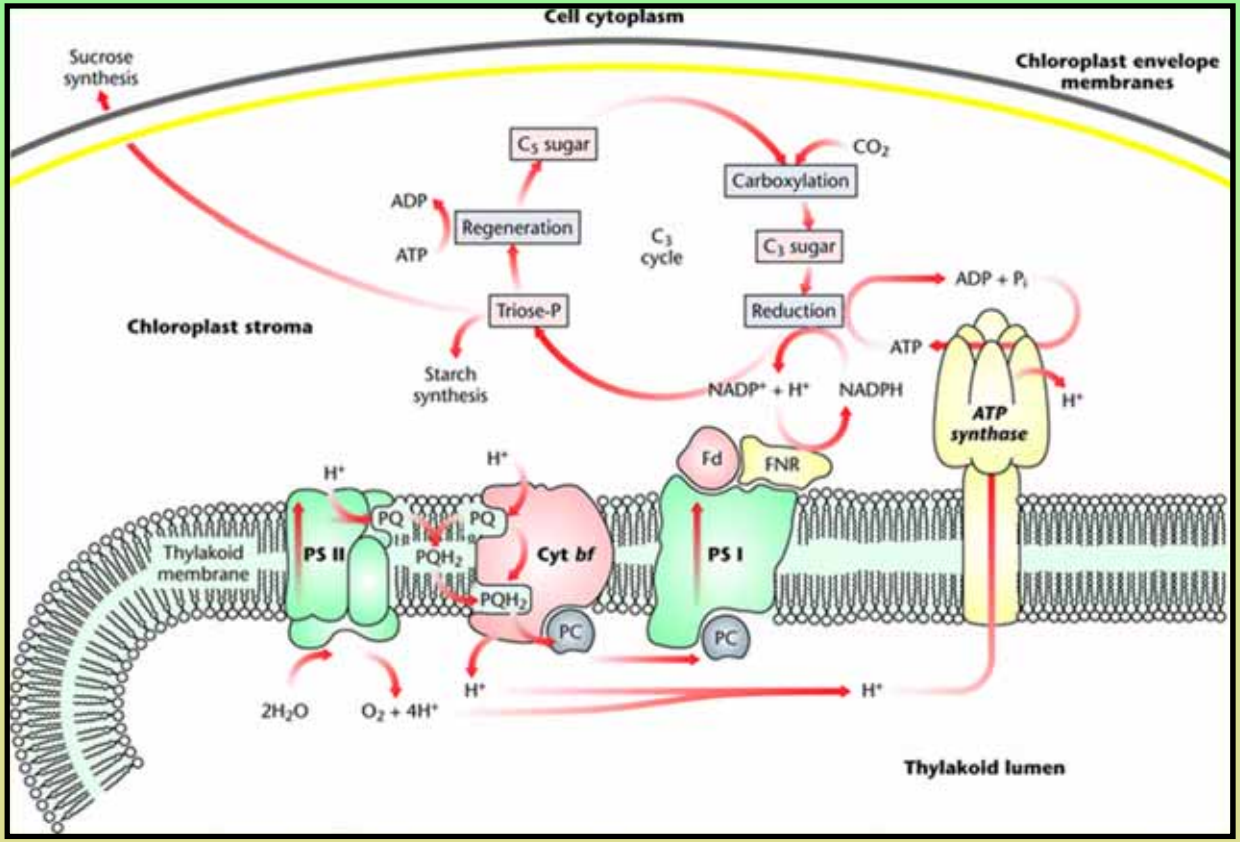
Fotosyntéza

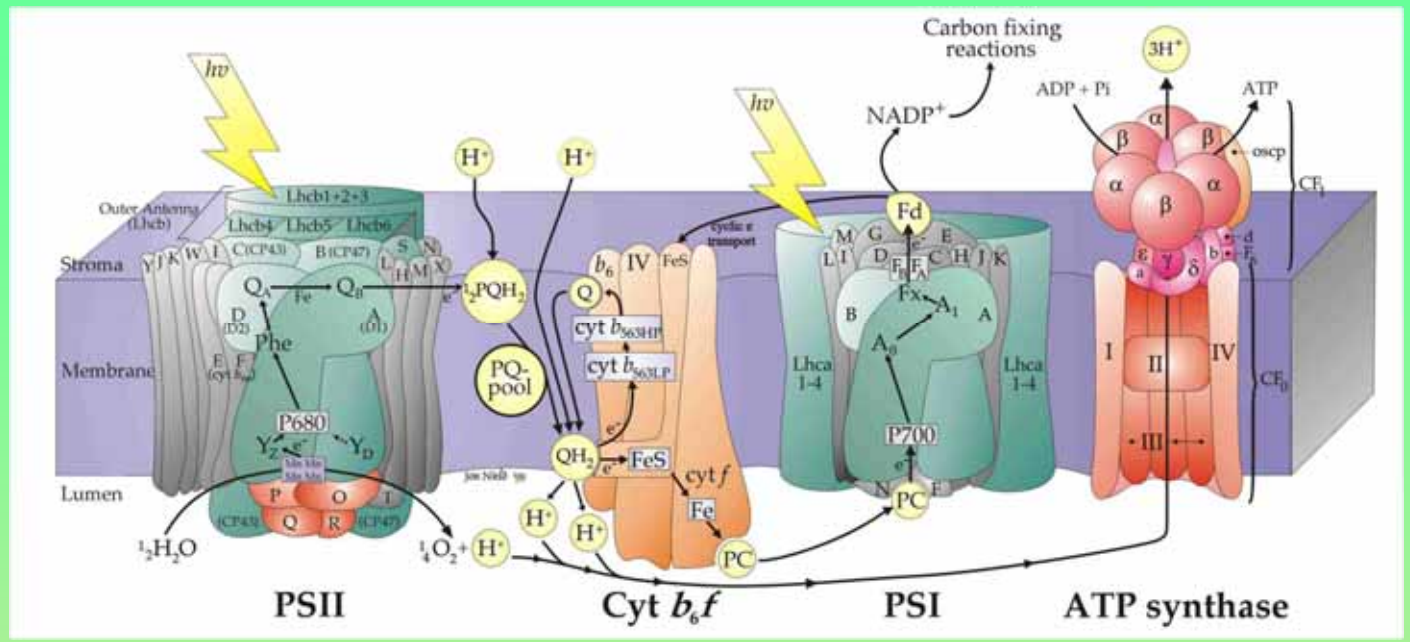
Uhlíkový metabolismus

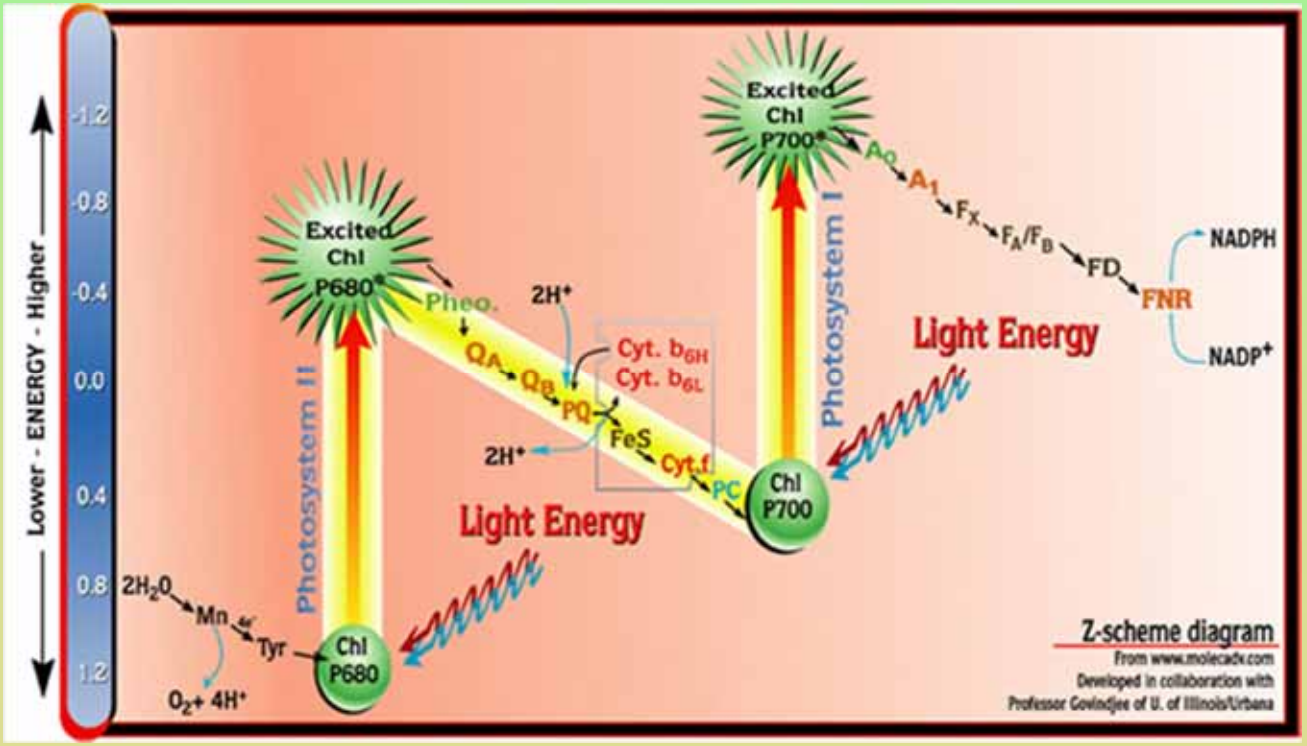
Ondřej Prášil
Mikrobiologický ústav AVČR
Laboratoř fotosyntézy v Třeboni

Čtyři fáze procesu přeměny energie ve fotosyntéze

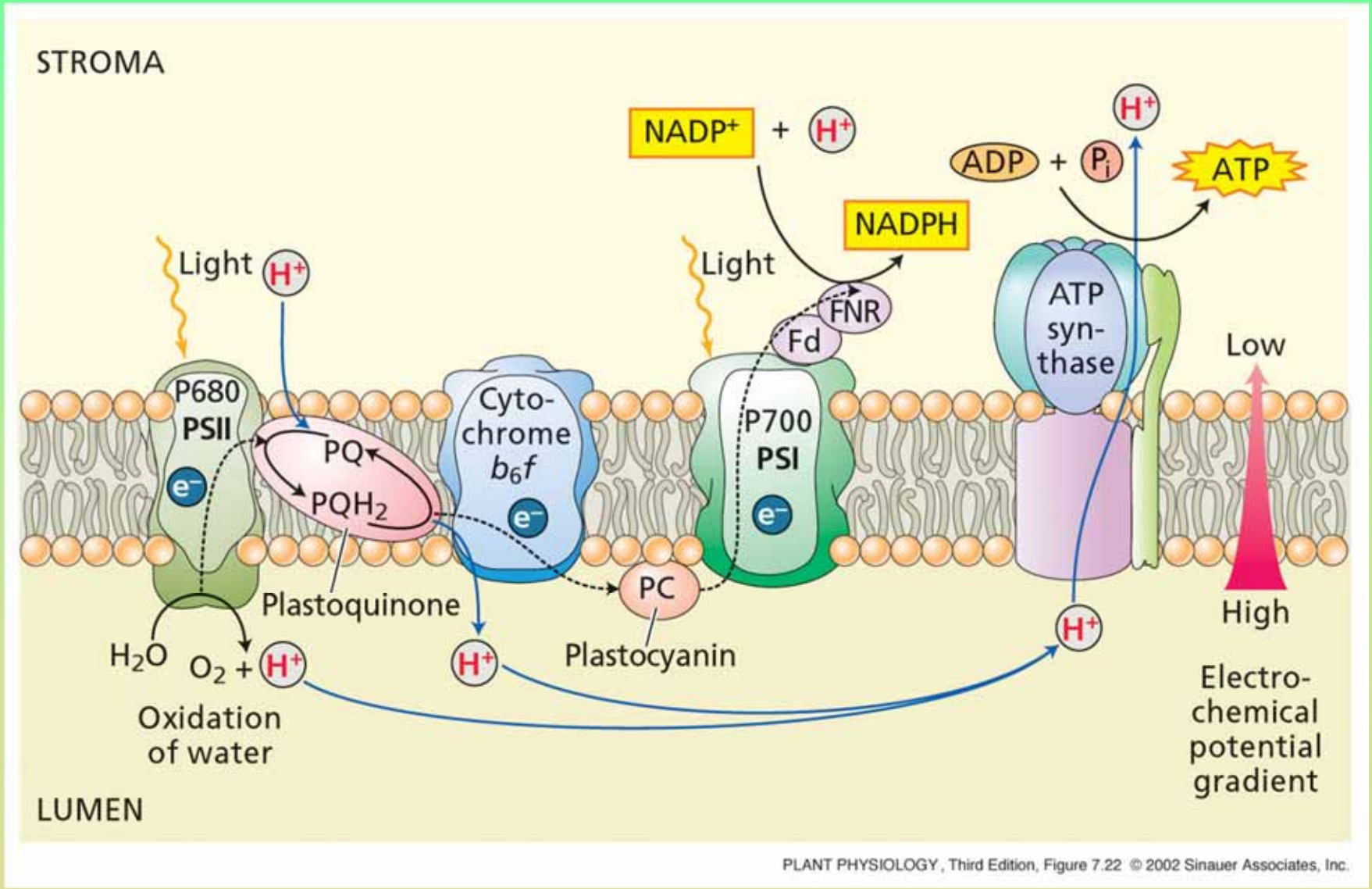
1. absorbce světla a přenos energie v anténních systémech
2. primární rozdělení nábojů a přenos elektronů v reakčních centrech
3. stabilizace energie v sekundárních procesech
4. syntéza a export stabilních produktů




Carbon fixing reactions
3H+
ADP + Pi
ATP
NADP+
hν
hν
H+
H+
Outer Antenna (Lhcb)
Lhcb1+2+3
Lhcb4
Lhcb5
Lhcb6
Stroma
Membrane
Lumen
Fd
oscp
CF1
CF0
Lhca 1-4
Lhca 1-4
P680
P700
PQ-pool
cyt b563H
cyt b563LP
FeS
cyt f
Fe
PC
QH2
PSII
Cyt b6f
PSI
ATP synthase


Lower - ENERGY - Higher
-1.2
-0.8
-0.4
0.0
0.4
0.8
1.2
Excited Chl P680*
Pheo.
2H+
QA
QB
PQ
Cyt. b6H
Cyt. b6L
FeS
Cyt.f
PC
Chl P700
2H+
Light Energy
Photosystem II
Photosystem I
Excited Chl P700*
A0
A1
FX
FA/FB
FD
FNR
NADPH
NADP+
Light Energy
2H2O
Mn
Tyr
Chl P680
O2+ 4H+
Z-scheme diagram
From www.molecadx.com
Developed in collaboration with
Professor Govindjee of U. of Illinois/Urbana

Vektoriální přenos elektronů a protonů



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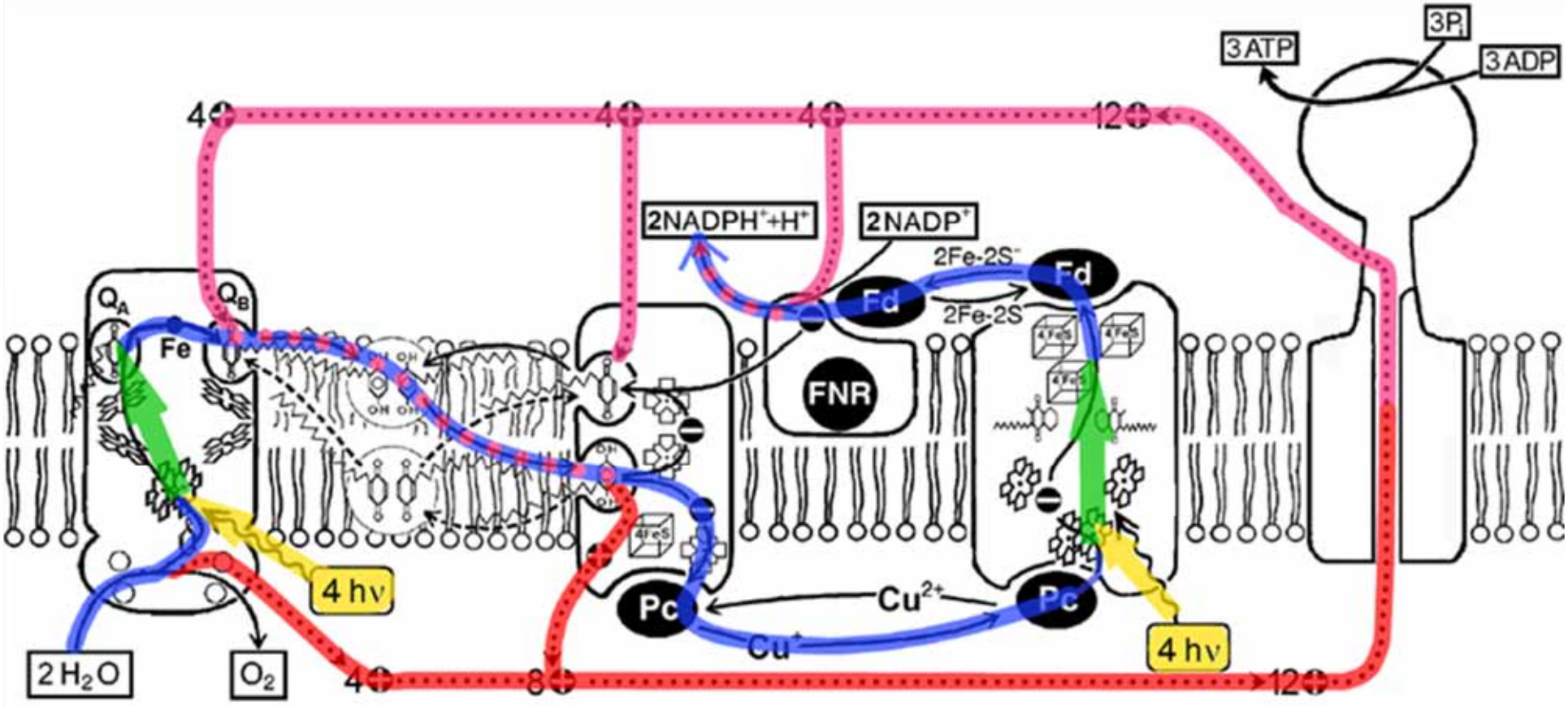
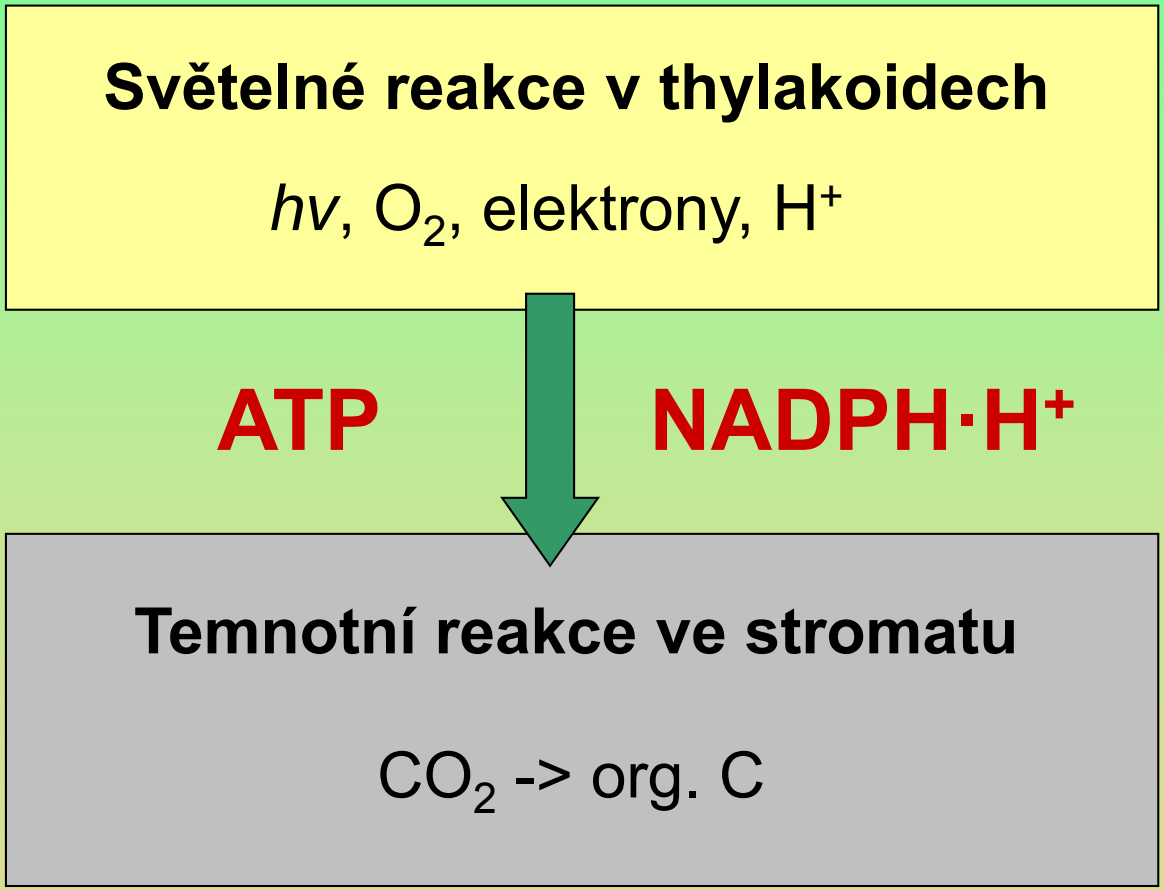


