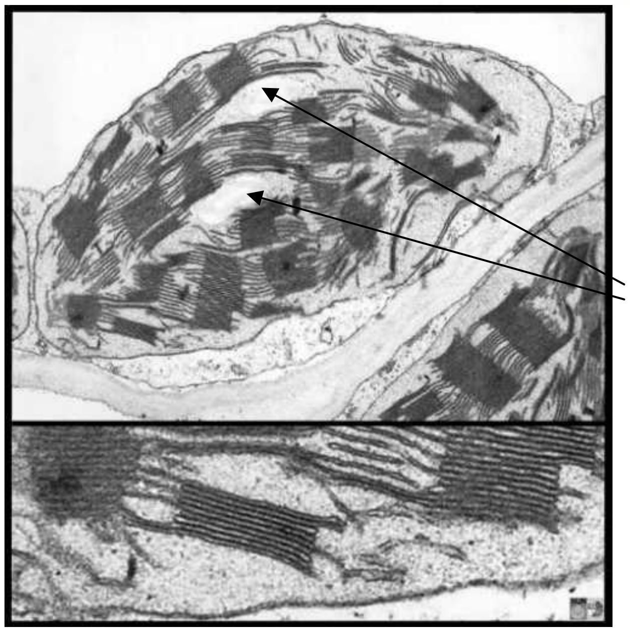
Morphological Adaptations to Sun & Shade

Sun Leaves



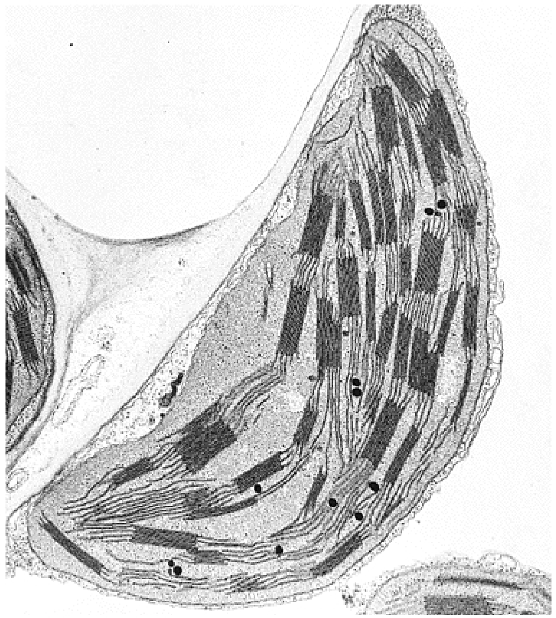
Shade Leaves





Starch Grains

See Lambers et al. Fig 2.10



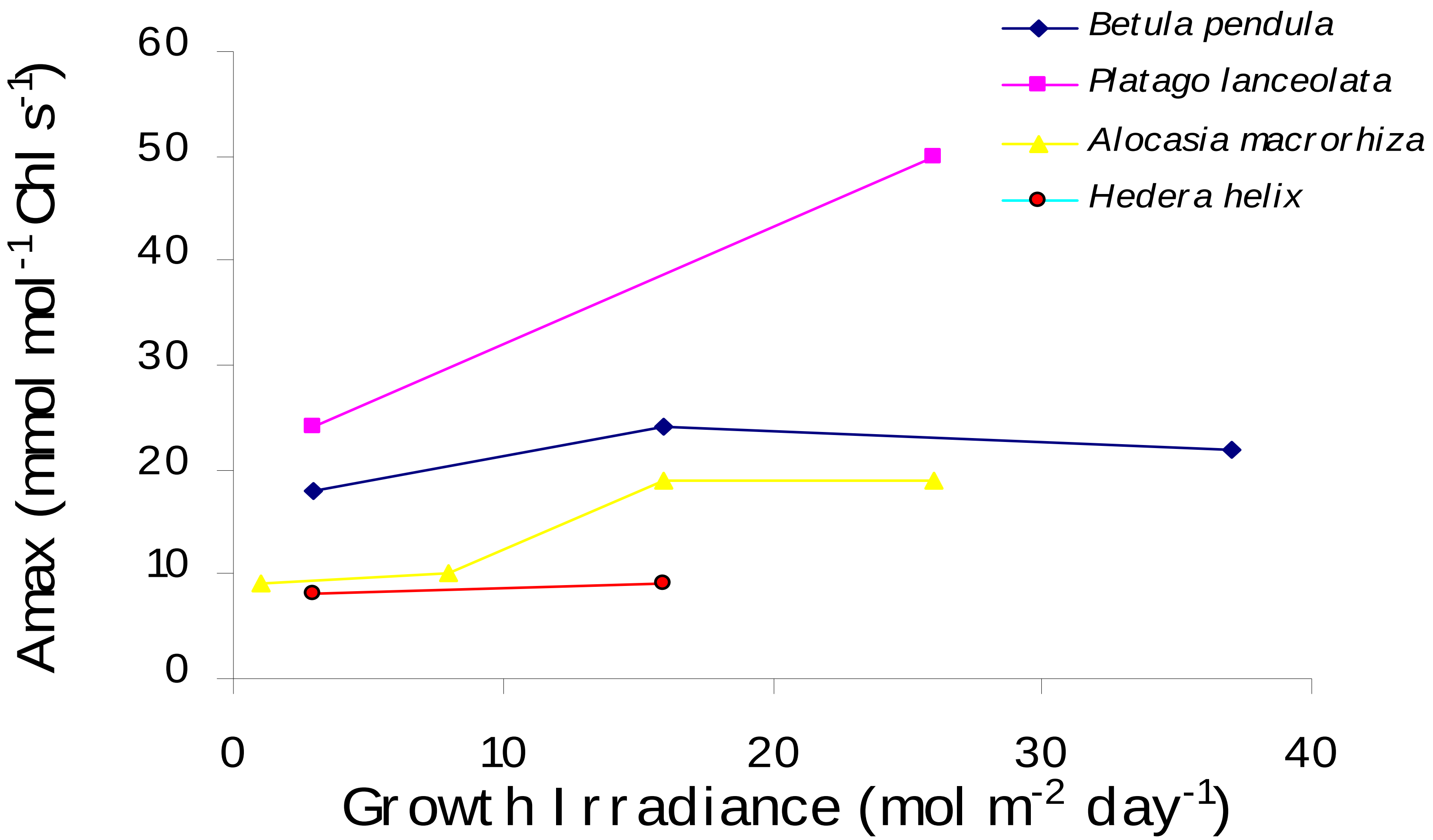
Summary of Sun / Shade Leaf Characteristics

TABLE 2. Overview of generalized differences in characteristics between shade- and sun-acclimated leaves.

	Sun	Shade
Structural		
Leaf dry mass per area	high	low
Leaf thickness	thick	thin
Palisade parenchyma thickness	thick	thin
Spongy parenchyma thickness	similar	similar
Stomatal density	high	low
Chloroplast per area	many	few
Thylakoids per stroma volume	low	high
Thylakoids per granum	few	many
Biochemical		
Chlorophyll per chloroplast	low	high
Chlorophyll per area	similar	similar
Chlorophyll per dry mass	low	high
Chlorophyll a/b ratio	high	low
Light-harvesting Complex per area	low	high
Electron transport components per area	high	low
Coupling factor (ATPase) per area	high	low
Rubisco per area	high	low
Nitrogen per area	high	low
Xanthophylls per area	high	low
Gas exchange		
Photosynthetic capacity per area	high	low
Dark respiration per area	high	low
Photosynthetic capacity per dry mass	similar	similar
Dark respiration per dry mass	similar	similar
Carboxylation capacity per area	high	low
Electron transport capacity per area	high	low
Quantum yield	similar	similar
Curvature of light-response curve	gradual	acute

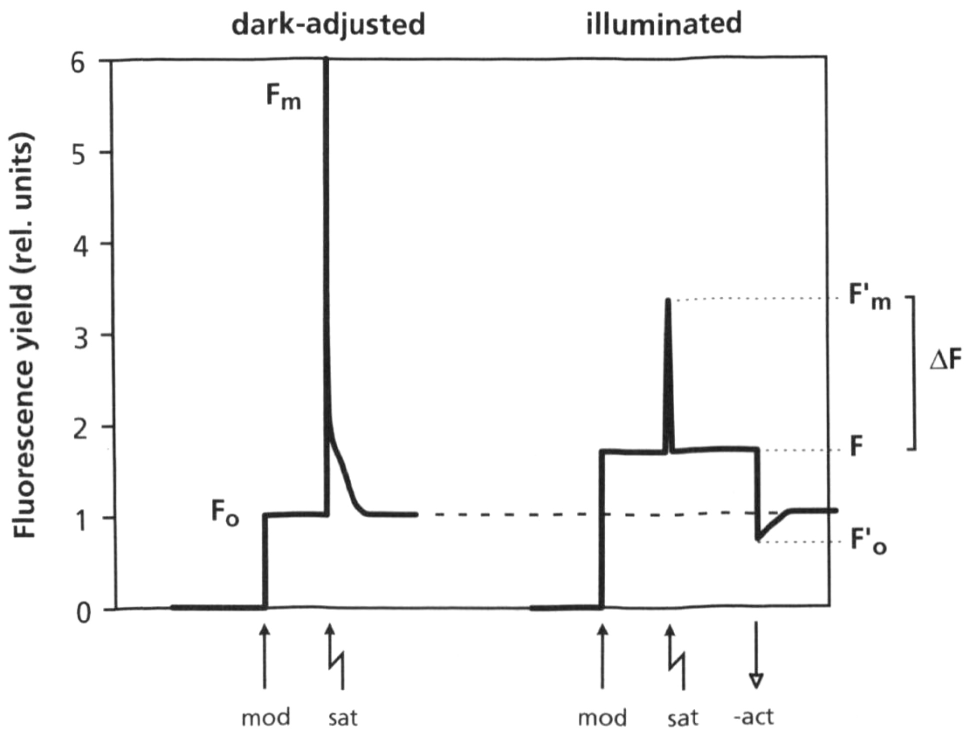
See Lambers et al. Table 2.2

Effect of Growth Irrandiance on A_{max} in Four Species



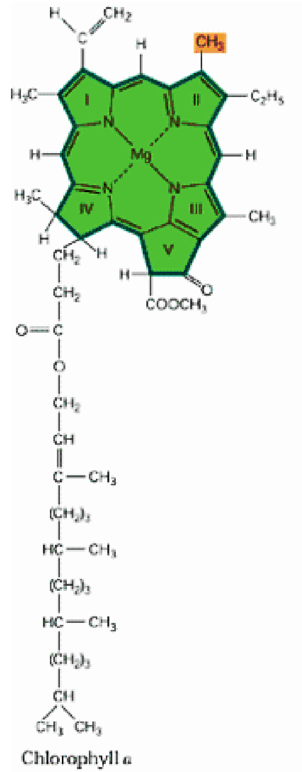
See Lambers et al. Fig 2.14

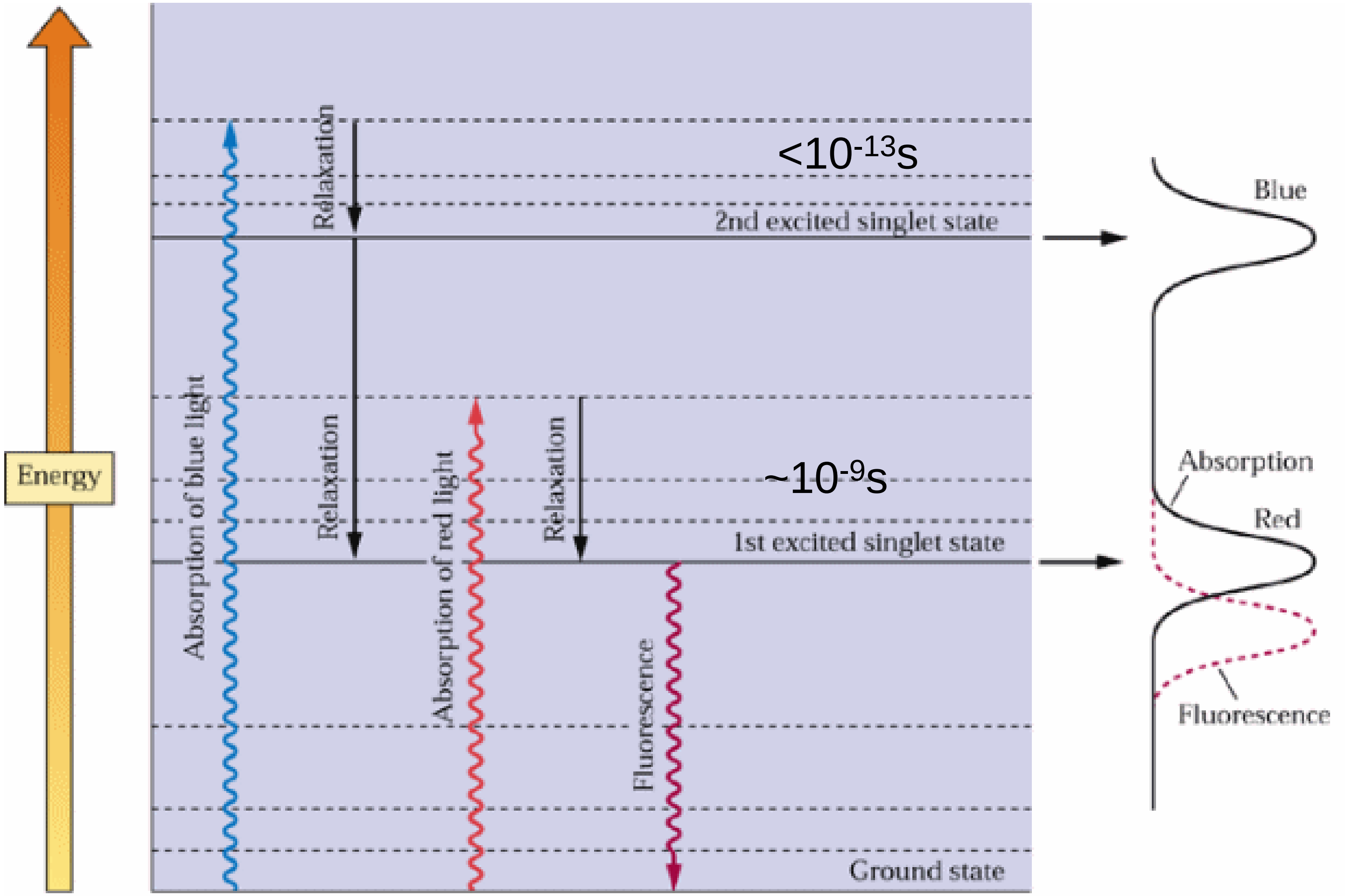
Chlorophyll Fluorescence (Box 4)



See Lambers et al. Chapter 2 Box 1 Fig 1

What is Fluorescence?





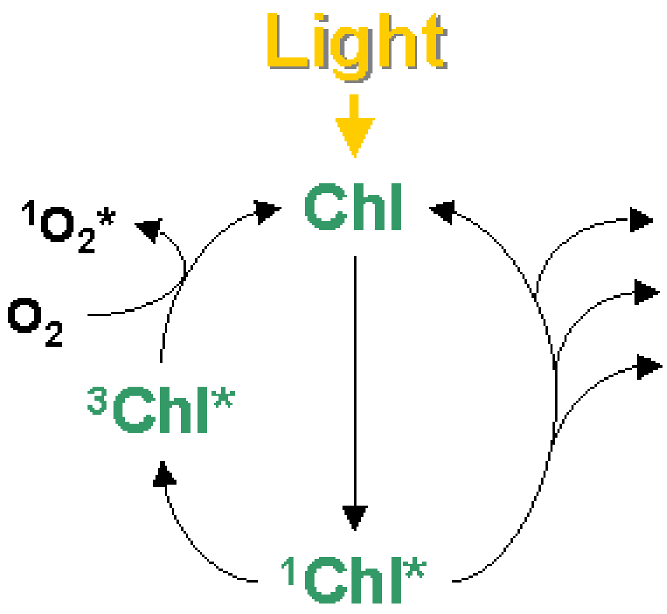
Blue Photons Are No More Effective At Driving PET Than Red Photons

Energy of a Photon, E = h.n = h. c/l

h is Plank's Constant ($6.626 \cdot 10^{-34}$ J-s); c is velocity of light ($3 \cdot 10^{8}$ m s^{-1}) ; l is wavelength (m)

Chlorophyll Fluorescence

- Light Energy absorbed by Chlorophyll in an LHC can undergo 3 *Competing* Fates



	Non-Stressed	Stressed	
photochemistry	~0.8	~0.2	F_{PSII}
heat	~0.1	~0.4	F_H
fluorescence	~ 0.1	~ 0.4	F_F

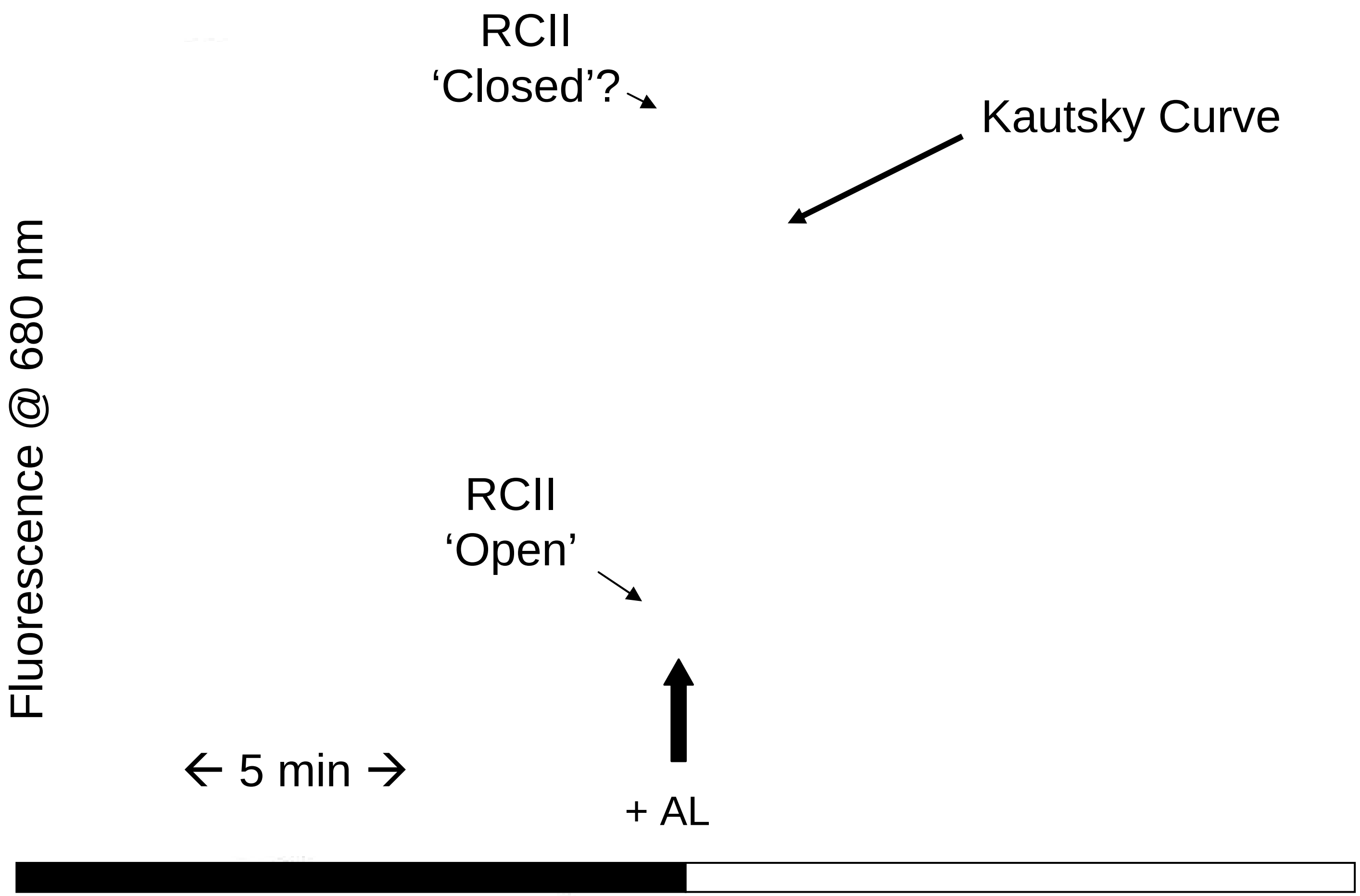
NB. PSI Does Not Emit Much Fluorescence At Room Temperature; Most Comes From PSII

Chlorophyll Fluorescence

- Light Energy (Exciton) Transfer to RCII is always much faster (~10^{-10}s) than Photosynthetic Electron Transport (PET, ~10^{-3}s).
- Initially, Illumination of Dark Adapted PSII, ~80% of Excitons Drive Photochemistry (PET) – the Quantum Efficiency of PSII (F_{PSII}) is 0.8; and RCII is said to be 'Open'.
- Within 1s, PET Rates Limit RCII Turnover, RCII is said to be 'Closed' and $F_{PSII} \Rightarrow 0$

