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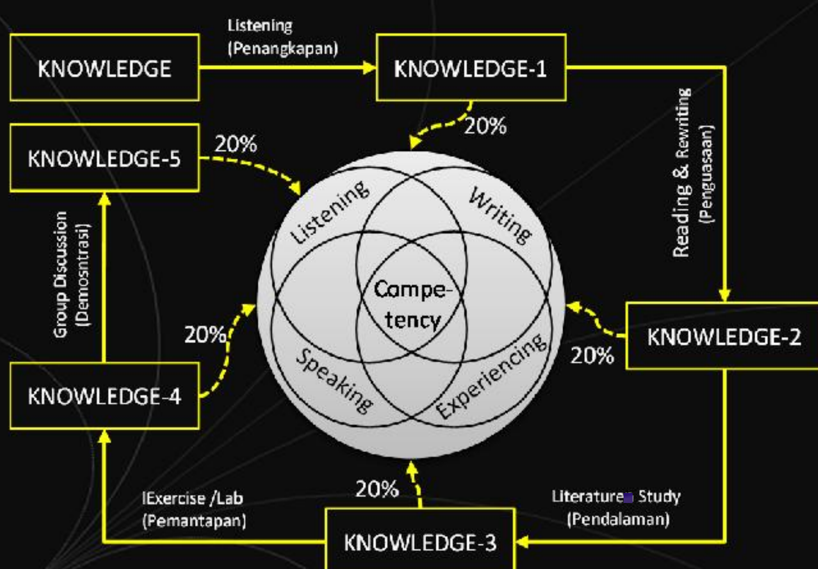
LECTURE 5:
C4 & CAM PHOTOSYNTHESIS

C4 and *CAM plants* are *plants* use certain CO_2 fixation to increase CO_2 concentration at the site of RUBISCO



VOCABULARY

Forget not, exam includes **ENGLISH WORDS**

1. Involve
2. Bundle
3. Sheath
4. Subsequent
5. Ambient
6. Stick together
7. Determine
8. Evolution
9. Thrive
10. Allow

LECTURE OUTCOMES

Students, after mastering the materials of Plant Physiology course, should be able:

1. To explain the assimilation of CO_2 to be carbohydrate (sugars) in C4 and CAM plants
2. To explain the diffusion of CO_2 from the atmosphere into the site of assimilation in the chloroplasts of C4 and CAM plants
3. To explain reactions, enzymes and products involved in the reduction of CO_2 to be carbohydrate in C4 and CAM plants
4. To explain the effect of several environmental factors on photosynthesis

LECTURE OUTLINE

1. C4 Plants

C4 Plant Evolution
Discovery C4 Pathway
Leaf Anatomy of C4 plants
CO_2 Reduction
Type of C4 Plants
Energetic of the C4 Photosynthetic System

2. CAM Plants

CAM Plant Evolution
CAM Plant Characteristics
CO_2 Reduction

1. C4 PLANTS

1. C4 Plant Evolution

1. C4 photosynthesis has evolved more than 60 times as a carbon-concentrating mechanism to augment the ancestral C3 photosynthetic pathway.
2. C_4 origins have all occurred over the past 30 Myr, with no difference in timing between monocot and eudicot lineages.
3. It is hypothesized that **atmospheric CO_2 depletion** coupled with high **temperatures**, **open habitat** and **seasonally dry subtropical environments** caused **excessive demand for water transport**, and **selected for C4 photosynthesis** to enable lower stomatal conductance as a water-conserving mechanism.

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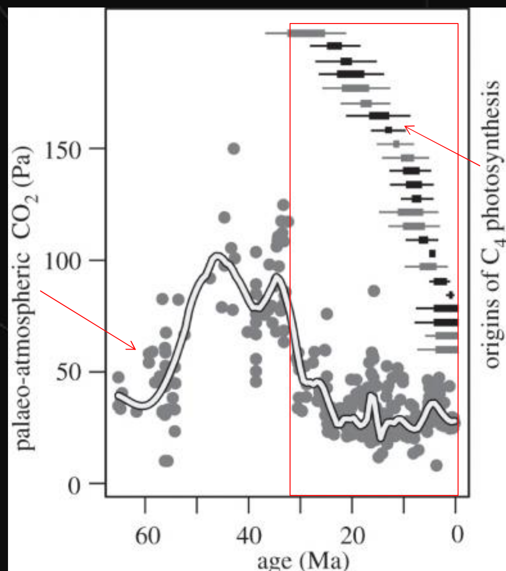
Geological history of atmospheric CO_2 and the estimated ages of C4 evolutionary origins.



Colin P. Osborne, and Lawren Sack Phil. Trans. R. Soc. B 2012;367:583-600

Geological history of atmospheric CO_2 and the estimated ages of C_4 evolutionary origins. The estimated ages of C_4 evolutionary origins in grasses (dark grey horizontal bars) and eudicots (black horizontal bars) were obtained using phylogenetic inference and calibration to fossils [35]. Thick bars represent uncertainty in the position of each C_4 evolutionary origin on the phylogeny, while thin bars indicate uncertainty in dating of the phylogeny (reproduced with permission from Christin *et al*. [35]).

2. Discovery C4 Pathway

1. In the late 1950s, H. P. Kortschack and Y. Karpilov observed early labeling of 4-carbon acids when “CO_2 was provided to sugarcane and maize.
2. After leaves were exposed to “CO_2 for a few seconds in the light, 70 to 80% of the label was found in the 4-carbon acids **malate** and **aspartate**—a pattern very different from the one observed in leaves that photosynthesize solely via the Calvin—Benson cycle.
3. M. D. Hatch and C. R. Slack elucidated C4 cycle, and established that malate and aspartate are the first stable, detectable intermediates of photosynthesis in leaves of sugarcane.
4. The carbon 4 of malate subsequently becomes carbon 1 of 3-phosphoglycerate (Hatch and Slack 1966).

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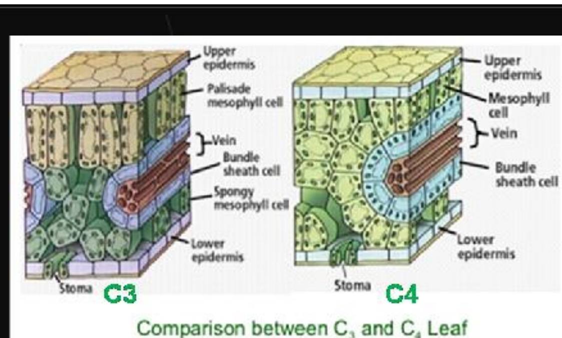
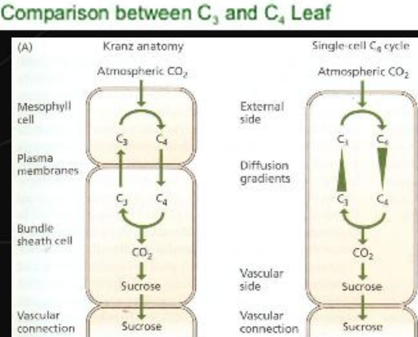
3. Leaf Anatomy of C4 Plants

1. The key features of the C4 cycle are the presence of two distinctive photosynthetic cell types: an internal ring of bundle sheath cells where RUBISCO is located, which is wrapped with an outer ring of mesophyll cells.
2. The chloroplasts in bundle sheath cells are concentrically arranged and exhibit large starch granules and unstacked thylakoid membranes.
3. On the other hand, mesophyll cells contain randomly arranged chloroplasts with stacked thylakoids and little or no starch.
4. However, there are now clear examples of single-cell C4 photosynthesis in a number of green algae, diatoms, and aquatic and land plants (Edwards *et al*. 2004; Muhaidat *et al*. 2007) (Fig. 8.12A).

Fig. 8.12 The photosynthetic pathway in leaves. (A) In almost all known C4 species, photosynthetic CO_2 assimilation requires the development of Kranz anatomy (right panel above and left panel below).

A few land plants, typified by Borszczowia aralocaspica and Bienertia cycloptera, contain the equivalents of the C4 compartmentalization in a single cell (right panel).





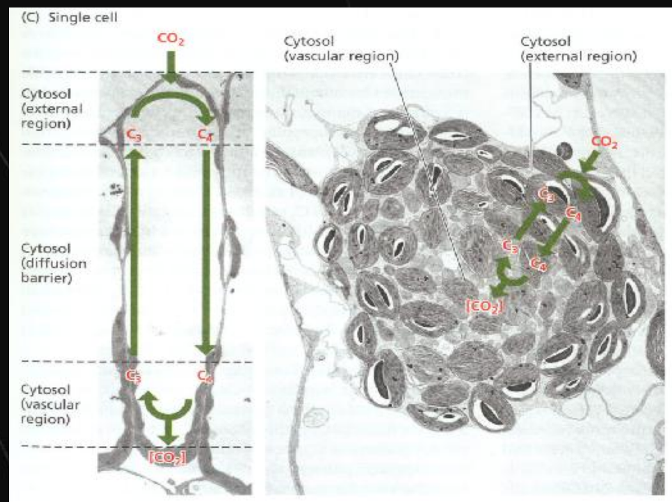
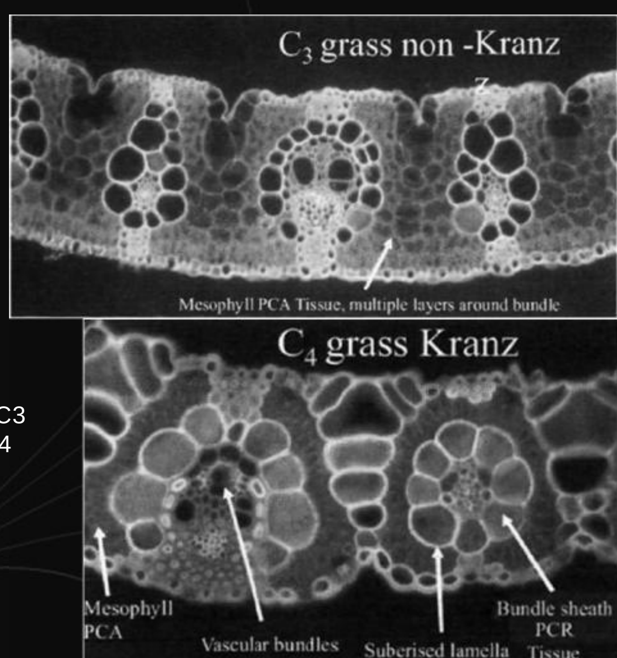
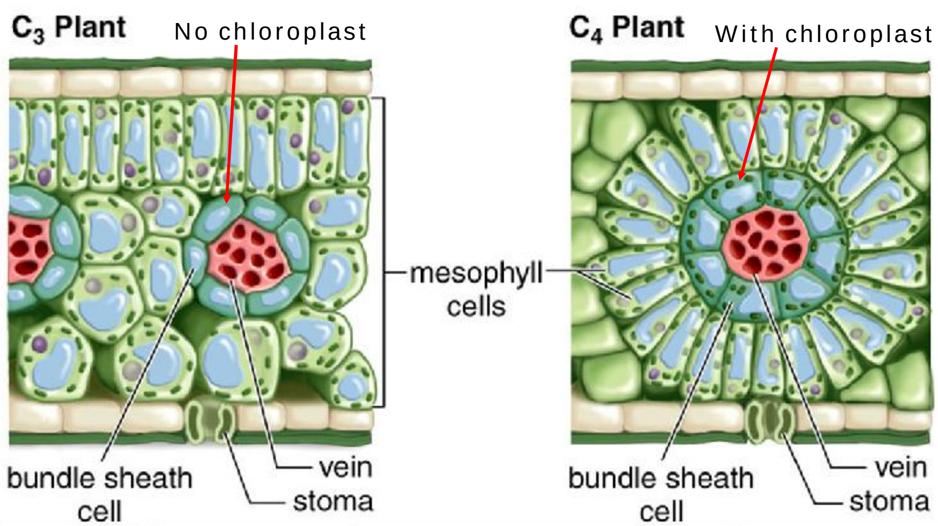


Fig. 12.8C. Single-cell C4 photosynthesis. Diagrams of the C4 cycle are superimposed on electron micrographs of *Borszczowia aralocaspica* (left) and *Bienertia cycloptera* (right). (B courtesy of Athena McKown; C from Edwards *et al*. 2004.)