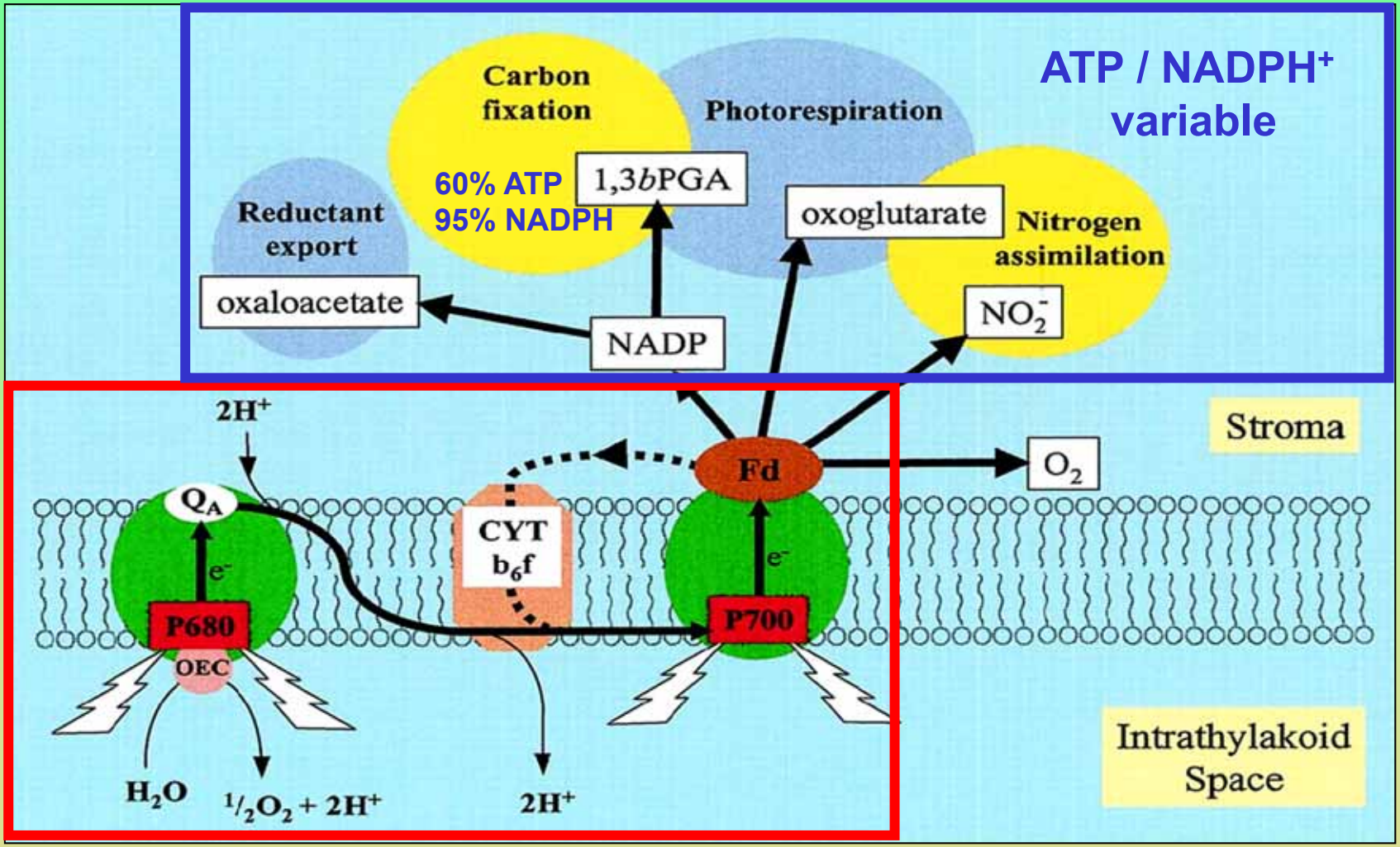
$2H_2O$ + **2NADP$^+$** +**2H$^+$** ->O_2 + **2NADPH** + $4H^+$

2NADPH + $12H^+$

Přeměna energie



Multiple pathways for spending the photosynthetic currency



Noctor and Foyer 2000

ATP / $NADPH^+$ ~ 1.5

ETM (membrány přeměny energie)

Přeměny energie:

Energie fotonů $h\nu$

Excitační energie chlorofylu a

Energie elektronů na různých redoxních potenciálech: membránové elektronové řetězce ΔE

Energie koncentrací iontů na membráně $\Delta \mu_{H^+}$

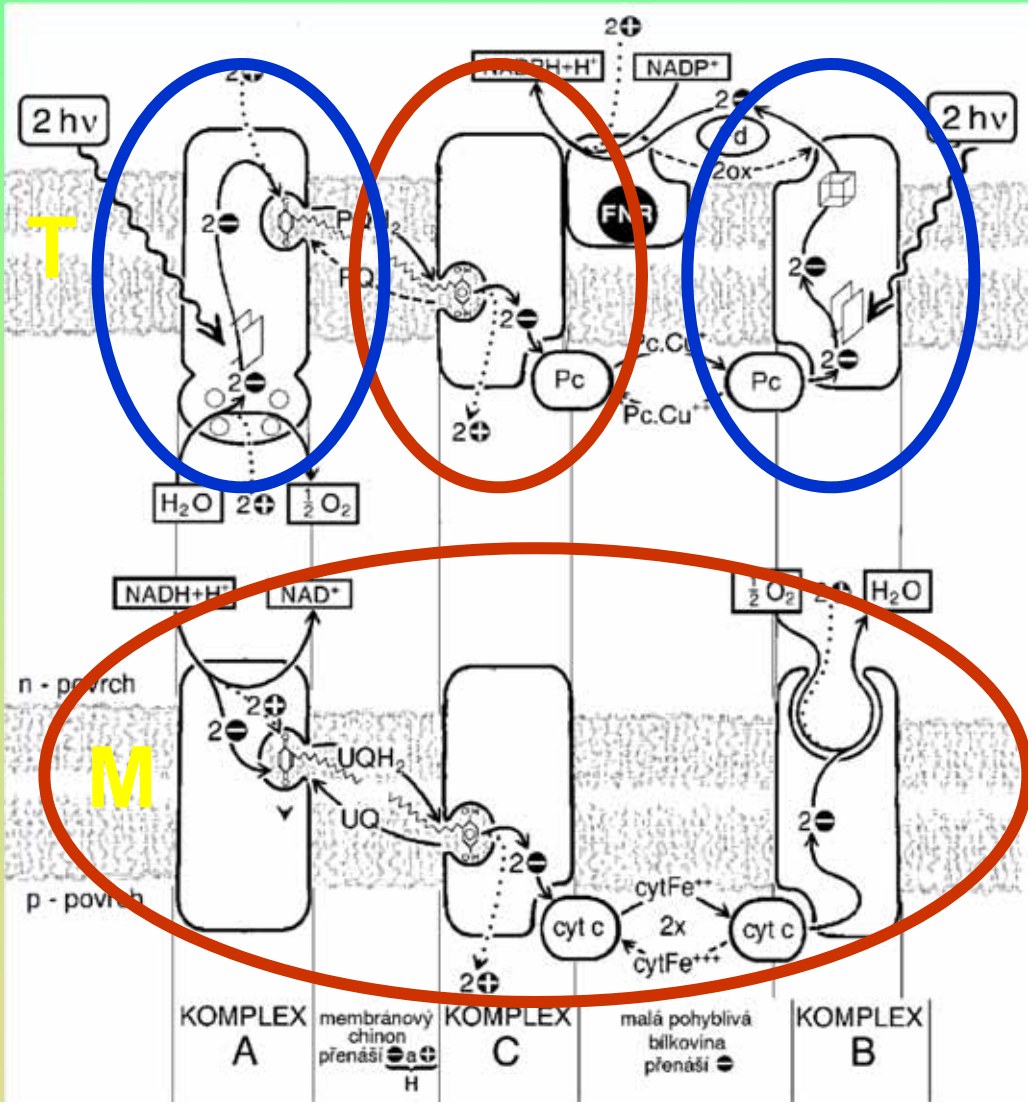
Energie anhydridové chemické vazby ATP ΔG_{ATP}

$$h\nu \rightarrow \Delta E \rightarrow \Delta \mu_{H}^{+} \rightarrow \Delta G_{ATP}$$

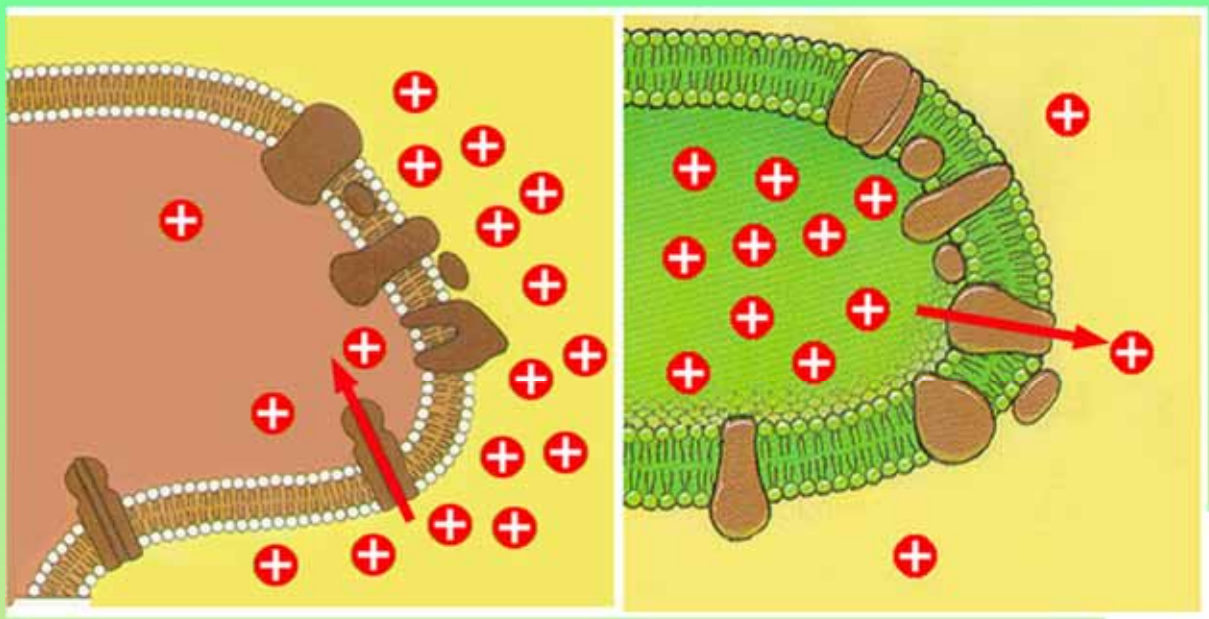
1. Generátory chemického potenciálu $\Delta \mu$**H+**

2. Generátory oxidačně redoxního potenciálu ΔE

$h\nu \rightarrow \Delta E$

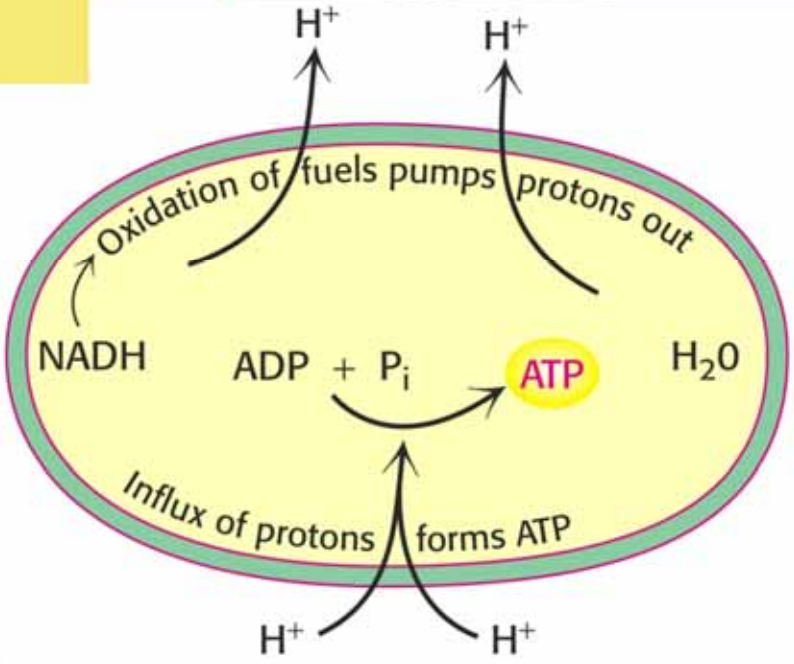


Vztah mezi různými formami volné energie

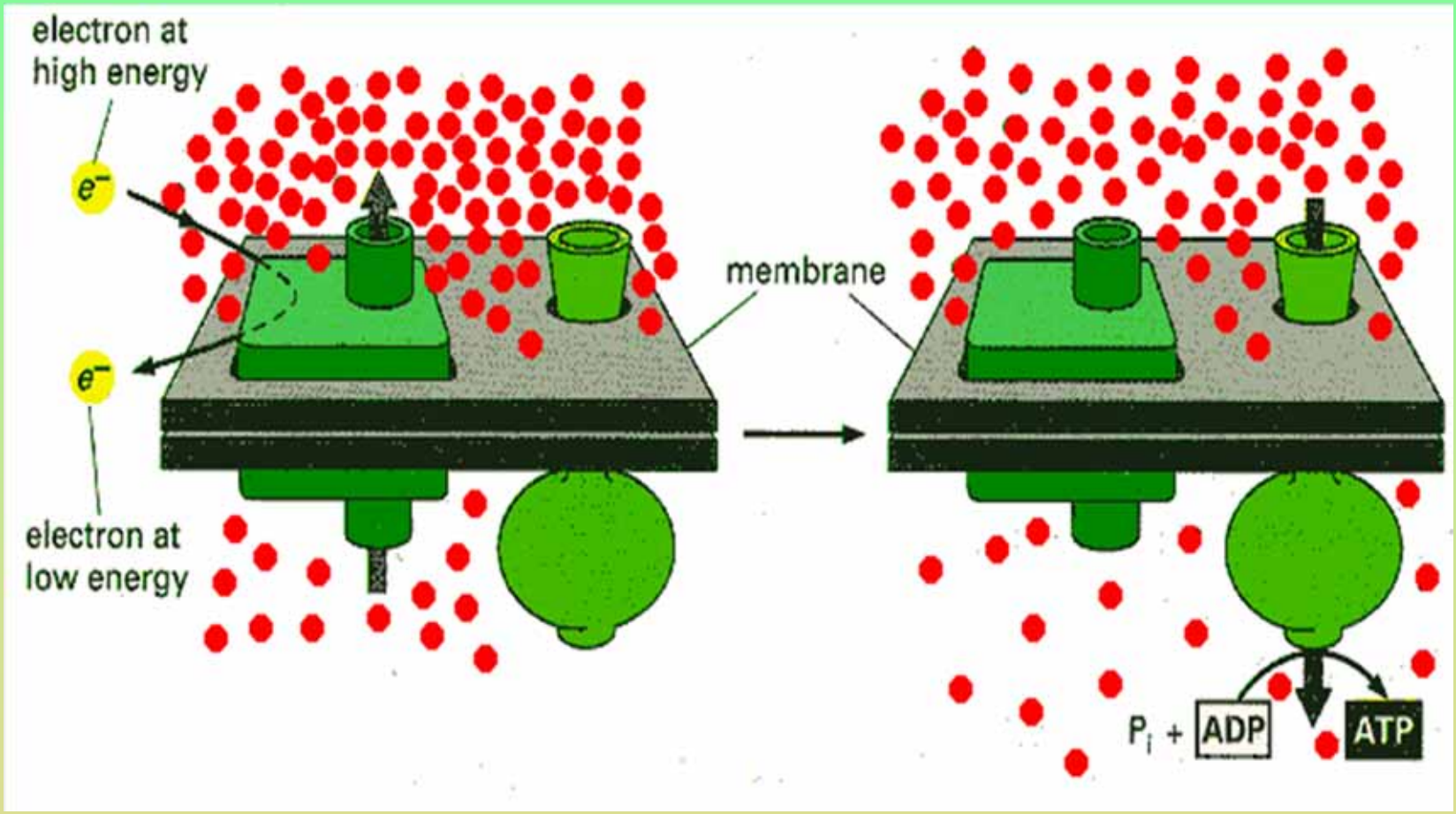


Peter Mitchell - Nobelova cena 1978
John Walker – Nobelova cena 1997
Paul Boyer – Nobelova cena 1997

- Rozdíl koncentrace iontů na membráně
- Protonmotorická síla ($\Delta\mu_H = \Delta pH + \Delta\psi$)

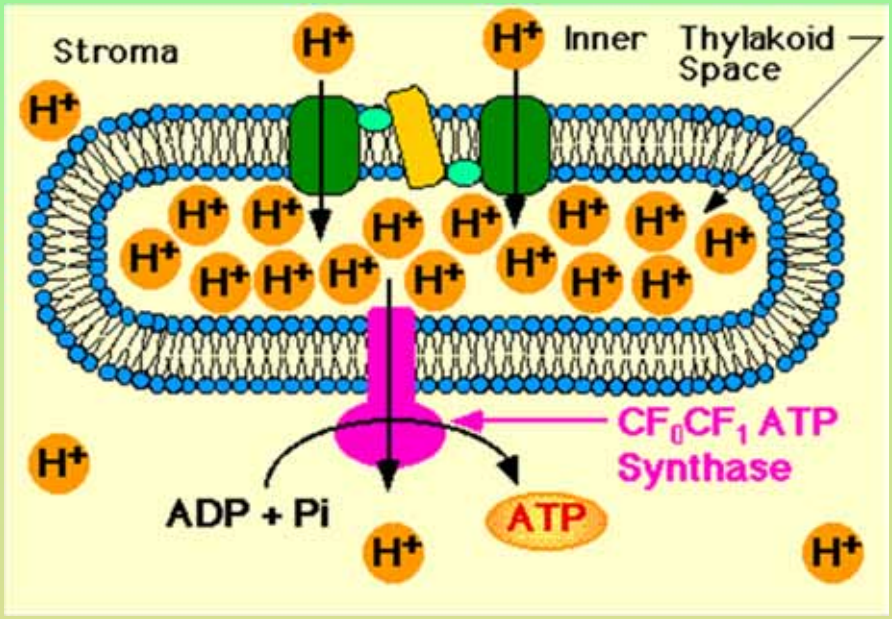


Principal of the ATP generation on the membrane



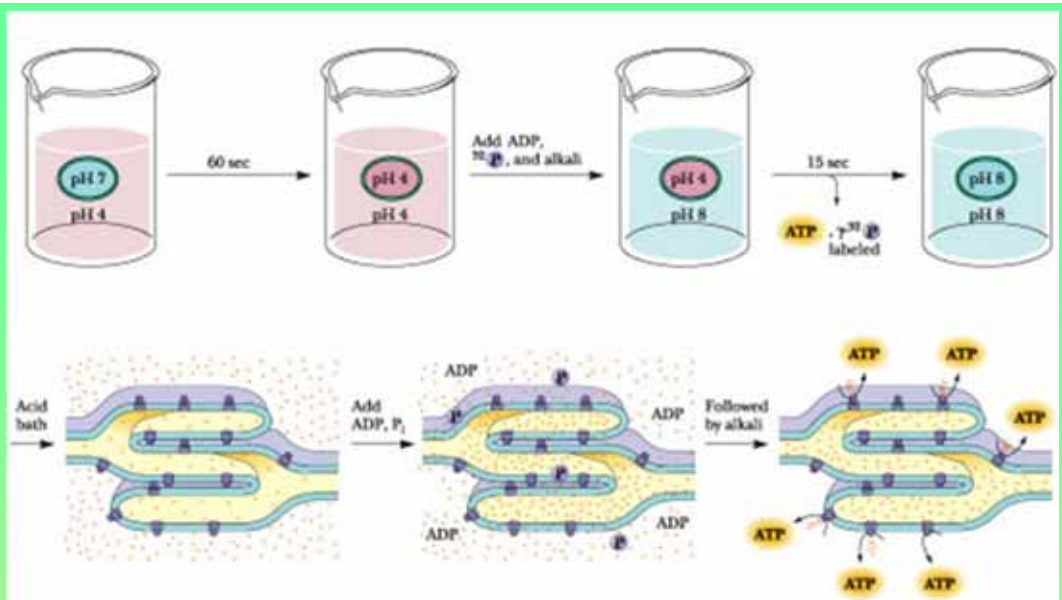
Chemiosmotic hypothesis

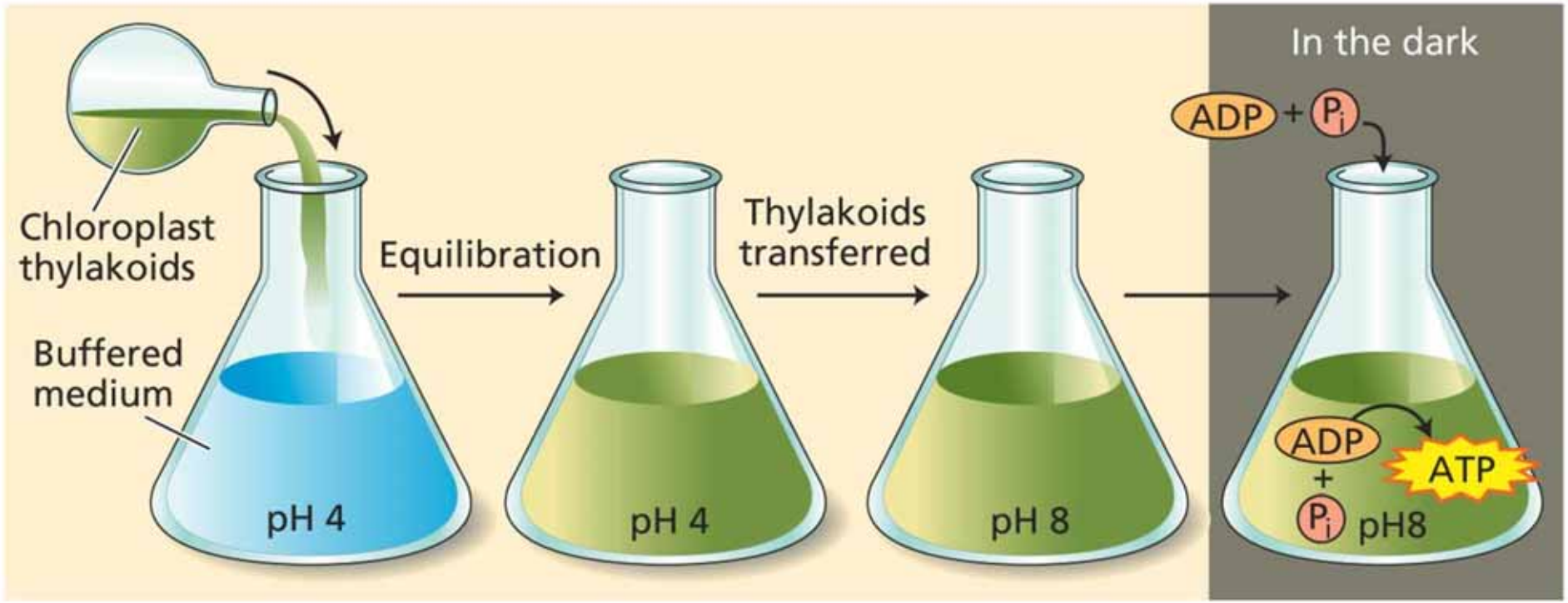
$$\Delta\mu_H^+ = F\,\Delta\Psi - 2.3\,RT\,\Delta pH$$