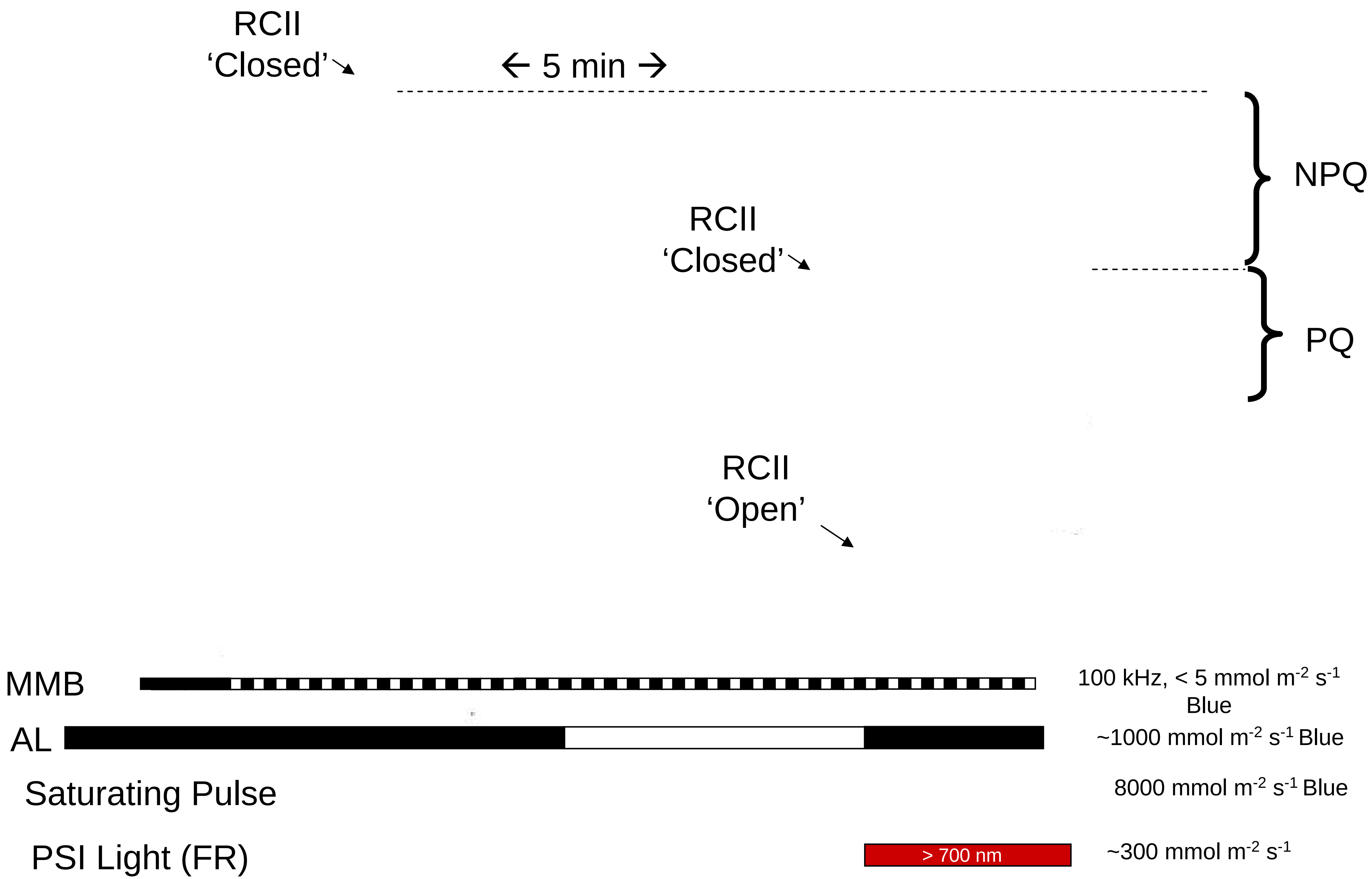
Chlorophyll Fluorescence

- As F_{PSII} Decreases With Illumination, F_F Rises,
- **So PSII Fluorescence is Inversely Related to Activity of RCII**



AL = Actinic Light ~ 1000 mmol m^{-2} s^{-1}

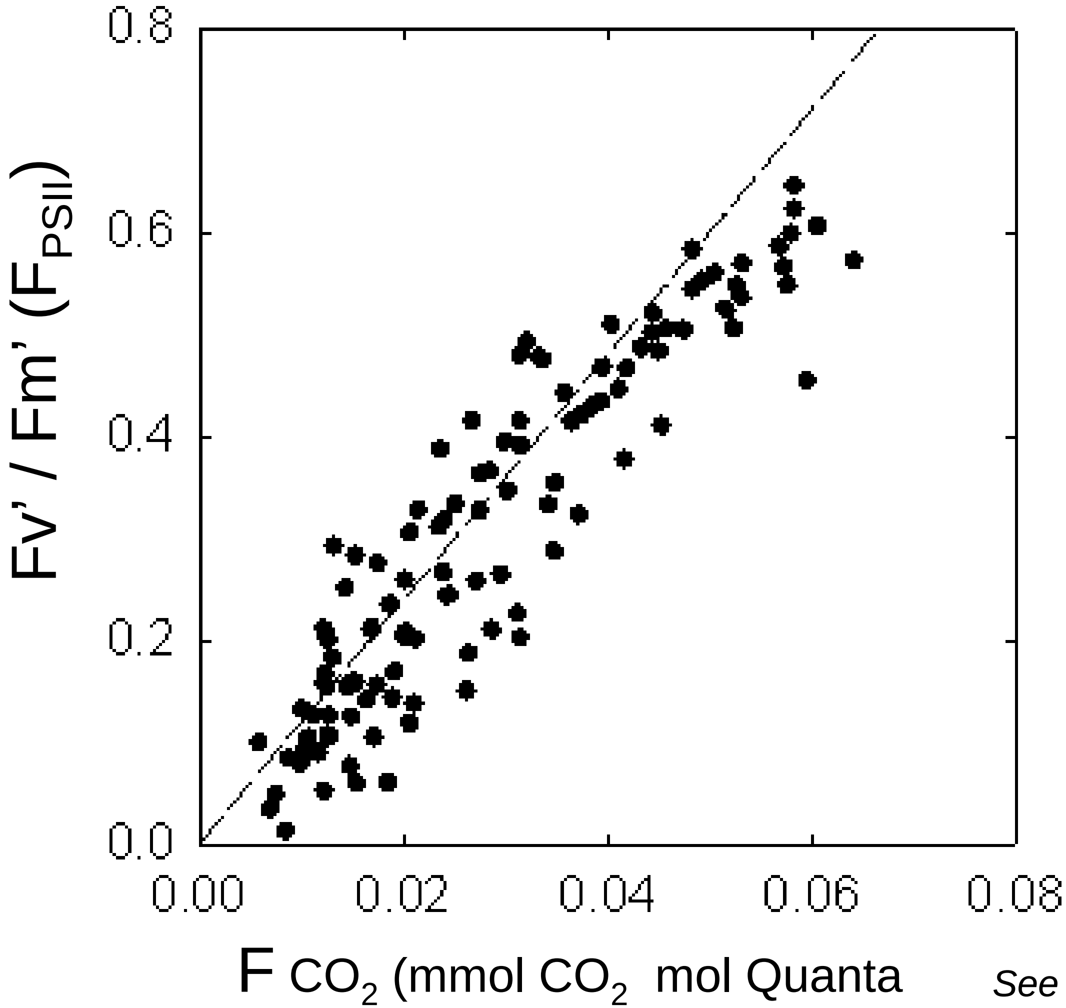
Pulse Modulated Chlorophyll Fluorescence



Important Chlorophyll Fluorescence Parameters

F_o	All RCII ‘Open’
F_M	All RCII ‘Closed’
$F_v = F_M - F_o$	Variable Fluorescence (Measure of Photochemistry)
F_v / F_M	F_{PSII} in Dark
Fq'/Fm'	F_{PSII} in Light (or DF/Fm’)
Fq'/Fm' · A · 0.5	= ETR_{PSII} , or J_F
Fq'/Fv'	= PQ (Photochemical Quenching, Fraction of Open RCIIs)
(Fm/Fm') – 1	=NPQ (Non-Photochemical Quenching)

F_{PSII} is Linearly Related to F_{CO2}



C3 Plants

>8 Photons / CO_2 fixed

F_{CO2} max is 0.125

C4 Plants

>12 Photons / CO_2 fixed

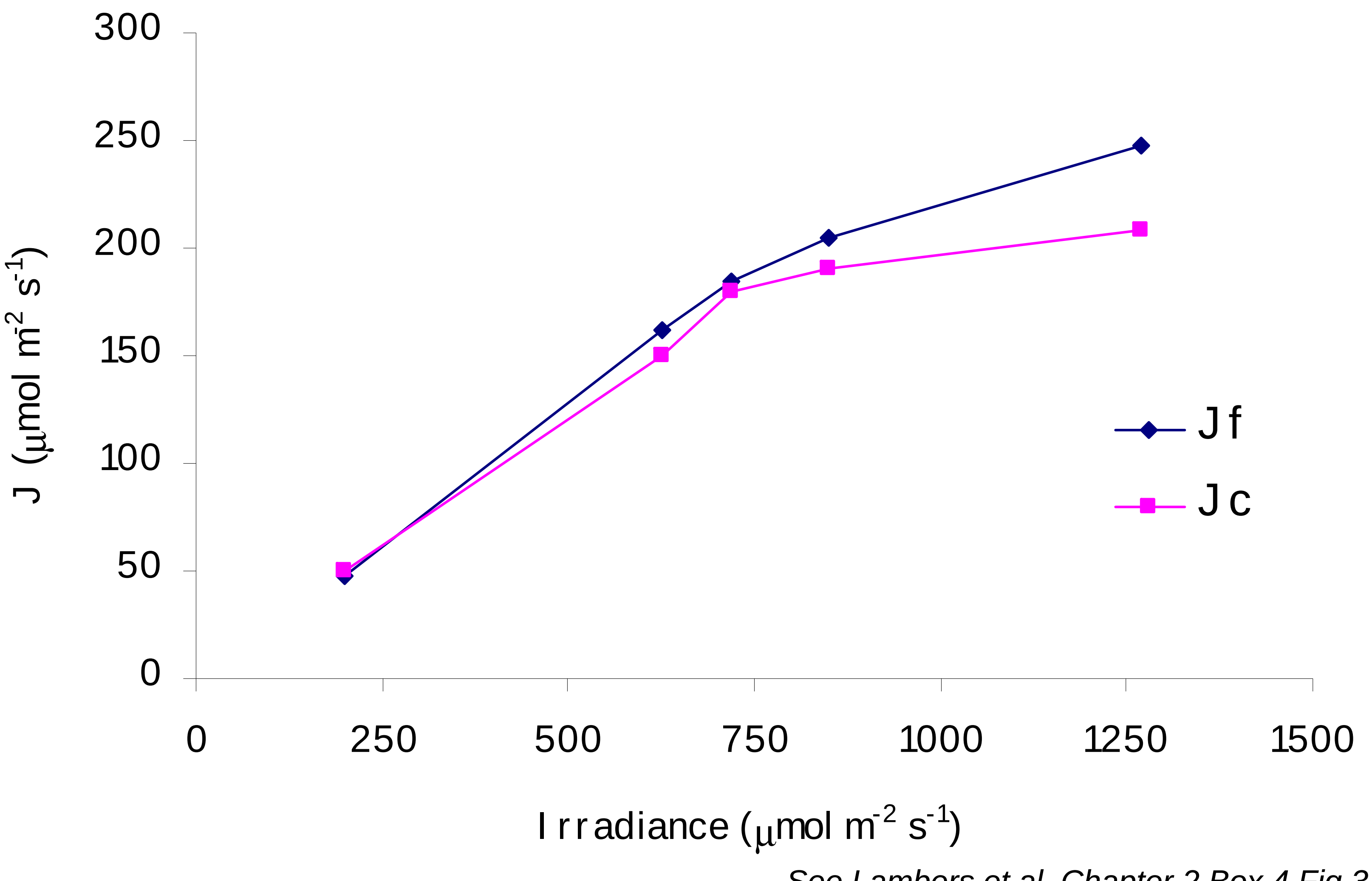
F_{CO2} max is 0.083

This C3 plant has F_{PSII} of ~0.6,
Expected F_{CO2} (0.6 x 0.125) = 0.075

~ 0.065/0.075 ⇨ **87% Electrons Flowing Through PSII fix CO_2**

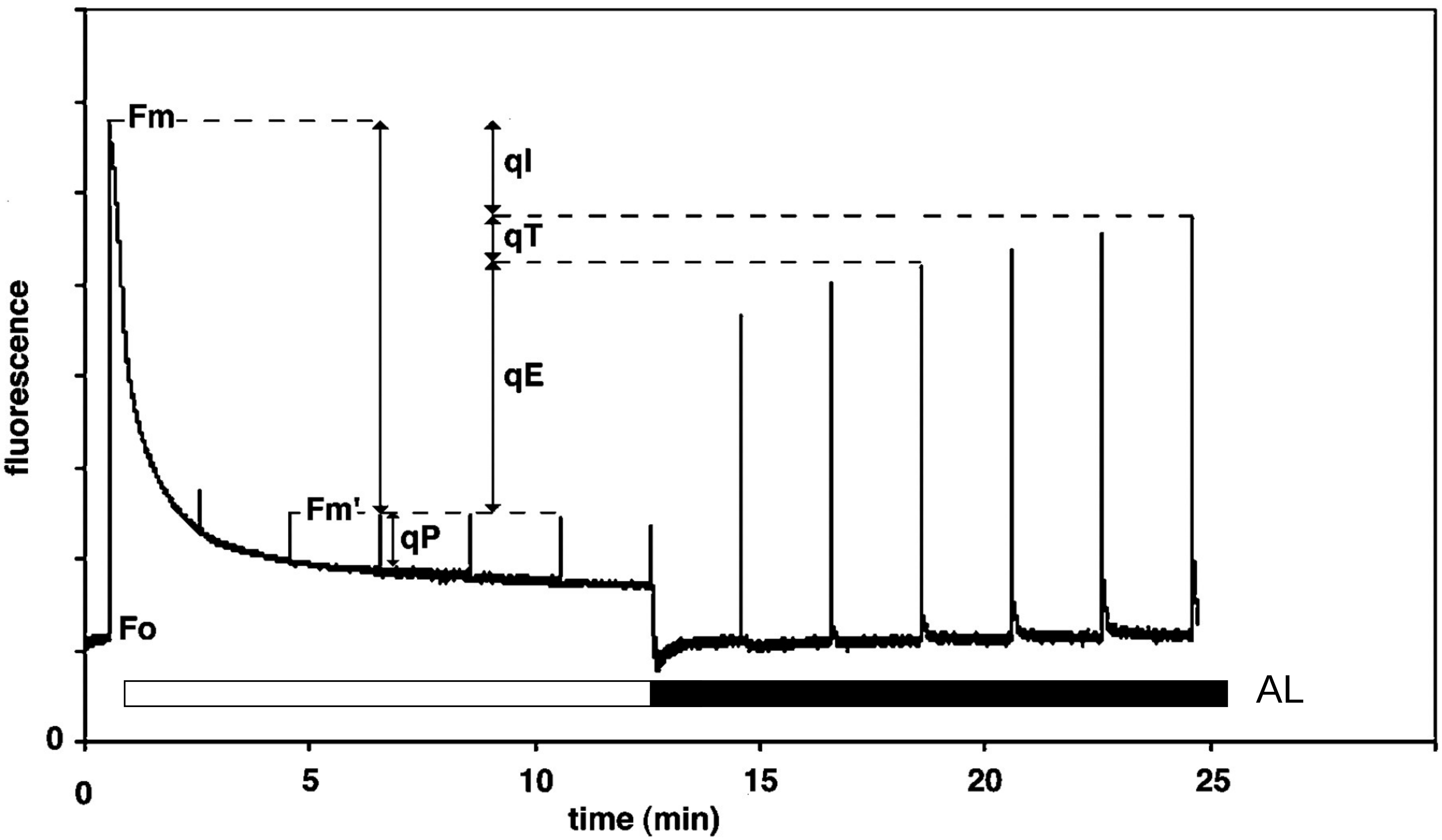
See Lambers et al. Chapter 2 Box 4 Fig 2

Electron Transport Rate Calculated From Fluorescence (J_F) & Assimilation Rates (J_C) are Similar



See Lambers et al. Chapter 2 Box 4 Fig 3

'Dark Relaxation' Experiments Show NPQ has 3 Components



qI ~ Photoinhibition

qT ~ State Transitions (State Adaptations)

qE ~ Xanthophyll Cycle

Magnitude of ‘Quenching’ Components Change with the Physiological State of the Leaf

- The qI Component (q by PhotoInhibition), varies with the physiological state of the leaf, and the Growth Irradiance

- The qT Component (quenching by Transfer) appears to be related to State Transitions (Adaptation) where excess energy is passed to PSI

- The qE Component (quenching of Energy) is related to the Xanthophyll Cycle and also dependent on the size of the pH gradient across the thylakoid membrane.

High Light - Excess Light is Dissipated

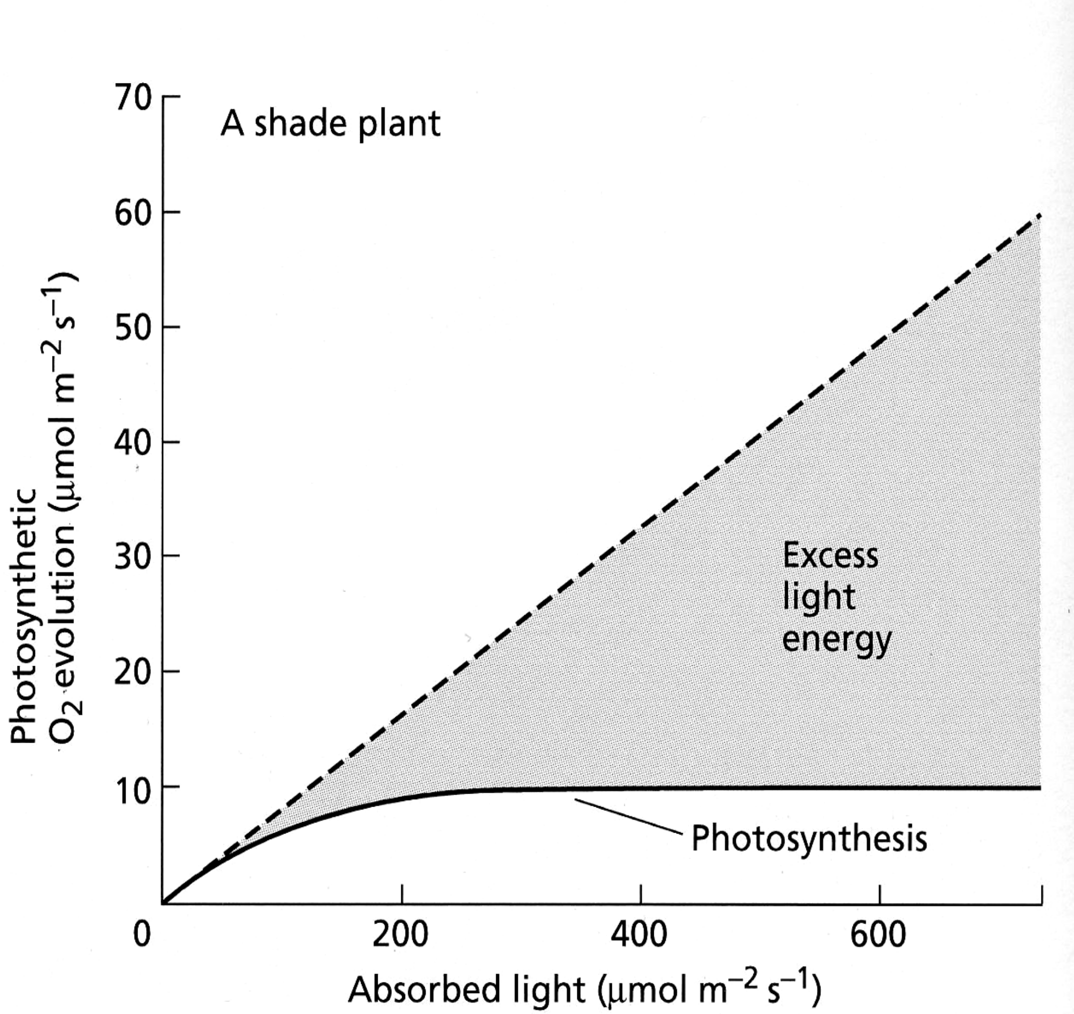
Too Much Light Can Cause the Production of Excessive Levels of $^1O_2$
⇨ other ROSs (O^-_2, $^*OH^-$, etc.)