Comparison between leaf structure of C3 plants and C4 plants under lectron microscope





Leaf structure model of C3 plants (leaft) and C4 plants (right)

4. CO_2 Reduction

1. The transport of CO_2 from the external atmosphere to the bundle sheath cells proceeds through five successive stages (Fig. 8.11).
2. In the C4 cycle, the enzyme phosphoenolpyruvate carboxylase (PEPCase), rather than rubisco, catalyzes the primary carboxylation, the reaction of HCO_3^- with PEP (phosphoenolpyruvate) (Sage 2004).
3. The 4-carbon reaction product, **oxaloacetate**, is converted into **malate** or **aspartate** (depending on the species) by NADP-malate dehydrogenase or aspartate aminotransferase, respectively.
4. Malate or aspartate is exported to bundle sheath cells where it is decarboxylated, releasing CO_2 that is refixed by rubisco via the Calvin cycle.

5. The specific paths by which CO_2 is concentrated in the vicinity of rubisco vary substantially between different C4 species.

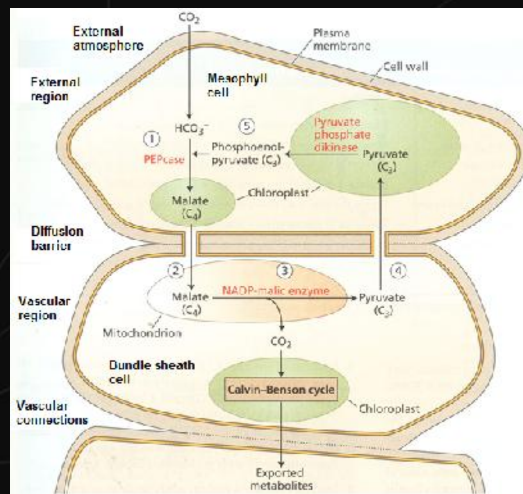


Fig. 8.11 The C4 photosynthetic carbon cycle involves five successive stages in two different compartments as indicated in the figure

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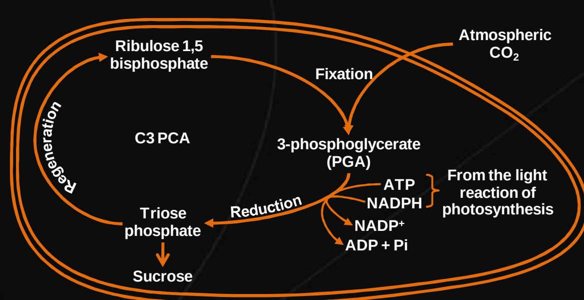
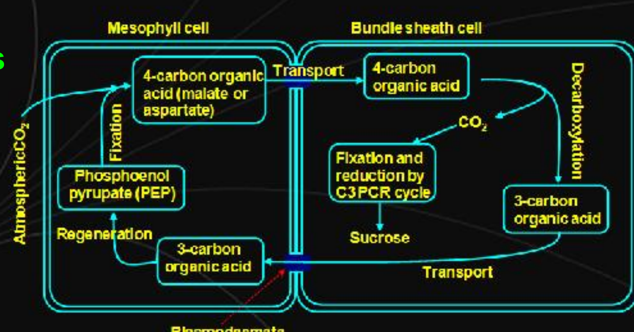
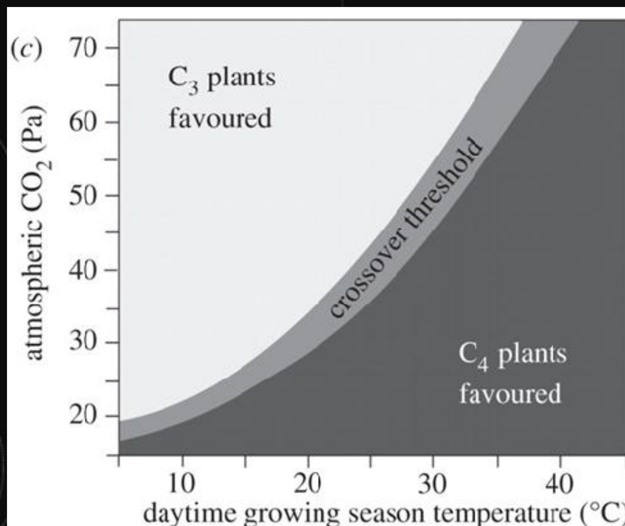
C3 plants



C4 plants





Condition favoured by C3 plants and C4 plants. Osborne & Sack (2012)

5. Types of C4 Plants

Principal C4 acid transported to the BSC	Decarboxylating enzyme	Variant name	Principal C3 acid returned to MC	Examples
Malate	NADP-dependent malic enzyme (chloroplast)	NADP-ME	Pyruvate	Maize, crabgrass, sugarcane, sorghum
Aspartate	NAD-dependent malic enzyme (mitochondria)	NAD-ME	Alanine	Millet, Pigweed (Panicum miliaceum)
Aspartate	Phosphoenolpyruvate carboxykinase	PEP-CK	Alanine/ pyruvate	Guinea grass (Panicum maximum)

BSC, bundle sheath cells; MC, mesophyll cells

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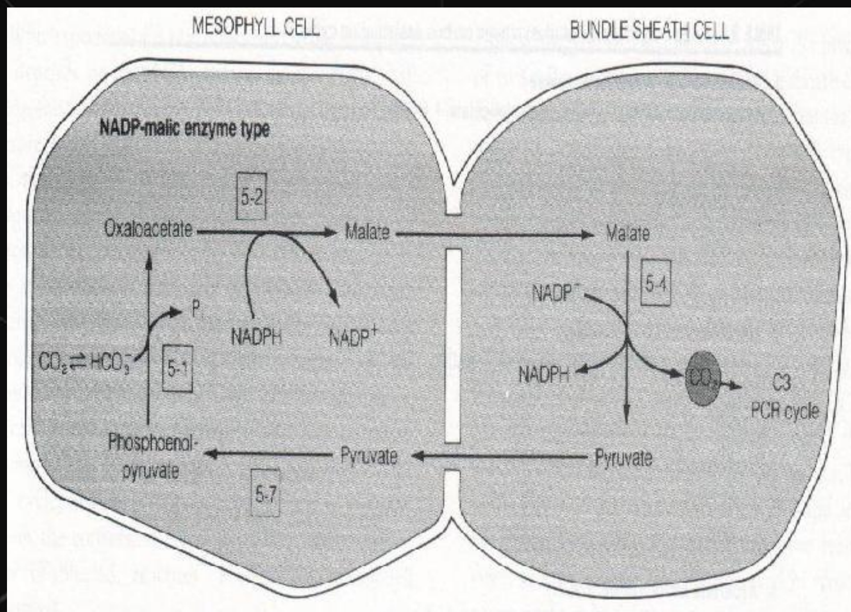
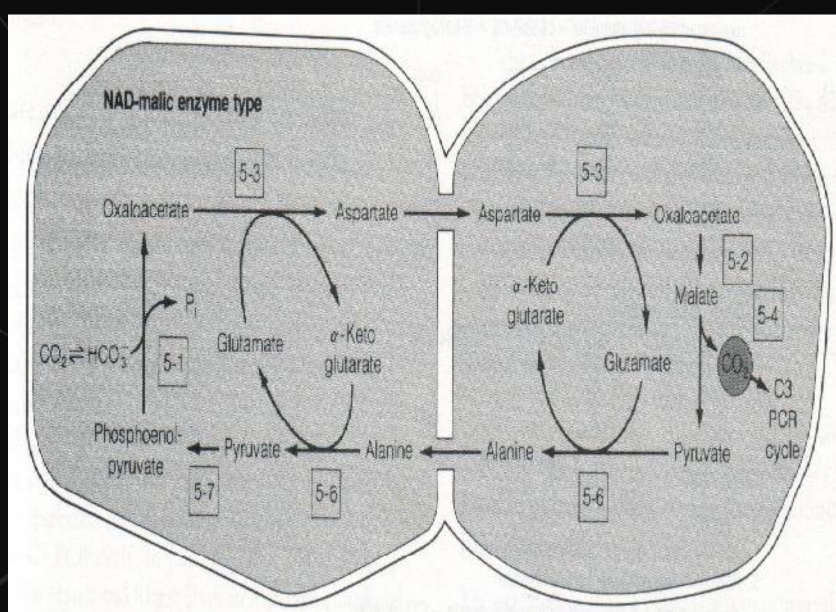
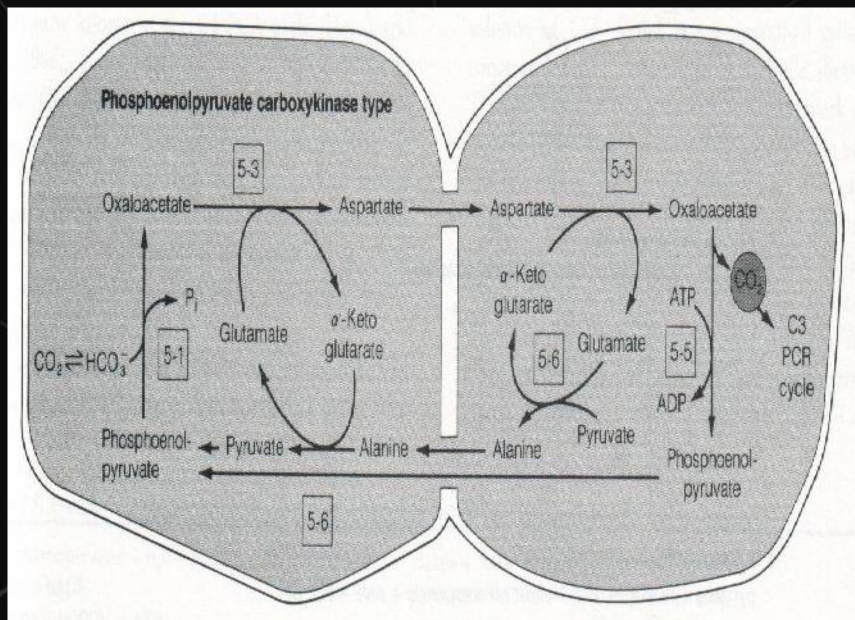
1. NADP-malic enzyme type



2. NAD-malic enzyme type



3. Phosphoenolpyruvate carboxykinase type



6. Energetics of the C4 Photosynthetic System

phosphoenolpyruvate + H_2O + NADPH + CO_2 (mesophyll)	→ malate + $NADP^+$ + $HOPO_3^{2-}$
malate + $NADP^+$	→ pyruvate + NADPH + CO_2 (bundle sheath cell)
pyruvate + $HOPO_3^{2-}$ + ATP	→ phosphoenolpyruvate + AMP + $2H^+$ + $P_2O_7^{4-}$
$P_2O_7^{4-}$ + H_2O	→ $2HOPO_3^{2-}$
AMP + ATP	→ 2ADP
Net: CO_2 (mesophyll) + 2ATP + $2H_2O$	→ CO_2 (bundle sheath cell) + 2ADP + $2HOPO_3^{2-}$ + $2H^+$

Cost of concentrating CO_2 within bundle sheath cell =
2ATP per CO_2

The reduction cost of 1 mol CO_2 via PCR =
2mol NADPH+3 mol ATP

Total reduction cost of 1 mol CO_2 in C4 plants =
?