ΔΨ	electrochem. potential
ΔpH	proton potential
F	Faraday constant
R	gas constant
T	temperature (in K)

Tvorba ATP v chloroplastech i v nepřítomnosti světla





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$\Delta p = \Delta\Psi - 59\ \Delta pH$

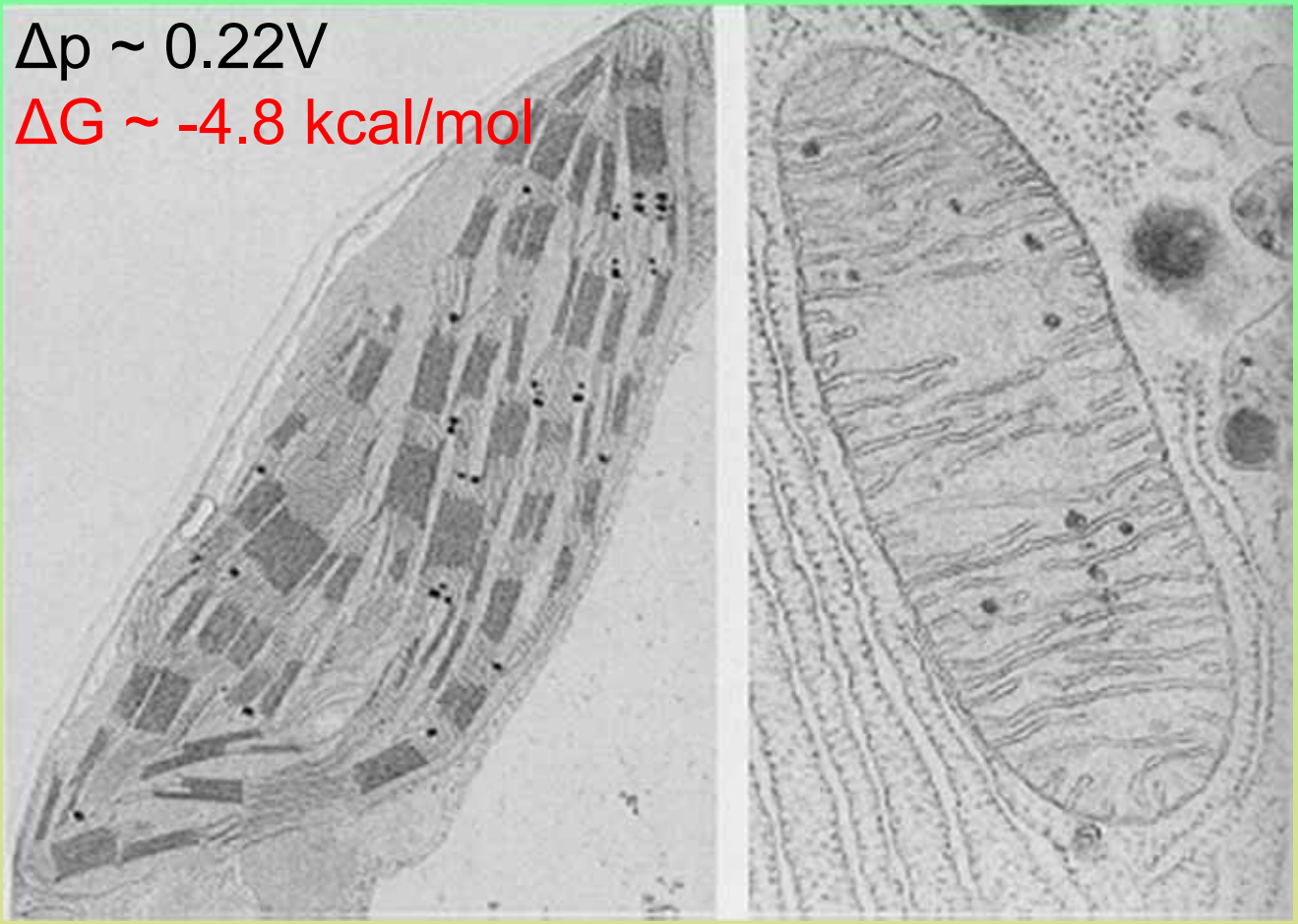
$\Delta pH > 3$

$\Delta p = \Delta\Psi - 59\ \Delta pH$

$\Delta\psi > 180$ mV

$\Delta p \sim 0.22V$

$\Delta G \sim -4.8$ kcal/mol



Difference due to thylakoid membrane permeability to Cl^- and Mg^{2+}

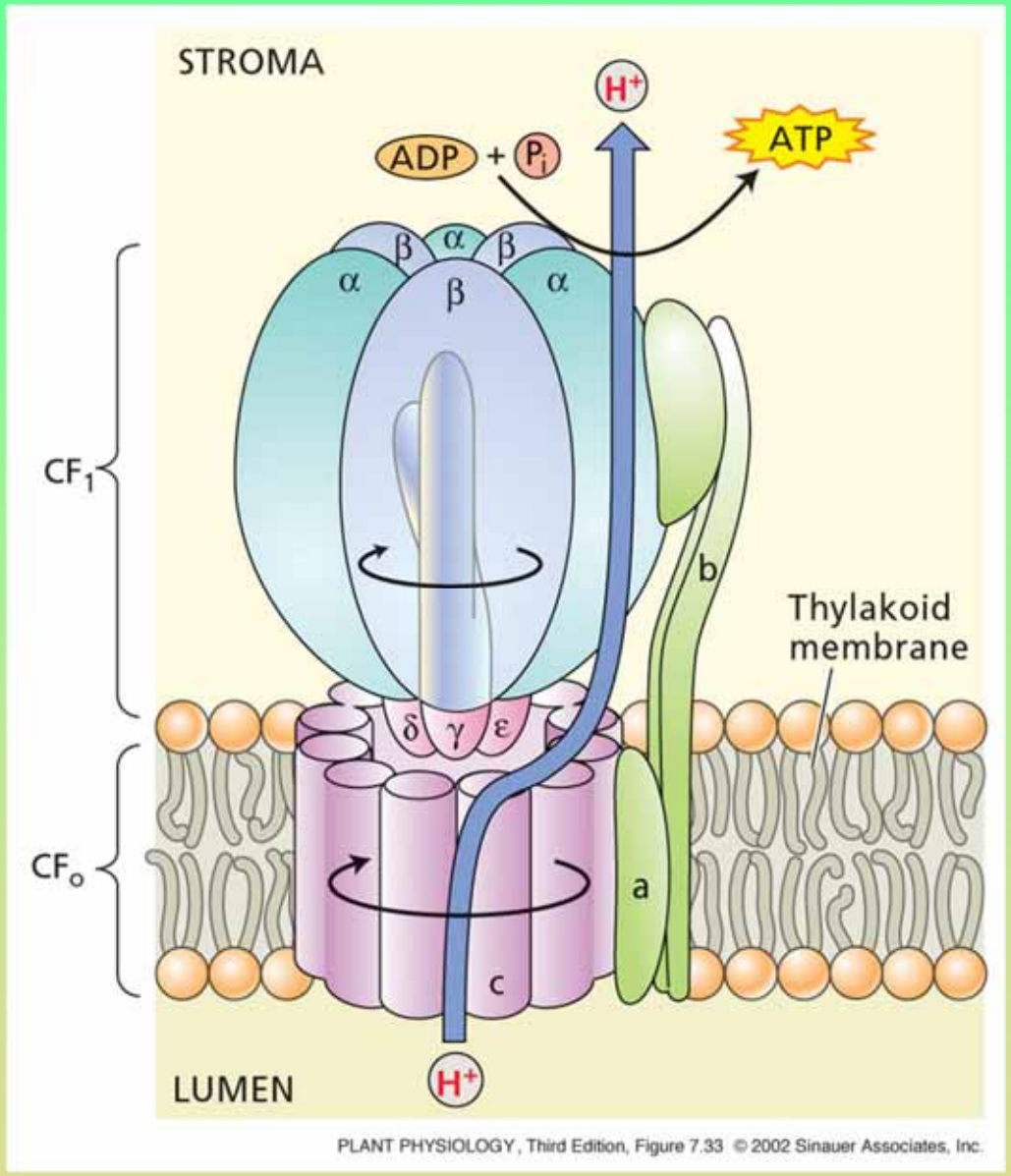
CF_0-CF_1 ATPáza (reverzibilní protonová)

10-13 c podjednotek CFo spojeny s γ podjednotkou CF1 = rotor

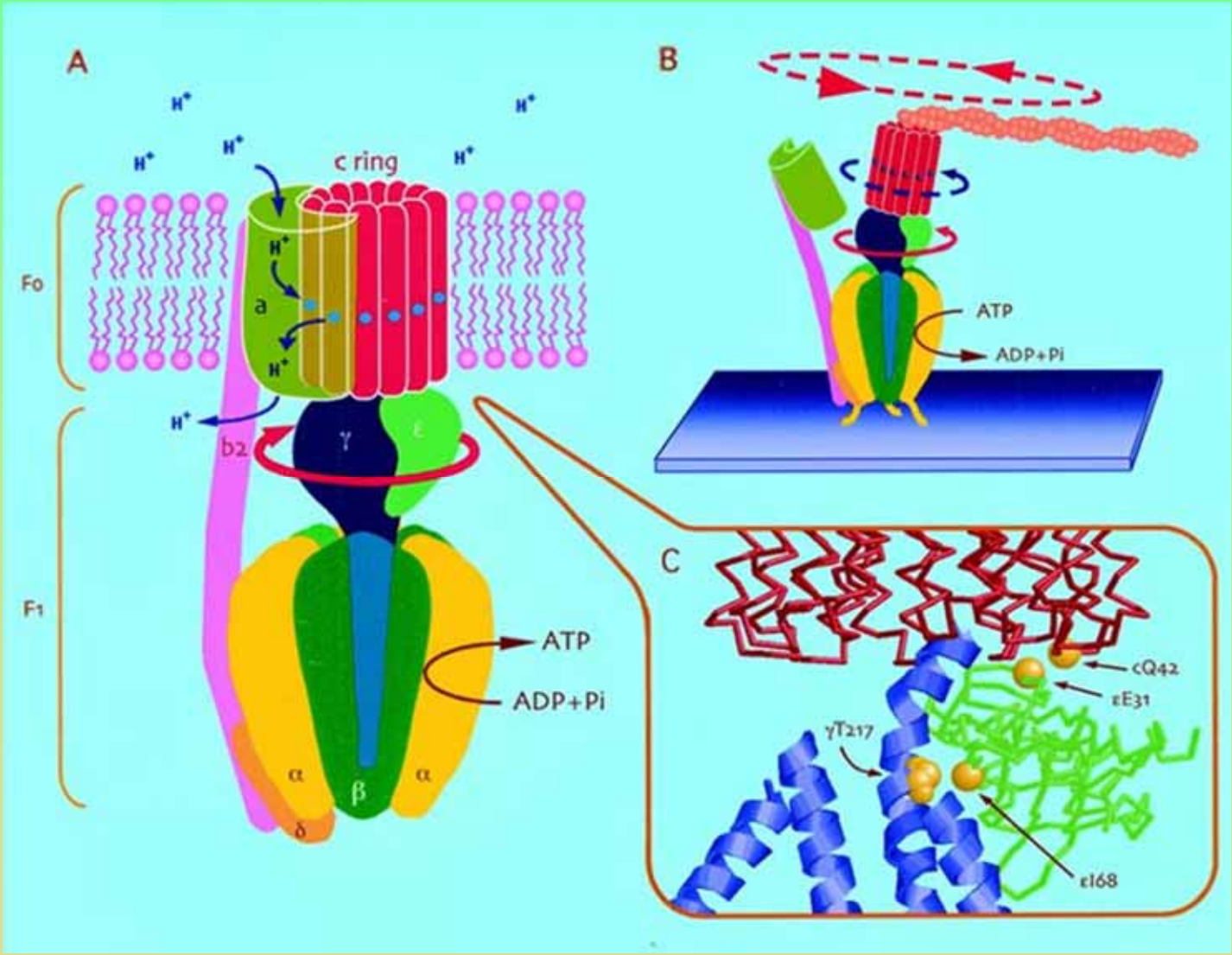
zbytek = stator

brzda = disulfidické můstky

$$\Delta \mu_{H^+} \rightarrow \Delta G_{ATP}$$

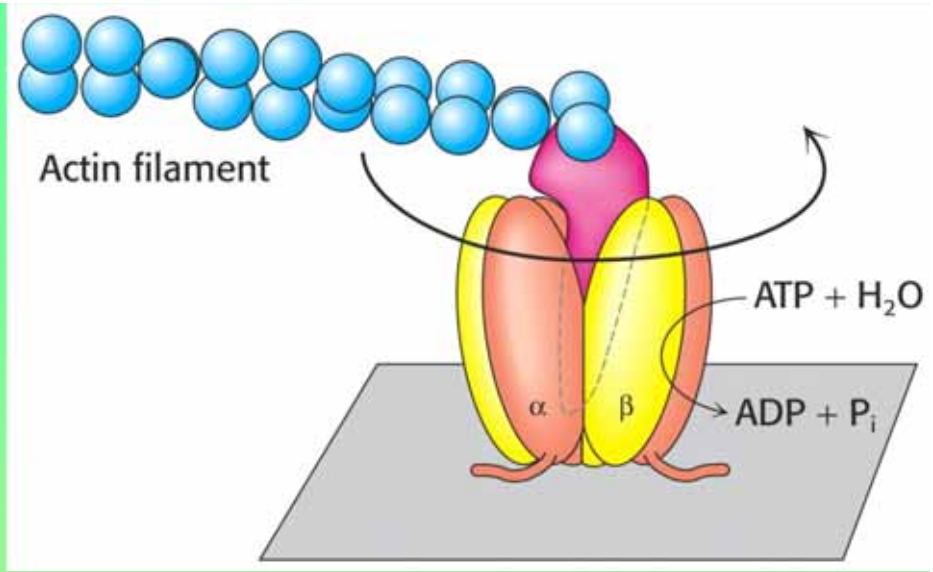


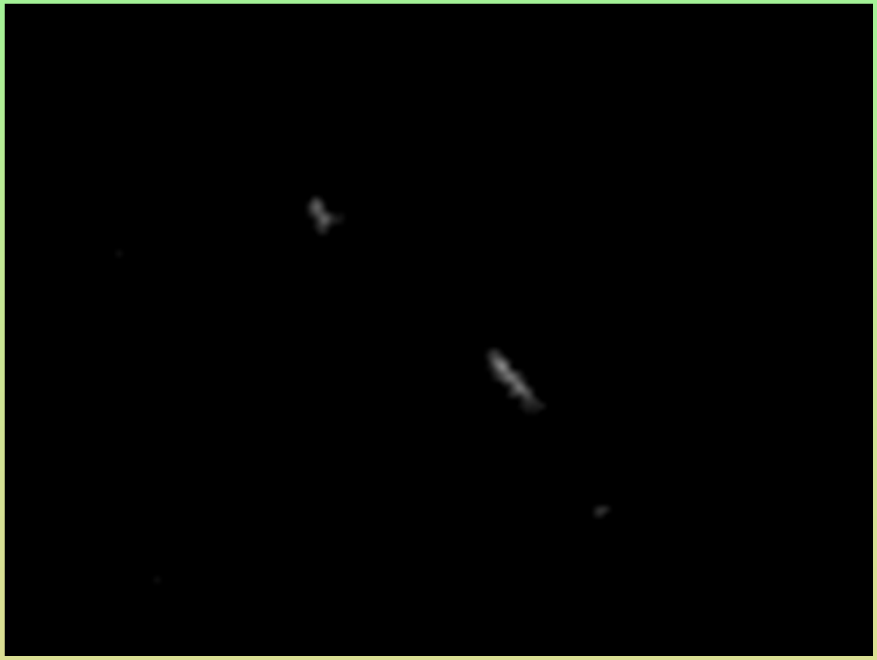
F_1 subunits α, β and δ together with F_0 subunits a and b comprise the stator while remaining χ, ε of F_1 and c ring of F_0 form the rotor during rotational synthesis of ATP. One ATP is formed during single rotation of the rotor that is related to the transfer of 3 H^+.

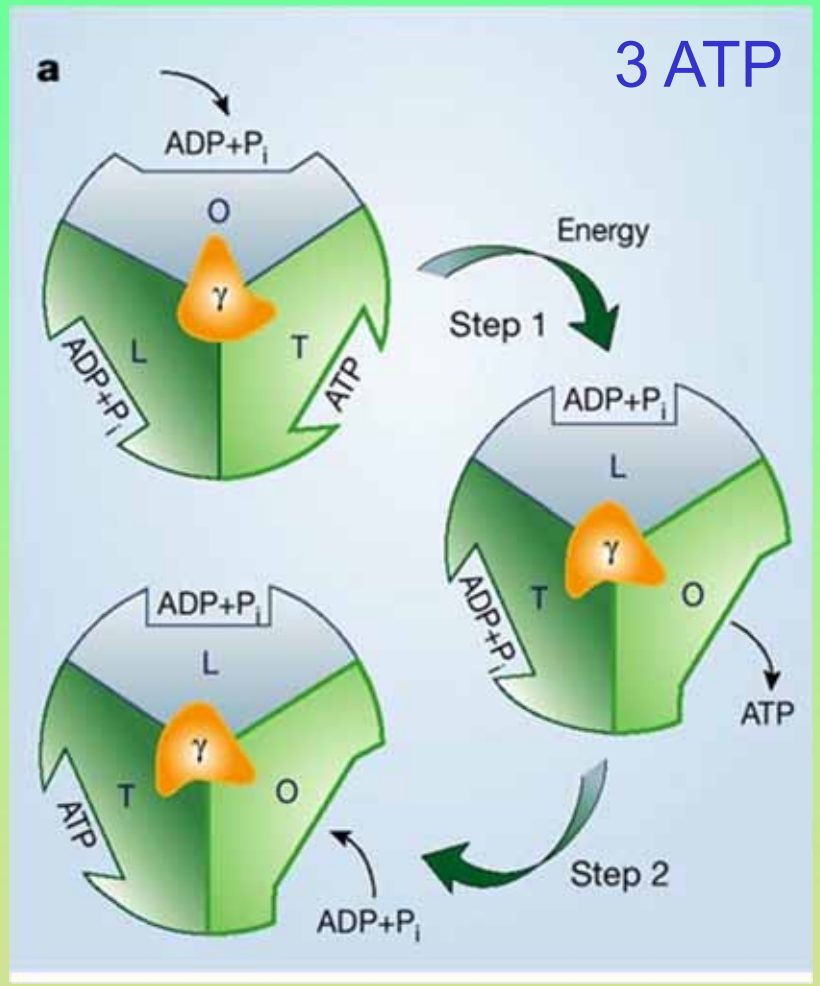


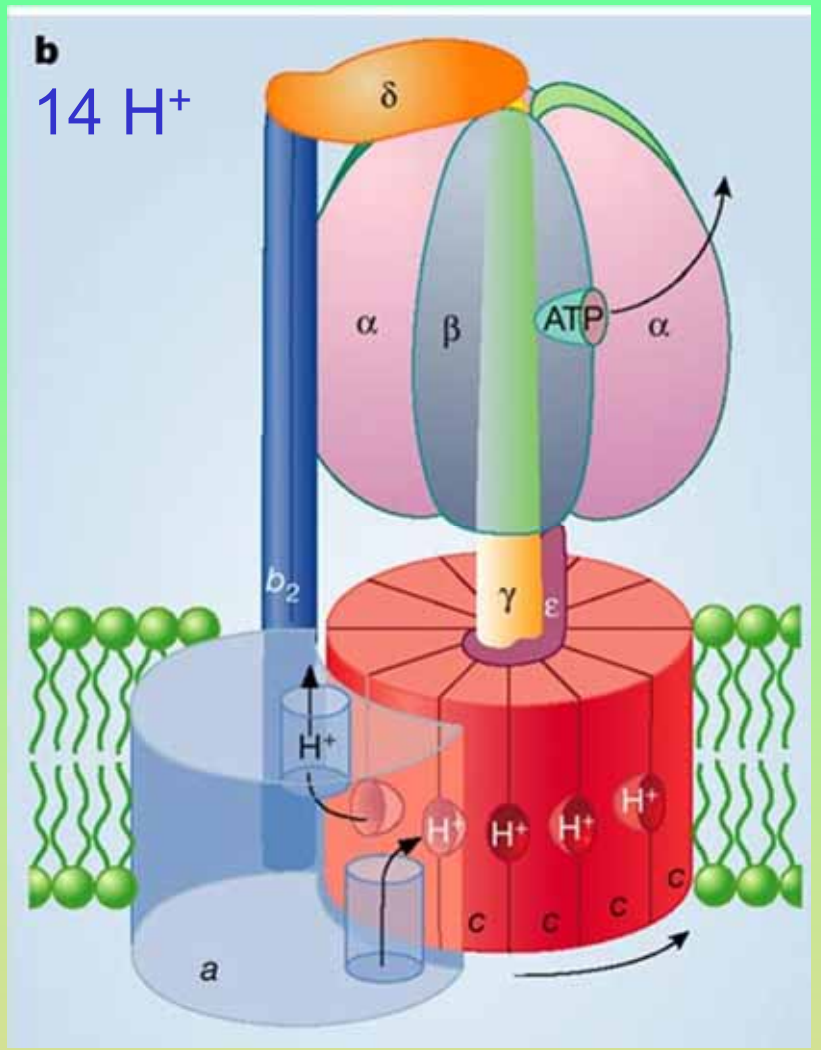
Videorecord of the $\chi\varepsilon F_1cF_0$ rotation during the ATP synthesis

.