⇨Photo-Oxidation (Photobleaching)

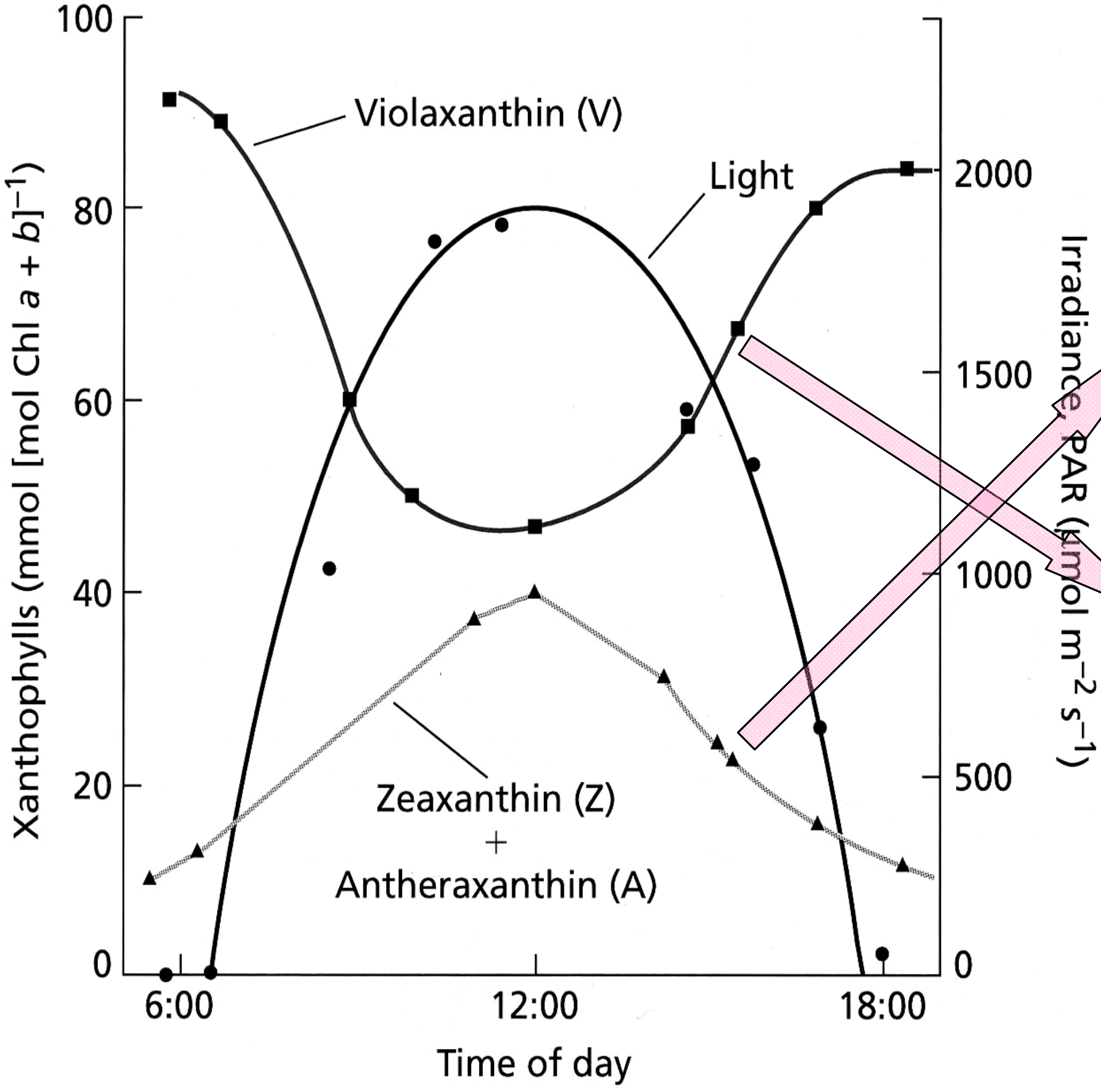
Protective Mechanisms Operate to Dissipate Absorbed Light

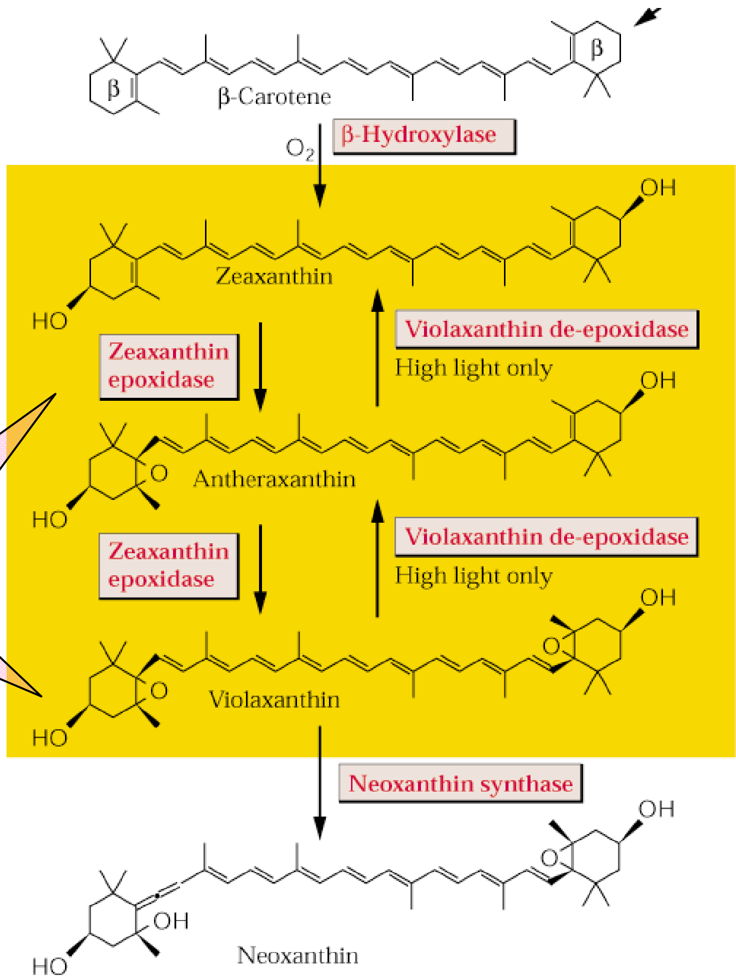
Wasteful but Essential for Survival

?



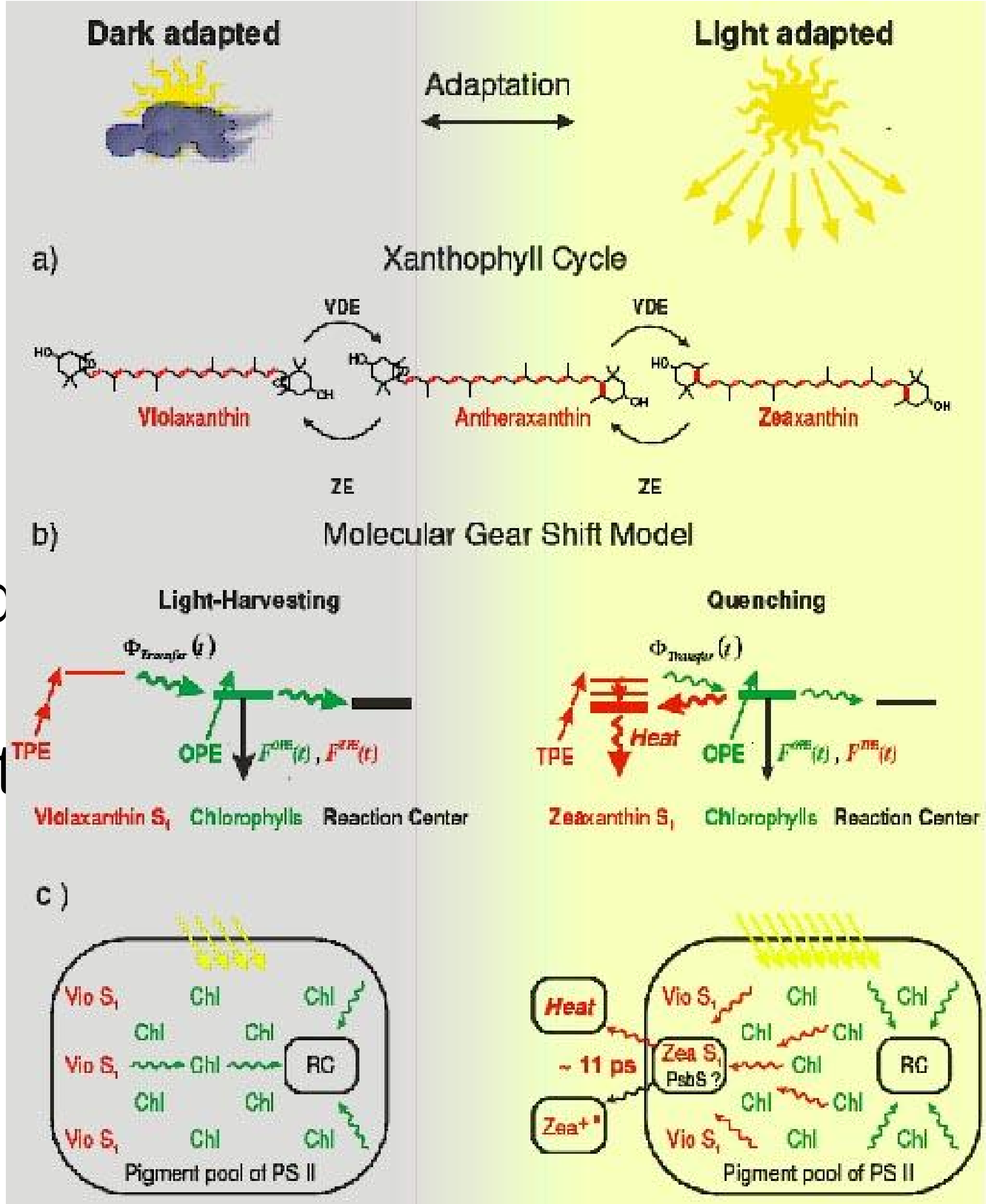
Xanthophyll Cycle Operates in Light Harvesting Complexes (LHCs) with Changing Irradiance Levels





See Lambers et al. Fig 2.15 & 16

Zeaxanthin / Antheraxanthin 'Quench' Captured Energy by Conversion to Heat

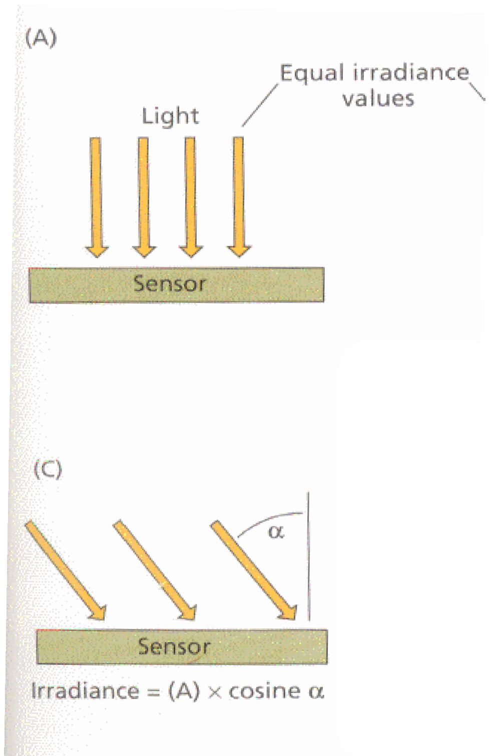


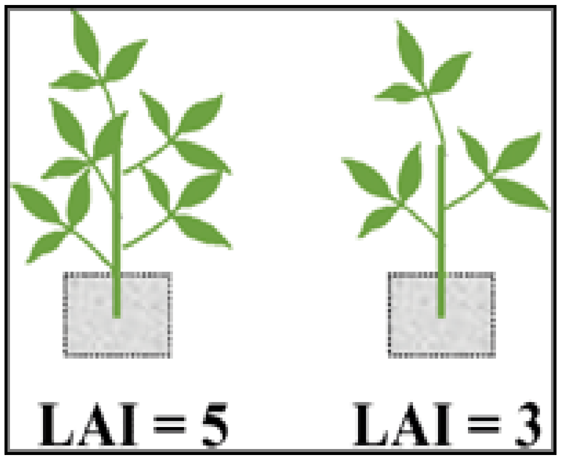
See Lambers et al. Fig 2.9C

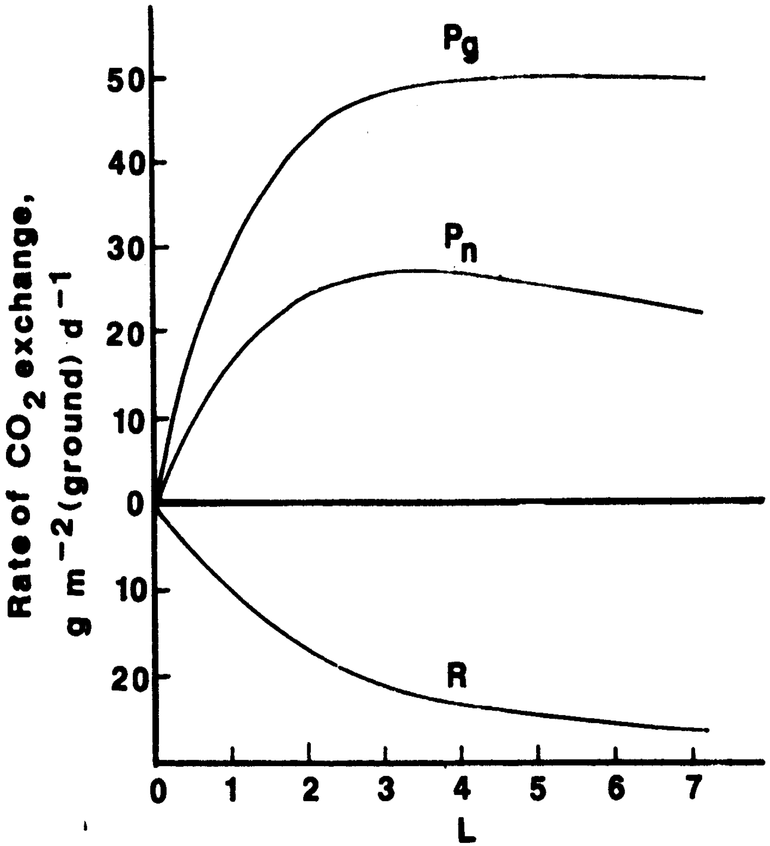
Improving Light Interception: Leaf Area Index

• Increasing LAI (Leaf Area Index - the total area of leaf / m^2 ground) will increase light absorbance

• but Rd will also increase.



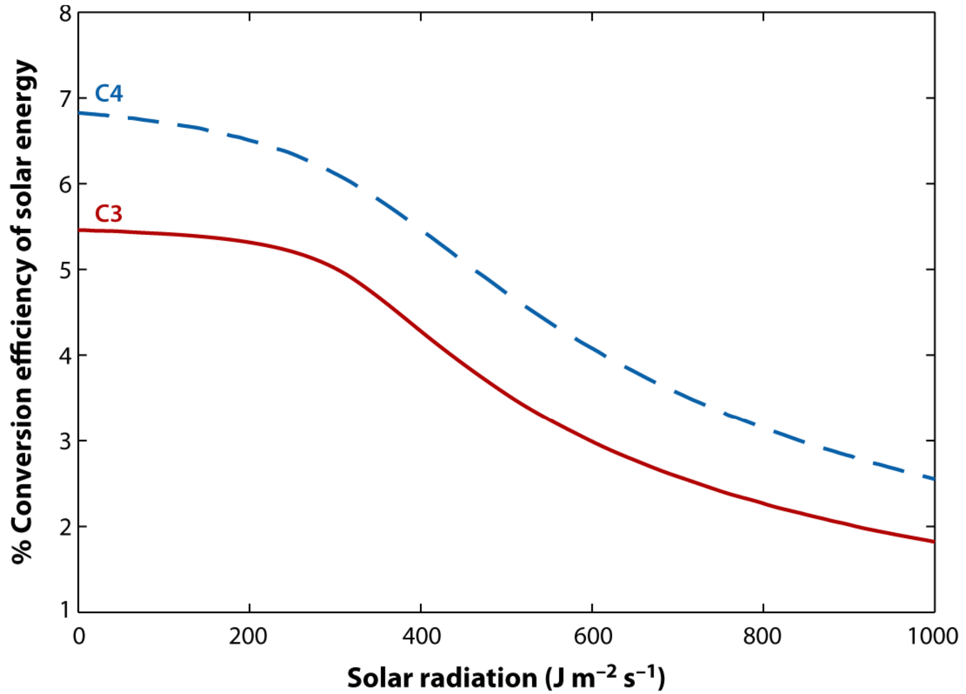




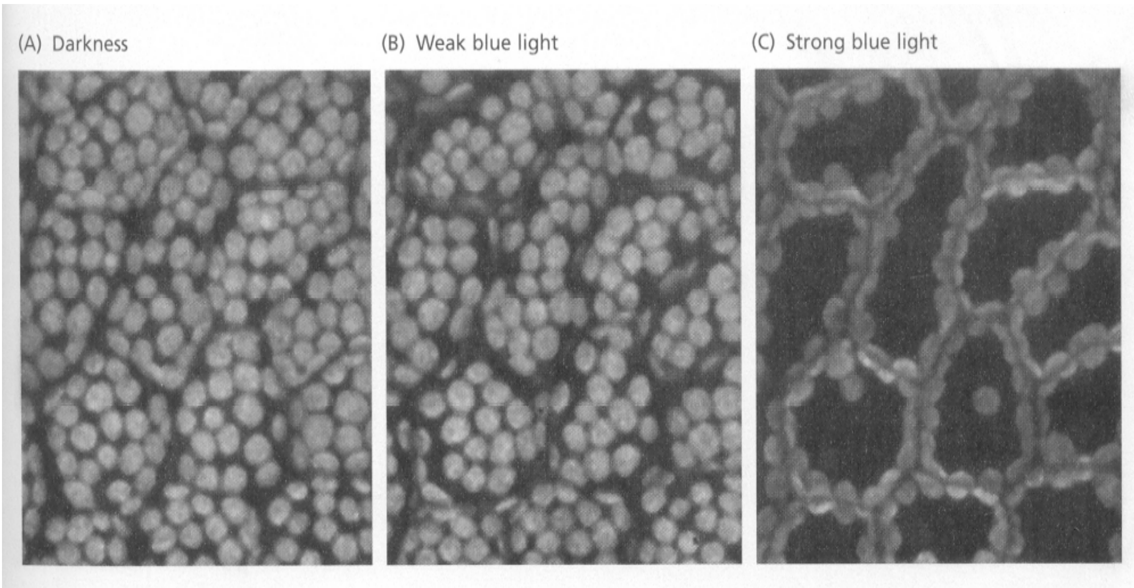
Response to Variable Light

Increasing Light Penetration into the Canopy May Increase Efficiency

? Reducing Chlorophyll Levels?



Zhu X-G, et al. 2010.
Annu. Rev. Plant. Biol. 61:235–61



Chloroplast Movement: Self-shading in bright light

Improved Light Interception: Heliotropism

- Minimizing Reflection / Transmission

▪Improved Sun tracking decreases reflection –

Sunflower (*Helianthus annus*) leaves and flowers show 'Heliotropism'

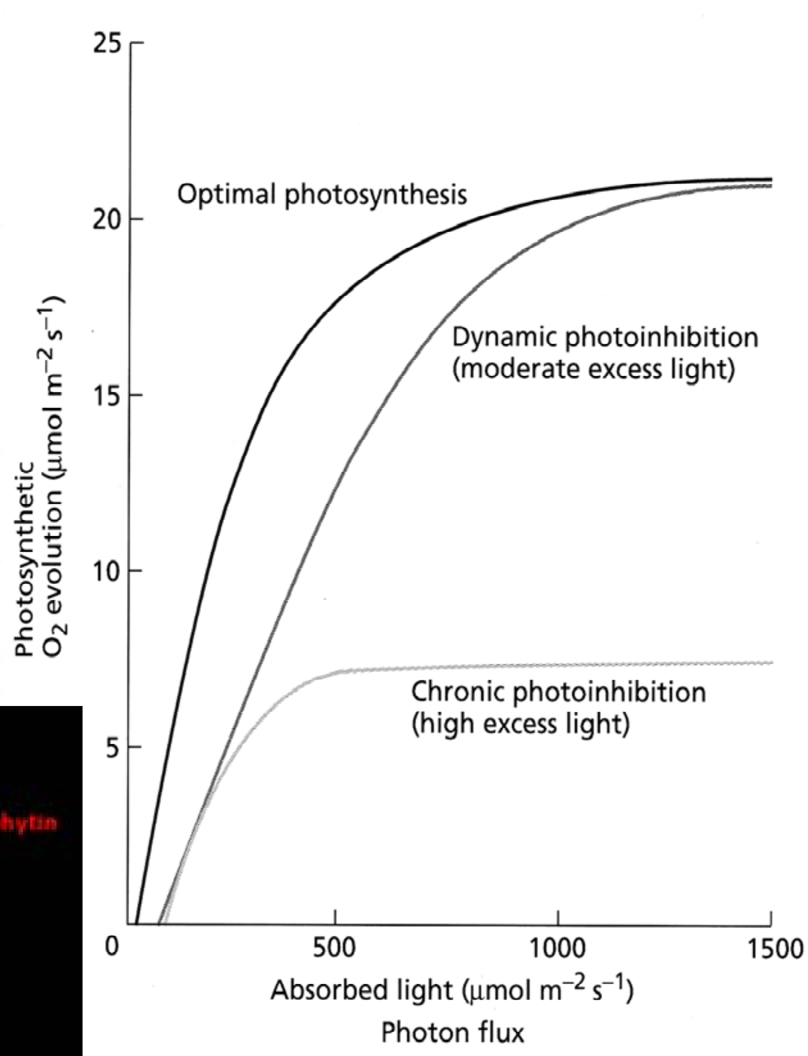
See Heliotropism Movie

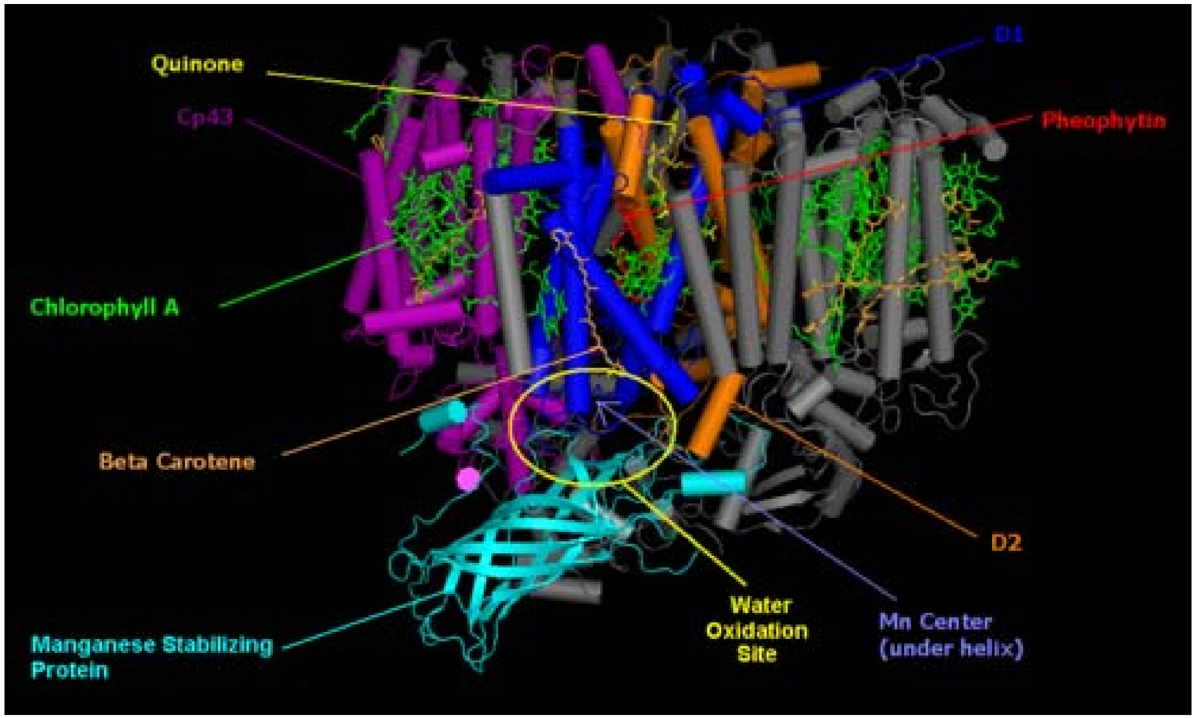
- *And so do Cress seedlings*

Maximizing Light Capture.. Heliotropism

- Plants can ‘track’ the sun through the sky to maximize light capture (Heliotropism).
- Many Herbaceous Plants do this to Varying Degrees
- Leaf Movement is Effected by Adjusting the Turgor Pressure in Pulvini Cells at the Base of the Petioles

Energy Quenching is
Reversible in Moderately High Light –
But Causes Damage in Excess Light
PSII Core has Half-Life of 90 Minutes!