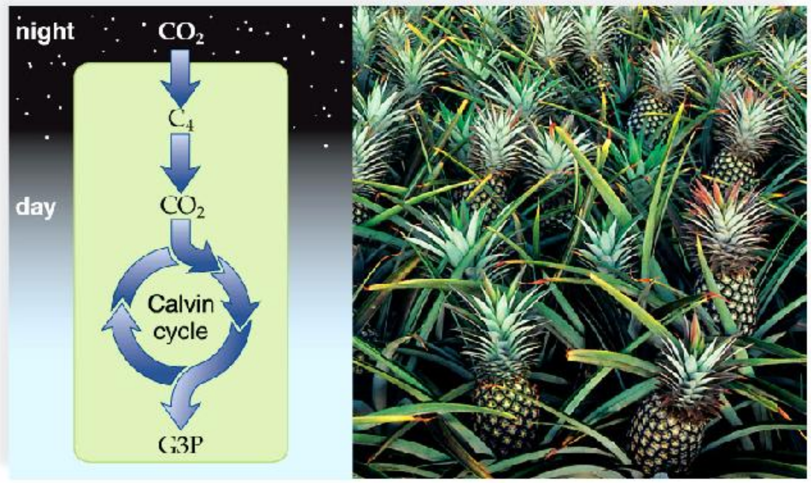
2. CAM PLANTS

1. CAM Plant Evolution

1. Many plants that inhabit arid environments with seasonal water availability such as pineapple (*Ananas comosus*), agave (*Agave* spp.), cacti (*Cactaceae*), and orchids (*Orchidaceae*), exhibit another mechanism for concentrating CO_2 at the site of rubisco.
2. CAM is an ancient pathway that likely has been present since the Paleozoic era (570 and 230 Mya) in aquatic species from shallow-water palustrine habitats.
3. The selective factors driving aquatic CAM are autogenic, and CAM is widespread within the plant kingdom across at least 343 genera in 35 plant families comprising ~6% of flowering plant species.

4. The oldest lineage with CAM described to date is represented by Isoetes, a mostly aquatic or semi-aquatic group distributed in oligotrophic lakes or mesotrophic shallow seasonal pools (Keeley 1998).

http://www.mobot.org/mobot/photoessays/guizhou/images/Isoetes_yunguiense.jpg



CO_2 fixation in a CAM plant, pineapple, *Ananas comosus*

A typical well known CAM plant is pineapple

25

2. CAM Plant Characteristics

1. An important attribute of CAM plants is their capacity to attain high biomass in habitats where precipitation is inadequate, or where evaporation is so great that rainfall is insufficient for crop growth.
2. CAM is generally associated with anatomical features that minimize water loss, such as thick cuticles, low surface-to-volume ratios, large vacuoles, and stomata with small apertures.
3. In addition, tight packing of the mesophyll cells enhances CAM performance by restricting CO_2 loss during the day.
4. Typically, a CAM plant loses 50 to 100 grams of water for every gram of CO_2 gained, compared with 250 to 300 grams for C4 plants and 400 to 500 grams for C3 plants.

3. CO_2 Reduction

1. In CAM plants, the uptake of atmospheric CO_2 takes place at night when stomata are open.
   - At this stage, gaseous CO_2 in the cytosol, coming from both the external atmosphere and mitochondrial respiration, increases levels of HCO_3^- [$CO_2 + H_2O \leftrightarrow HCO_3^- + H^+$].
2. Then cytosolic PEPCase catalyzes a reaction between HCO_3^- and PEP provided by the nocturnal breakdown of chloroplast starch.
3. The resulting four-carbon acid, oxaloacetate, is reduced to malate which, in turn, proceeds to the acid milieu of the vacuole.
4. During the day, the malic acid that was stored in the vacuole at night flows back to the cytosol. Malate decarboxylase (NAD-malic enzyme) acts on malate to release CO_2, which is refixed into carbon skeletons by the Calvin—Benson cycle.

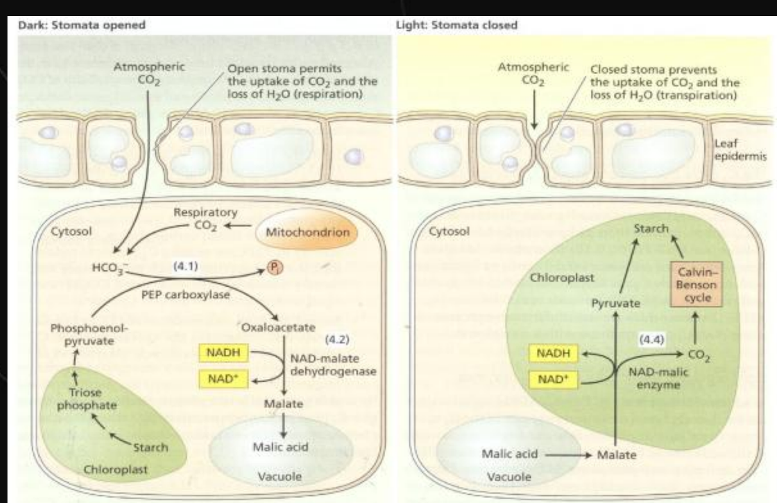


Fig. 8.13 Crassulacean acid metabolism (CAM). In CAM metabolism, CO_2 uptake is separated temporally from fixation via the Calvin—Benson cycle.

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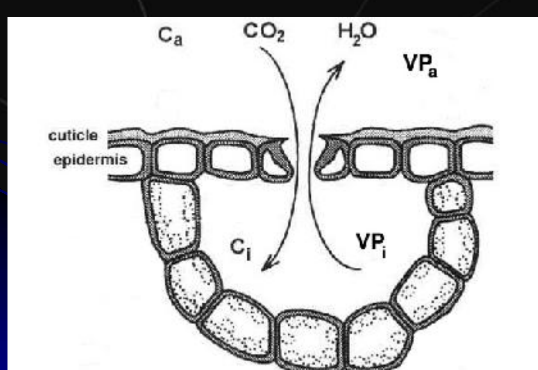
3. Physiological and Ecological Aspects of PHOTOSYNTHESIS

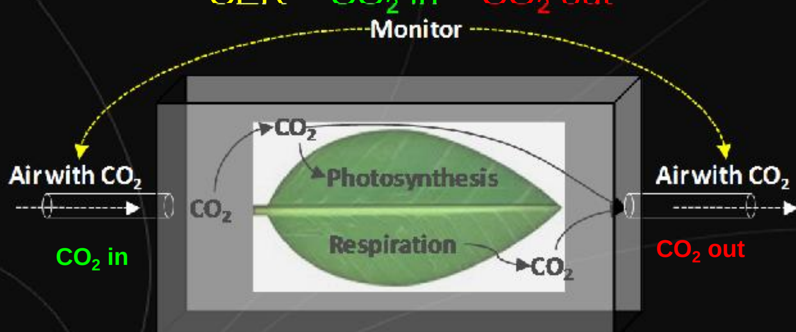


1. Light
2. Water
3. Temperature
4. CO_2
5. Nutrients

Etc.

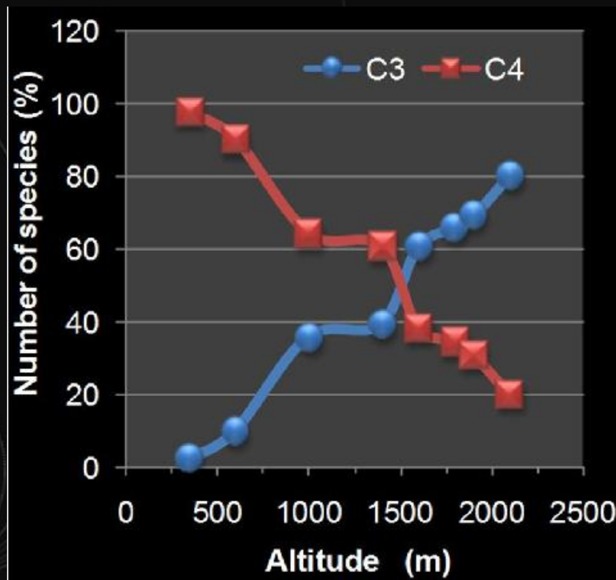
CER = CO_2 Exchange Rate

CER = CO_2 in – CO_2 out



CO_2 in = CO_2 out

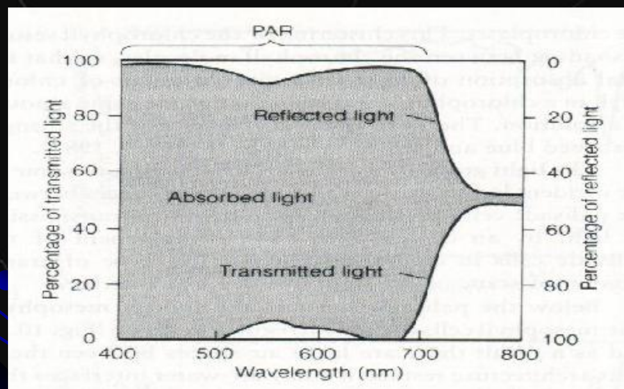
No Carbohydrate accumulation
NO GROWTH



EFFECT OF LIGHT ON PHOTOSYNTHESIS

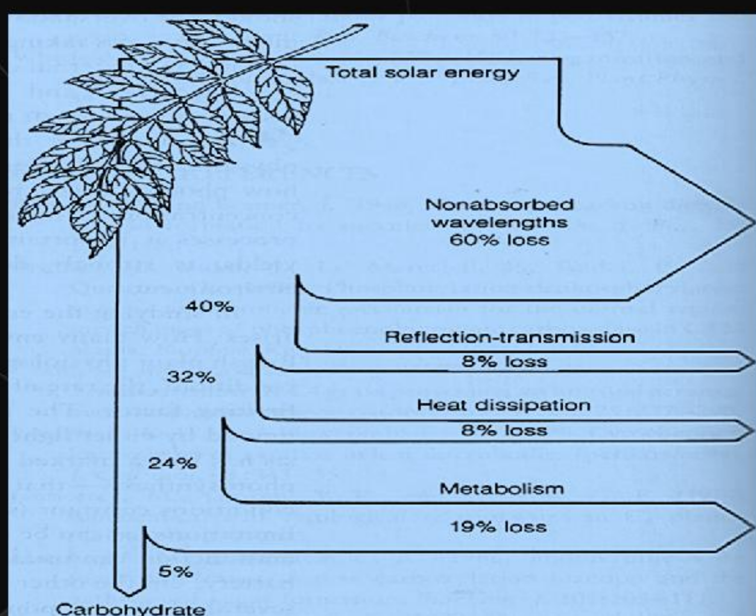
LIGHT = PAR = PPFD

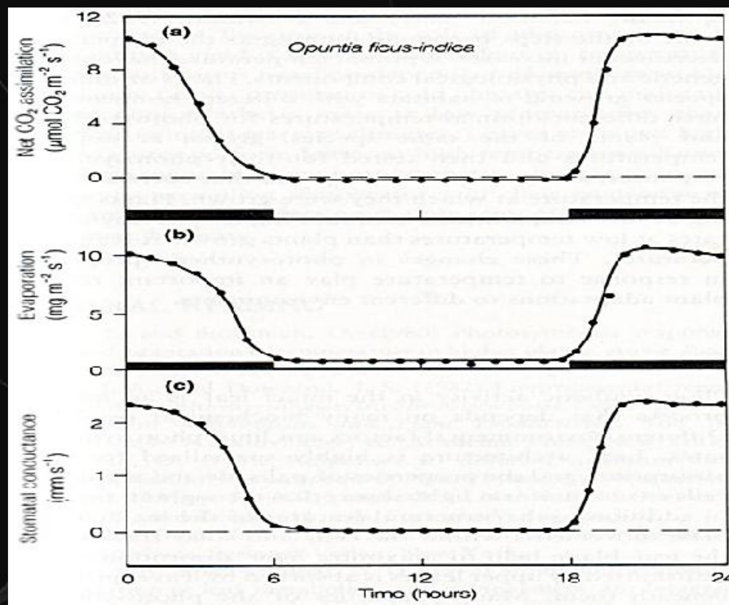
(Photosynthetic photon flux density)