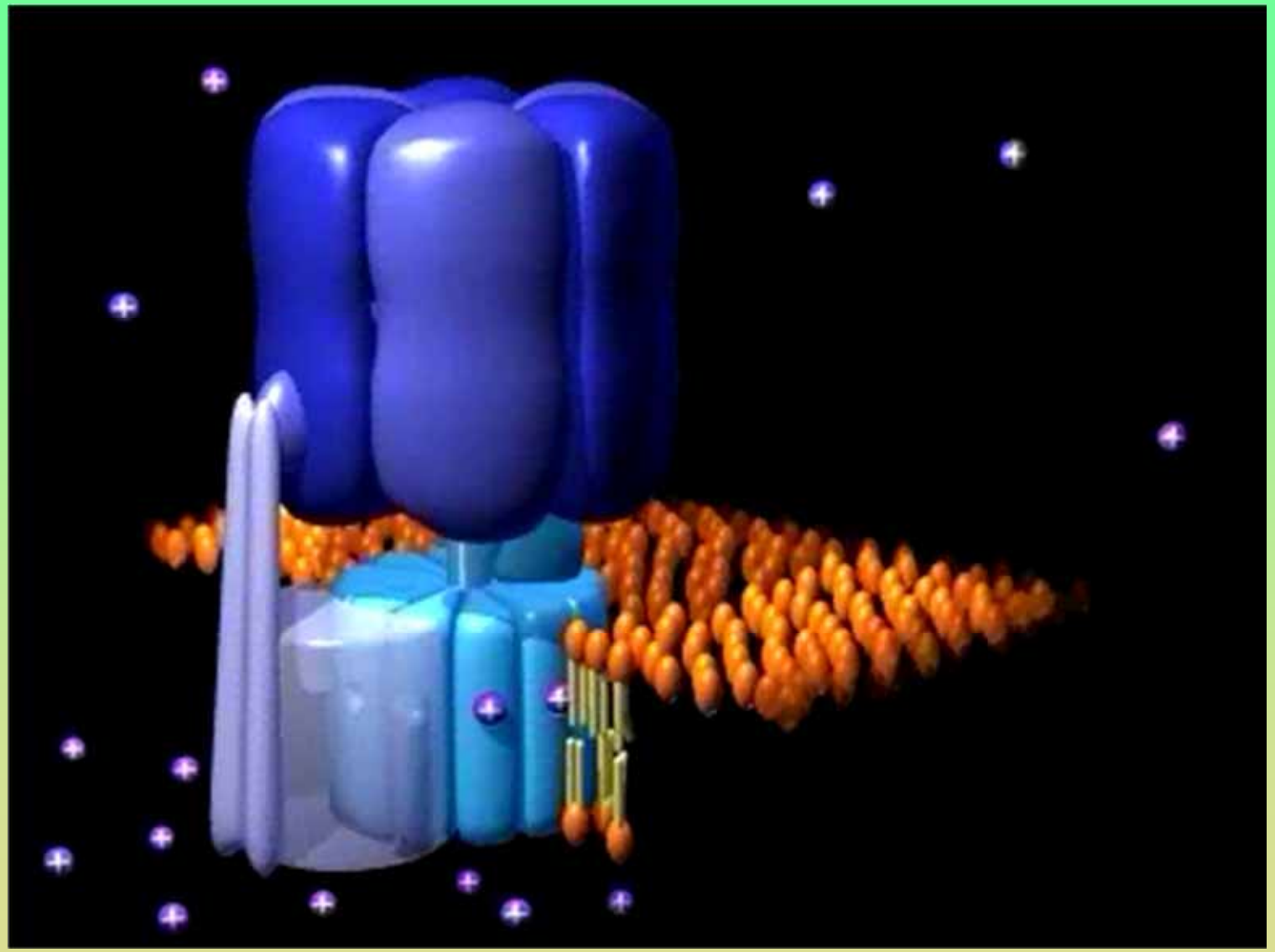


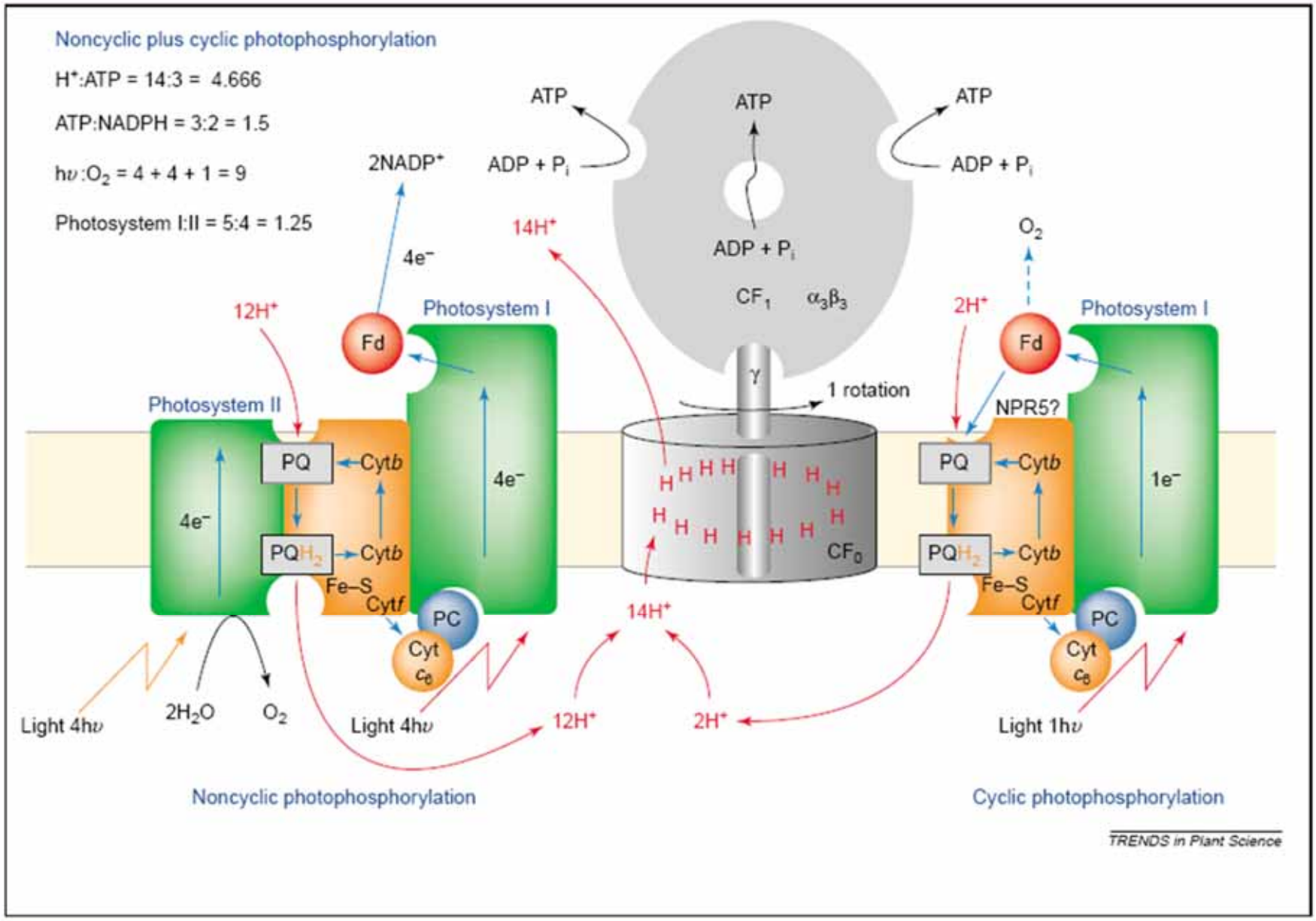






„binding change mechanism“ (P.Boyer)




Noncyclic plus cyclic photophosphorylation
H+:ATP = 14:3 = 4.666
ATP:NADPH = 3:2 = 1.5
hν:O2 = 4 + 4 + 1 = 9
Photosystem I:II = 5:4 = 1.25
ATP
ATP
ATP
ADP + Pi
ADP + Pi
ADP + Pi
2NADP+
4e−
14H+
O2
12H+
Photosystem I
Photosystem I
2H+
Fd
Fd
CF1 α3β3
γ
1 rotation
Photosystem II
NPR5?
PQ
Cytb
PQH2
Cytb
Fe–S
Cytf
PC
Cyt c6
4e−
4e−
1e−
CF0
14H+
Light 4hν
2H2O
O2
Light 4hν
12H+
2H+
Light 1hν
Noncyclic photophosphorylation
Cyclic photophosphorylation
TRENDS in Plant Science

Obsah přednášky

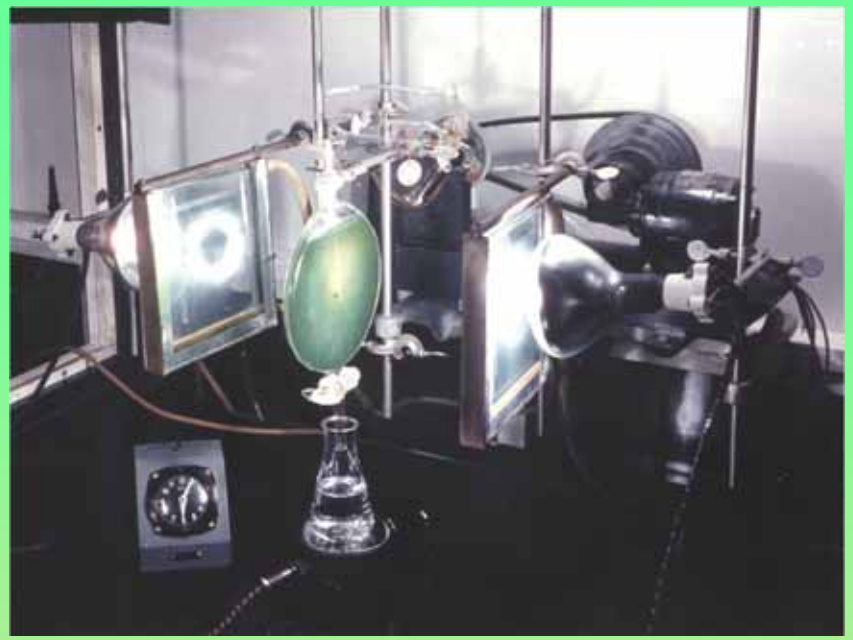
- **C3 dráha: fixace a redukce CO_2**
- **Fotorespirace a C2 dráha**
- **mechanismy koncentrace CO_2**
- **C4 metabolismus**
- **CAM metabolismus**

Melvin Calvin

Nobel 1961

Andrew Benson

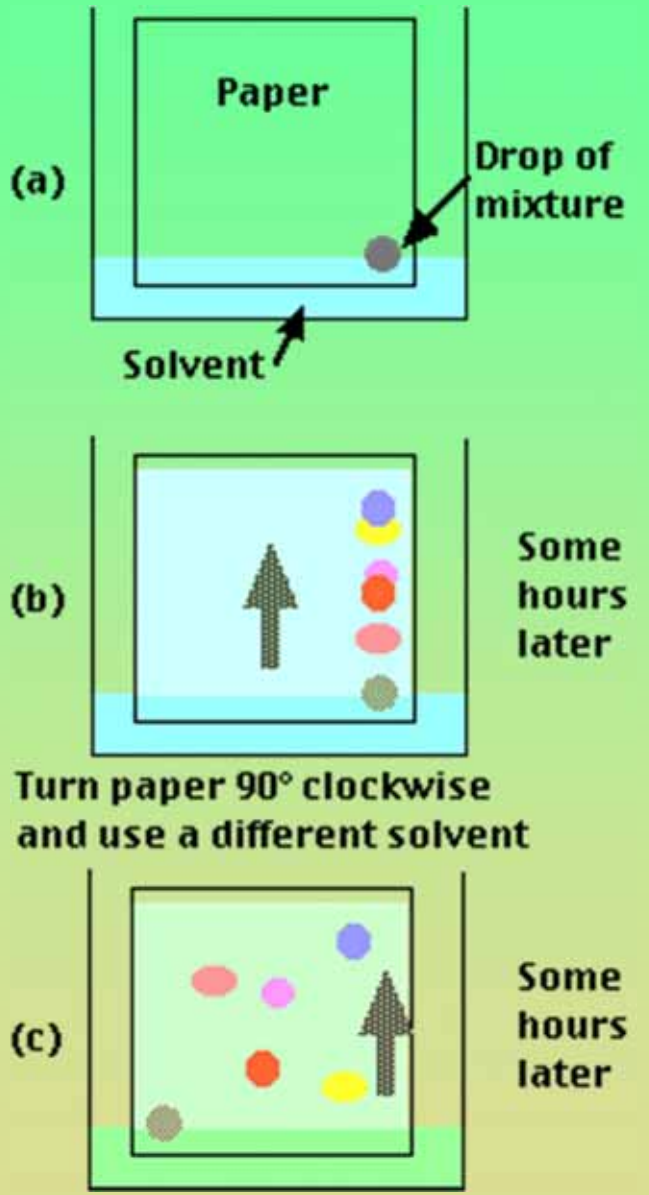
Calvinův, Calvin-Bensonův, Redukční pentosový cyklus, **C_3 cesta**

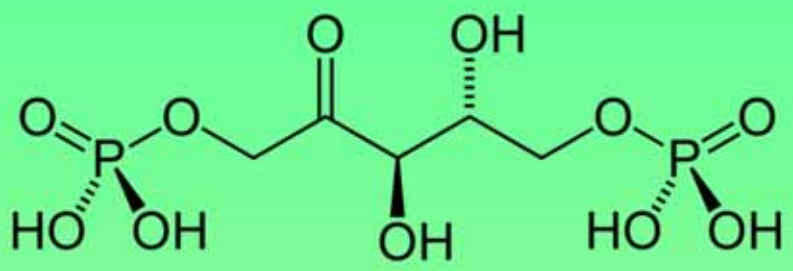


značení $^{14}CO_2$

2D papírová chromatografie
autoradiografie

akumulace substrátu
při limitaci CO_2



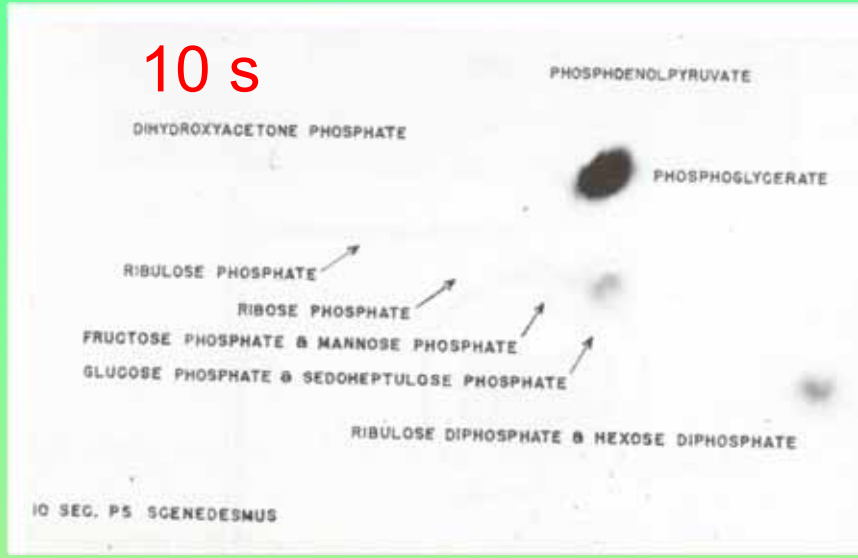


ribulosa-1,5-bisfosfát (RuBP)
fosfoglycerát PGA

RuBP + $CO_2 \rightarrow$ 2 x 3PGA

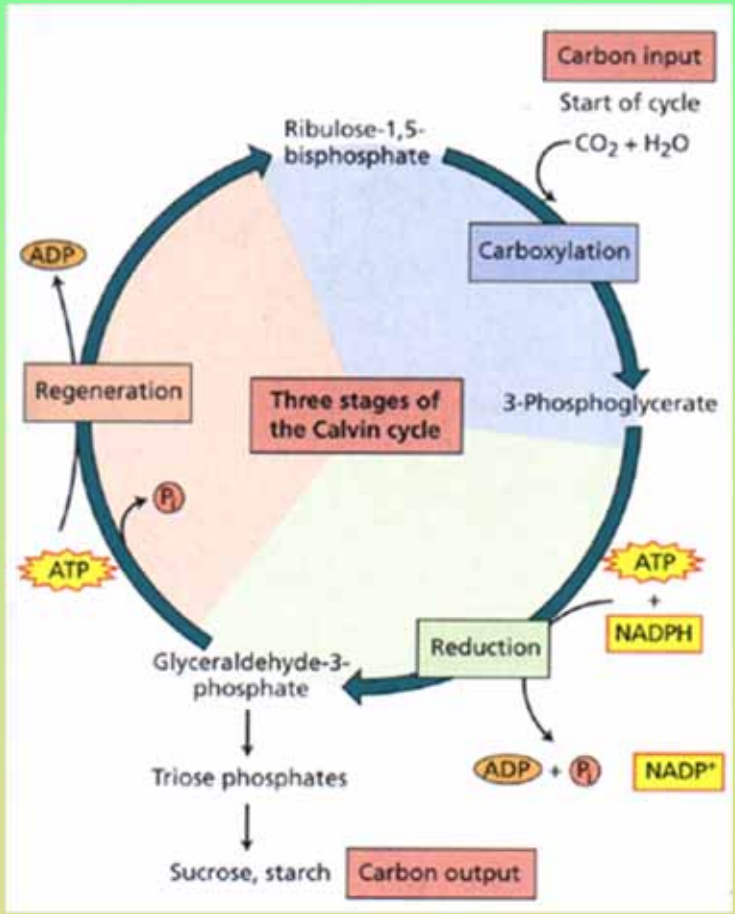
Rubisco = karboxydismutáza
RuBP karboxyláza/oxygenáza

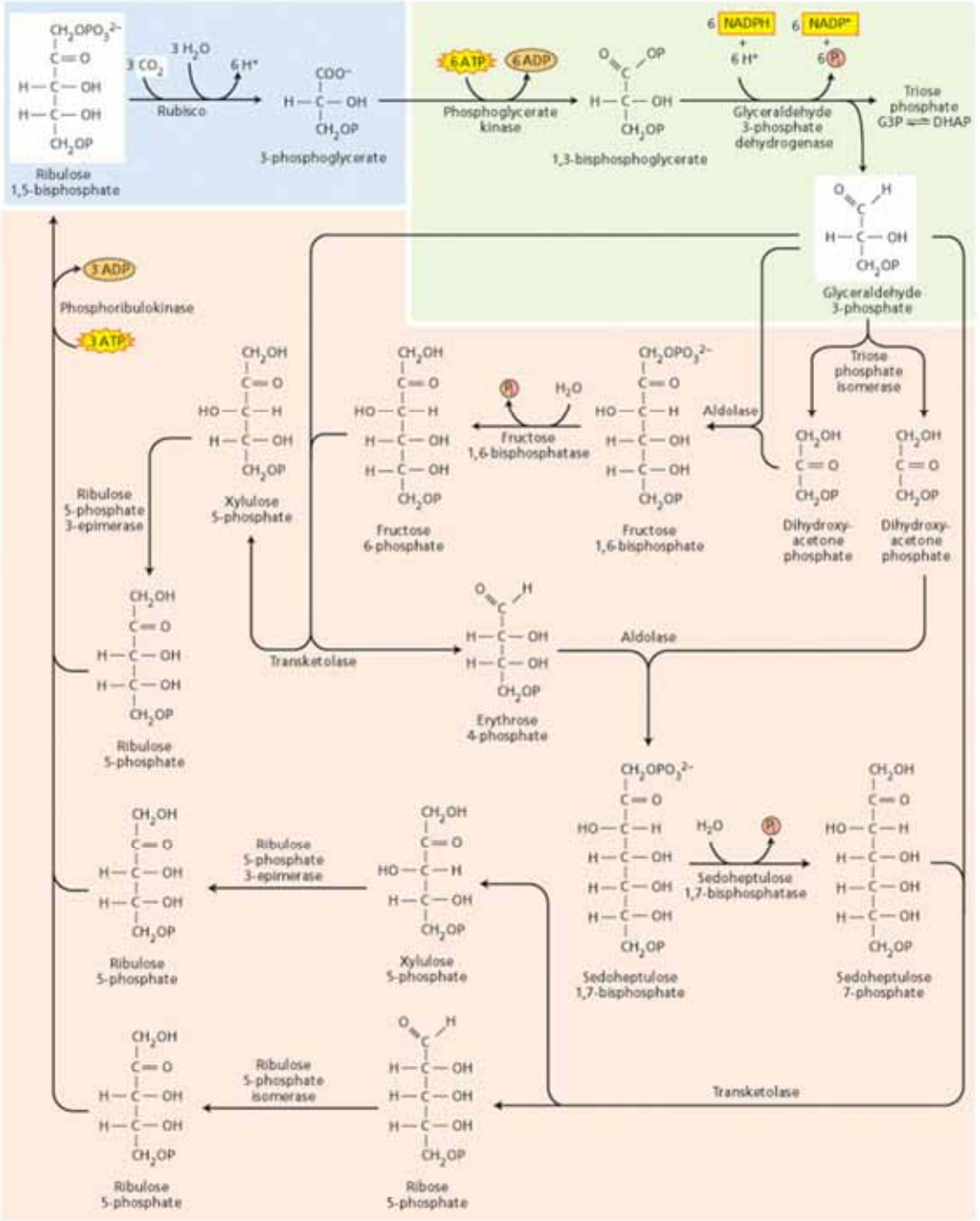
Karboxylace není reduktivní



Calvinův cyklus:

celkem 12 reakcí
autokatalytický





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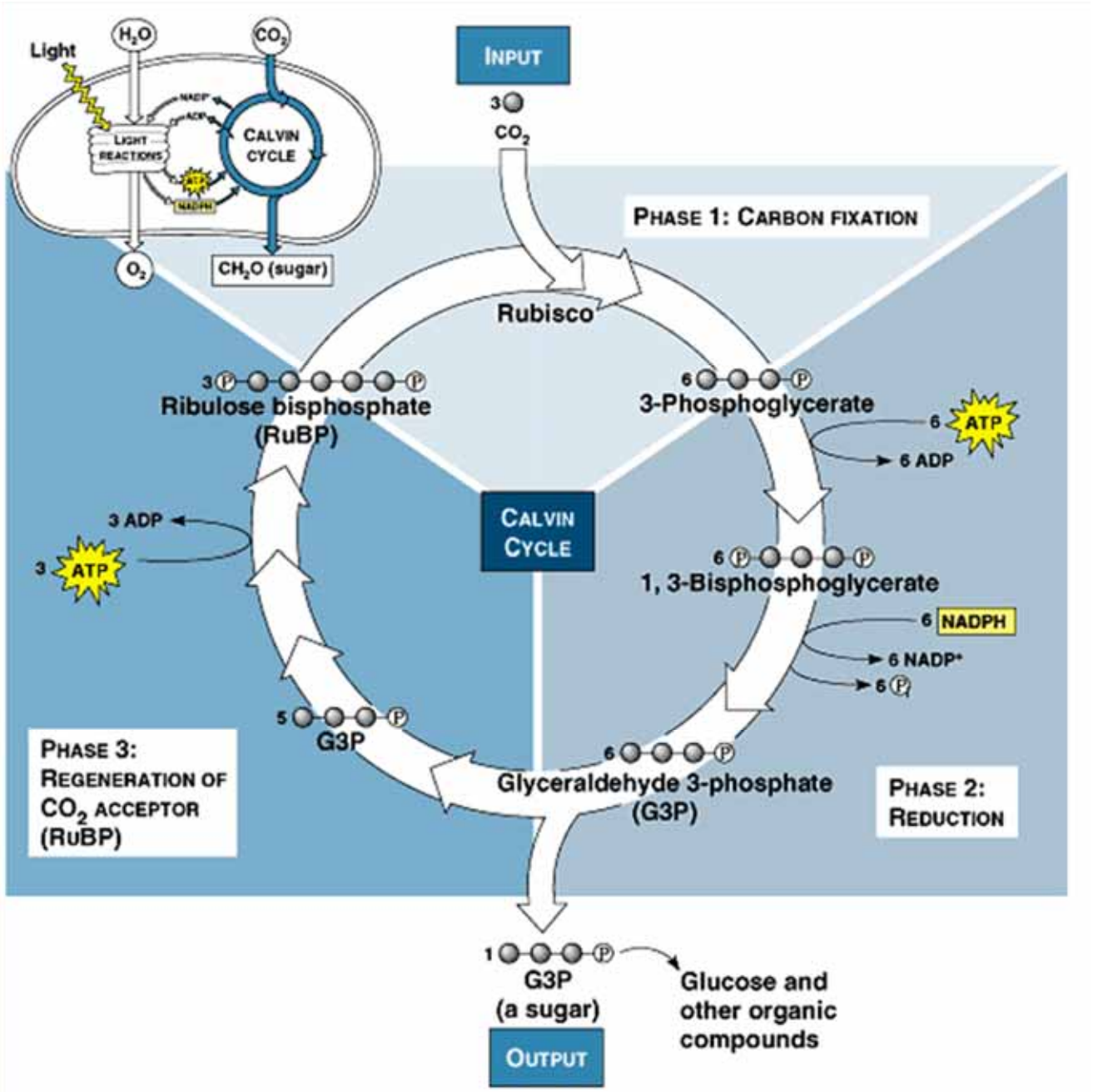
Calvinův cyklus:

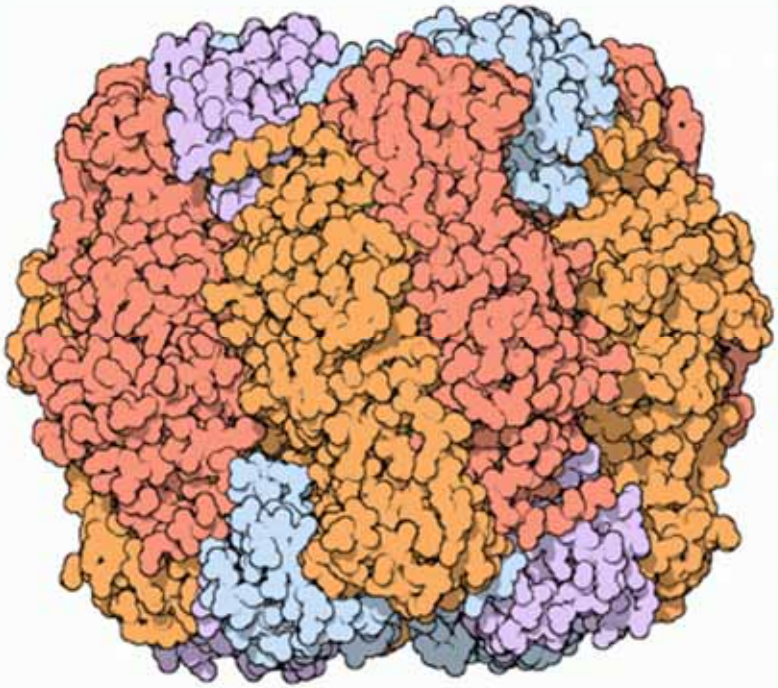
celkem 12 reakcí
autokatalytický

Karboxylace:

- -ΔG karboxylace
- velká afinita CO_2 k Rubiscu



$3\ CO_2 + 3\ H_2O + 6\ NADPH + 9\ ATP \rightarrow G3P + 6\ NADP^+ + 3\ H^+ + 9\ ADP + 8\ P_i$



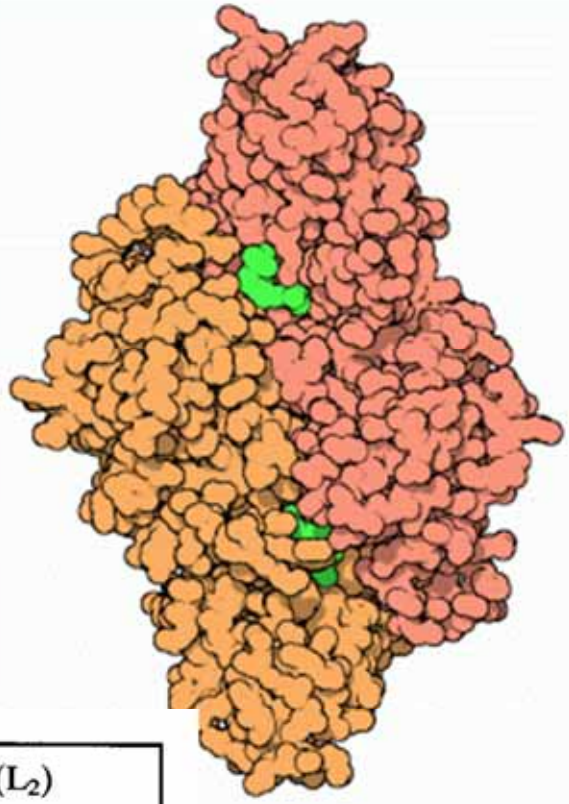
Rubisco

velký enzym
pomalý
(3 CO_2 za sec)

Nejpočetnější…

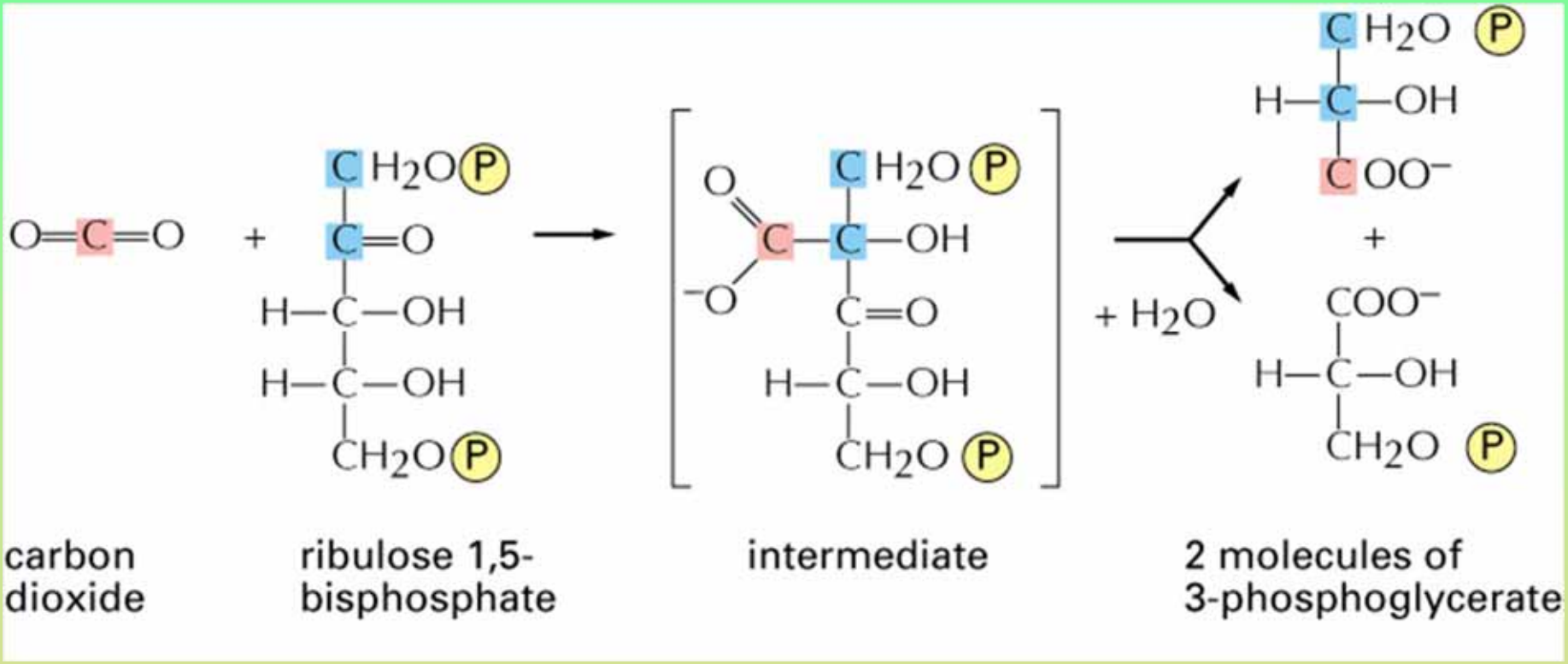
nespecifický (O_2)

Aktivní část: L2

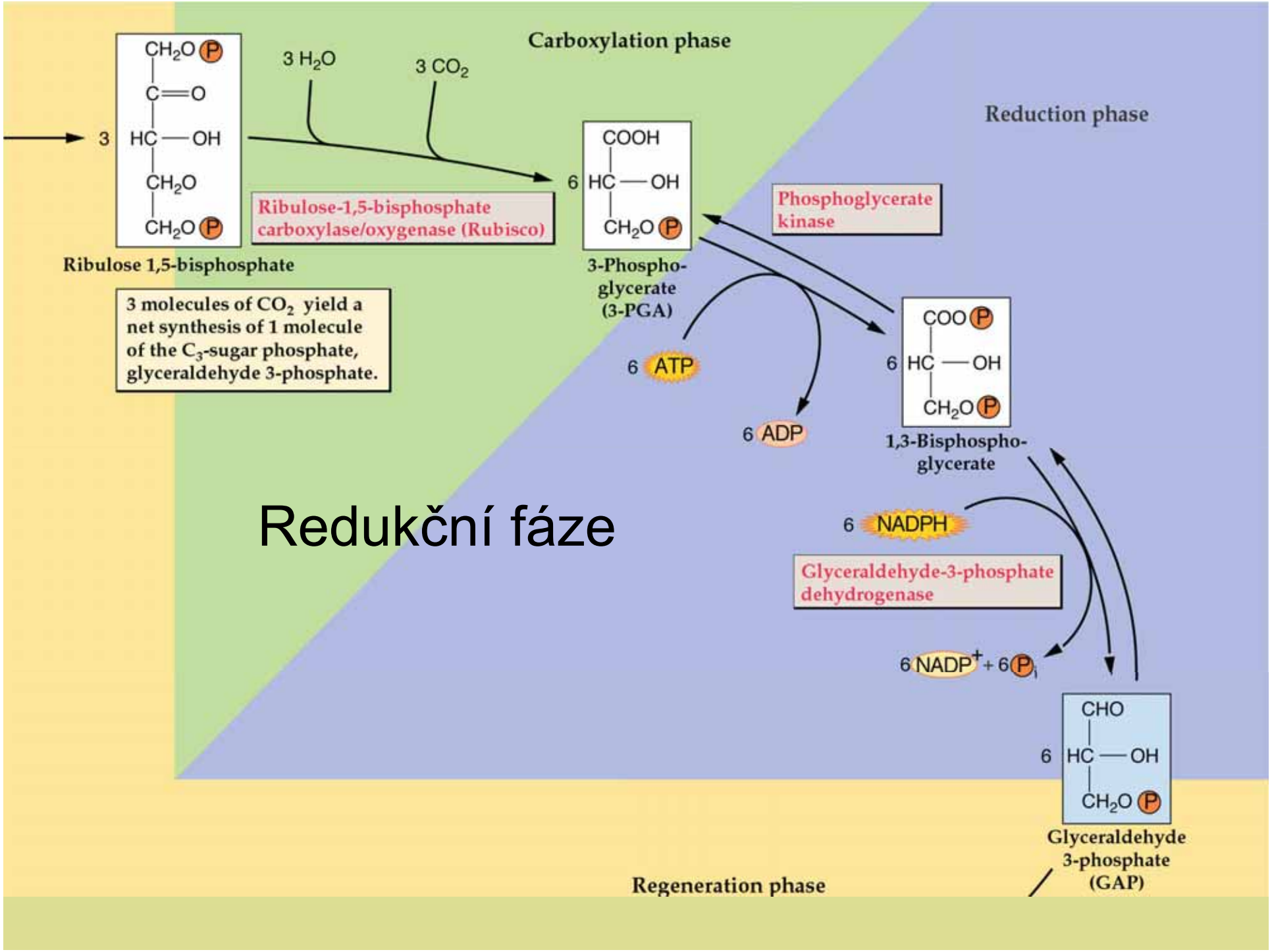


Form (subunit organisation)	Form I (L_8S_8)		Form II (L_2)
Origin	Cyanobacterial	β-Proteobacterium	α-Proteobacterium
Taxa	Form 1B (green type) Cyanobacteria Chlorophyta Chlorophyceaea Prasinophyceae Eugleophyceae	Form 1D (red type) Rhodophyta Cryptophyta Haptophyta Heterokonta Bacillariophyceae Chrysophyceaea Diophyta	Dinophyta
Location of gene	Chloroplastic *rbc*L Nuclear *rbc*S	Chloroplastic *rbc*L Chloroplastic *rbc*S	Nuclear *rbc*L

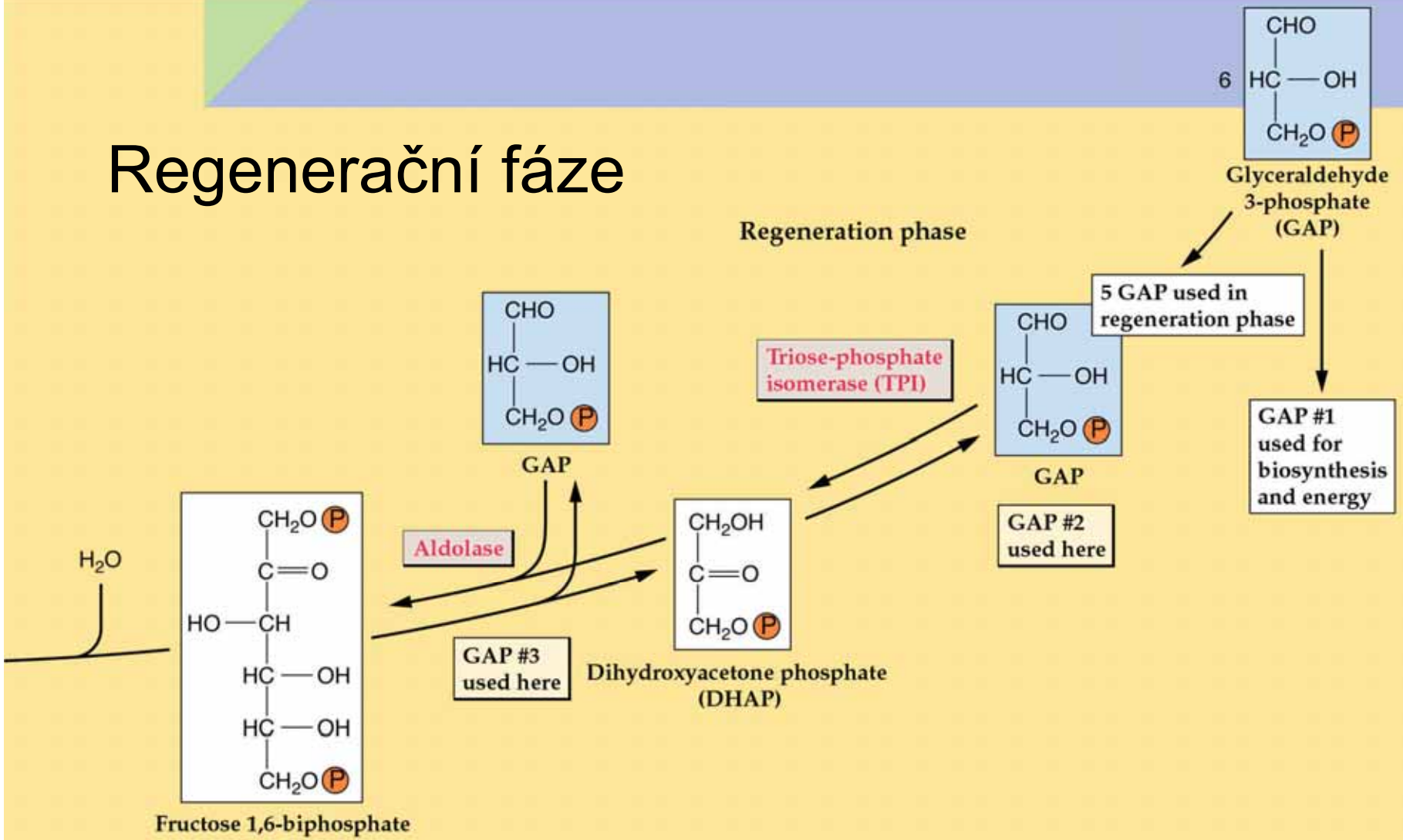
Rubisco – karboxylace RuBP



Karboxylační fáze


Carboxylation phase
Reduction phase
Regeneration phase
3 H_2O
3 CO_2
Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco)
Ribulose 1,5-bisphosphate
3 molecules of CO_2 yield a net synthesis of 1 molecule of the C_3-sugar phosphate, glyceraldehyde 3-phosphate.
3-Phospho-glycerate (3-PGA)
Phosphoglycerate kinase
6 ATP
6 ADP
1,3-Bisphospho-glycerate
6 NADPH
Glyceraldehyde-3-phosphate dehydrogenase
6 $NADP^+$ + 6 P_i
Glyceraldehyde 3-phosphate (GAP)
Redukční fáze