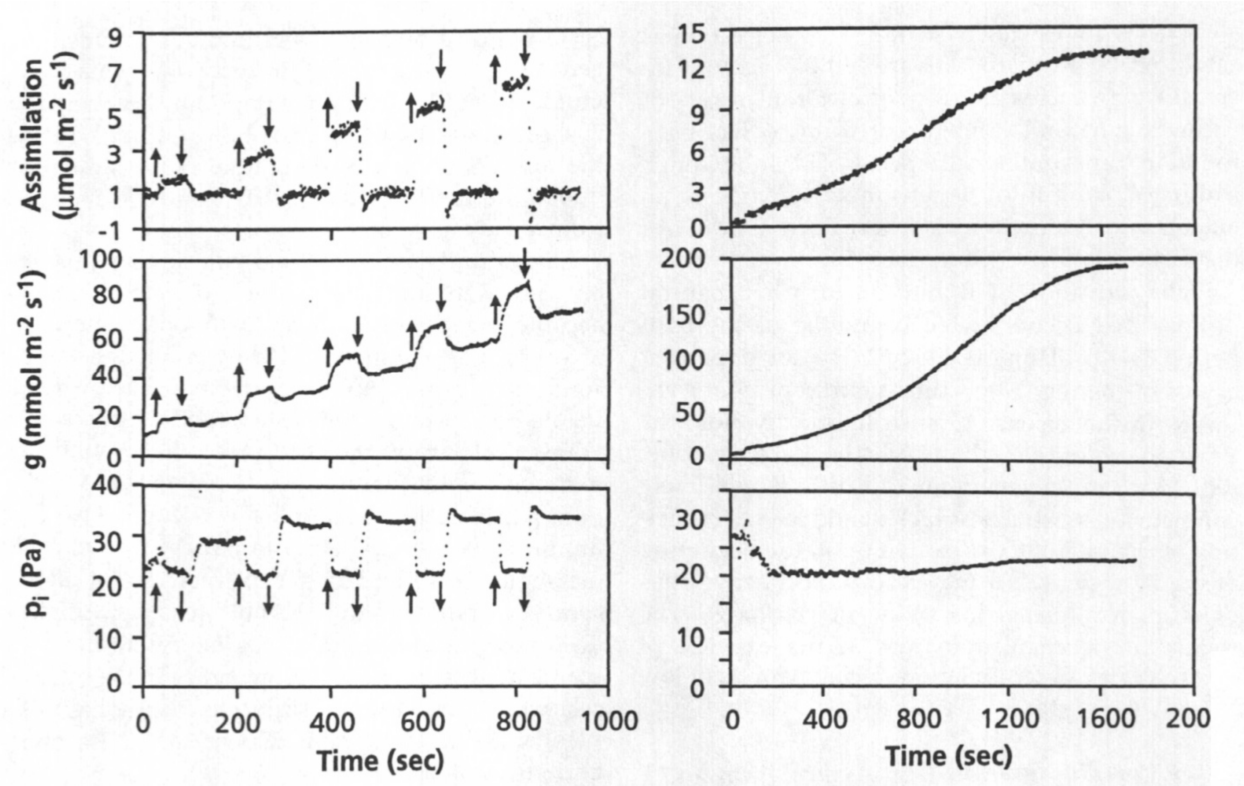


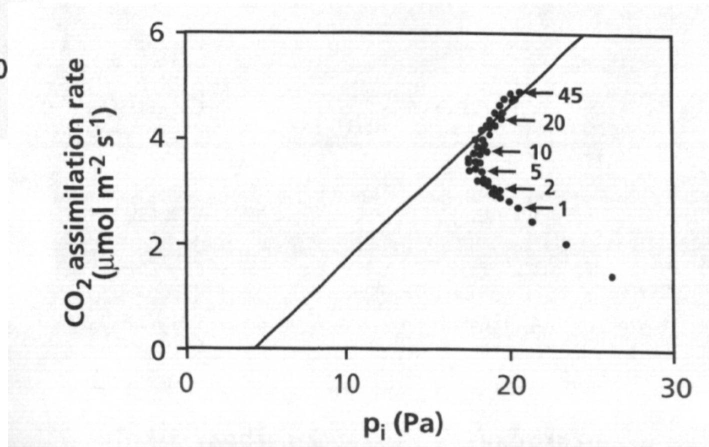
Structure of PS II

Sunflecks

Energy Quenching (or Non-Photochemical Quenching – NPQ) is an Important Mechanism for Preventing Photinhibition and Photobleaching

Photosynthetic Induction

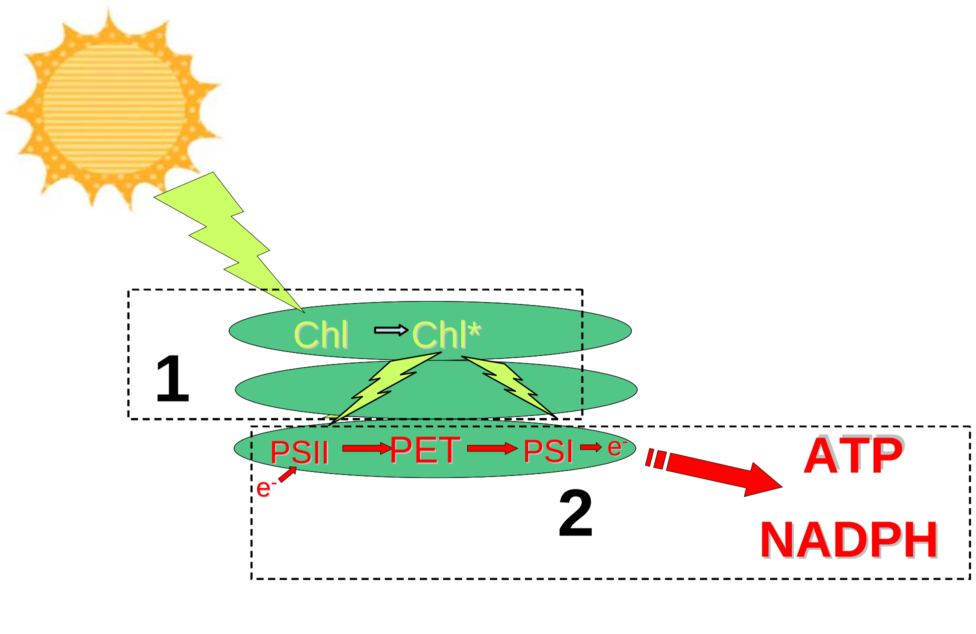


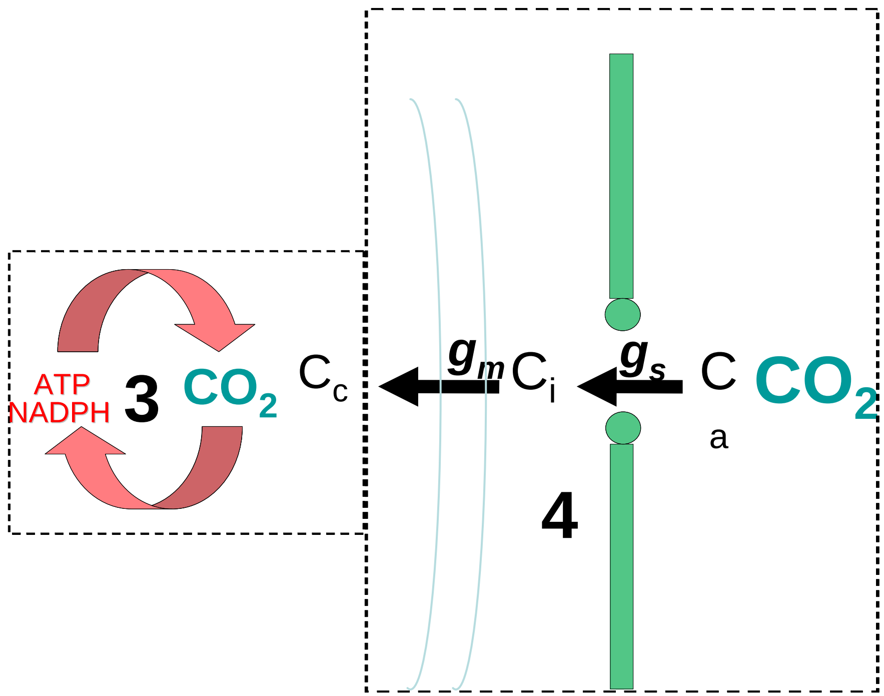


See Lambers et al. Fig 2.18 & 19

2. Maximizing CO_2 Capture & Photosynthetic Efficiency

What Limits C3 Photosynthesis?





Limitation of Carbon Assimilation Rates

1. Light Harvesting Capacity
2. Photosynthetic Electron Transport / Chemiosmosis
3. C3 Cycle Kinetics (RuBisCO Activase?)
4. CO_2 Supply / g_s / g_m

Ca, Ci, Cc ~ CO_2 Levels in Air, Intercellular Space, Chloroplast

gs & *gm* ~ Stomatal Conductance & Mesophyll Conductance

Rate Limiting Enzymes of the C_3 (Calvin) Cycle.

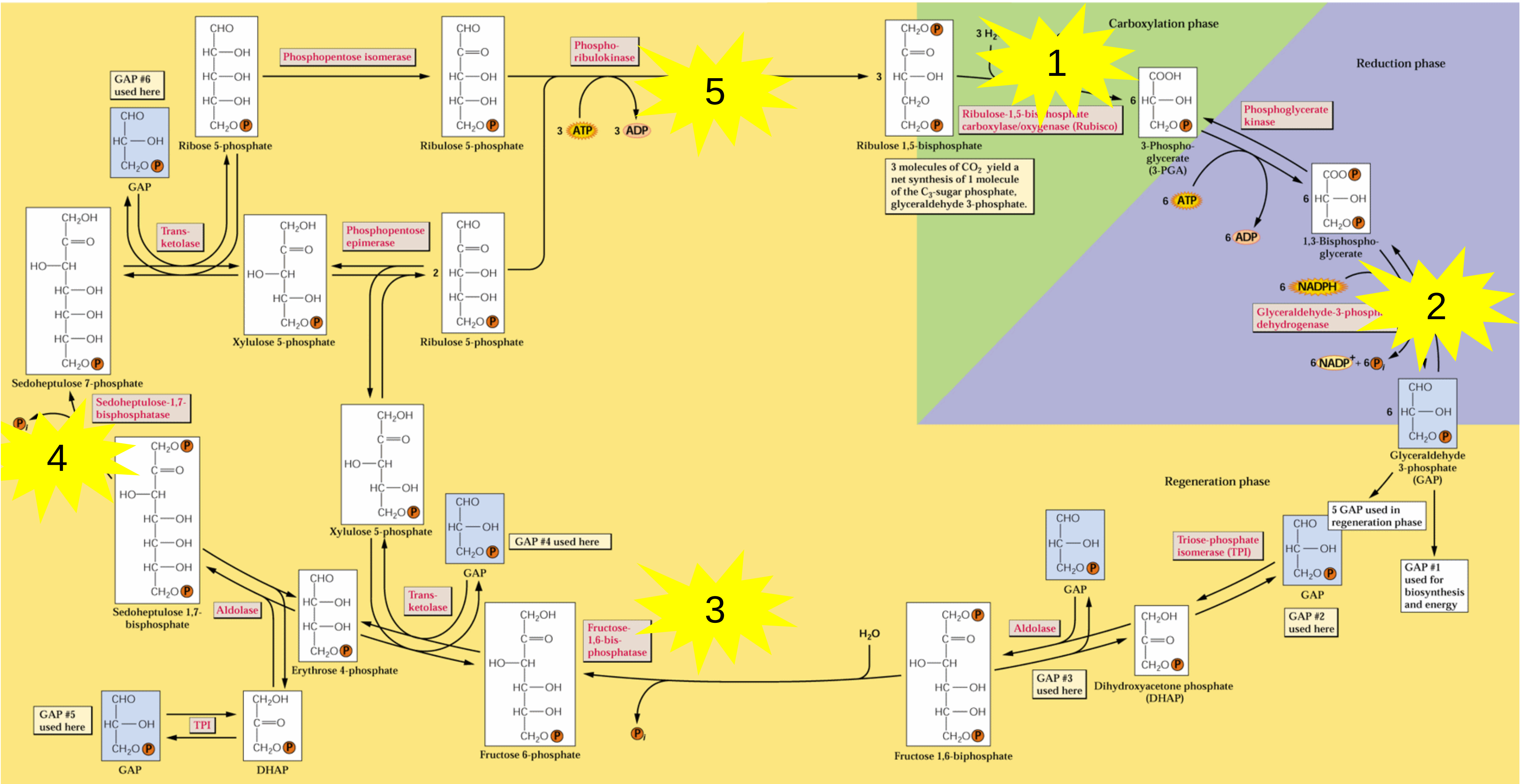
3 Fructose-1,6-bis-phosphatase

1 Rubisco

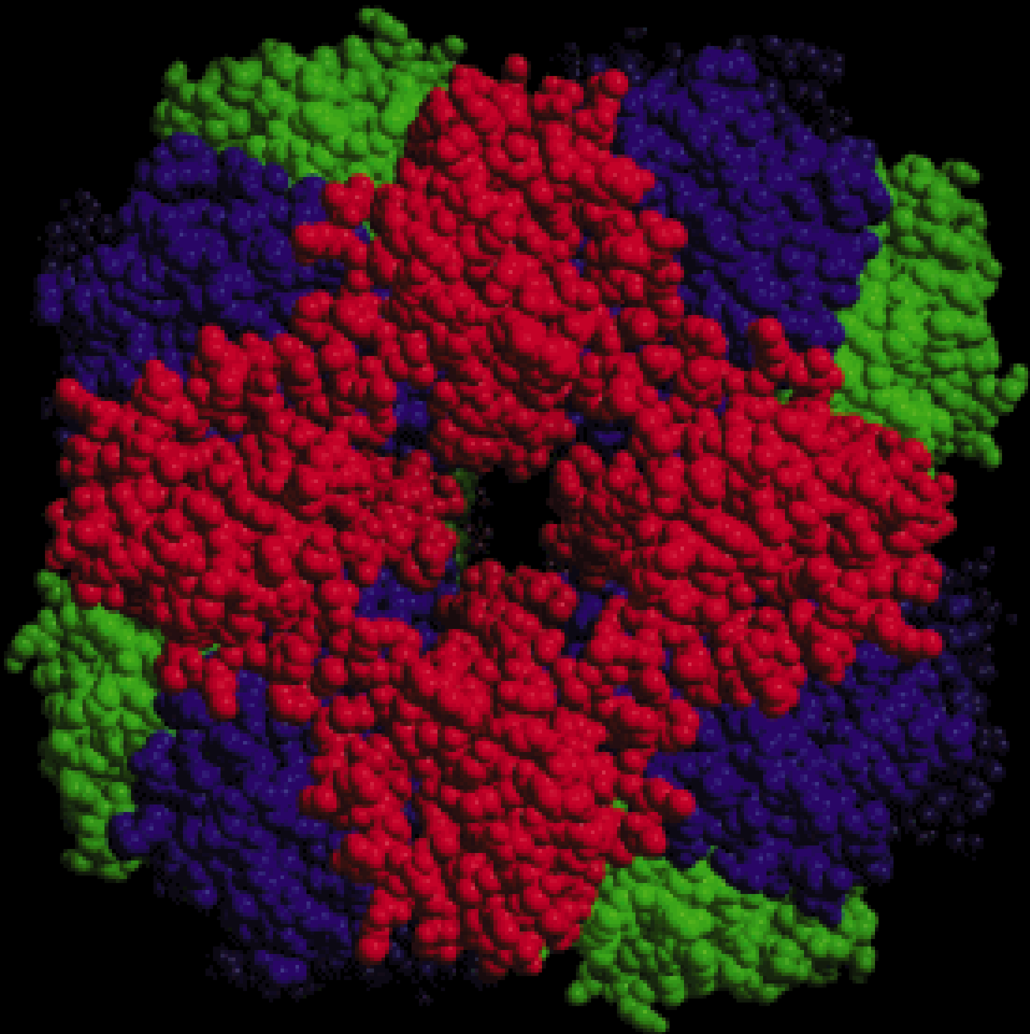
5 Ribulose-5 phosphate kinase

4 Sedoheptulose-1,7 bis-phosphatase

2 NADPH G3P dehydrogenase



The 3-D Structure of RuBisCO is Known



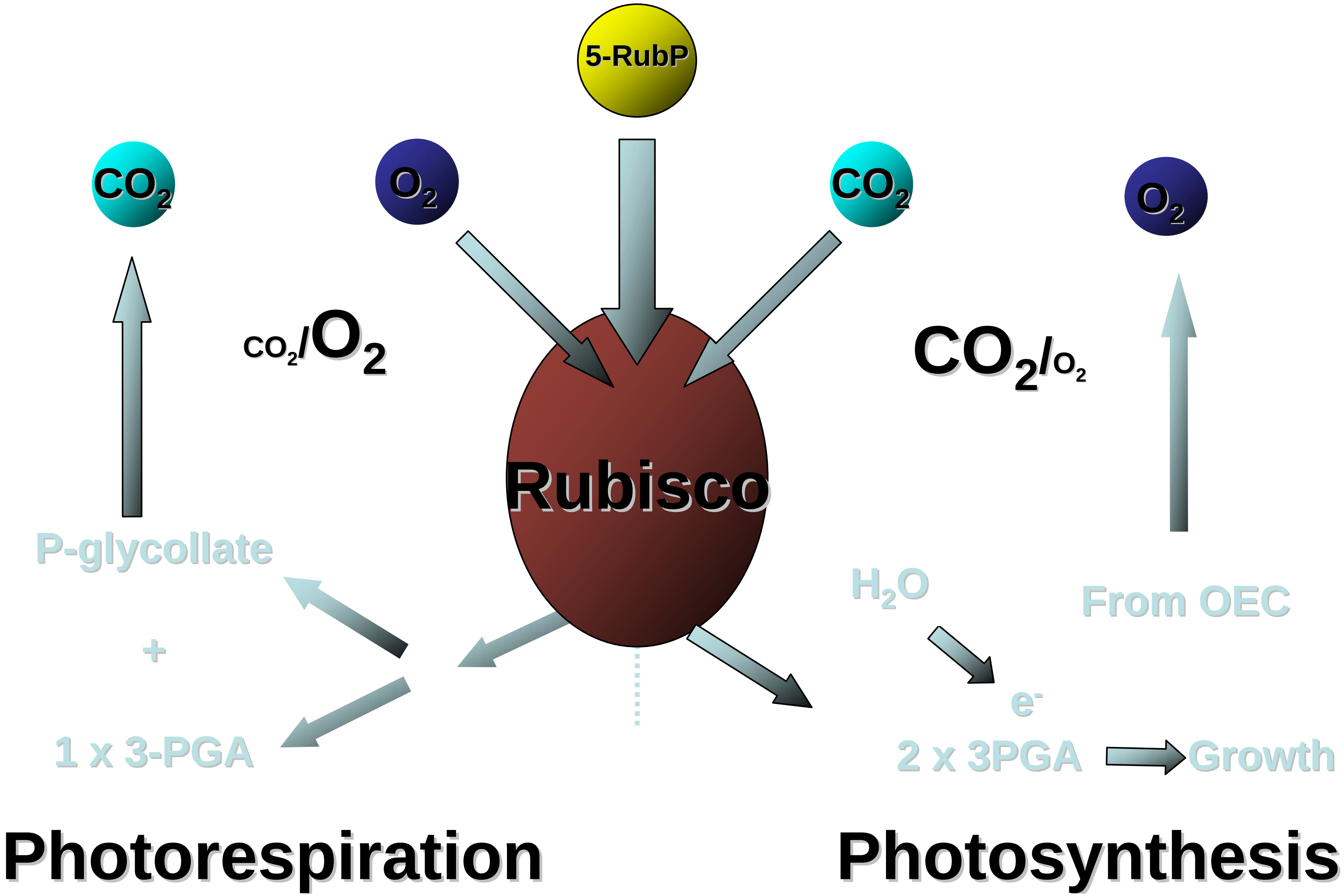
The Chemistry of Primitive Life: V

- Rubisco was responsible for depleting $[CO_2]^{air}$
- OEC was responsible for increasing $[O_2]^{air}$
- Why are $[CO_2]^{air}$ levels ~0% and $[O_2]^{air}$ >25%?