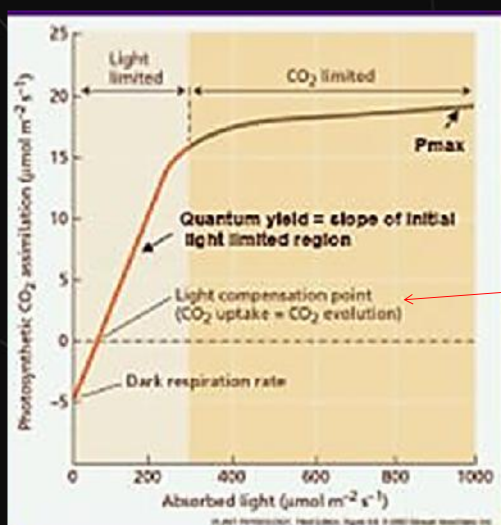


Sifat optis dari daun kacang panjang

Light transmitted and reflected increases with wavelength







Features of the Light Response Curve

Quantum yield (ϕ)

Photosynthetic capacity with respect to light = Pmax

LCP
Photosynthesis=respiration+ photorespiration

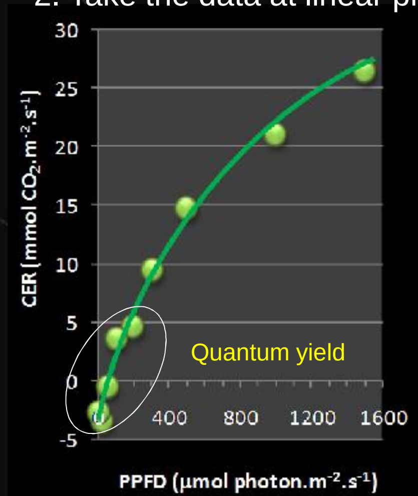
Light saturation point. PFD at which sat. occurs

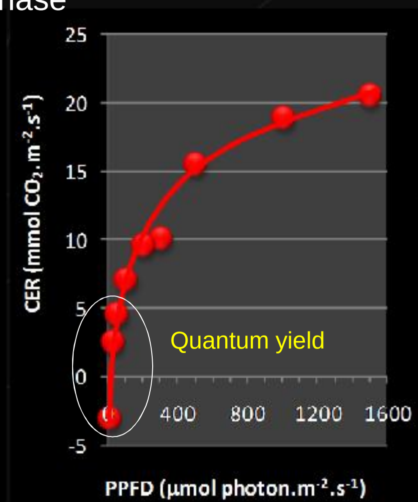
Dark respiration rate. Mitochondrial respiration.

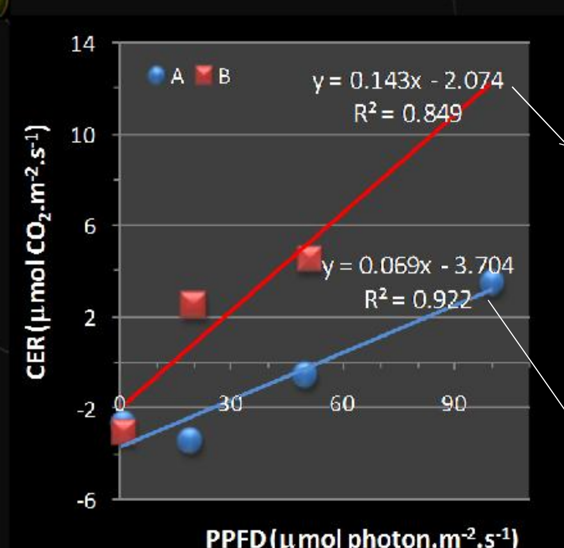
Quantum yield (Q_E, ¤) = mol CO_2/mole photon

Analysis of quantum yield and light compensation point

1. Assume you have data as shown below
2. Take the data at linear phase







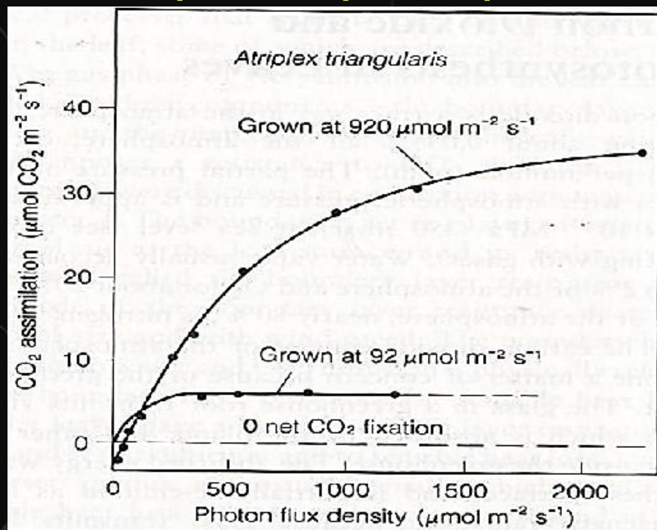
Quantum yileld
Q_E = 0.069 **«mol photon m^{-2} s^{-1}**

Light Compensation point
= 2.074/1.143
= **14.5** «mol **photon m^{-2} s^{-1}**

Quantum yileld
Q_E = 0.069 **«mol photon m^{-2} s^{-1}**

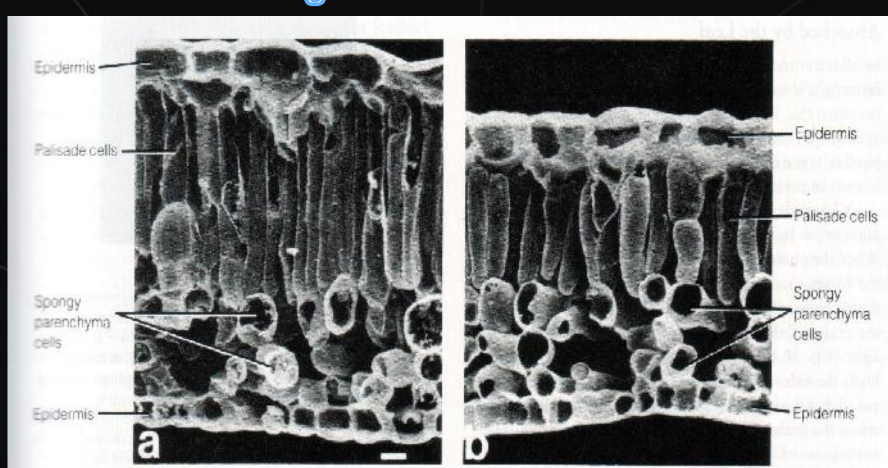
Light Compensation point
= 3.704/0.069
= **53.7** «mol **photon m^{-2} s^{-1}**

Effect of previous plant experience

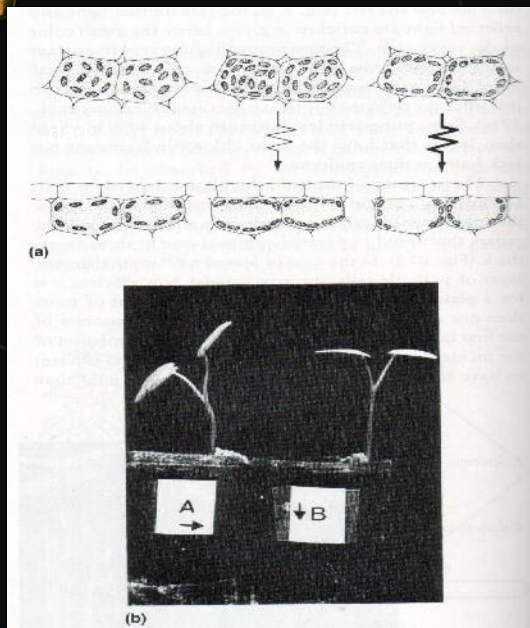


Plants growing usually at low light cannot harness high light

Effect of light on the struture of cells



Keadaan terbuka Keadaan ternaungi



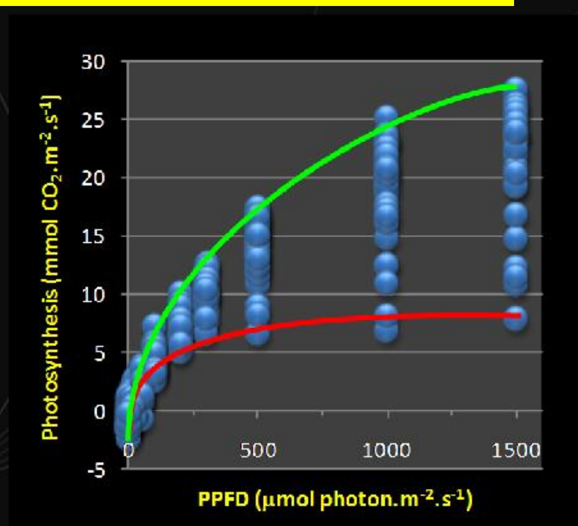
Distribusi khloroplast dalam sel

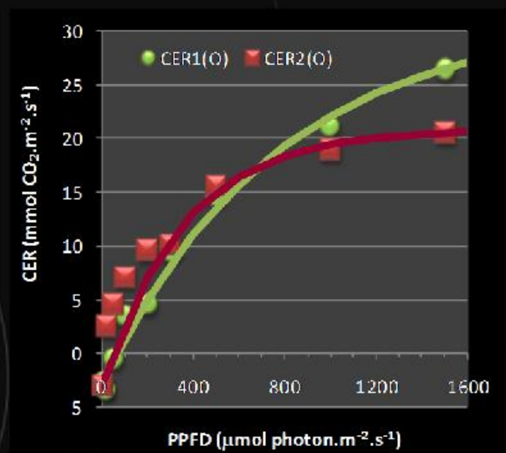
Atas : penampang membujur

Bawah : Penampang melintang

Soybean in Malang

$$P = P_{max}\left[1 - EXP\left(-Q_E PPFD / P_{max}\right)\right]$$





	Pmax	Q_E	$1/Q_E$
CER1	34.0	0.044	22.6
CER2	23.9	0.067	14.9

$1/Q_E$ = mole photon/mol CO_2

$$P = P_{max}\left[1 - EXP\left(-Q_E PPFD / P_{max}\right)\right]$$

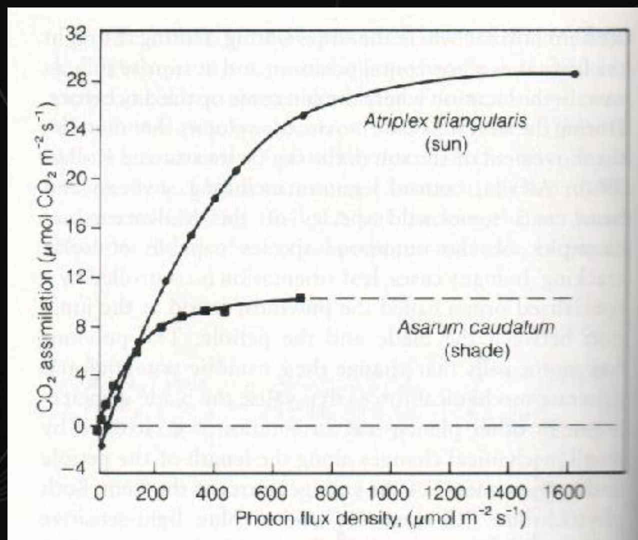
$$\frac{P}{P_{max}} = 1 - EXP\left(-Q_E PPFD / P_{max}\right)$$