Regenerační fáze



3 RuBP (15C) + 3 CO_2 (3C) -> 6 G3P (18C) -> 3 RuBP (15C) + GAP (3C)

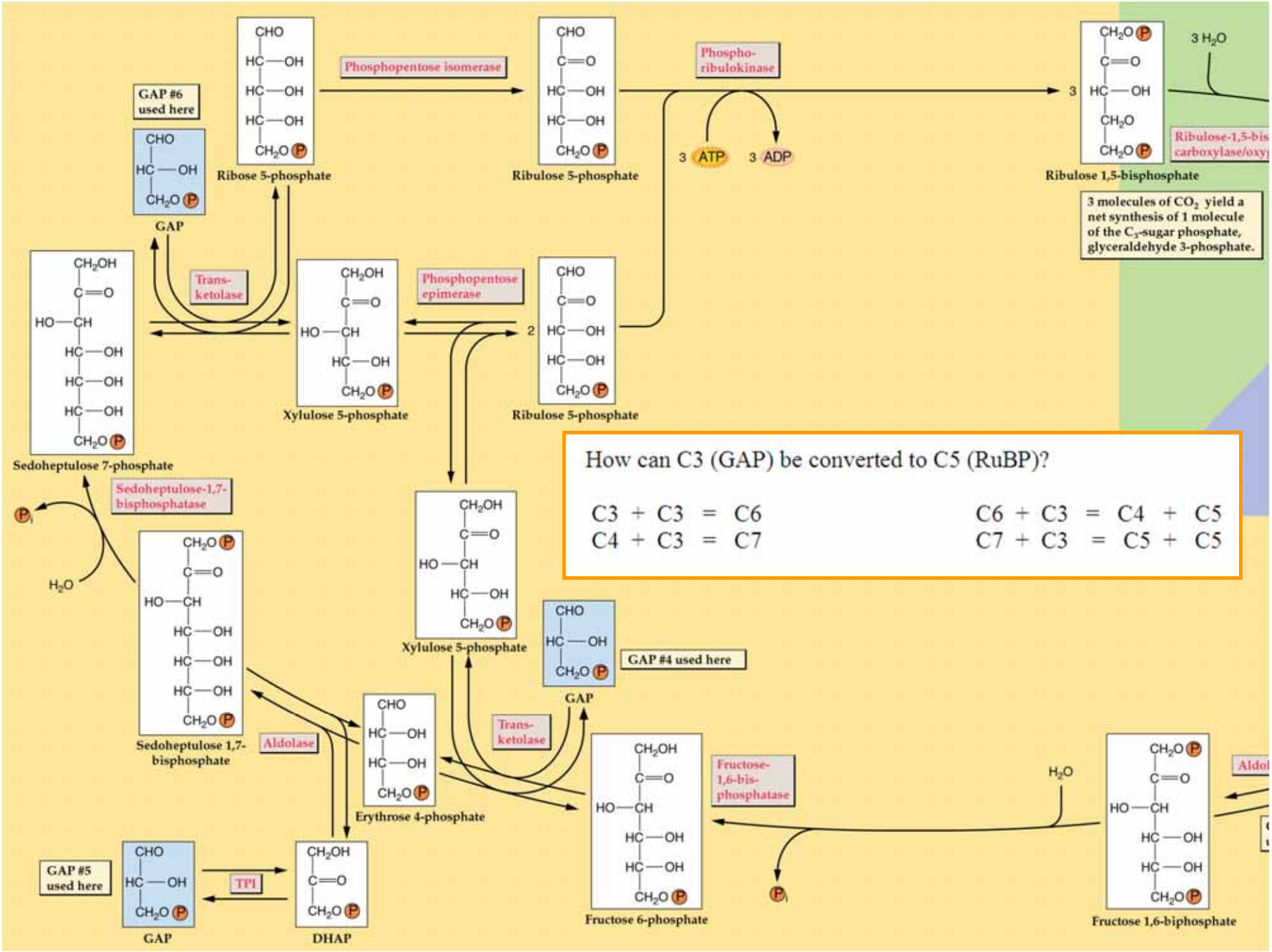

Ribose 5-phosphate
Phosphopentose isomerase
Ribulose 5-phosphate
Phospho-ribulokinase
3 ATP
3 ADP
3
Ribulose 1,5-bisphosphate
3 H2O
Ribulose-1,5-bis carboxylase/oxy
3 molecules of CO2 yield a net synthesis of 1 molecule of the C3-sugar phosphate, glyceraldehyde 3-phosphate.
GAP #6 used here
GAP
Trans-ketolase
Xylulose 5-phosphate
Phosphopentose epimerase
2
Ribulose 5-phosphate
Sedoheptulose 7-phosphate
How can C3 (GAP) be converted to C5 (RuBP)?
C3 + C3 = C6
C4 + C3 = C7
C6 + C3 = C4 + C5
C7 + C3 = C5 + C5
Sedoheptulose-1,7-bisphosphatase
Pi
H2O
Xylulose 5-phosphate
GAP #4 used here
GAP
Sedoheptulose 1,7-bisphosphate
Aldolase
Trans-ketolase
Erythrose 4-phosphate
Fructose-1,6-bis-phosphatase
H2O
Pi
Fructose 6-phosphate
Fructose 1,6-biphosphate
Aldol
GAP #5 used here
TPI
GAP
DHAP

TABLE 8.1
Reactions of the Calvin cycle (Part 1)

Enzyme	Reaction
1. Ribulose-1,5-bisphosphate carboxylase/oxygenase	6 Ribulose-1,5-bisphosphate + 6 CO_2 + 6 H_2O → 12 (3-phosphoglycerate) + 12 H^+
2. 3-Phosphoglycerate kinase	12 (3-Phosphoglycerate) + 12 ATP → 12 (1,3-bisphosphoglycerate) + 12 ADP
3. NADP:glyceraldehyde-3-phosphate dehydrogenase	12 (1,3-Bisphosphoglycerate) + 12 NADPH + 12 H^+ → 12 glyceraldehye-3-phosphate + 12 $NADP^+$ + 12 P_i
4. Triose phosphate isomerase	5 Glyceraldehyde-3-phosphate → 5 dihydroxyacetone-3-phosphate
5. Aldolase	3 Glyceraldehyde-3-phosphate + 3 dihydroxyacetone-3-phosphate → 3 fructose-1,6-bisphosphate
6. Fructose-1,6-bisphosphatase	3 Fructose-1,6-bisphosphate + 3 H_2O → 3 fructose-6-phosphate + 3 P_i
7. Transketolase	2 Fructose-6-phosphate + 2 glyceraldehyde-3-phosphate → 2 erythrose-4-phosphate + 2 xylulose-5-phosphate

Note: P_i stands for inorganic phosphate.

3 CO_2 + 3RuBP+ 3 H_2O + 6 NADPH + 9 ATP -> 6G3P + 6 $NADP^+$ + 3 H^+ + 9 ADP + 8 P_i

Regenerace součástí Calvinova cyklu

Ve tmě je nízká koncentrace meziproduktů C cyklu
Na světle se musí nejprve regenerovat meziprodukty – indukční perioda

Energetická bilance Calvinova cyklu

Množství energie na syntézu hexósy ≥ energie oxidace (spálení) 1 molu hexosy = 2804 kJ

$6CO_2 + 12\ NADPH + 18\ ATP \rightarrow C_6H_{12}O_6$

Spotřebuje se 3126 kJ na oxidaci 12 molů NADPH (12 x 217) a na hydrolýzu 18 molů ATP (18 x 29 kJ)

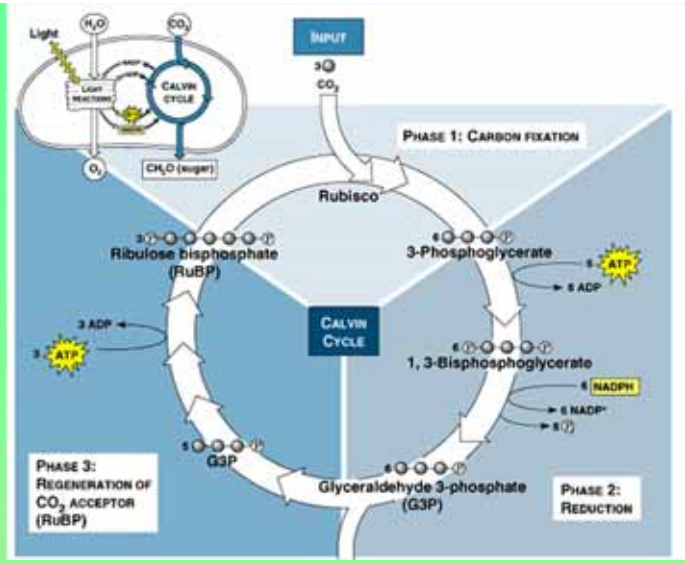
Termodynamická účinnost je tedy **90%** (2804/3126)
Většina (83%) energie jde na redukční proces

1 CO_2 ~ min. 8 fotonů
Celková termodynamická účinnost:
6 x 8fotonů x 175 kJ(energie 680nm) = 8400 kJ
Celkem maximální účinnost **33%** (2804/8400)

Velká část energie se ztratí při tvorbě NADPH a ATP

Reálná účinnost přeměny světelné energie je **0.1 – 0.4**%, optimálně **2**%

Regulace Calvinova cyklu

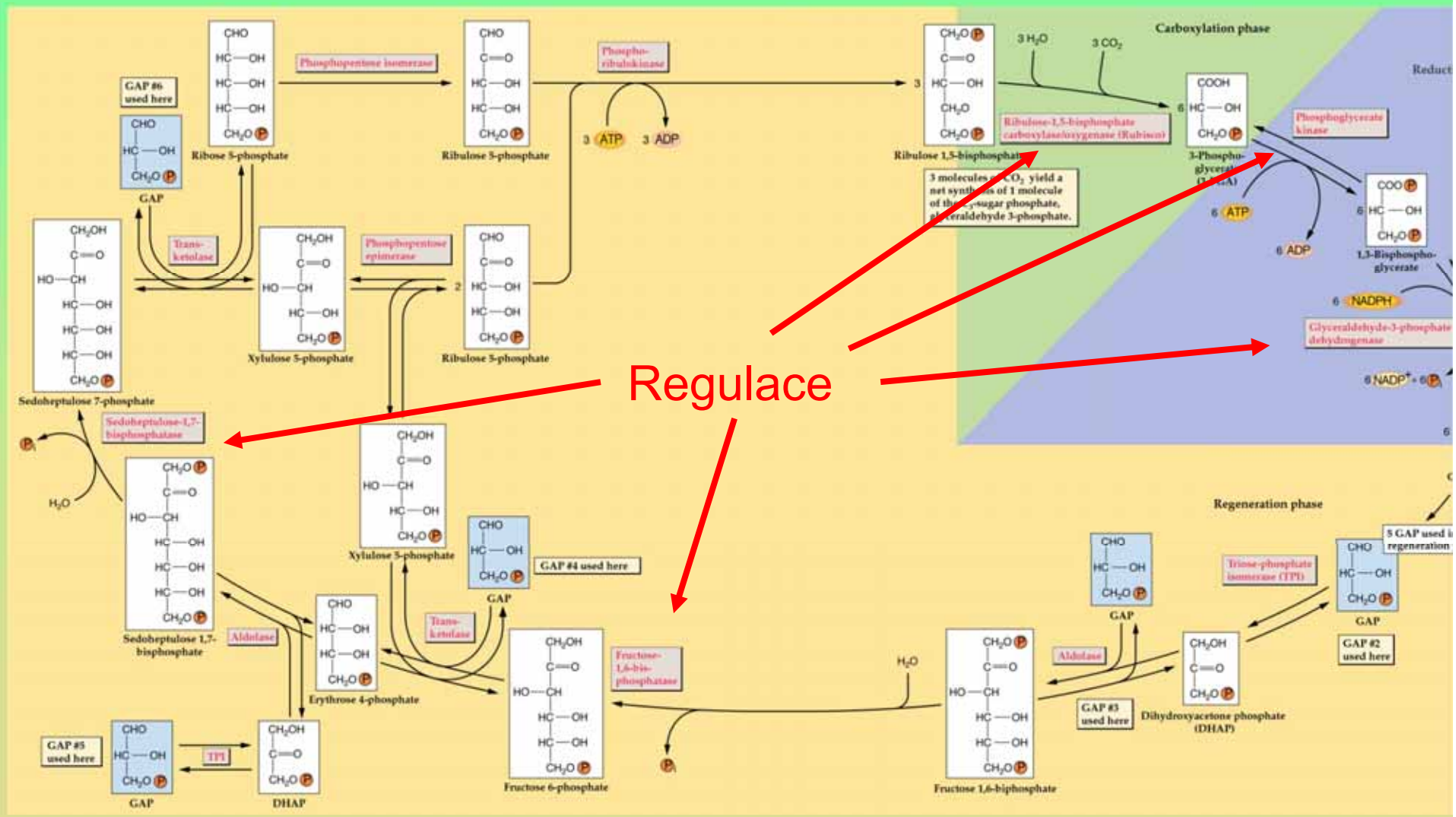


- regulace – na úrovni syntézy proteinů (signály jádro – chloroplast). Anterográdní regulace (J → Ch). Pomalé (hod)…

- posttranslační modifikace – rychlé změny aktivity během minut
  - změny v kovalentních vazbách (disulfidické vazby, karbamace)
  - nekovalentní modifikace (vazba metabolitů, změny v pH)

Regulace světlem

Moduluje aktivitu enzymů v závislosti na přenosu elektronů

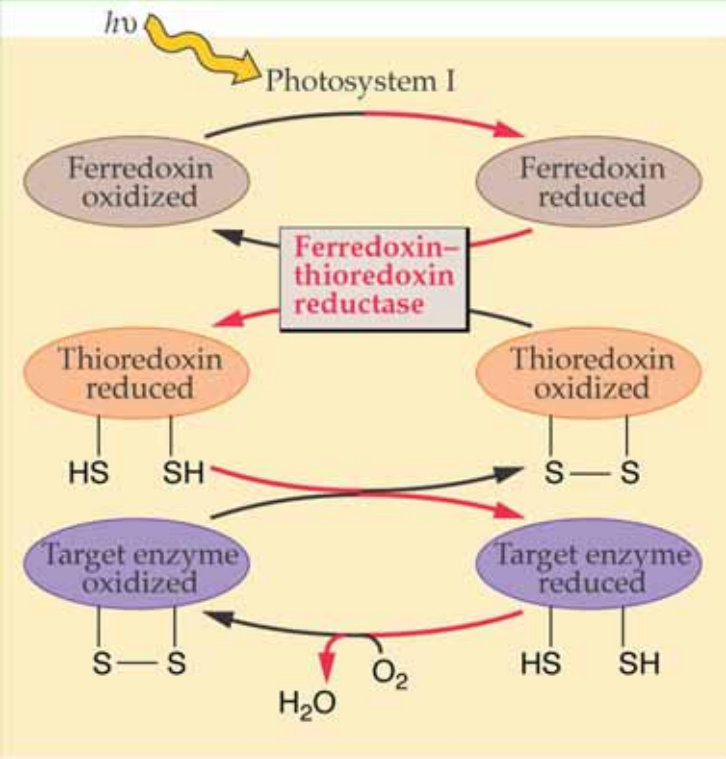


Aktivace cyklu fixace uhlíku

Fotochemické změny

Table 1 Stromal conditions of darkened and illuminated chloroplasts

	Dark	Light
pH	7.0–7.3	8.0–8.5
Mg^{2+} (mM)	1–3	3–6
ATP/ADP ratio	0.2–1.0	1–5
Thioredoxin (% reduced)	8–30	62–67

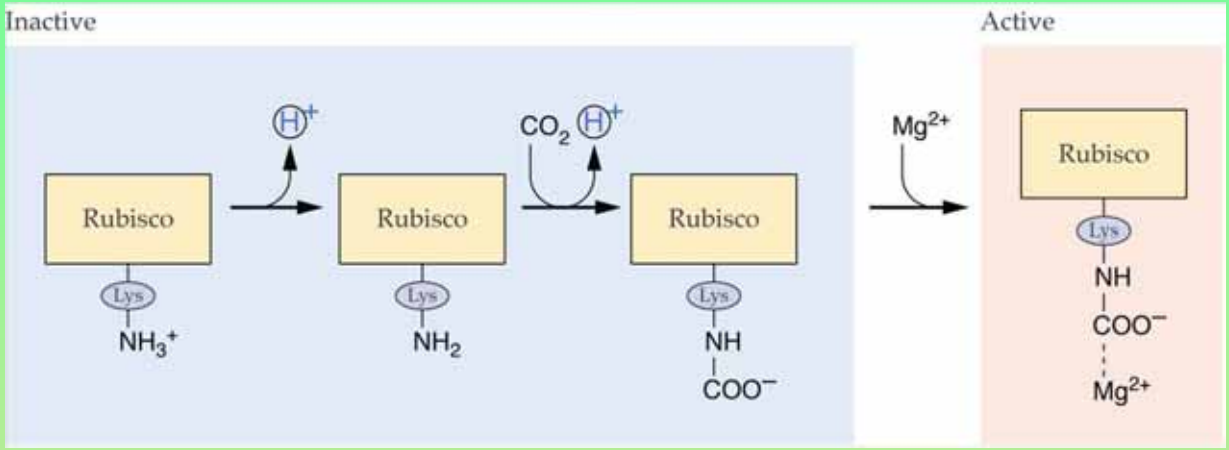


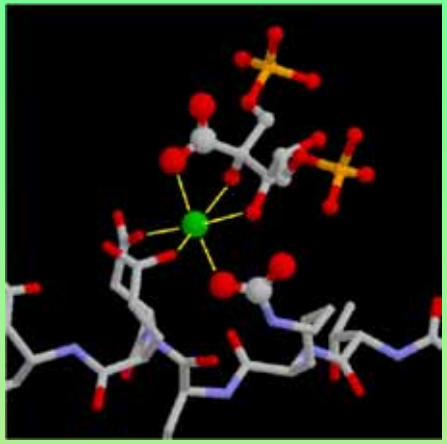
Aktivace 4 enzymů CC systémem ferredoxin – thioredoxin

(inhibice katabolických procesů)

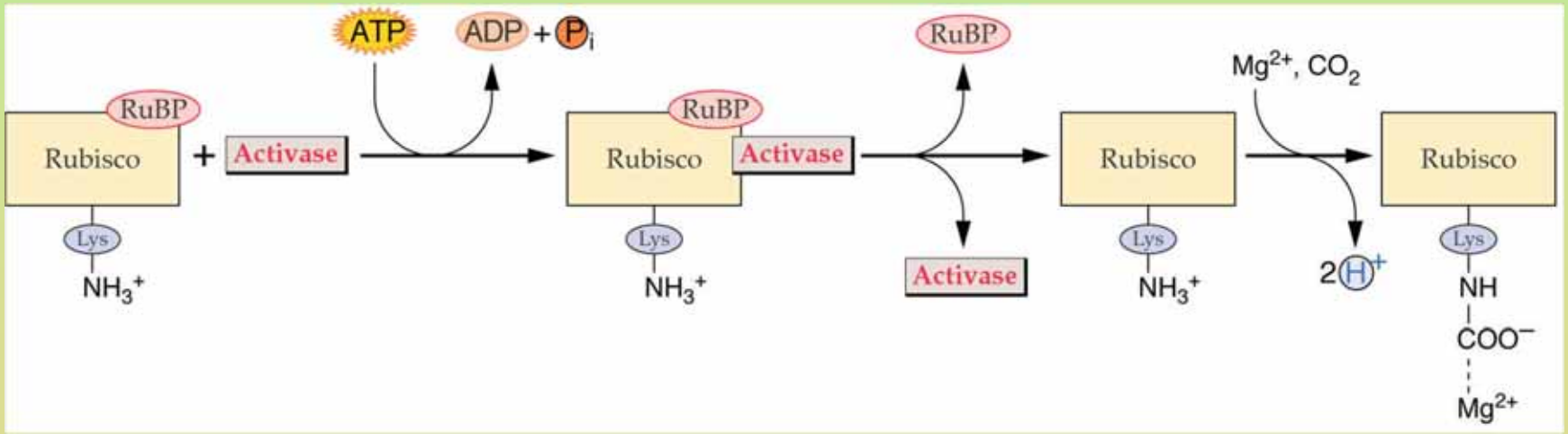
Aktivace cyklu fixace uhlíku - Rubisco

Karbamylace Lys^{201} probíhá lépe za zvýšení Mg^{2+} a pH





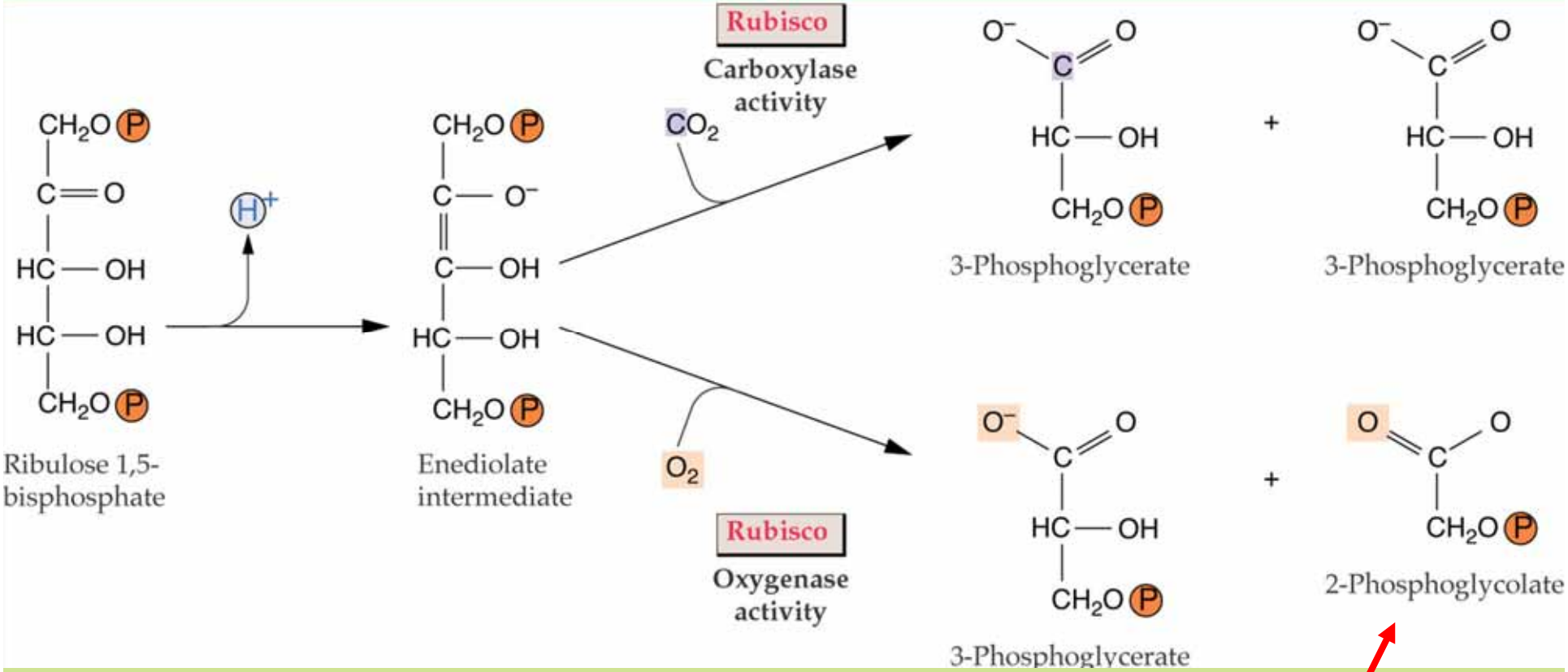
Rubisco aktiváza odstraní pevně navázané cukry



Obsah přednášky

- C3 dráha: fixace a redukce CO_2
- Fotorespirace a C2 dráha
- mechanismy koncentrace CO_2
- C4 metabolismus
- CAM metabolismus