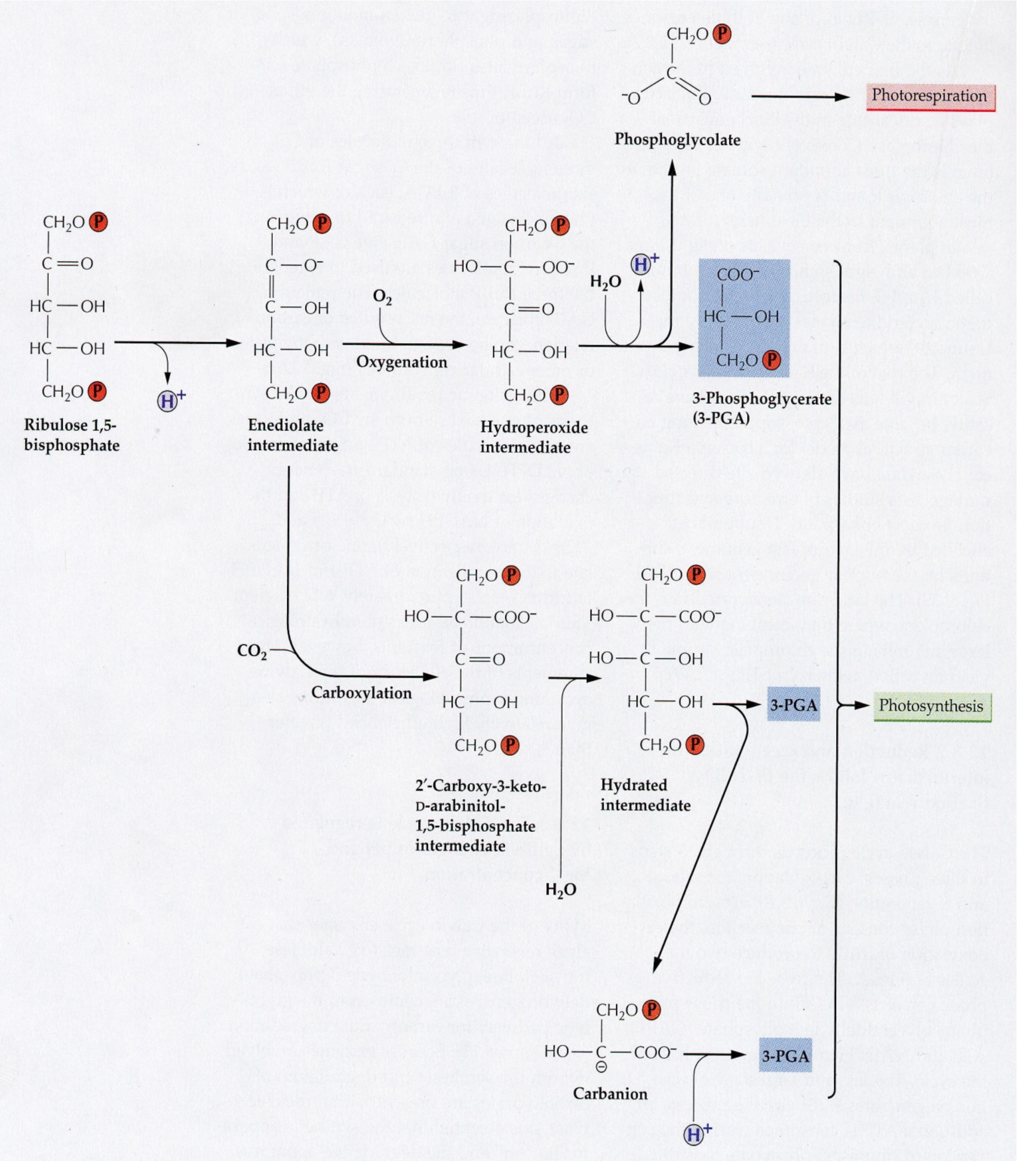
Rubisco has a Design Flaw!

Rubisco Catalyses 2 Reactions

An Example of Negative Feedback



The Carboxylation and Oxygenation Mechanisms of RuBisCO



Rubisco Catalyses 2 Reactions.

- Rubisco Evolved ~3.5 10^9 years ago in an Anaerobic Atmosphere.
- Aerobic Atmosphere Arose ~2 10^9 y.a.
- In Aerobic Atmospheres Rubisco Catalyses Additional Reaction
  - Carboxylation: 5-RuBP (5-C) + CO_2 ➔

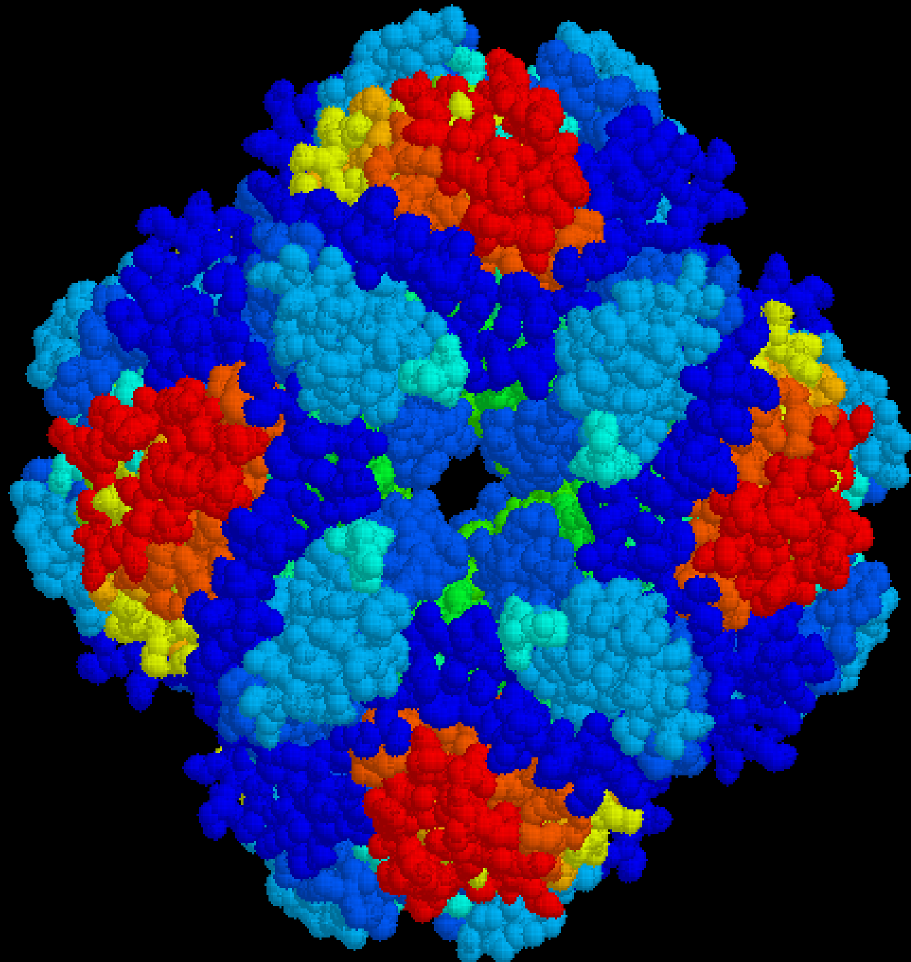
    2 x 3-PGA (3-C)
  - Breakdown: 5-RuBP ➔

    1x 3-PGA & 1 x 2-P glycollate
- Atmospheric O_2 produced by oxygenic photosynthesis (~ 0 to 21kPa between 2 10^9 & 1.8 10^9 y.a.)
- Stability of Atmosphere (21kPa O_2 & 0.35 kPa CO_2) due to Design Flaw in Rubisco.

Properties of Rubisco

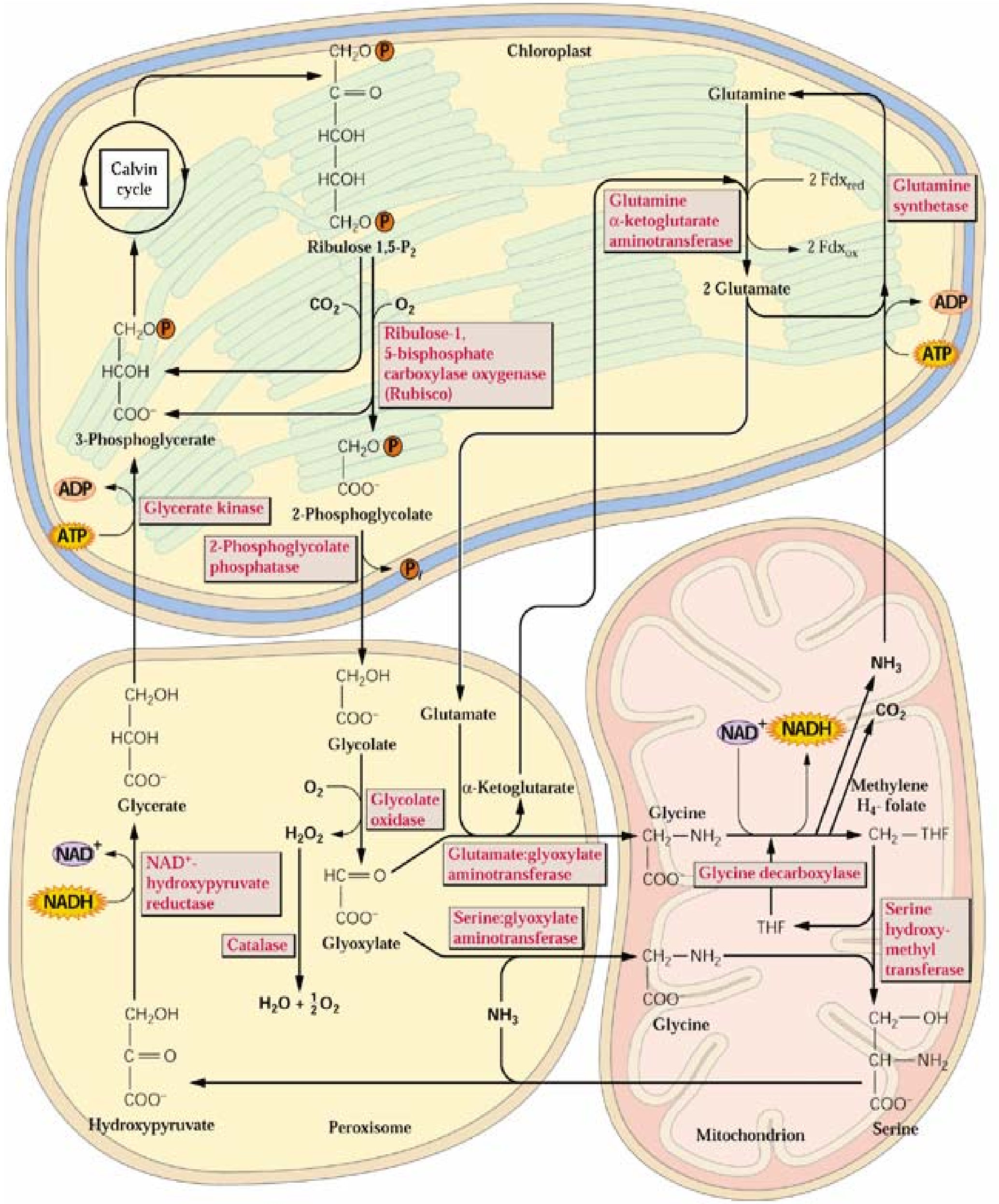
- Rubisco is Comprised of Large (~55 kD) & Small (~15 kD) subunits
- In Higher Plants L_8S_8 ~ 550 kD
- LSU encoded in Chloroplast Genome
  SSU encoded in Nuclear Genome
- ~50% of Leaf Protein
- Specific Activity ~ 3 nmol / s / mg
  - turn over number ~ 10^1 / s
- Substrate Affinities (Km)

CO_2	~ 12	M
O_2	~ 250	M
5-RuBP	~ 40	M



Photorespiration.....

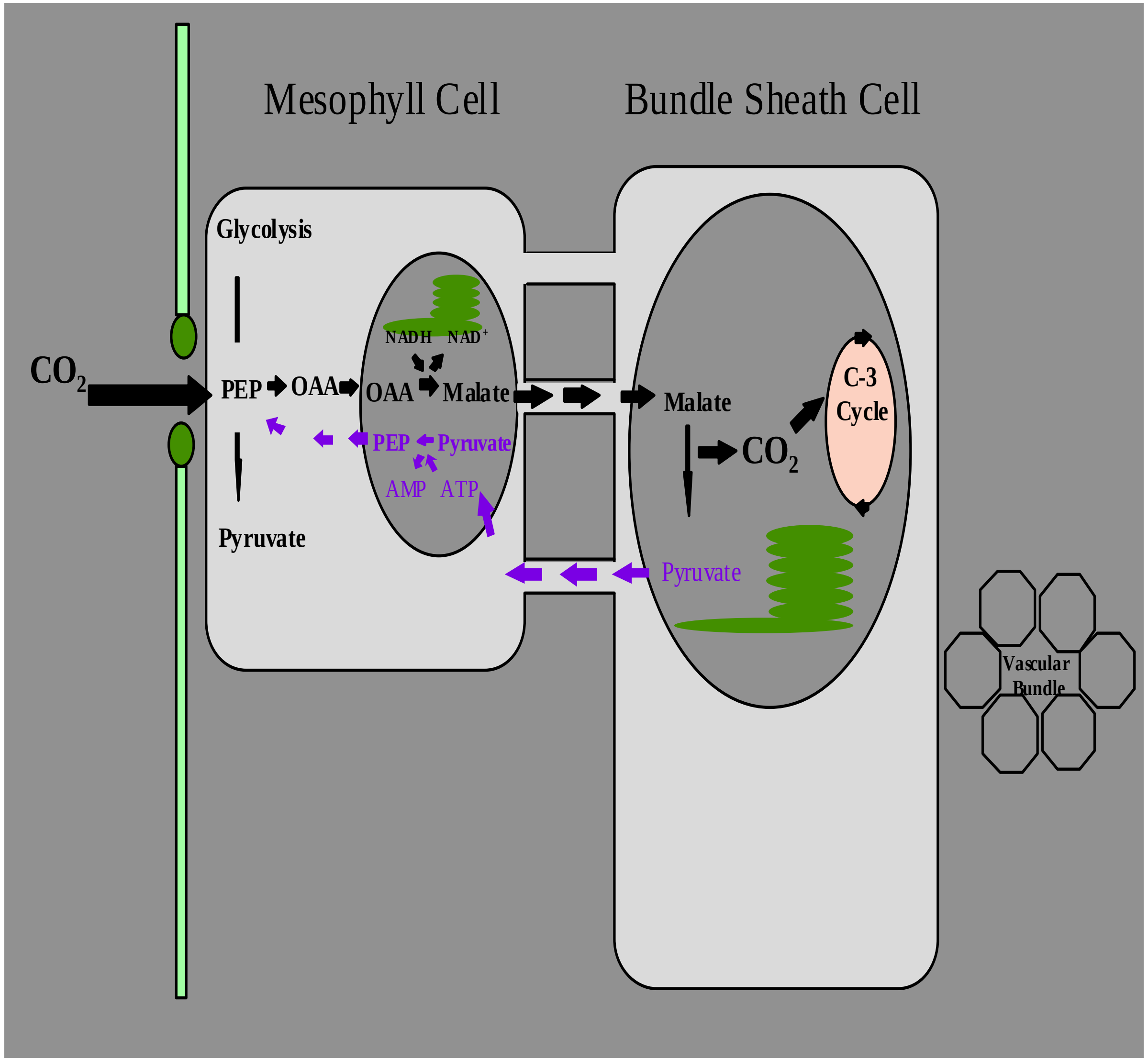
Photorespiration involves the chloroplast, peroxisomes & mitochondria

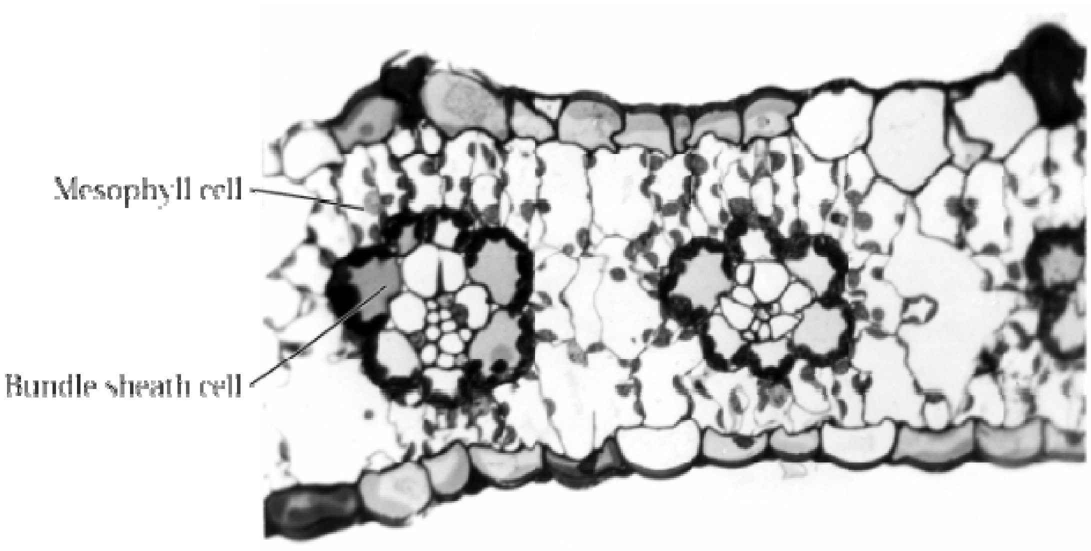


Solving the Photorespiration Problem

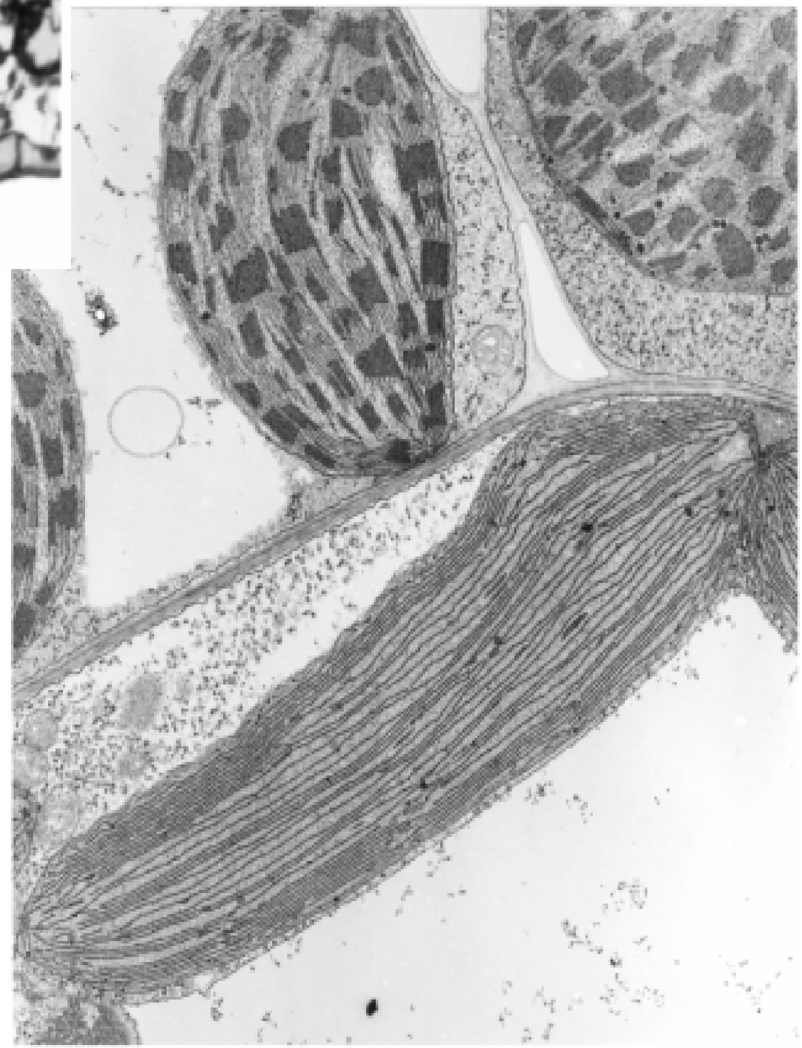
- C_3 Plants lose ~ 25-50% of Carbon by Photorespiration
- Despite 2 10^9 years of Evolution, the Rubisco 'Design Flaw' has not been corrected in higher plants
- However, Plants have learned to reduce Photorespiration by developing 'CO_2 Pumps'
- 'CO_2 Pumps' elevate CO_2 levels around Rubisco thereby forcing carboxylation
- Essentially, there are 2 types of Pump Mechanism
  - Some Aquatic Phototrophs - HCO_3^- pump on plasma membrane
  - Some Terrestrial Phototrophs - C_4 mechanism