$$1 - \frac{P}{P_{max}} = EXP\left(-Q_E PPFD / P_{max}\right)$$

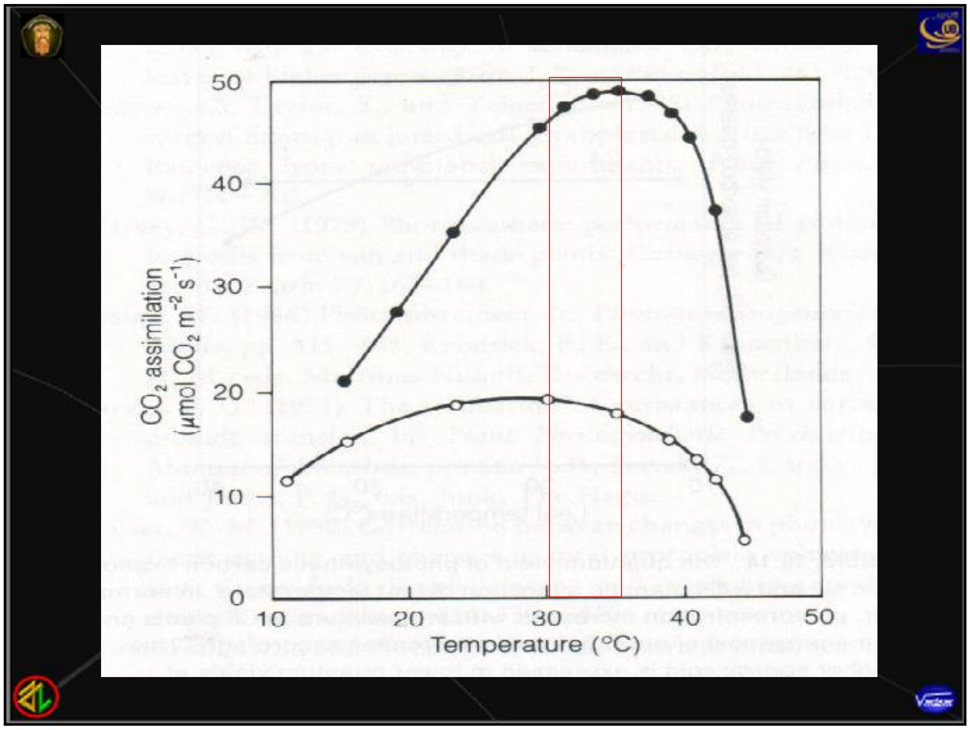
$$\ln\left(1 - \frac{P}{P_{max}}\right) = \frac{-Q_E}{P_{max}} PPFD + 0$$

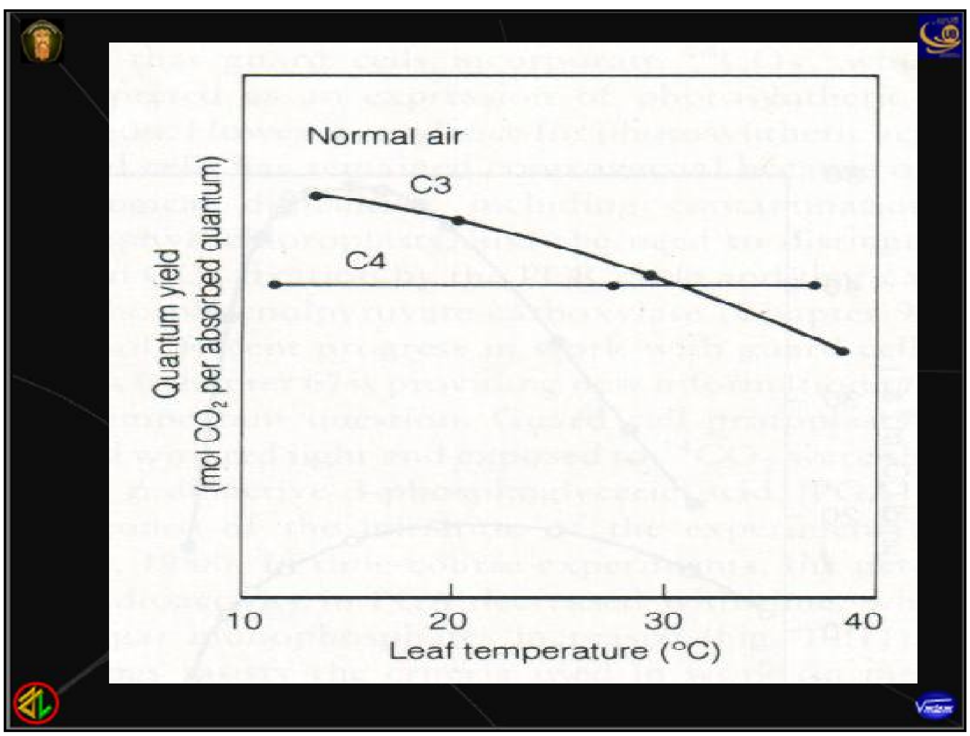
y b x a

LIGHT: Sun and Shade Plants

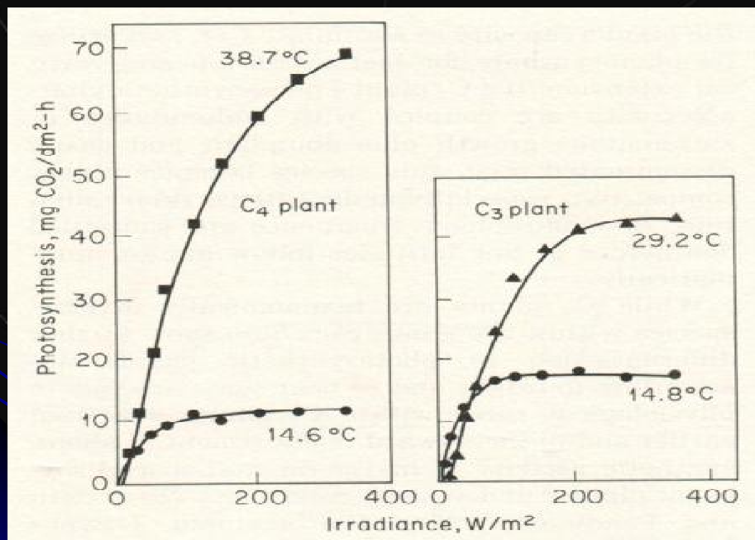


EFFECT OF TEMPERATURE ON PHOTOSYNTHESIS

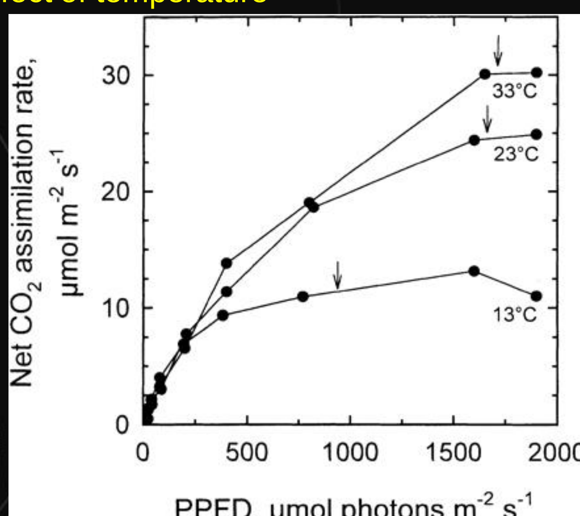

50
40
30
20
10
0
CO_2 assimilation
(μmol CO_2 m^{-2} s^{-1})
10
20
30
40
50
Temperature (°C)


Normal air
C3
C4
Quantum yield
(mol CO_2 per absorbed quantum)
10
20
30
40
Leaf temperature (°C)

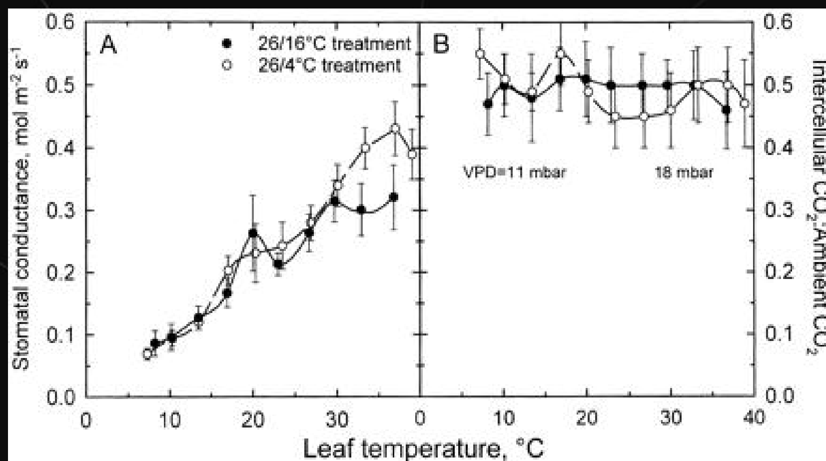
TEMPERATURE & LIGHT

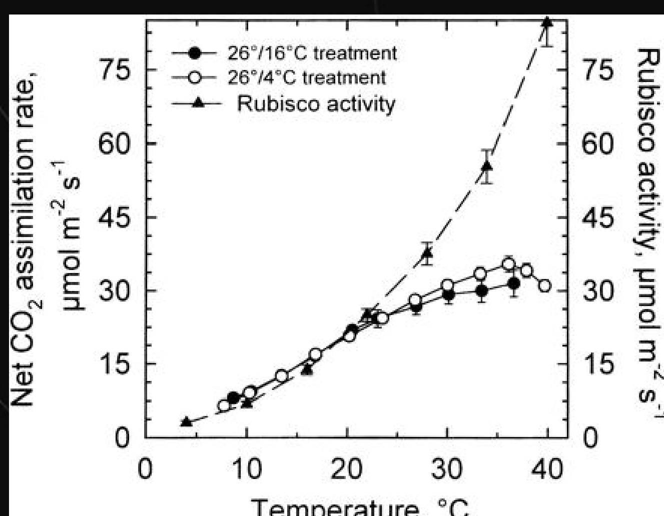


Effect of temperature



Muhlenbergia montana plants grown at 26/16 °C day/night temperature. Arrows indicate the estimated light saturation points used in subsequent temperature response measurements.