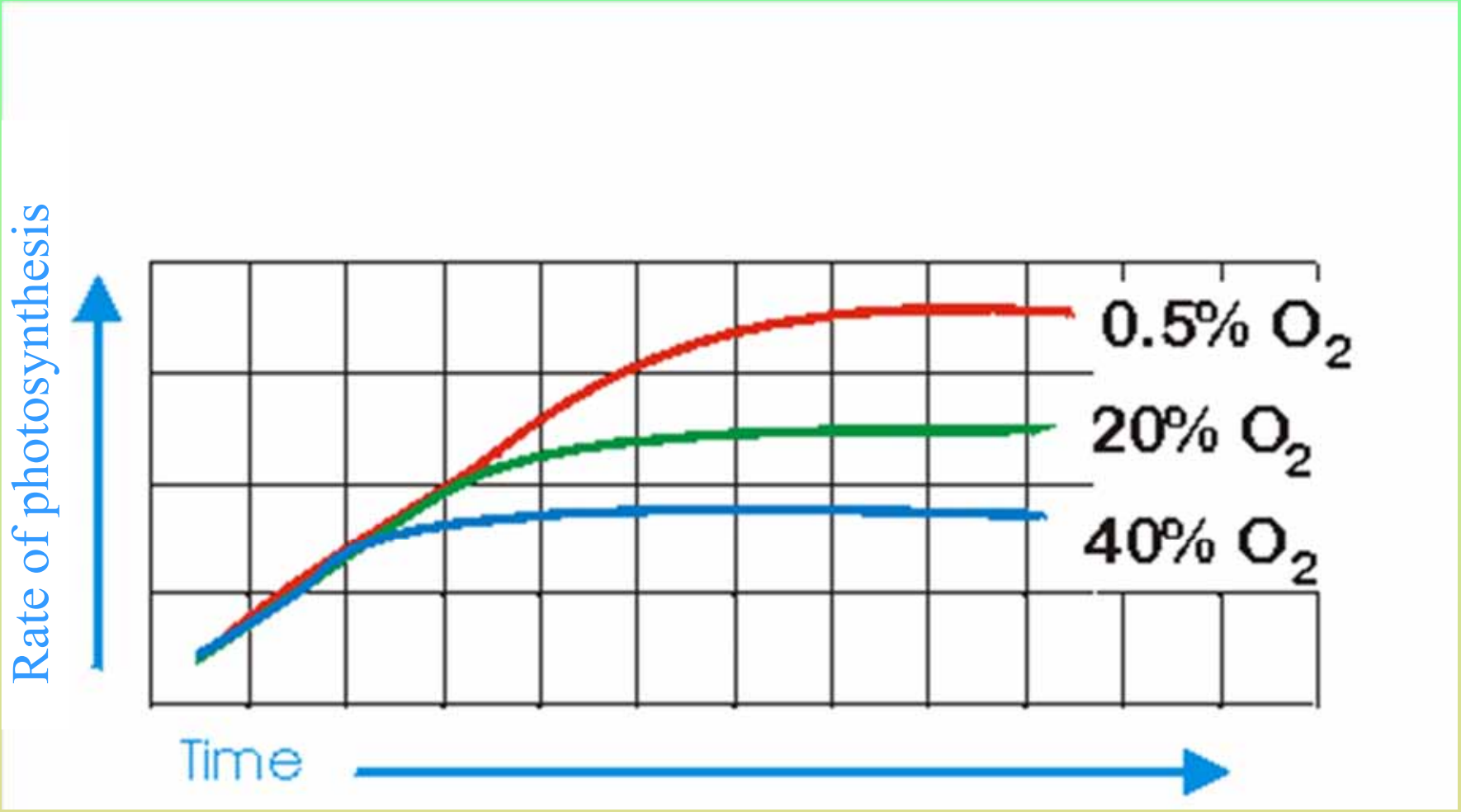
Fotorespirace – oxygenázová aktivita rubisca



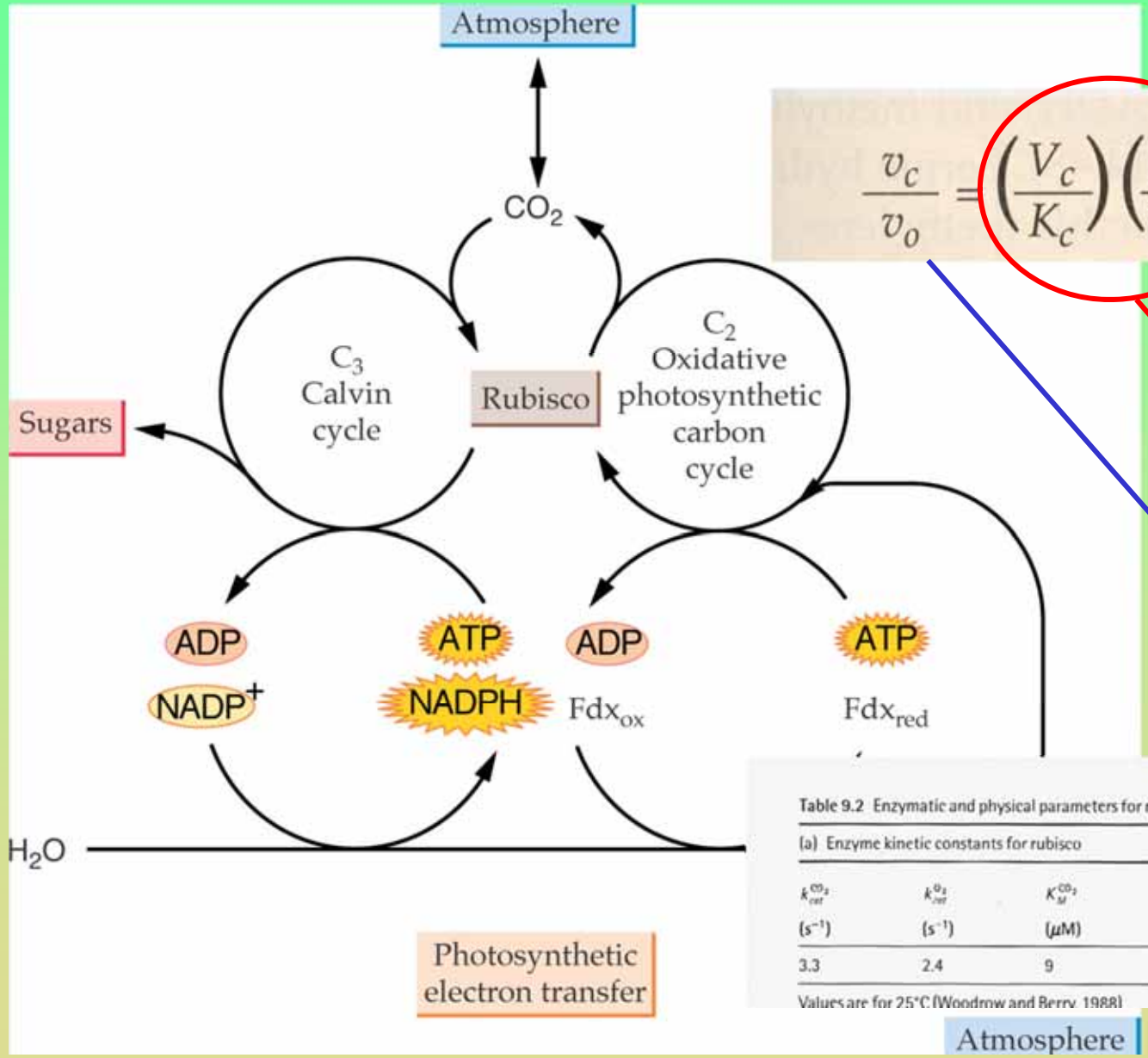
RUBISCO vzniklo v době, kdy nebyl O_2 v atmosféře

inhibuje rubisco

Fotorespirace snižuje fixaci uhlíku při vyšších koncentracích kyslíku



Co určuje poměr fotosyntézy a fotorespirace?



Kinetické vlastnosti Rubisca

$$\frac{v_c}{v_o} = \left(\frac{V_c}{K_c}\right)\left(\frac{K_o}{V_o}\right)\left(\frac{[CO_2]}{[O_2]}\right)$$

CO_2 8 μM
O_2 260 μM

faktor specificity
~ 30-80

~ 2.5

Table 9.2 Enzymatic and physical parameters for rubisco

(a) Enzyme kinetic constants for rubisco

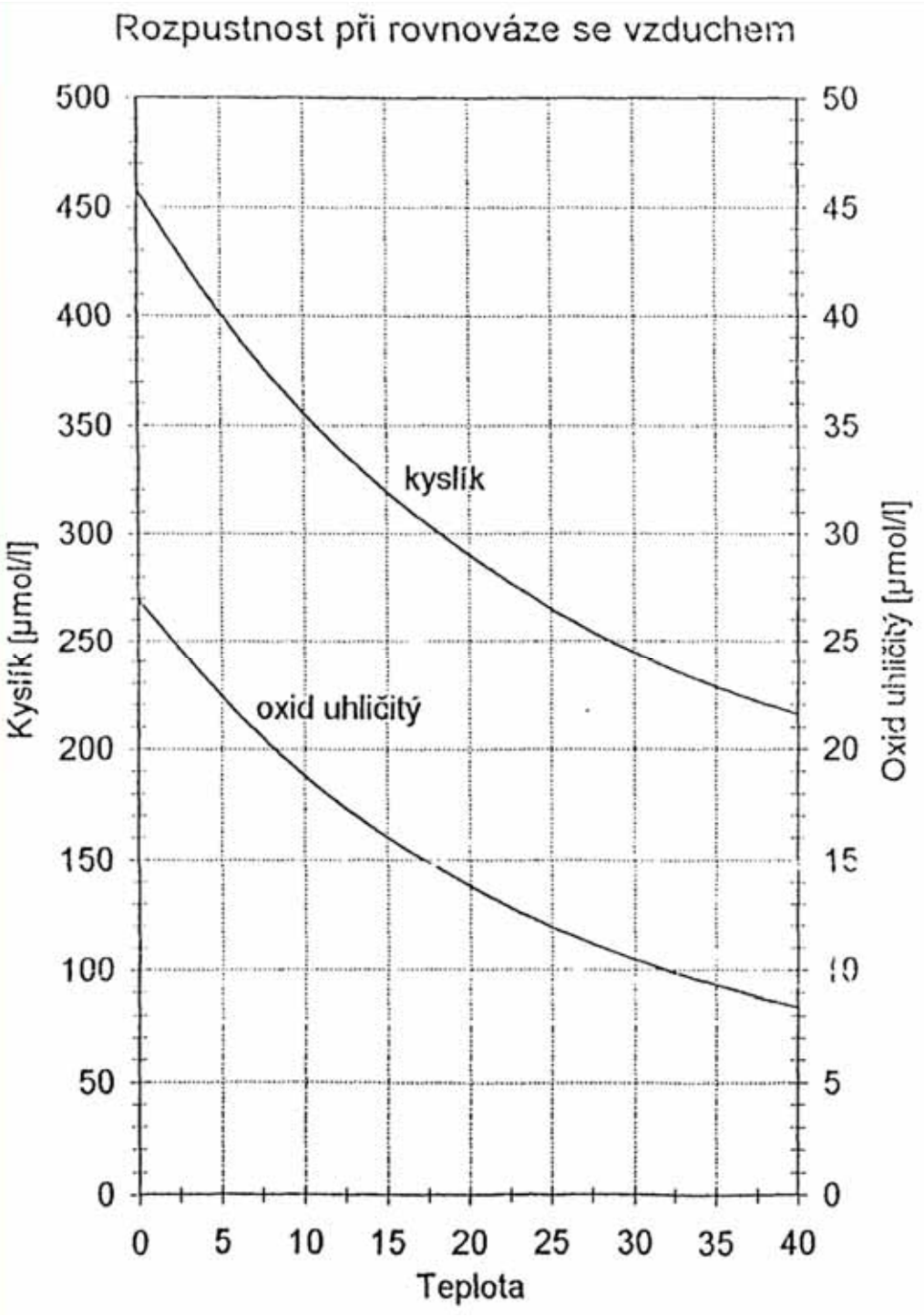
$k_{cat}^{CO_2}$ (s^{-1})	$k_{cat}^{O_2}$ (s^{-1})	$K_M^{CO_2}$ (μM)	$K_M^{O_2}$ (μM)	$\frac{k_{cat}^{CO_2}}{K_M^{CO_2}}$ ($s^{-1}M^{-1}$)	$\frac{k_{cat}^{O_2}}{K_M^{O_2}}$ ($s^{-1}M^{-1}$)
3.3	2.4	9	535	3.7×10^5	4.5×10^3

Values are for 25°C (Woodrow and Berry, 1988)

Vliv teploty na oxygenázovou aktivitu

rozpustnost O_2 a CO_2

kinetiku a aktivitu Rubisca



C2 oxidativní fotosyntetický cyklus

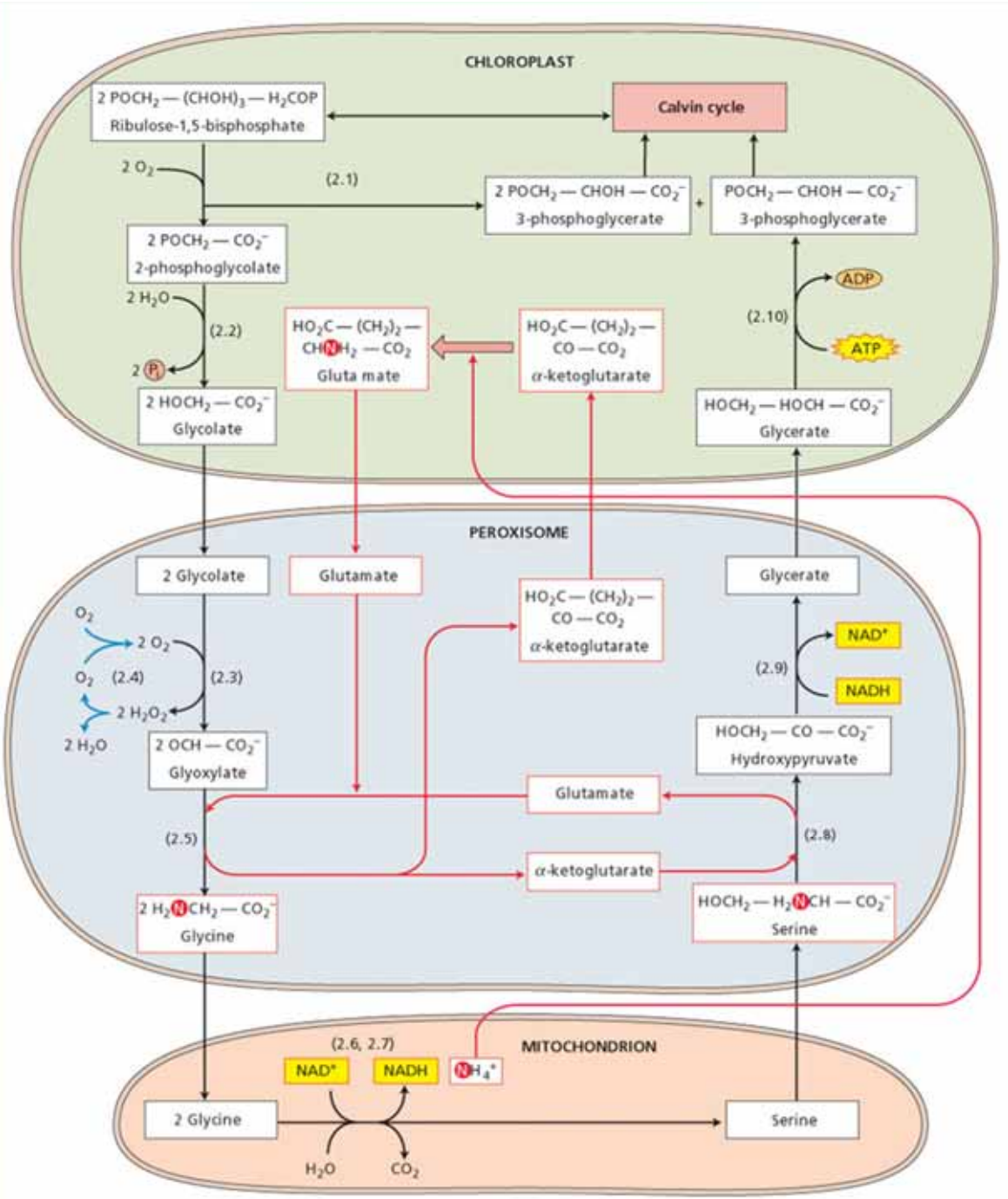
snižuje ztráty fixovaného C způsobené fotorespirací – oxygenázovou aktivitou Rubisca

kooperace 3 organel:
- chloroplast
- peroxisom
- mitochondrie

~50% energie spotřebované na karboxylaci

2 Pglycolate -> 1 Pglycerate

4C -> 3C (25% C loss)



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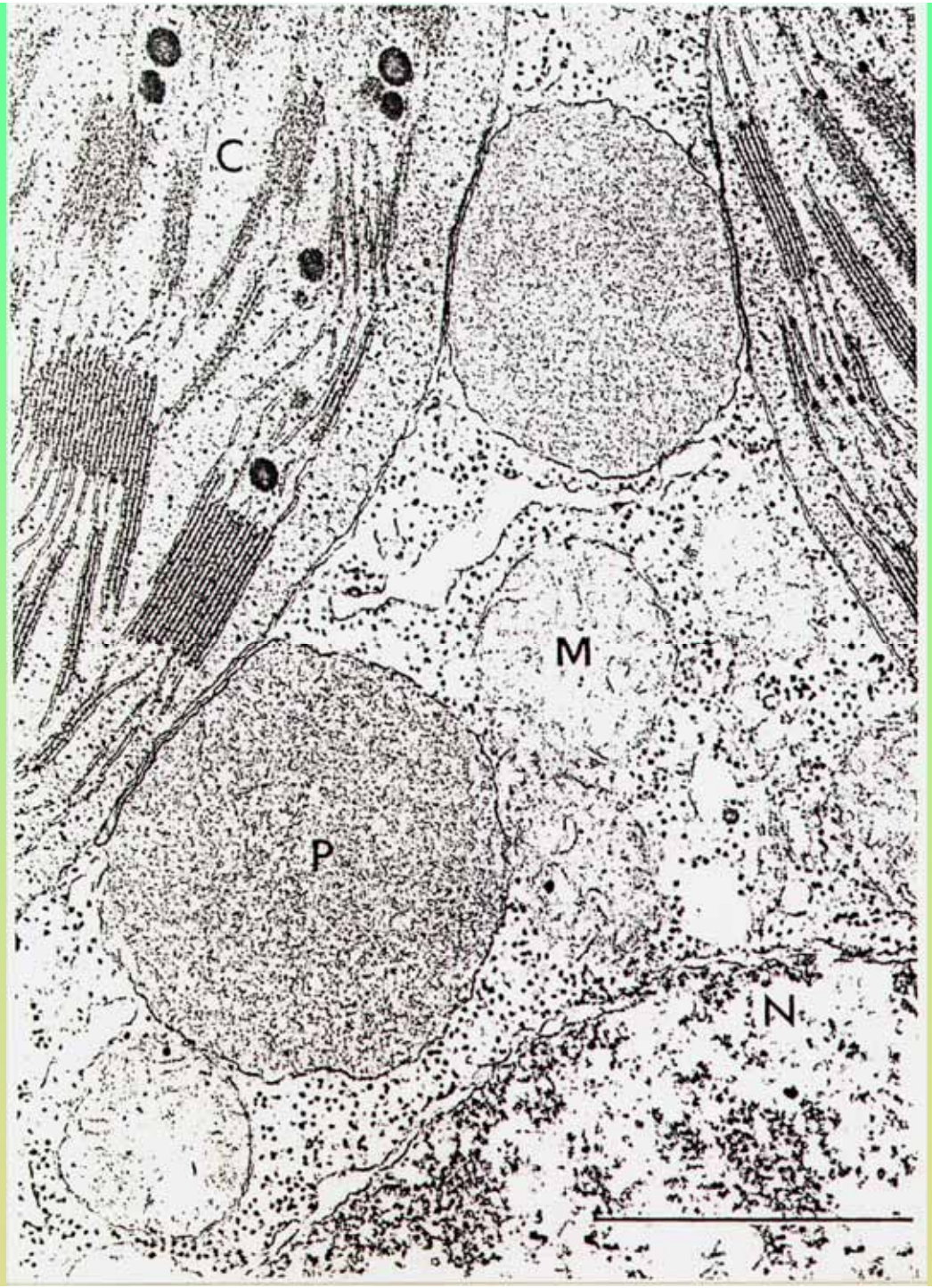
C2 oxidativní fotosyntetický cyklus

Elektronově mikroskopický snímek rostlinné buňky

kooperace 3 organel:

chloroplast (C)
peroxisom (P)
mitochondrie (M)