One Variant of the C4 Mechanism

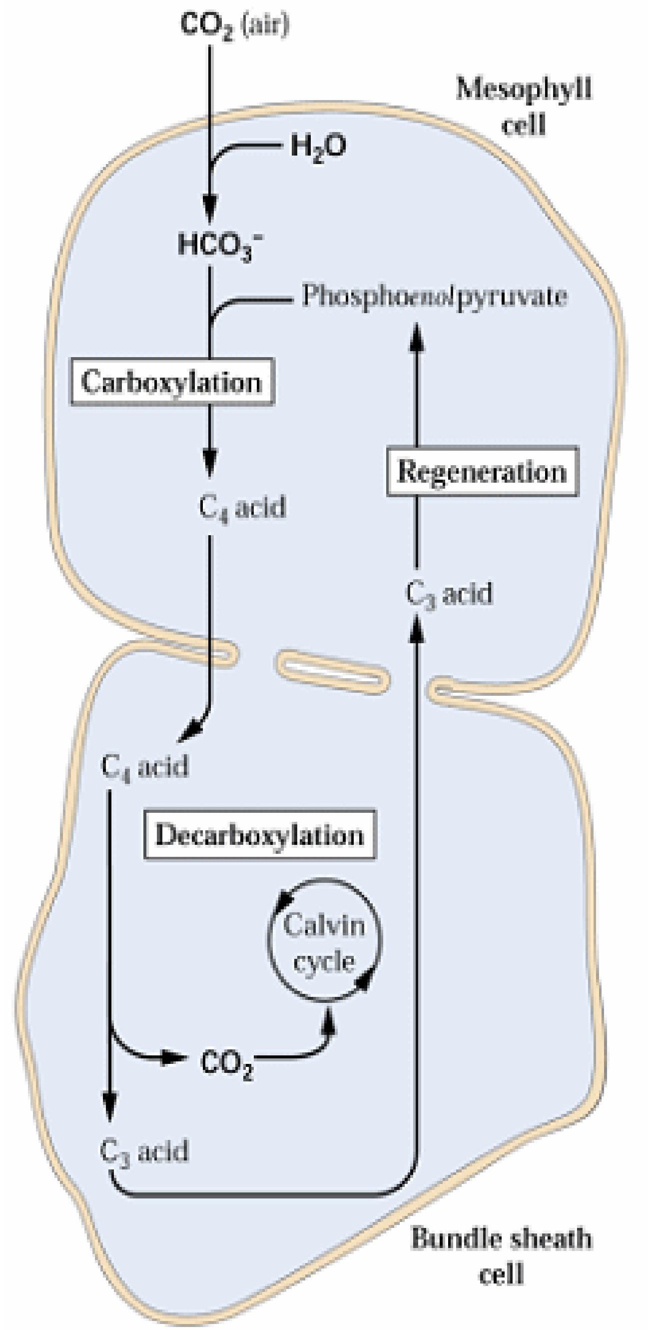


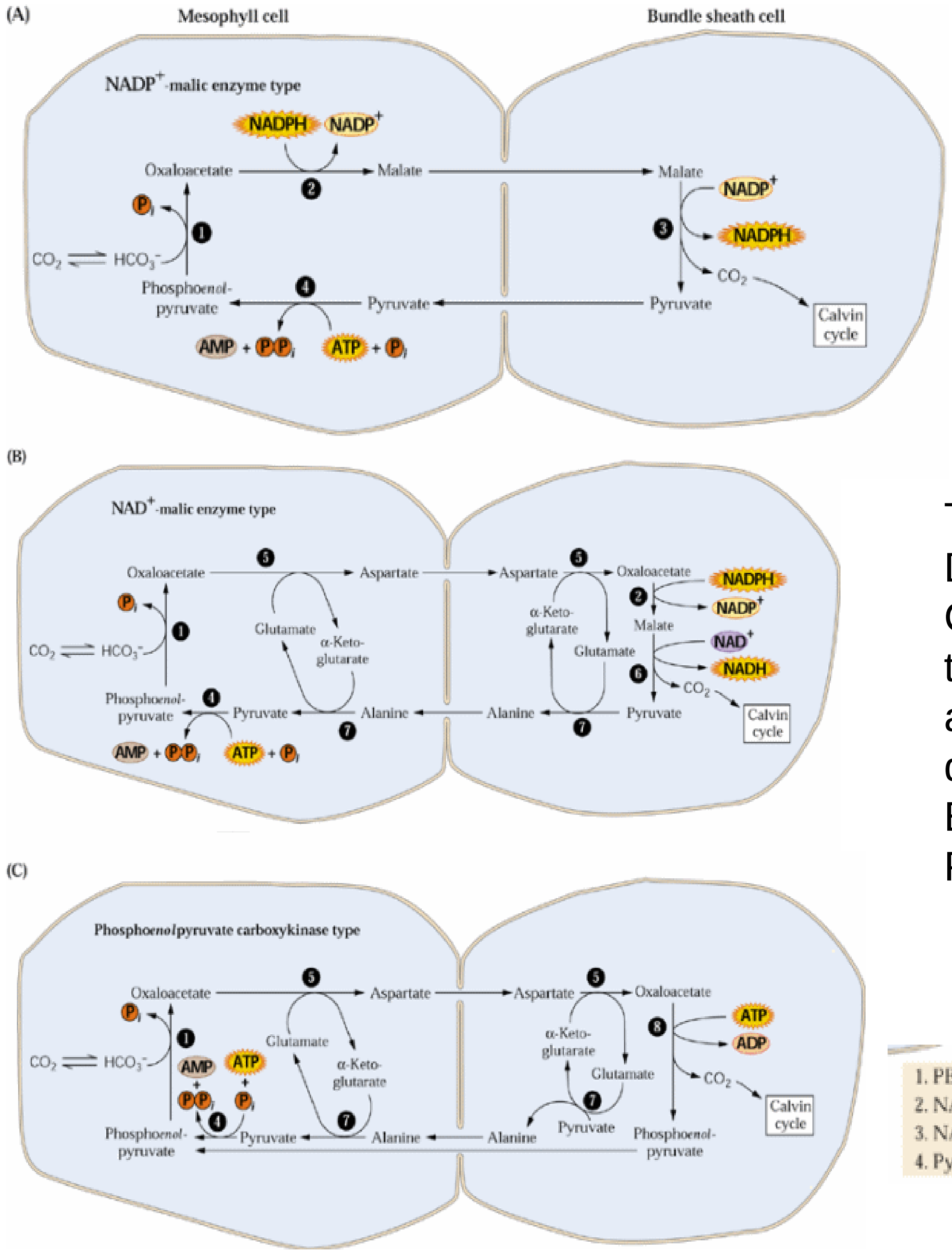


The C4 Mechanism



The C4 Mechanism



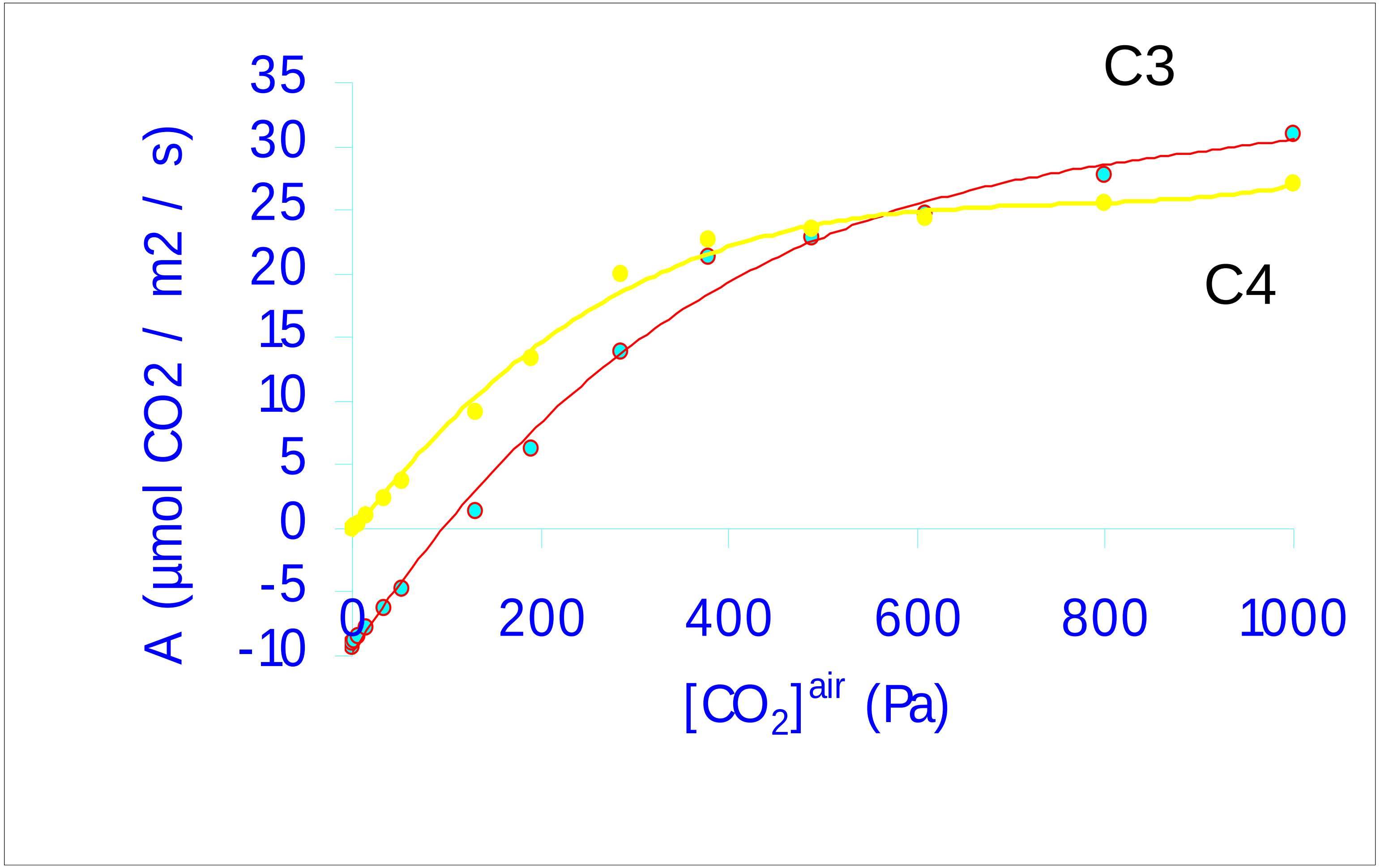


The C4 Mechanisms

There are 3 Variants in Plants that Differ in the Transfer of Fixed Carbon from the Mesophyll Cells to the Bundle Sheath Cells (malate or aspartate), and the method of their decarboxylation ($NADP^+$-Malic Enzyme, NAD^+ Malic Enzyme, or PEP Carboxykinase)

1. PEP carboxylase
2. $NADP^+$-malate dehydrogenase
3. $NADP^+$-malic enzyme
4. Pyruvate-orthophosphate dikinase (PPDK)
5. Aspartate aminotransferase
6. NAD^+-malic enzyme
7. Alanine aminotransferase
8. PEP carboxykinase

Net Assimilation Rate (A) *versus* CO_2 Concentration C3 & C4 Plant

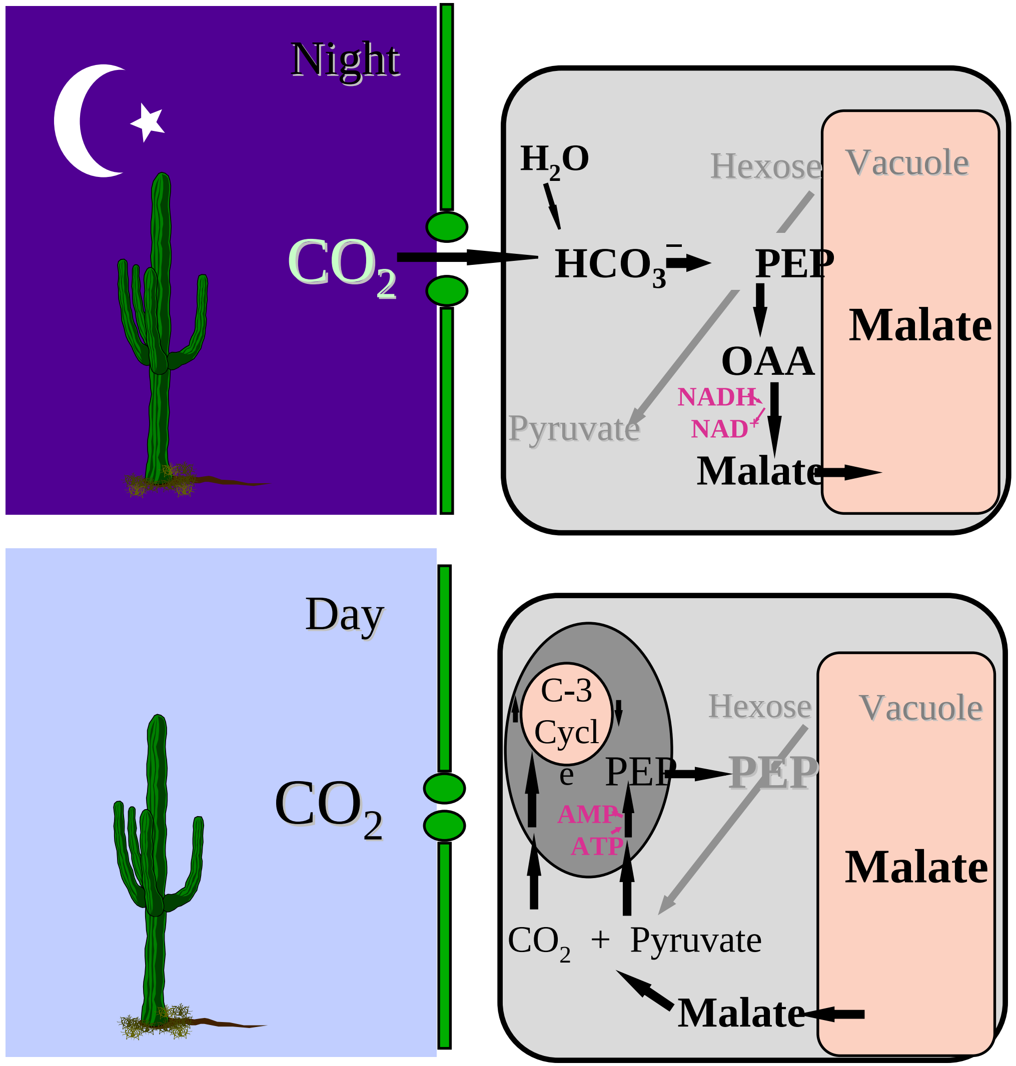


Plants and $[CO_2]^{air}$: Conclusions.

- Phototrophs utilizing the C3 mechanism have forged and stabilized our atmosphere (from >10% to 0.03% CO_2).
- CO_2 is a fertilizer and C3 plants should benefit from higher $[CO_2]^{air}$.
- C4 plants are rarely severely CO_2 limited; therefore increases in $[CO_2]^{air}$ should not benefit these plants.
- CAM (Crassulacean Acid Metabolism) plants, have evolved a variation on the C4 theme and like C4 plants, should not respond greatly to increases in $[CO_2]^{air}$.

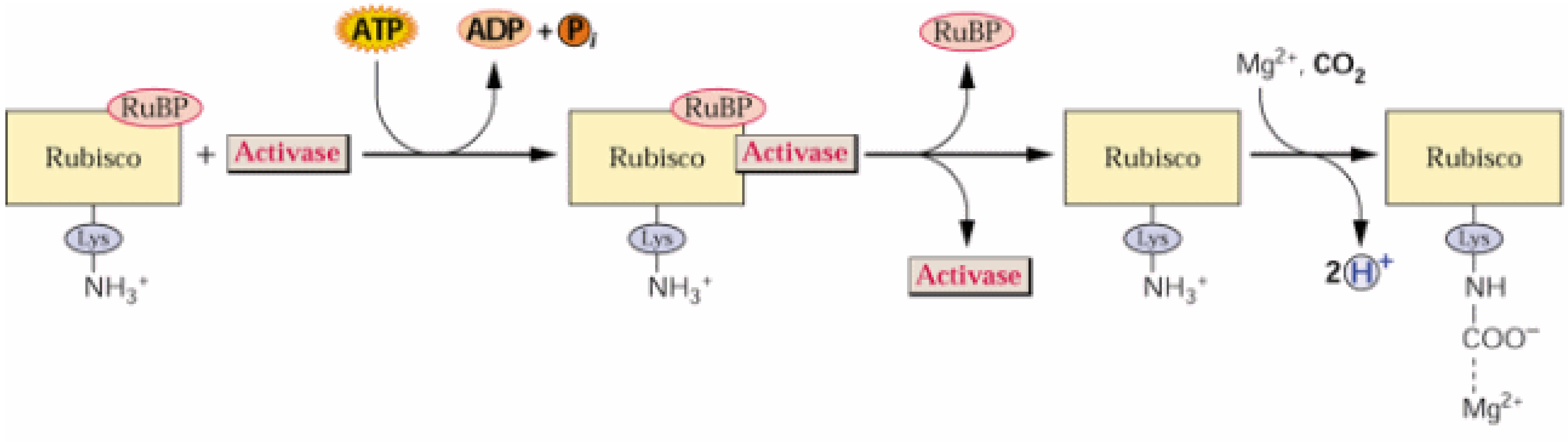
Crassulacean Acid Metabolism (CAM) - another C4 Variant

- Night: The enzyme *PEP carboxylase* adds HCO_3 to the 3-Carbon intermediate of glycolysis (PEP); the C4 acid product (OAA) is then reduced (by *NAD-malate dehydrogenase*) to malate which accumulates in the vacuole.
- Day: Malate is moved back into the cytoplasm and converted to the 3-C intermediate of glycolysis, pyruvate - CO_2 is released and fixed via the C3 cycle in the chloroplast; pyruvate is converted back to PEP.



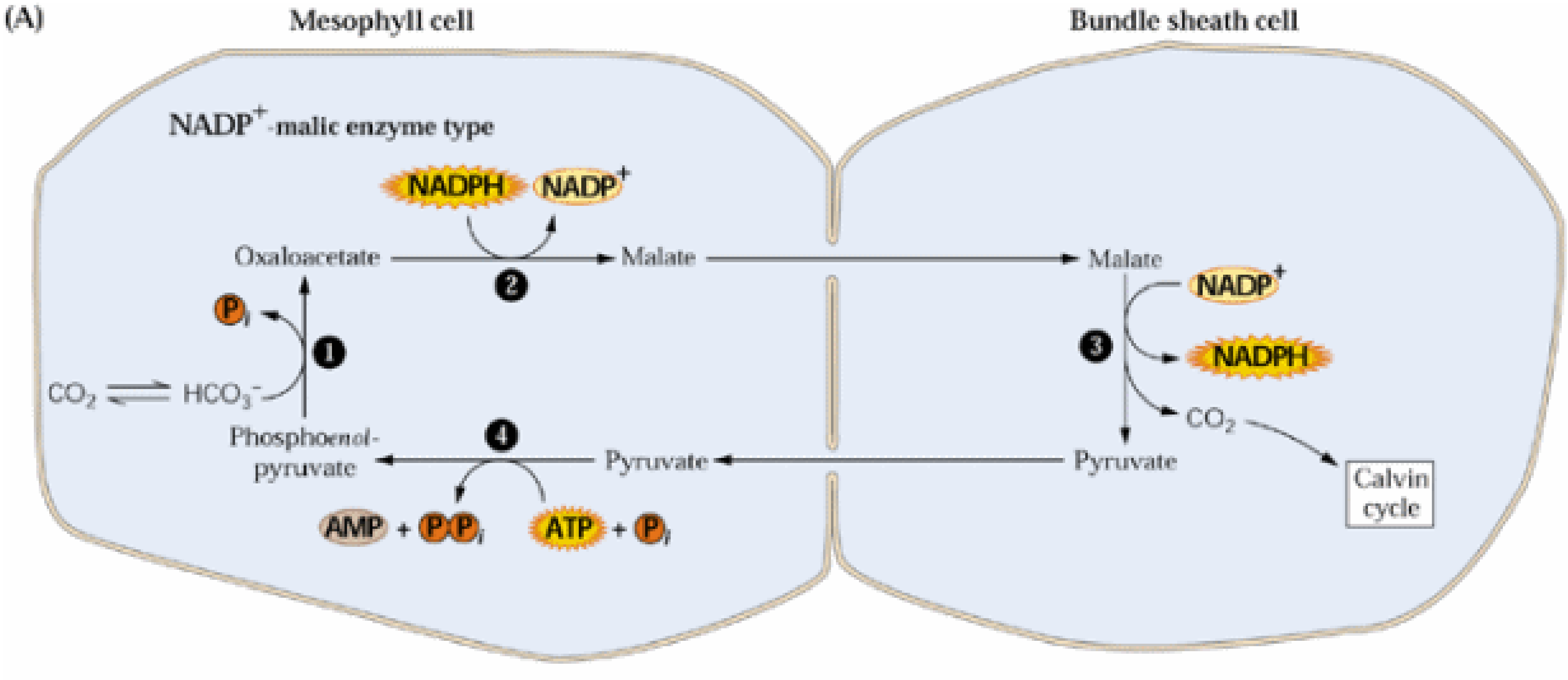
The C_3 (Calvin) Cycle.