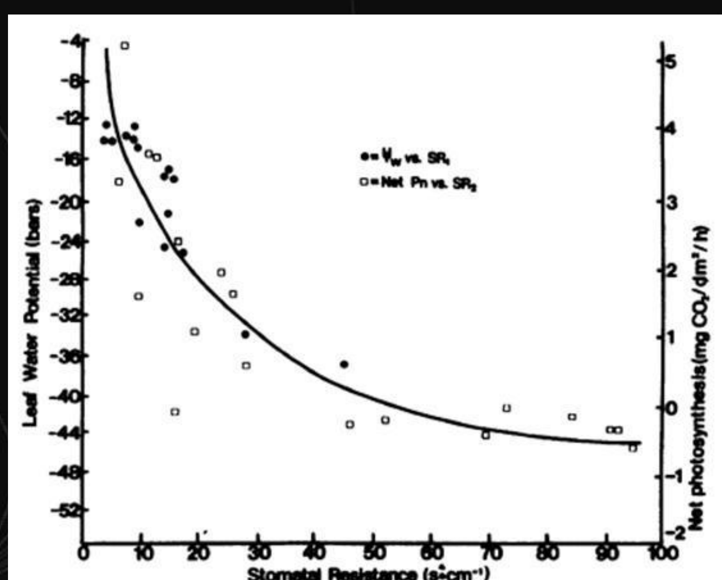


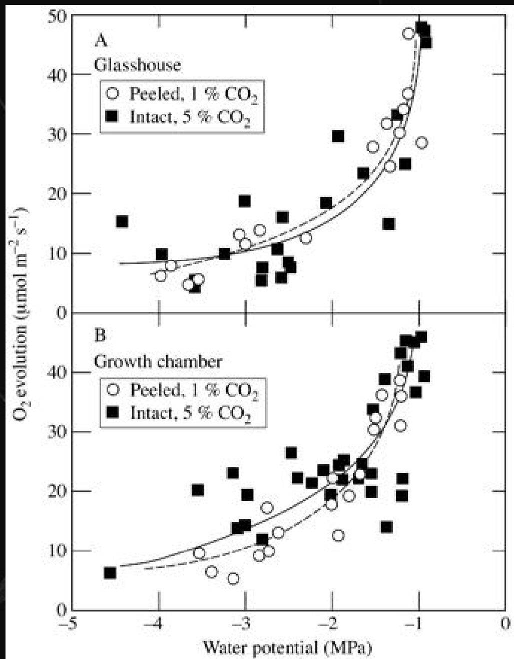


from *M. montana* grown at 26/16 °C or 26/4 °C day/night temperatures. Rubisco activity was determined on leaves of plants grown at 26/16 °C (mean±SE, *N*=4–6)

EFFECT OF WATER ON PHOTOSYNTHESIS

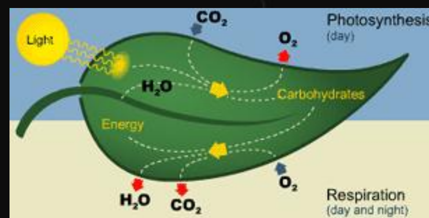
Water

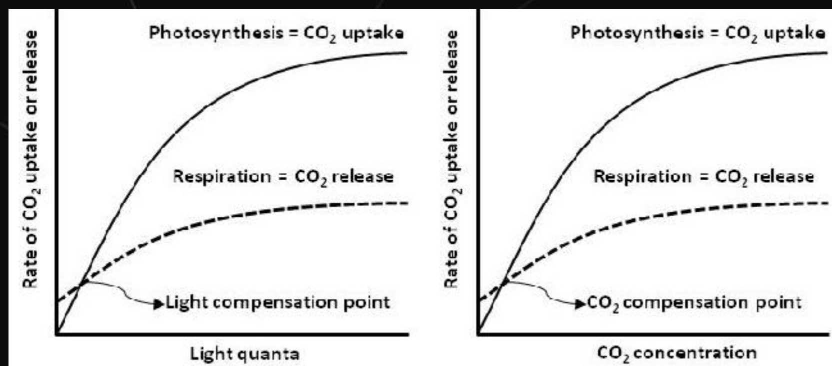




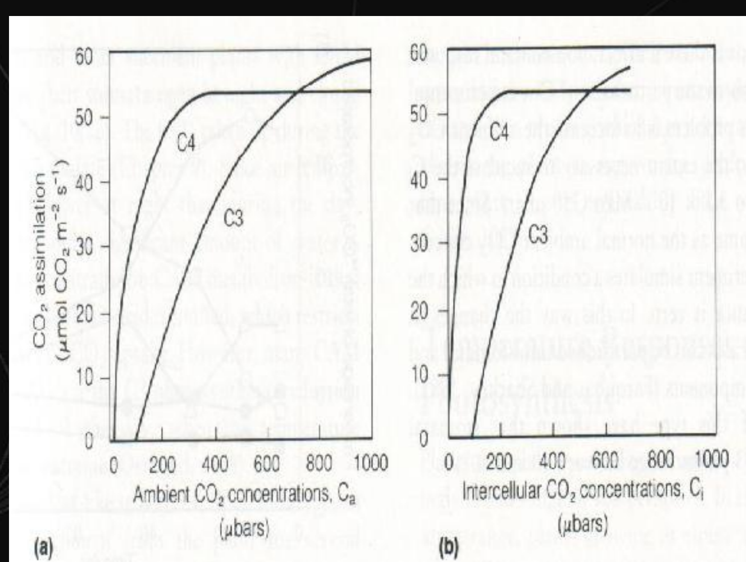
Maximum O_2 evolution at various Ψ_w in sunflower leaf discs. Tang *et al*., 2002

EFFECT OF CO_2 ON PHOTOSYNTHESIS


Light
CO_2
O_2
Photosynthesis
(day)
H_2O
Carbohydrates
Energy
O_2
H_2O
CO_2
Respiration
(day and night)


Photosynthesis = CO_2 uptake
Respiration = CO_2 release
Light compensation point
Rate of CO_2 uptake or release
Light quanta
Photosynthesis = CO_2 uptake
Respiration = CO_2 release
CO_2 compensation point
Rate of CO_2 uptake or release
CO_2 concentration

Ambient [CO_2]


CO_2 assimilation (μmol CO_2 m^{-2} s^{-1})
60
50
40
30
20
10
0
C4
C3
0 200 400 600 800 1000
Ambient CO_2 concentrations, C_a
(μbars)
(a)
60
50
40
30
20
10
0
C4
C3
0 200 400 600 800 1000
Intercellular CO_2 concentrations, C_i
(μbars)
(b)

- CO_2 compensation point
  - for C4 plants - CO_2 comp point is 0-5 ppm
  - for C 3 plants - CO_2 comp point is 30-70 ppm
- C 4 plants have developed mechanisms for surviving and thriving in hotter, drier climates.
- C 3 plants survive and thrive in more moderate climates.

CO_2 compensation

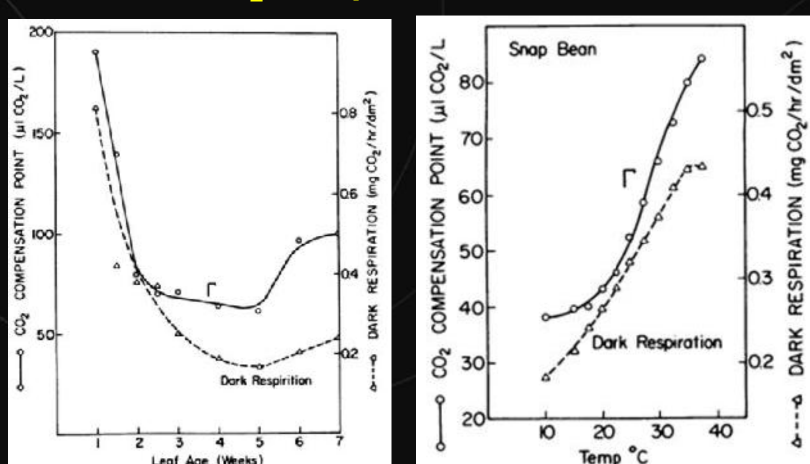
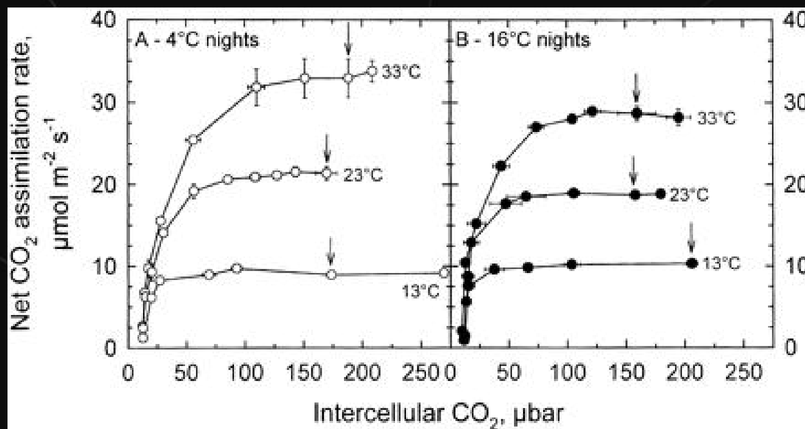
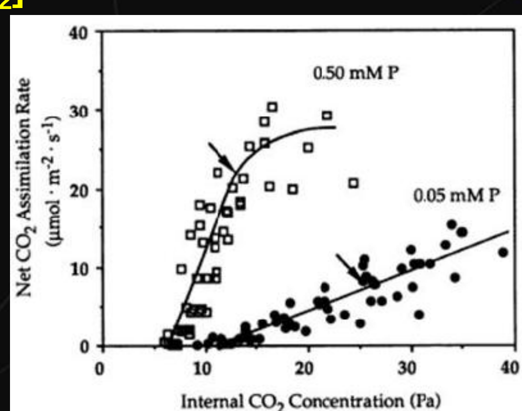


FIG. 1. Change in CO_2 compensation point and dark respiration with age of snapbean leaves. All assays were run on leaflets of the second trifoliate (Smith et al., 1976).



Intercellular [CO_2]

Net $C0_2$ assimilation rate versus leaf internal $C0_2$ concentration response curves for the 0.50 (open squares) and 0.05 mM Pi (closed circles) treatments. The arrows indicate the point on the curves which correspond to the mean photosynthetic rate of 34 Pa $C0_2$.



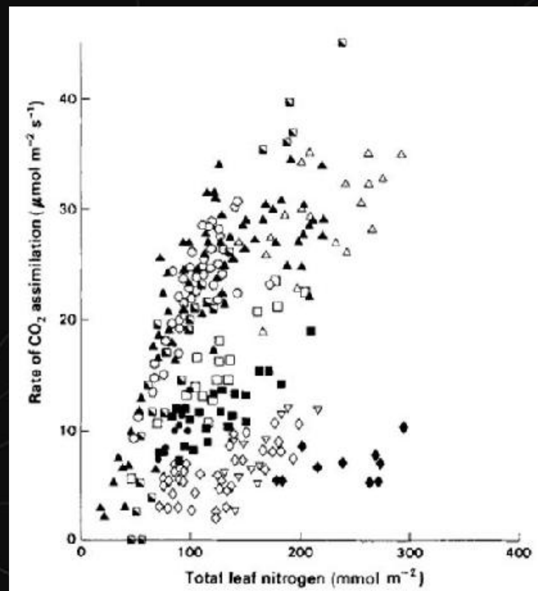
Greenhouse grown plants were allowed to adapt to the growth chamber for at least 48 h before measurement. Three separate experiments representing a total of eight leaves from each treatment were measured. Leaves were illuminated with saturating PPFD (>1100 lmol.m2. -s1). Each datum represents a single determination.). Lauer *et al*., 1989

EFFECT OF NUTRIENTS ON PHOTOSYNTHESIS

High Phosphate (0.5 mM Pi) | **Low Phosphate (0.05 mM Pi)**

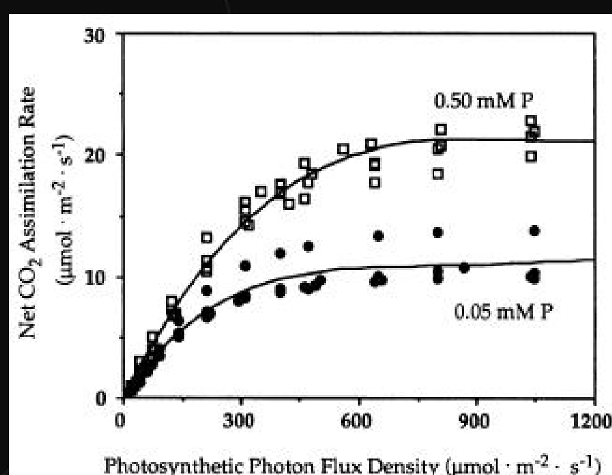
Heliotropic response of soybeans grown on 0.50 mM Pi (left) or 0.05 mM Pi (right). The photographs were taken at 1 p.m. (b, e). Lauer *et al*., 1989

NUTRIENTS: Nitrogen

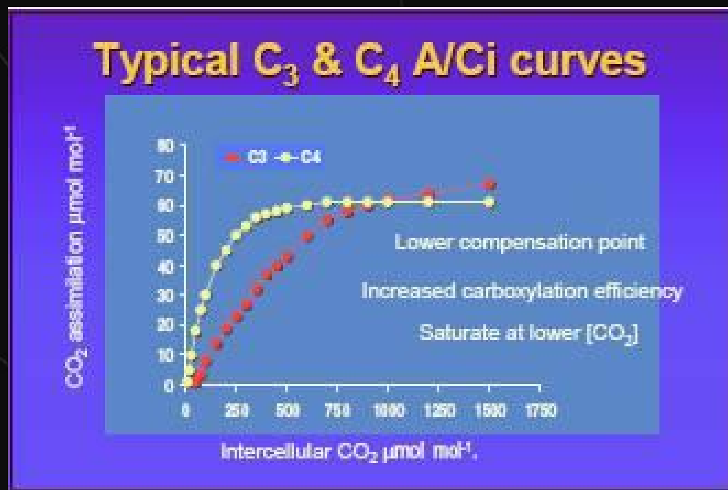


Rate of CO_2 assimilation at high irradiance versus leaf nitrogen content, both expressed per unit leaf area for several plant species. Evans, 1989

NUTRIENTS: Phosphate

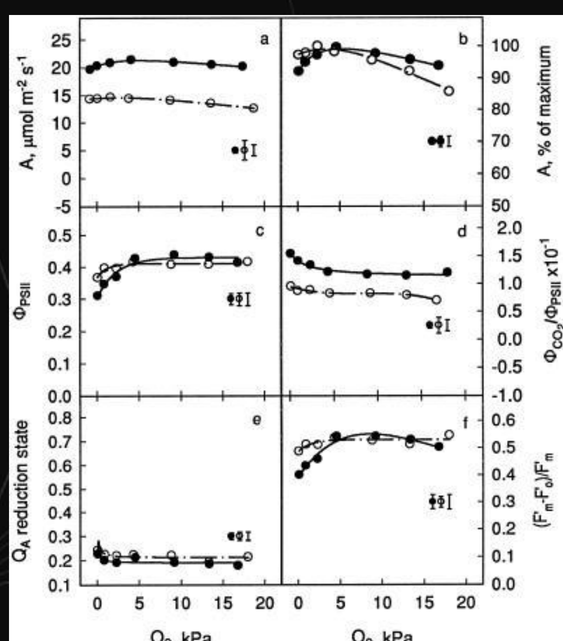


Light response curve (A versus PPFD) for the 0.50 (open squares) and 0.05 mm Pi (closed circles) treatments. Greenhouse grown plants were allowed to adapt to the growth chamber for 6 d before measurement. Leaves were oriented perpendicular to the light source during measurement. Four leaves of each treatment were measured. Each datum represents a single determination.). Lauer *et al*., 1989



- C4 saturates at a lower CO2 concentration
- C4 has higher carboxylation efficiency
- Maximum CO2 assimilation at high CO2 concentration is higher in C3.

O_2



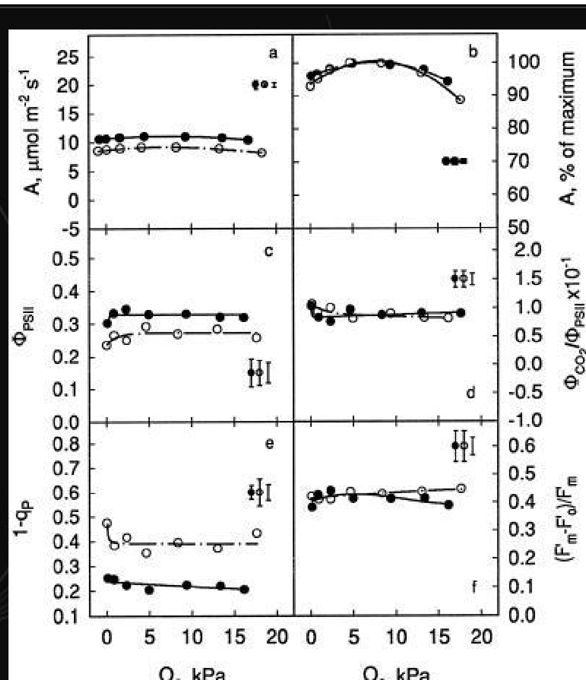
in *A. edulis* wild-type plants

F_m maximum fluorescence level after a saturating light pulse on a dark-adapted leaf

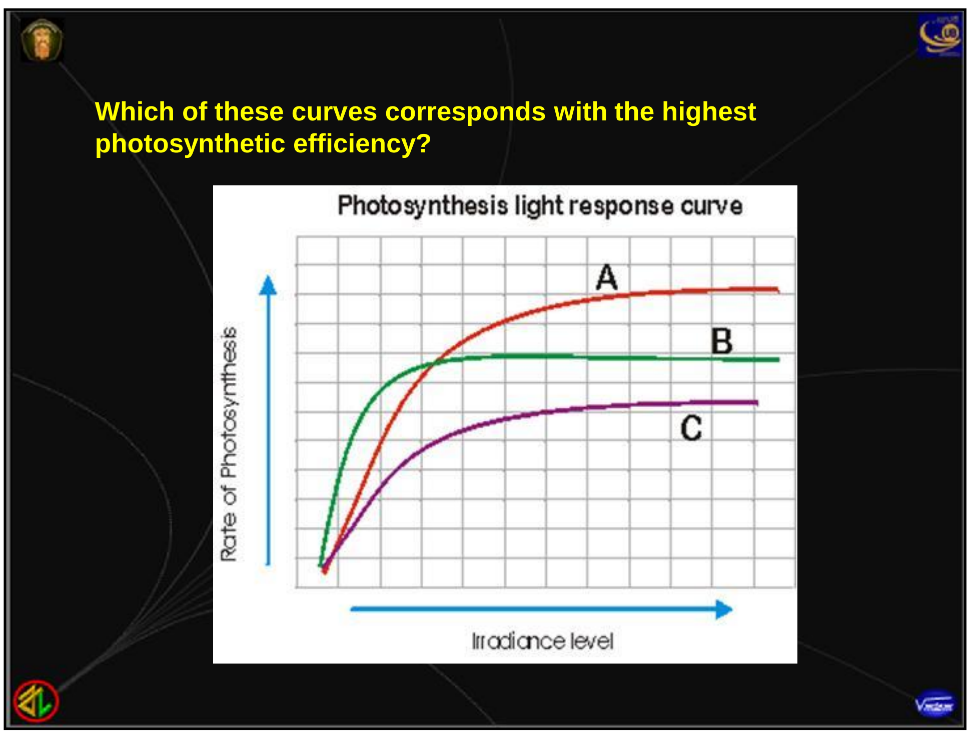
F'_m maximum fluorescence after a saturating light pulse from a leaf during steady-state photosynthesis$F_o$basal fluorescence level on a dark-adapted leaf

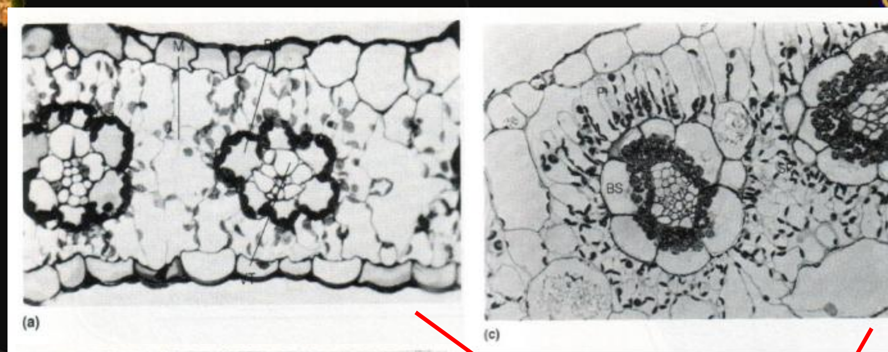
F'_o minimum fluorescence from a leaf following steady-state illumination and quickly dark adapted under a pulse of far-red light to fully oxidize PSI

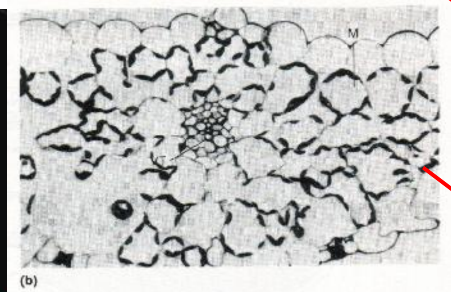
F_s steady-state fluorescence on an illuminated leaf




THANK YOU
http://leavingbio.net/TheStructureandFunctionsofFlowers%5B1%5D.htm
Спасибо
謝謝
شكراً

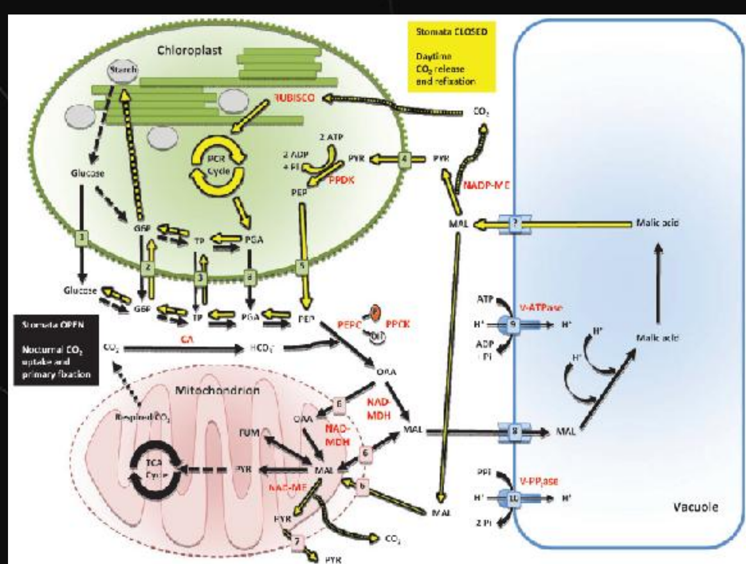

Which of these curves corresponds with the highest photosynthetic efficiency?
Photosynthesis light response curve
A
B
C
Rate of Photosynthesis
Irradiance level





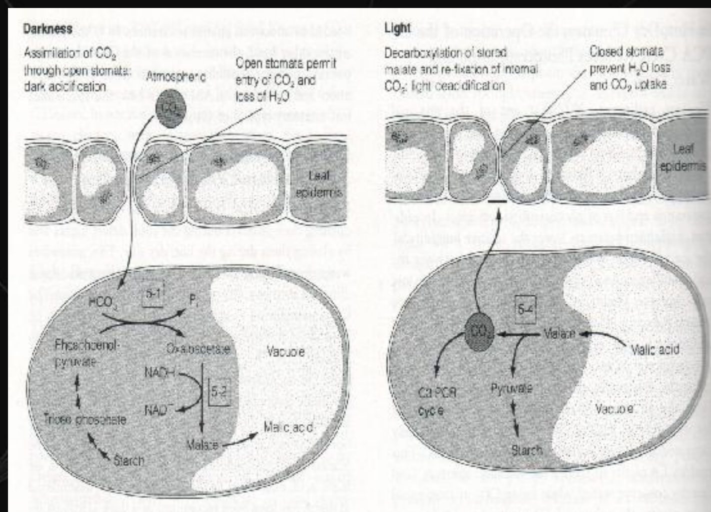
C4 Plants:
(a). *Zea maize* (350x)
(c). *Gomphrena* (740x)

C3 Plants: *Avena Sativa* (380x)



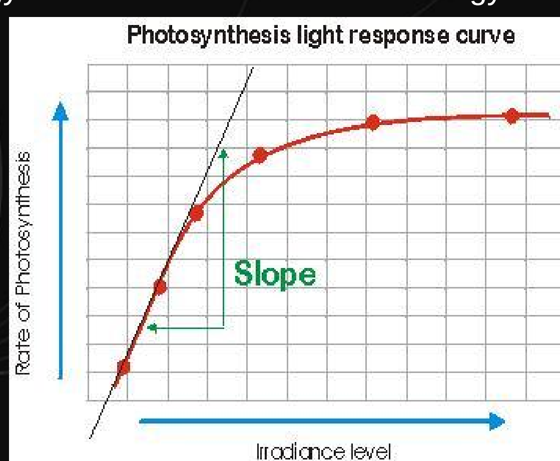
Phase I, black arrows; Phase II, the transition of PEPC to RUBISCO, Phase III, yellow arrows; Phase IV, CO_2 fixation

CO_2 Reduction in CAM (Crassulacean Acid Metabolism) Plants



Photosynthetic Efficiency

The slope of the linear phase of the response curve is a measure of "photosynthetic efficiency" -- how efficiently solar energy is converted into chemical energy.