- Rubisco Activase, is also required for Rubisco activation
- RuBP binds to Rubisco in the dark preventing carbamylation of Lys 201
- RA removes RuBP from Rubisco in an ATP-dependent reaction, opening the site for CO_2 access to Lys 201



The C_3 (Calvin) Cycle.

- Variant 1: $NADP^+$-malic enzyme



1 PEP carboxylase

2 NADP malate dehydrogenase

3 $NADP^+$ malic enzyme

4 Pyruvate-orthophosphate dikinase (PPDK)

5 Aspartae aminotransferase

6 NAD^+ malic enzyme

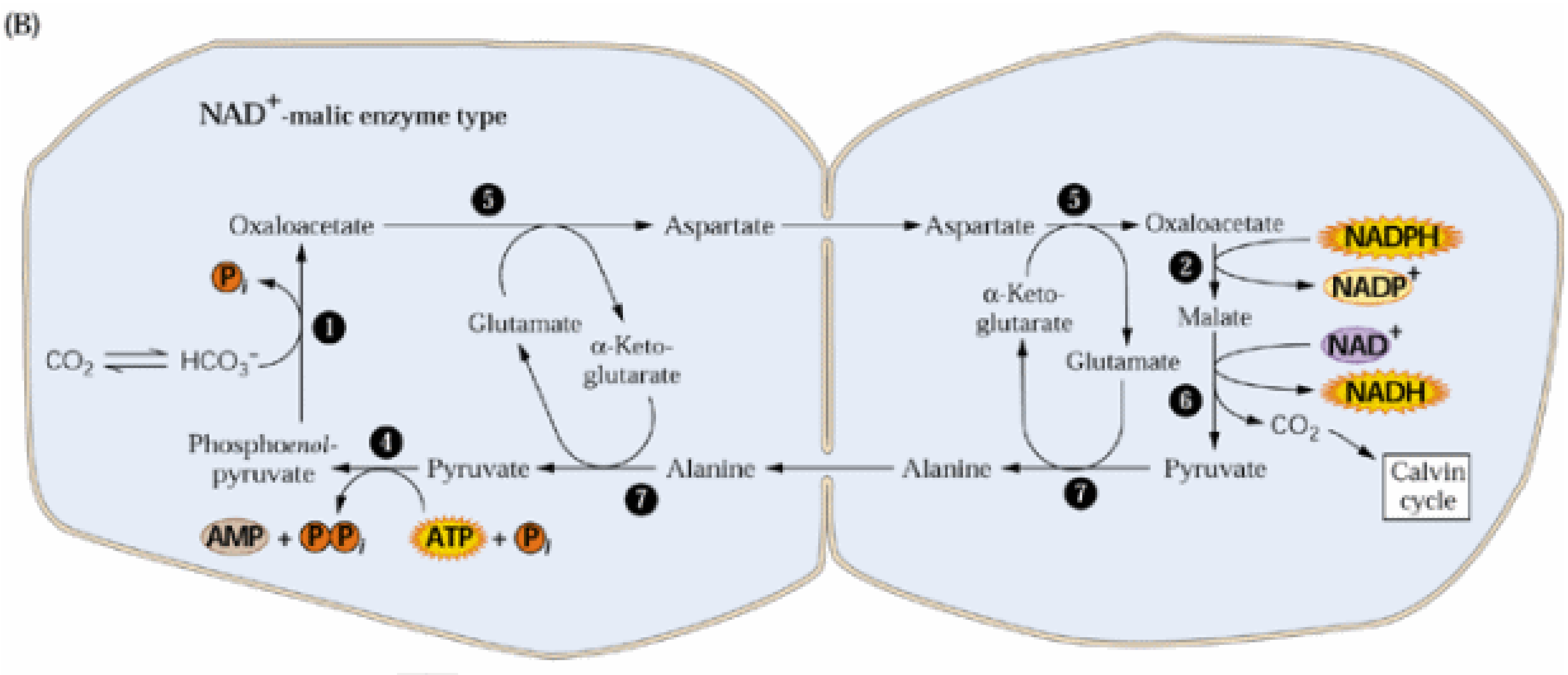
7 Alanime aminotransferase

8 PEP carboxykinase

The C_3 (Calvin) Cycle.

- Variant 2: NAD^+-malic enzyme

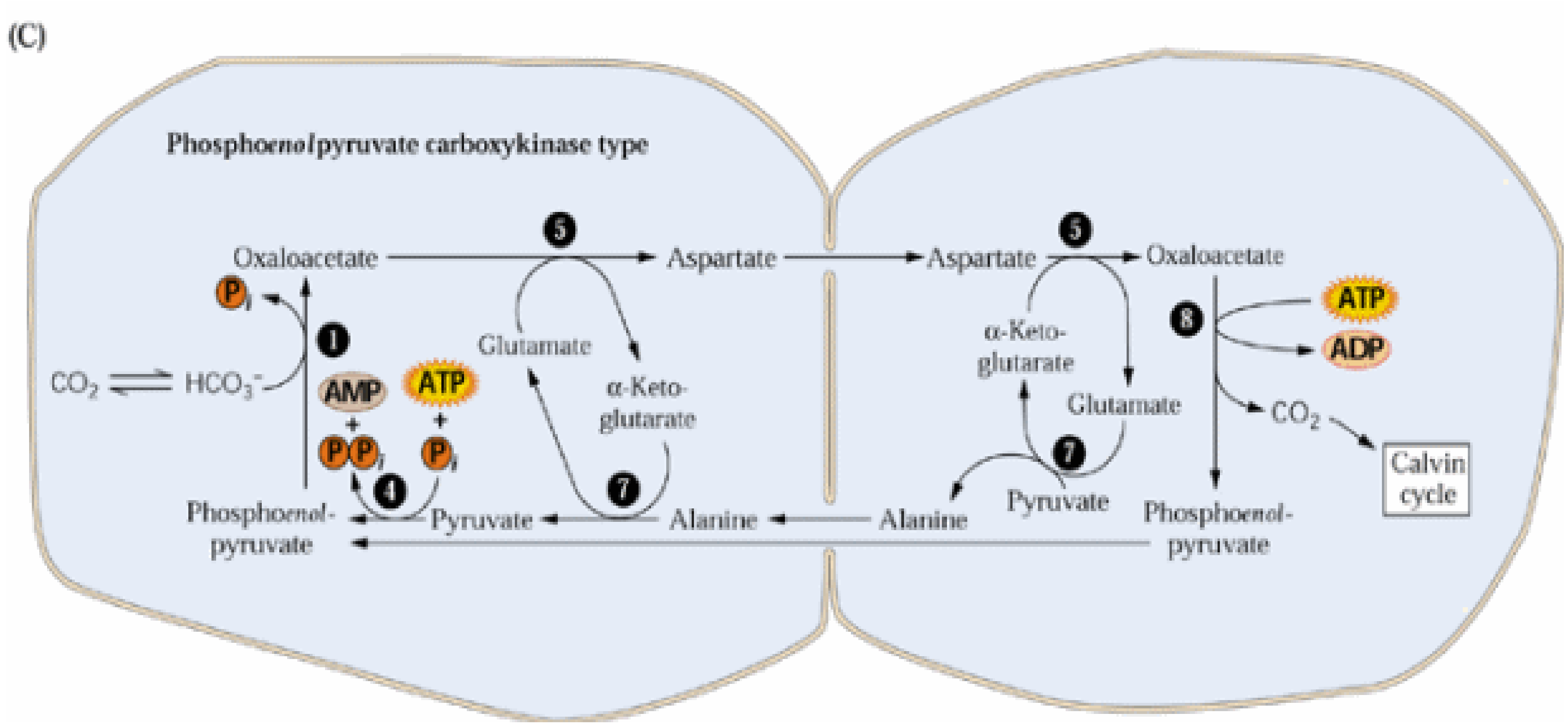
(B)



1 PEP carboxylase
2 NADP malate dehydrogenase
3 $NADP^+$ malic enzyme
4 Pyruvate-orthophosphate dikinase (PPDK)
5 Aspartae aminotransferase
6 NAD^+ malic enzyme
7 Alanime aminotransferase
8 PEP carboxykinase

The C_3 (Calvin) Cycle.

- Variant 3: PEP carboxykinase

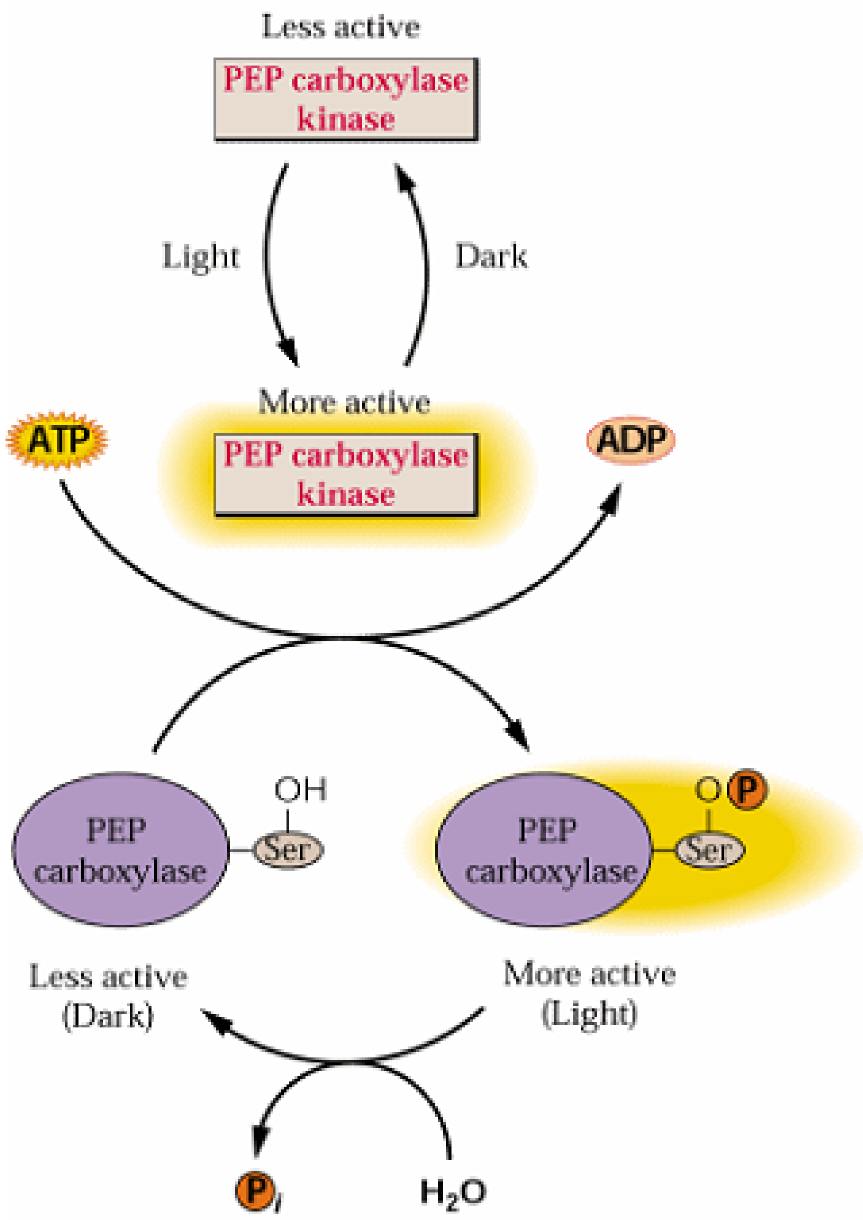


1 PEP carboxylase
2 NADP malate dehydrogenase
3 NADP$^+$ malic enzyme
4 Pyruvate-orthophosphate dikinase (PPDK)

5 Aspartae aminotransferase
6 NAD$^+$ malic enzyme
7 Alanime aminotransferase
8 PEP carboxykinase

The C_4 Cycle.

- PEPc activity is regulated by phosphorylation state
- Malate is a competetive inhibitor of PEPc
- Phospho-PEPc is active in the light (prevents malate binding)
- PEPc is dephosphorylated in the dark and is inactive

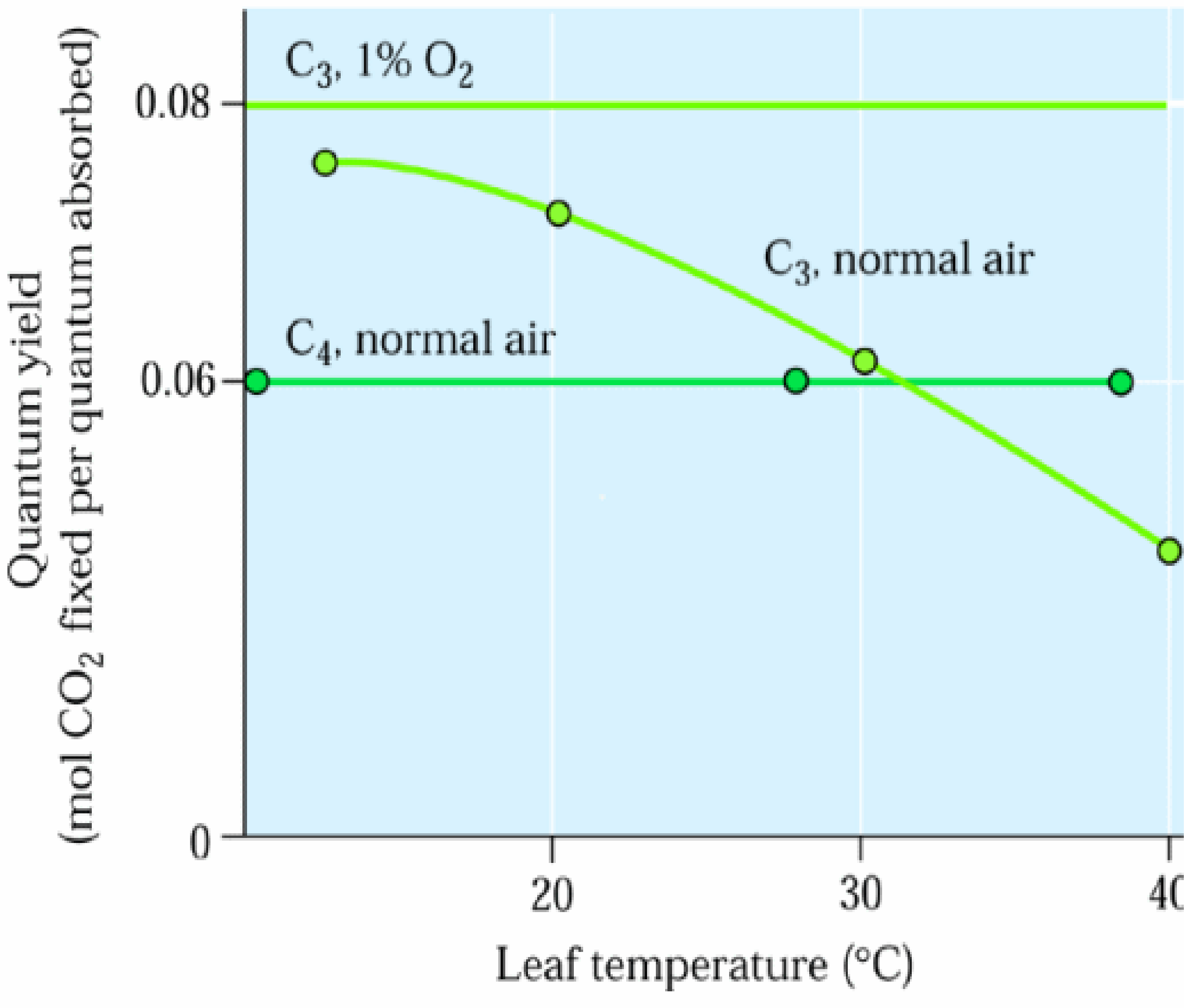


CO_2 Assimilation; the Effect of the Environment

The A_{max} Rates Of Crops & Wild Plants

Type of Plant	Example	Maximum Photosynthesis (CO_2 fixed, $\mu mol\ m^{-2}\ s^{-1}$)[a]
CAM	*Agave americana* (century plant)	0.6–2.4
Tropical, subtropical, and Mediterranean evergreen trees and shrubs; temperate zone evergreen conifers	*Pinus sylvestris* (Scotch pine)	3–9
Temperate zone deciduous trees and shrubs	*Fagus sylvatica* (European beech)	3–12
Temperate zone herbs and C-3 pathway crop plants	*Glycine max* (soybean)	10–20
Twelve herbacious alpine plants (Austrian alps, 2600 m elev.)	*Ligusticum mutellina* *Taraxacum alpinum* others	10–24
Tropical grasses, dicots, and sedges with C-4 pathway	*Zea mays* (corn or maize)	20–40

Photorespiration Increases (A Decreases) with Increasing Temperature

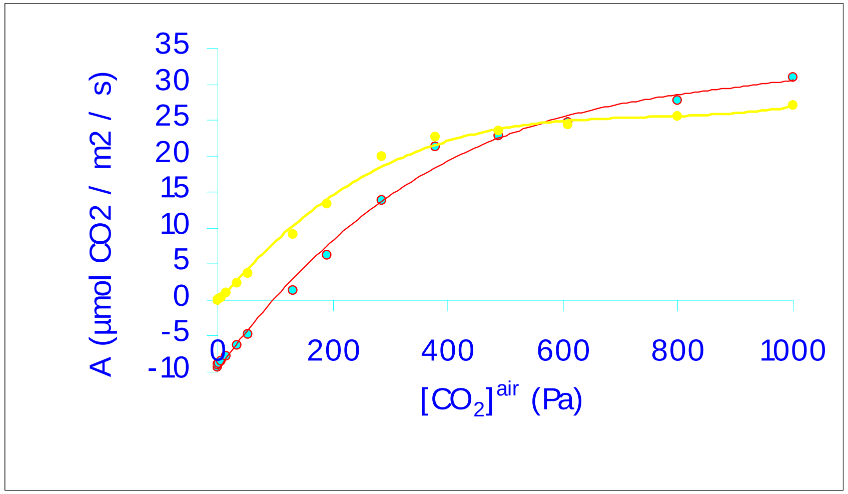


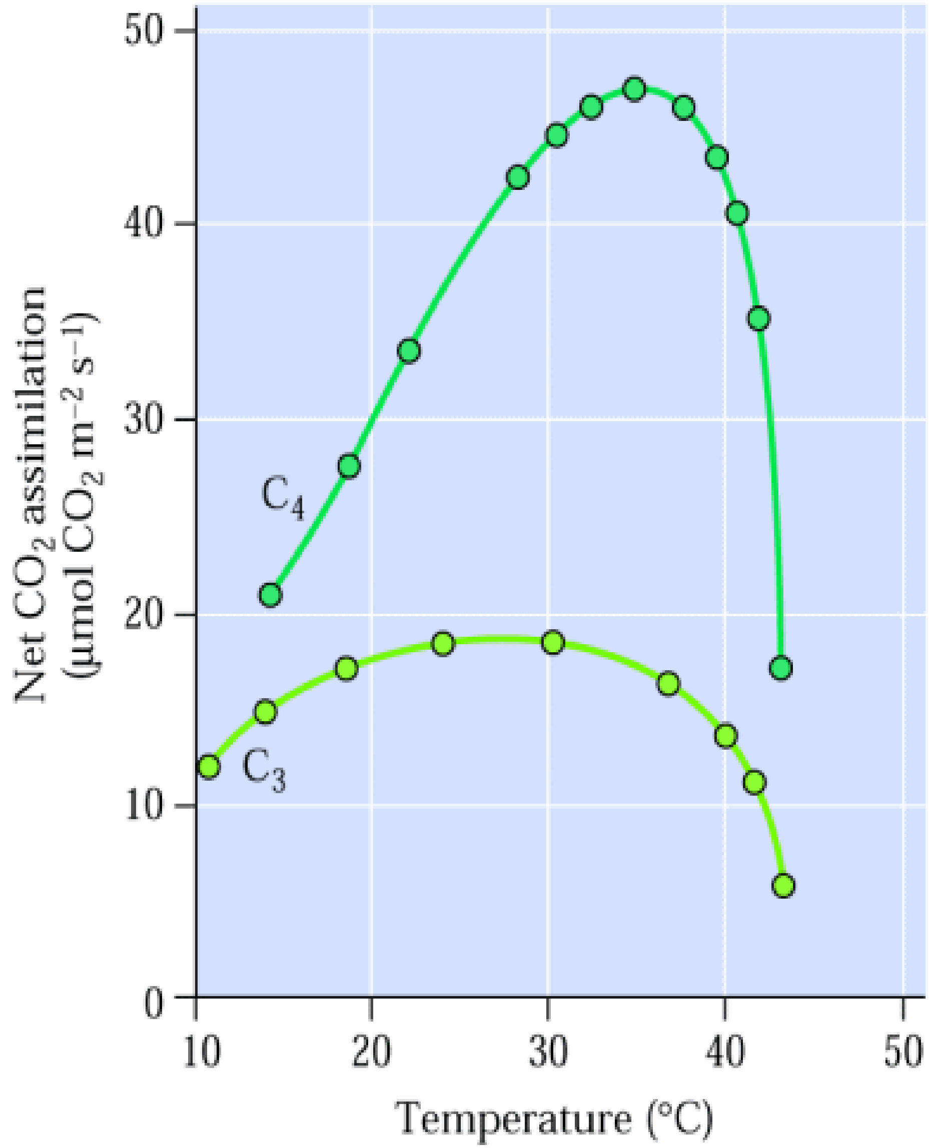
?