CO_2 Fixation in C_3 vs. C_4 Plants

a. CO_2 fixation in a C_3 plant, blue columbine, *Aquilegia caerulea*

b. CO_2 fixation in a C_4 plant, corn, *Zea mays*

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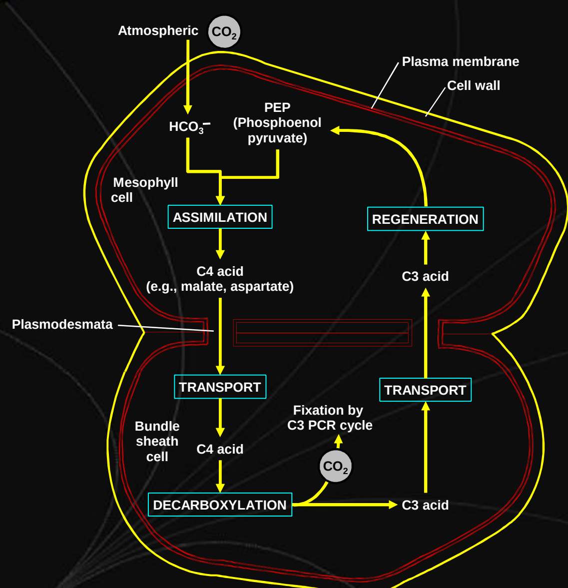

Basic Reaction of CO_2 reduction in C4 plants

Lycopodiella cernua, paku kawa

3. CO_2 Reduction

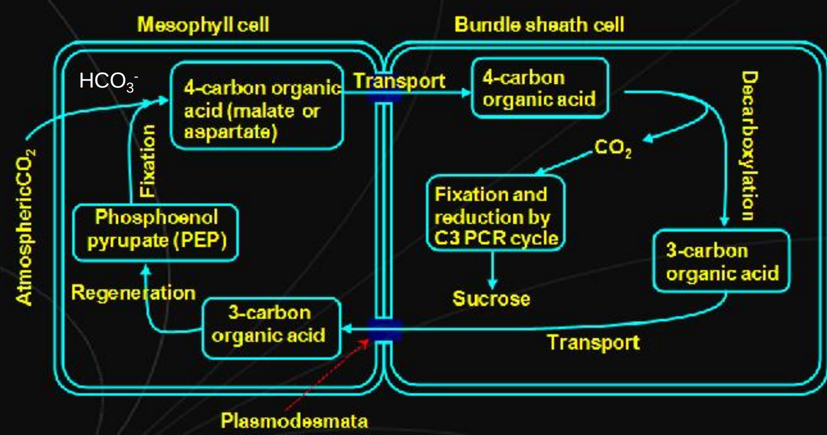

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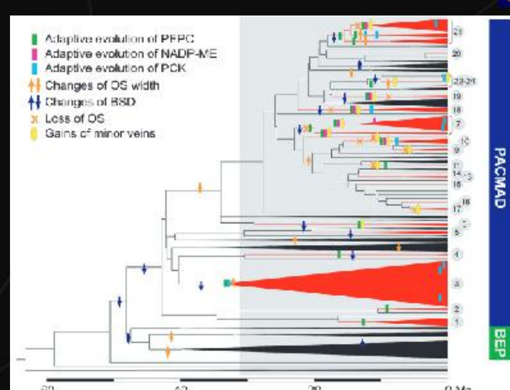
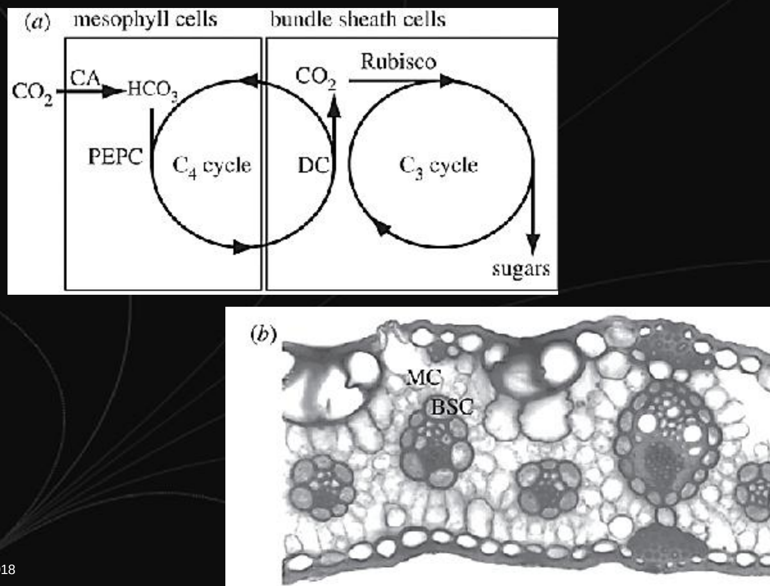
Fig. 3 Gradual accumulation of C4 characters inferred for grasses. The dated phylogenetic tree for grasses was obtained from Christin et al. (2013b), with the timescale given in millionyears (Myr). All groups containing only C3 or C2 species are compressed and in black. Monophyletic C4 groups are compressed in red, with their numbering on the right following GPWGII (2012).

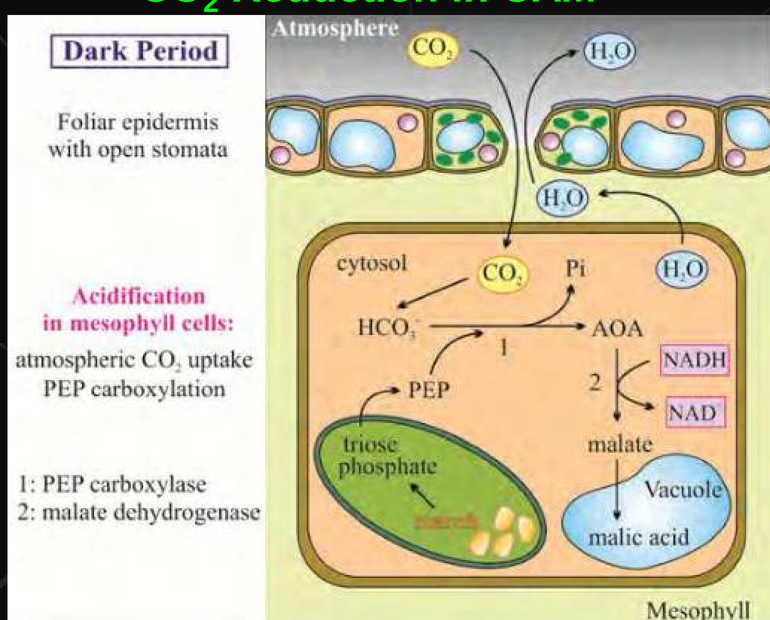


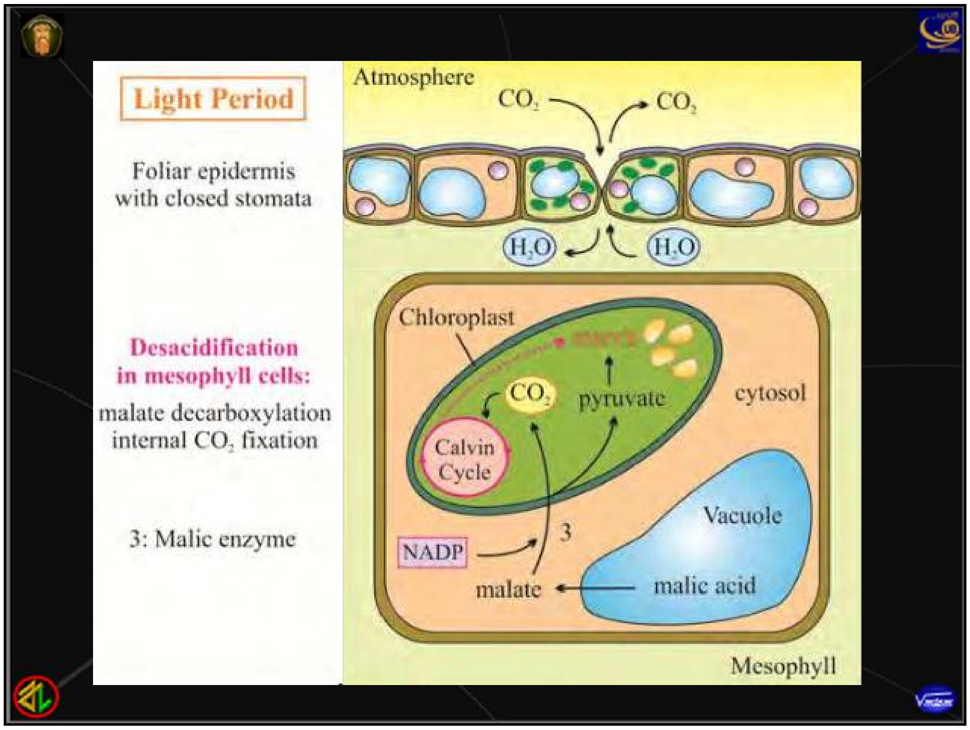
The two main grass clades are delimited on the right (BEP and PACMAD). Important changes in anatomical characters are reported based on Christin et al. (2013b).Episodes of adaptive evolution of C 4 enzymes are based on Christin et al. (2007,2009a,b). The changes shown here represent only a fraction of all changes linked to C4 evolution and their positioning is approximate because the species sampling was not identical in the different studies. The grey box represents the last 30 Myr, when atmospheric CO_2 stayed below 500 ppm. OS, outer bundle-sheath; BSD, distance between consecutive bundle-sheaths; PEPC, phosphoenol pyruvate carboxylase; NADP-ME, NADP-malic enzyme; PCK, phosphoenol pyruvate carboxykinase.

3. CO_2 Reduction



CO_2 Reduction in CAM




Light Period
Foliar epidermis
with closed stomata
Desacidification
in mesophyll cells:
malate decarboxylation
internal CO_2 fixation
3: Malic enzyme
Atmosphere
CO_2
CO_2
H_2O
H_2O
Chloroplast
CO_2
pyruvate
cytosol
Calvin
Cycle
Vacuole
3
NADP
malate
malic acid
Mesophyll