Because the solubility of CO_2 decreases rapidly with temperature?

Because Rubisco or Rubisco Activase is Temperature sensitive?

Climate Change: Increasing Temperatures will Favour C4 Plants

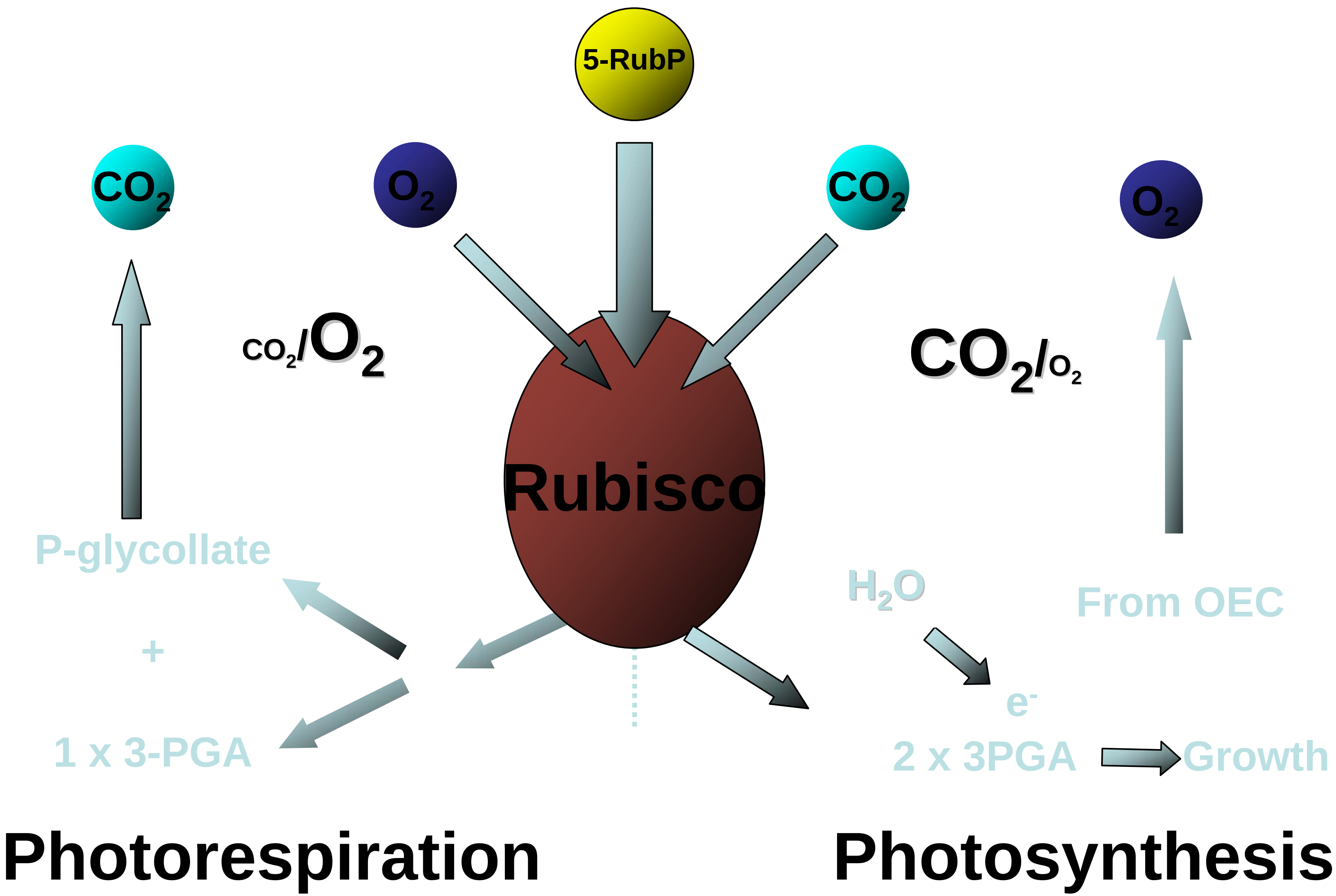


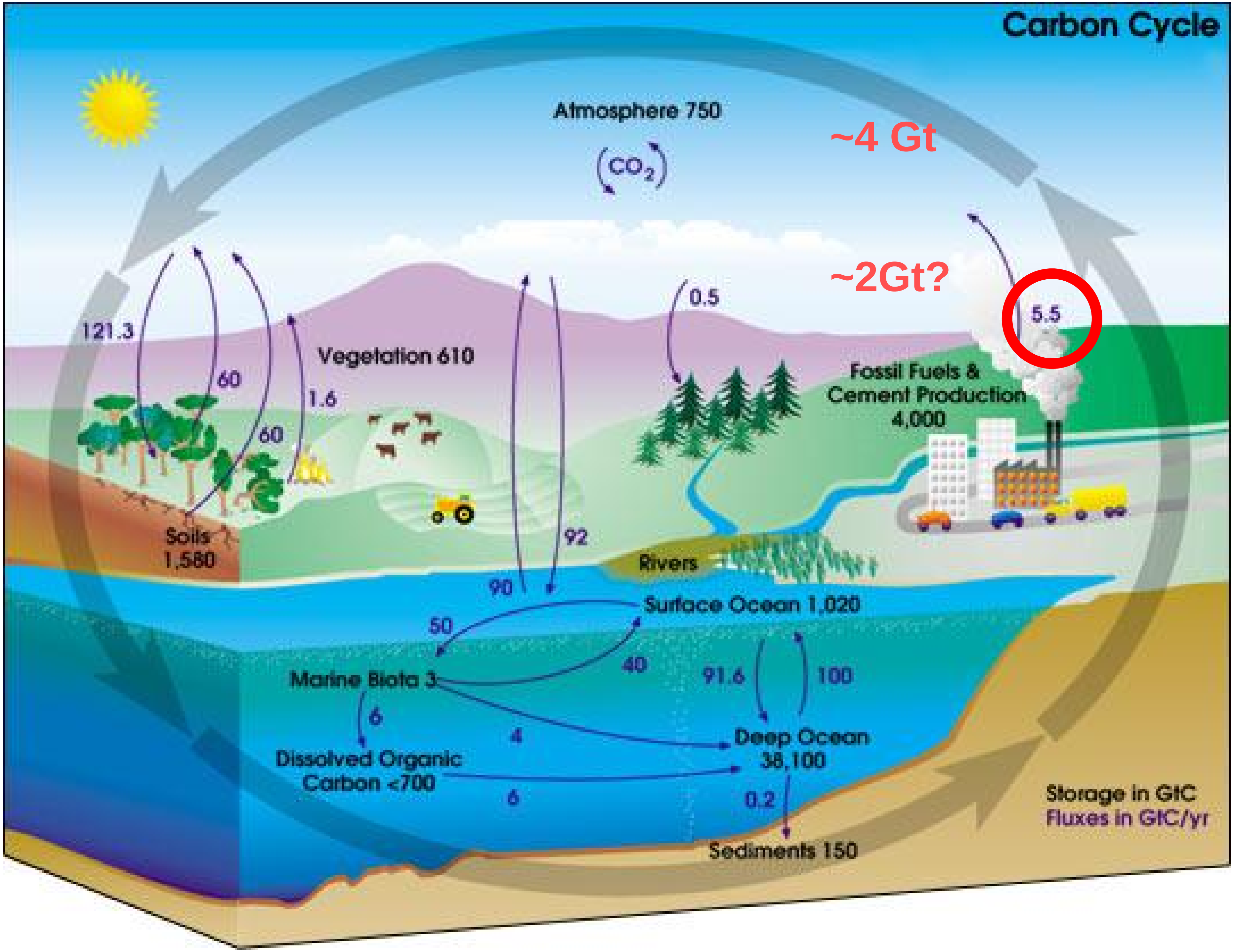


…But Increasing CO_2 Will Favour C3 > C4….

So What Will Happen?

Rubisco Catalyses 2 Reactions




Carbon Cycle
Atmosphere 750
CO_2
~4 Gt
~2Gt?
0.5
5.5
121.3
60
60
1.6
Vegetation 610
Fossil Fuels &
Cement Production
4,000
Soils
1,580
92
90
Rivers
Surface Ocean 1,020
50
40
91.6
100
Marine Biota 3
6
4
Deep Ocean
38,100
Dissolved Organic
Carbon <700
6
0.2
Sediments 150
Storage in GtC
Fluxes in GtC/yr

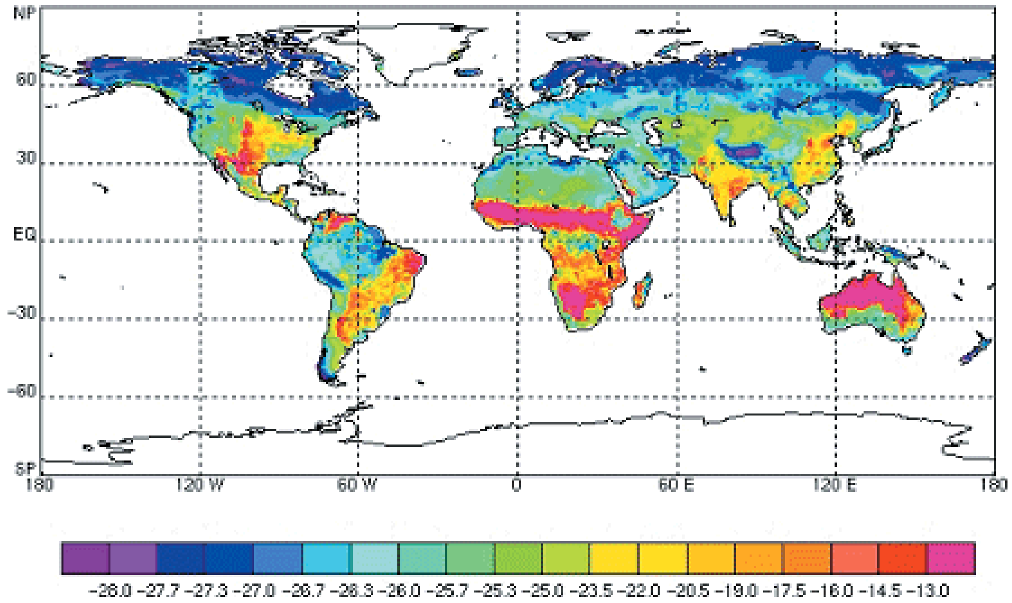
How Will Plants Plants Respond to Rising CO_2?

Modelling Change $d^{13}C$ Measurements 1982-1991

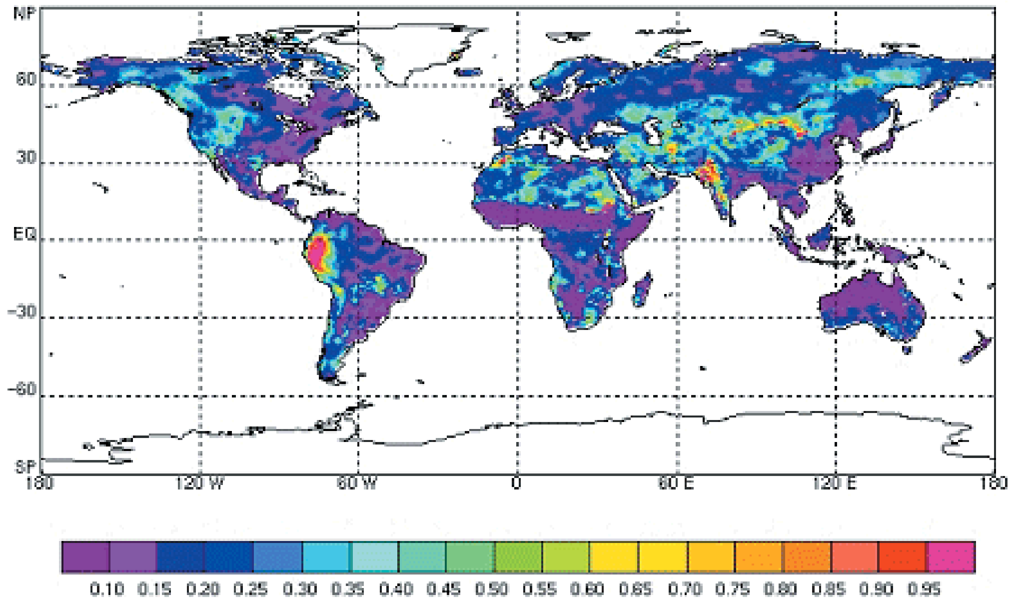
- C3 Plants have a $d^{13}C$ signature of -25 to -28
- C4 Plants have a $d^{13}C$ signature of -12 to -15

Models Show changes in C3 / C4 Plant Distibution are not where expected

A. Mean Annual



B. Standard Deviation in Annual



CO_2 Enrichment Experiments Using Enclosed Leaf Chambers Suggest ~ 25% Yield Increase in x2 Senario

Source	Rice	Wheat	Soybeans	C_4 crops
		Yield		
Kimball (1983)	19	28	21	–
Cure and Acock (1986)	11	19	22	27
Allen *et al*. (1987)	–	–	26	–
Enclosure studies	–	31	32	18
FACE studies	12	13	14	0*
		Biomass		
Cure and Acock (1986)	21	24	30	8
Allen *et al*. (1987)	–	–	35	–
FACE studies	13	10	25	0*
		Photosynthesis		
Cure and Acock (1986)	35	21	32	4
FACE studies	9	13	19	6

*Data from only 1 year in Leakey *et al*. (*30*).

Long *et al.* 2006 Science 312.

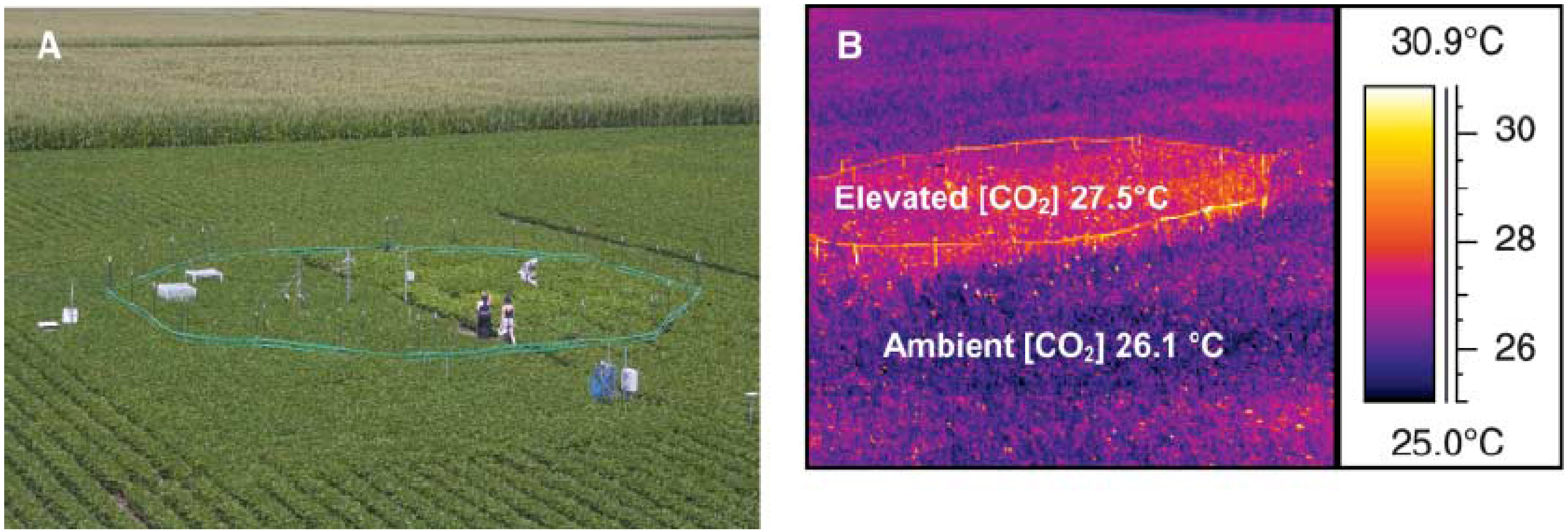
Free Air Concentration Enrichment (FACE) Studies

RESEARCH ARTICLES

Food for Thought: Lower-Than-Expected Crop Yield Stimulation with Rising CO_2 Concentrations

30 JUNE 2006 VOL 312 SCIENCE

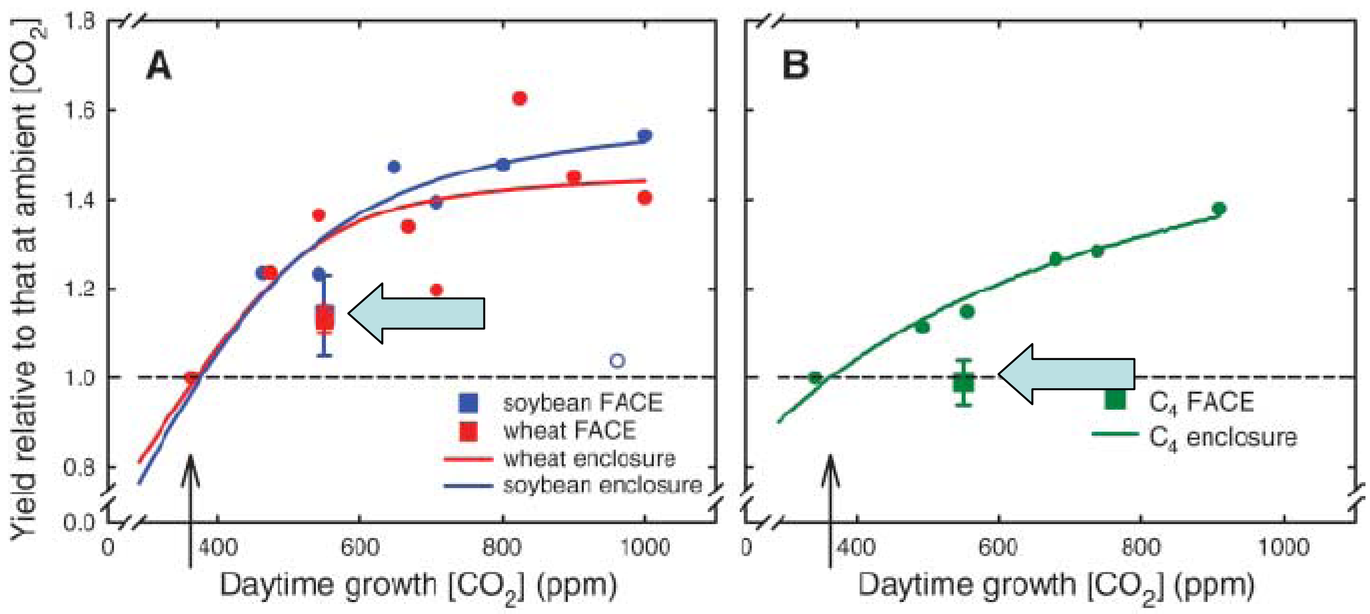
Stephen P. Long,[1,2,3]* Elizabeth A. Ainsworth,[4,1,3] Andrew D. B. Leakey,[3,1]
Josef Nösberger,[5] Donald R. Ort[4,1,2,3]



FACE Experiments Suggest Only 10% Yield Increase in C3 and No Increase in C4!

C3 Plants

C4 Plants



Reliable Biological Data, not More Complex Maths, is Urgently Required

- Clearly, a Much Better Understanding of the Effects of Temperature & CO_2 on Primary Production is Required *Before* Climate Models Become Reliable
- 9 Billion Citizens will require feeding in 2050. Projected Yields are based on Enclosed CO_2 Enrichment Experiments and now appear to be a Gross Overestimate.