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- C3 dráha: fixace a redukce CO_2
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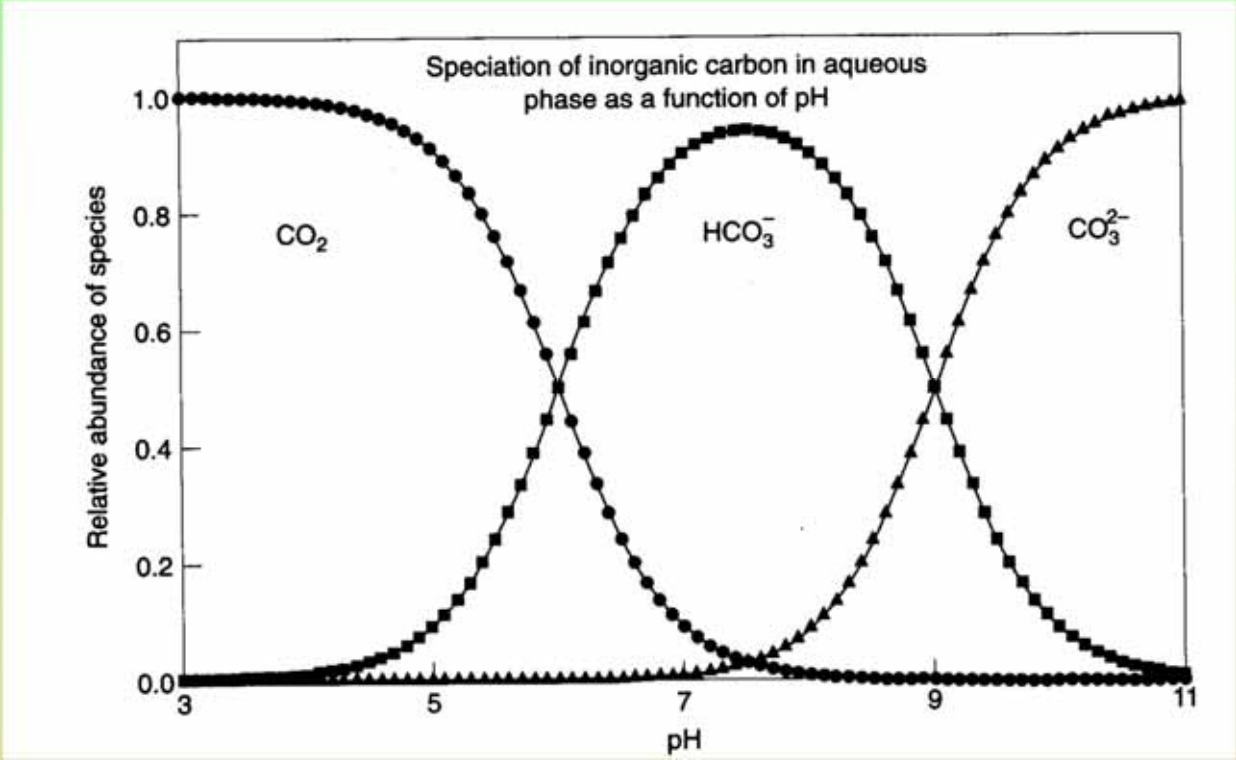
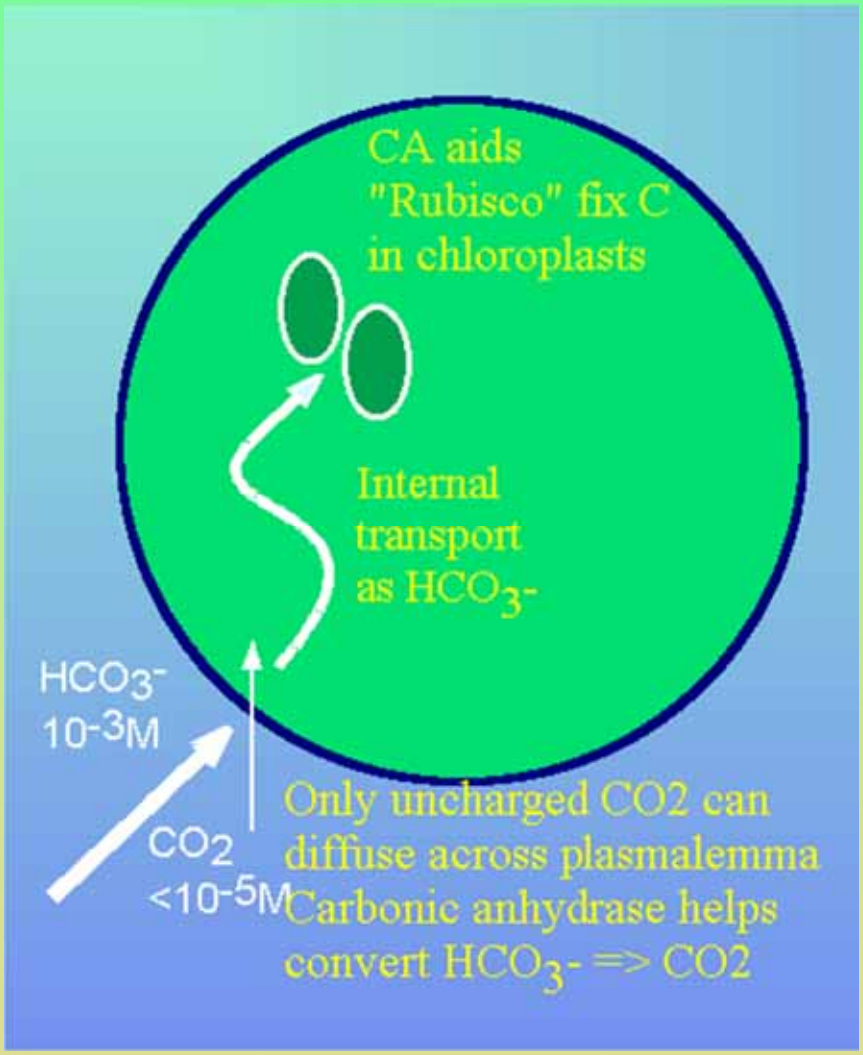
- CAM metabolismus

Formy CO_2 ve vodě

ve vzduchu ~ 360 μmol CO_2
ve vodě :
$H_2O + CO_2 \Leftrightarrow H_2CO_3 \Leftrightarrow H^+ + HCO_3^- \Leftrightarrow 2H^+ + CO_3^{2-}$
chemické rovnováhy CO_2 a protonů určují pH vody



CCM – mechanismus koncentrace uhlíku v řasách



Reverzibilní hydratace CO_2

$H_2O + CO_2 \Leftrightarrow H_2CO_3$

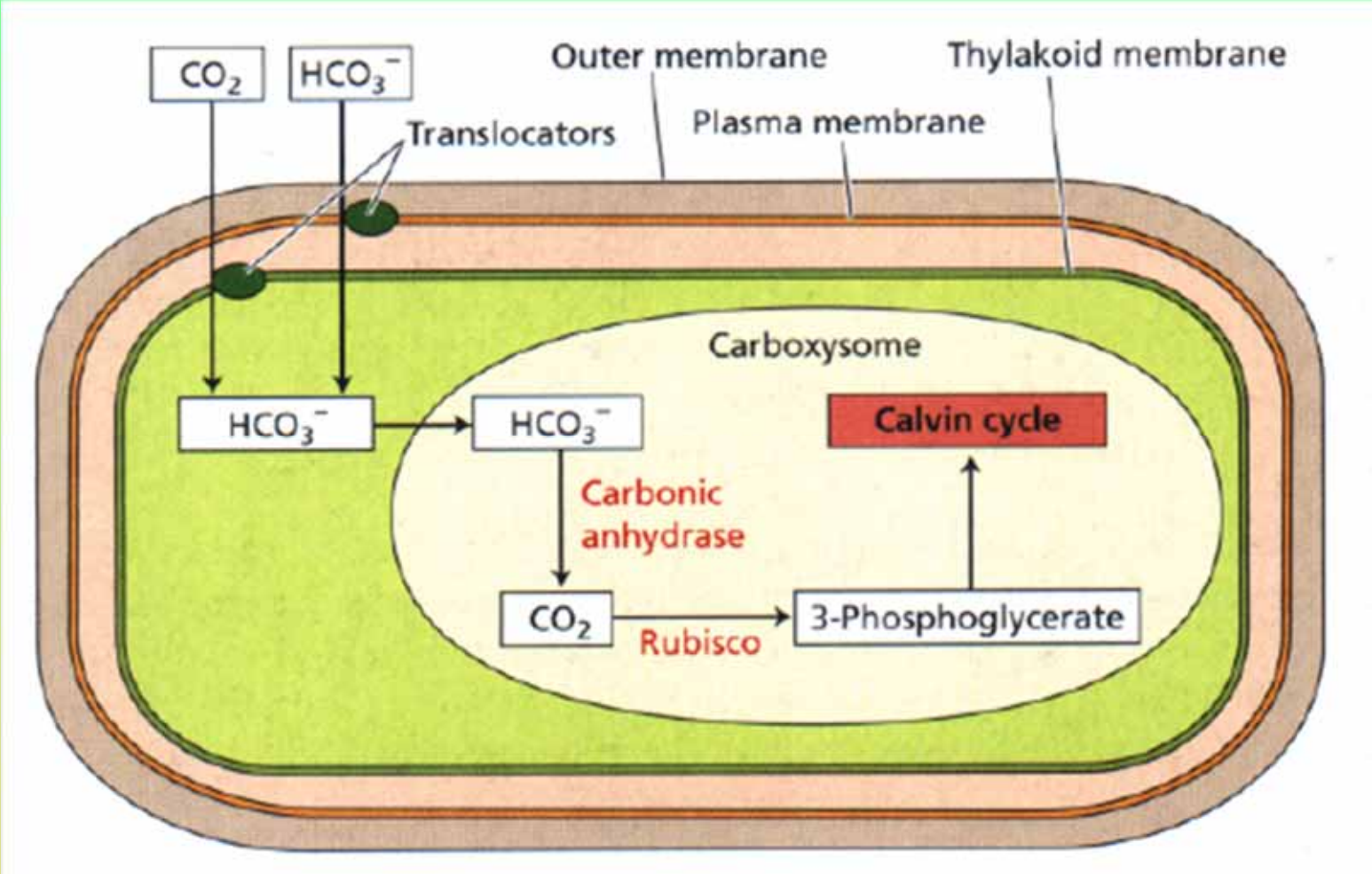
pomalá bez katalýzy

CA = karbonátdehydratáza
Až 600000 s^{-1}
jeden z nejrychlejších enzymů

CCM spotřebovává ATP

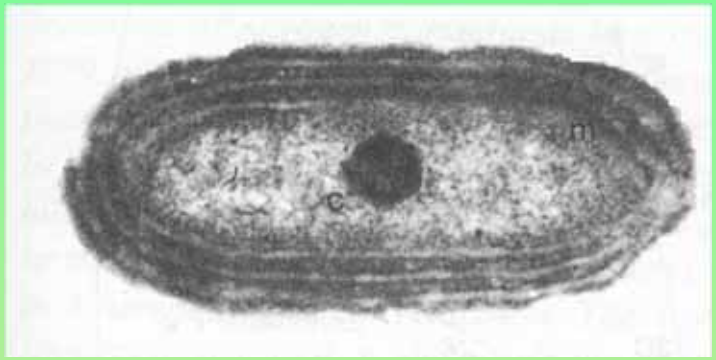
Pumpy CO_2 v cytoplasmatické membráně

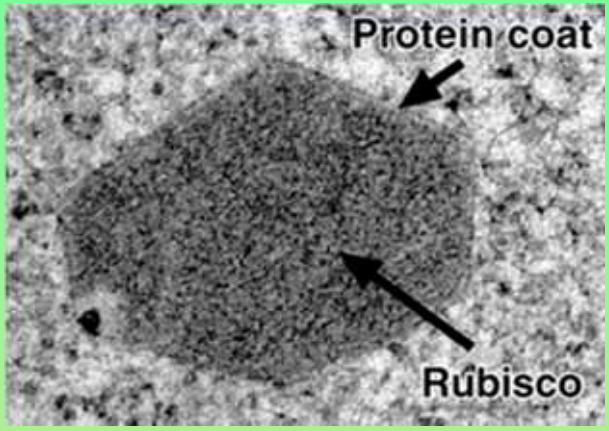
vodní rostliny, řasy ,sinice



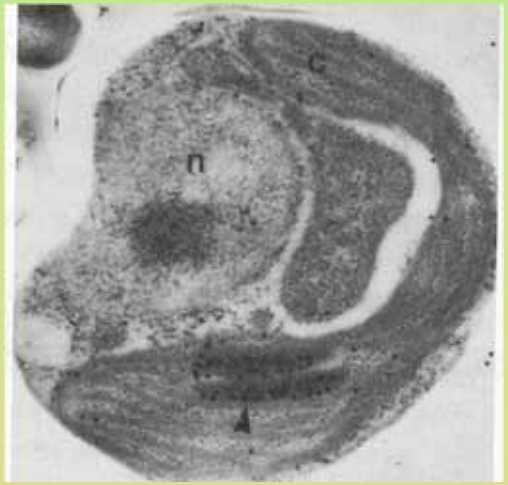
Strukury, ve kterých dochází k fixaci uhlíku

Sinice: karboxysomy





Řasy: pyrenoid



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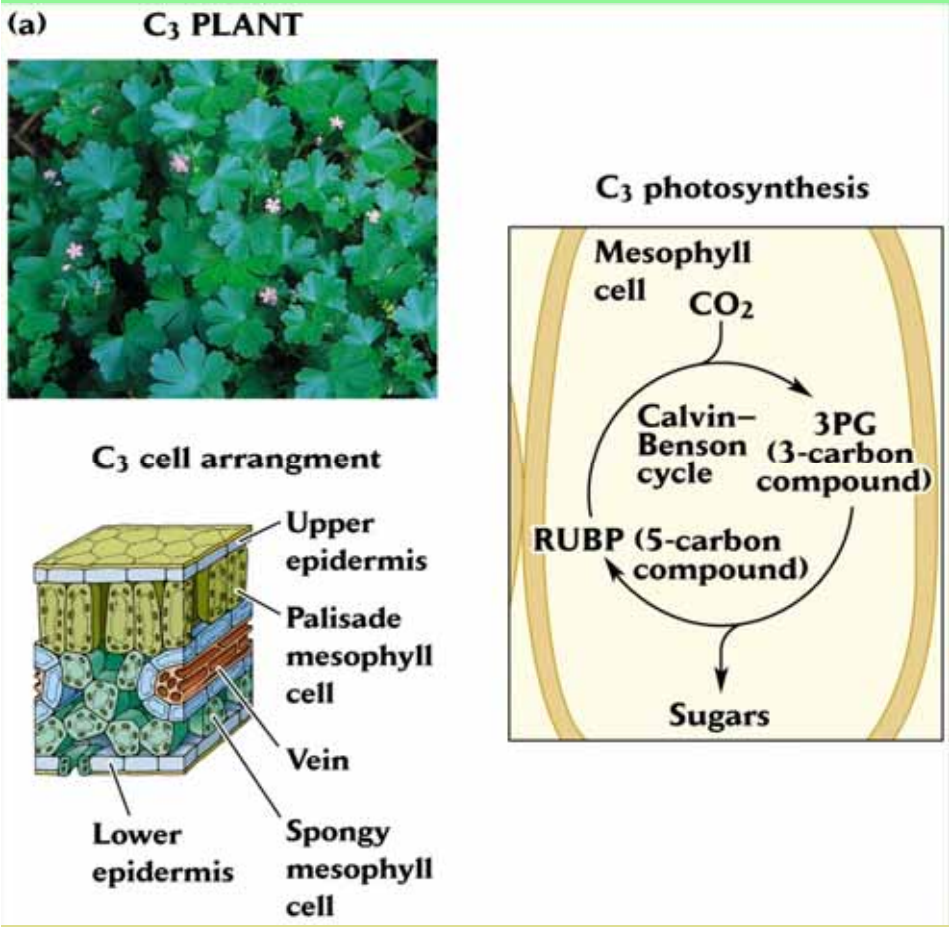
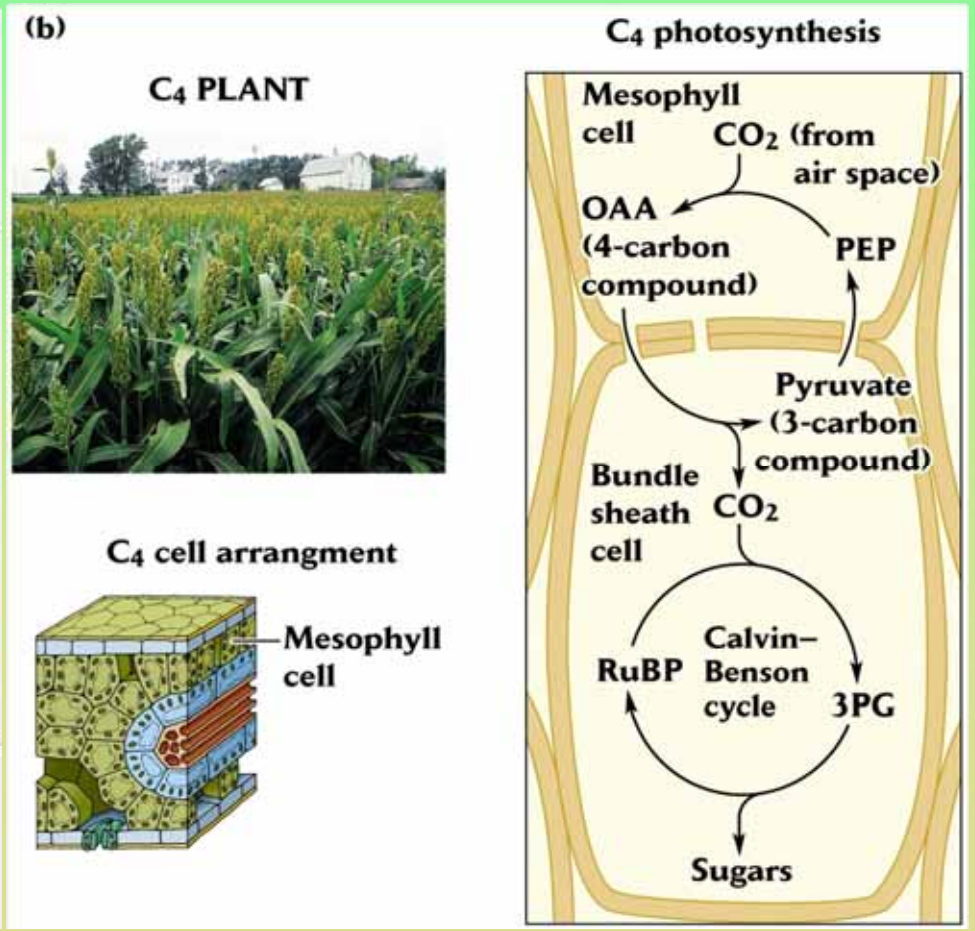
- CAM metabolismus

Jak se mohou adaptovat cévnaté rostliny?

C3 rostliny

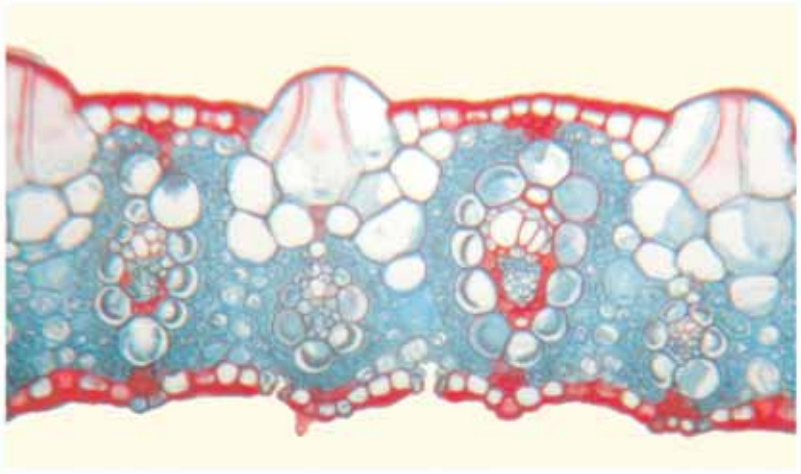
Věnčitá anatomie C4 rostlin –
velké buňky pochev cévních svazků
max. 2-3 vrstvy mesofylních buněk





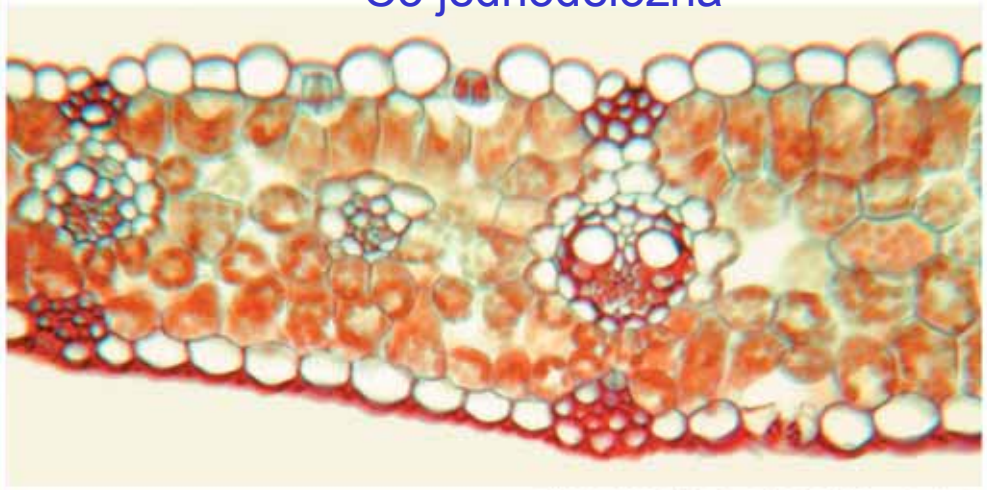
(A)

C4 jednoděložná



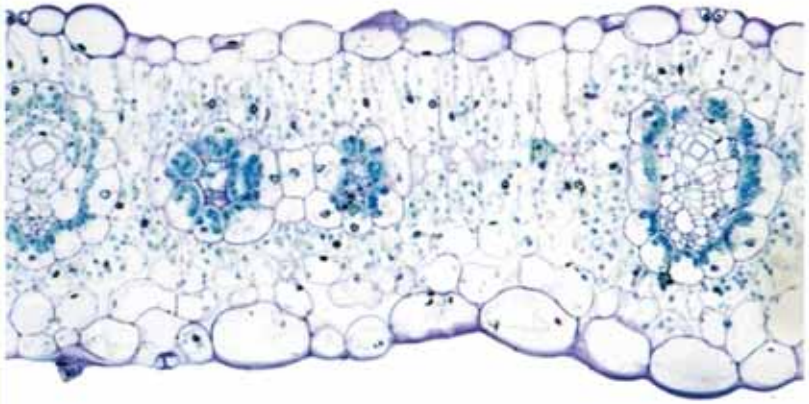
(B)

C3 jednoděložná

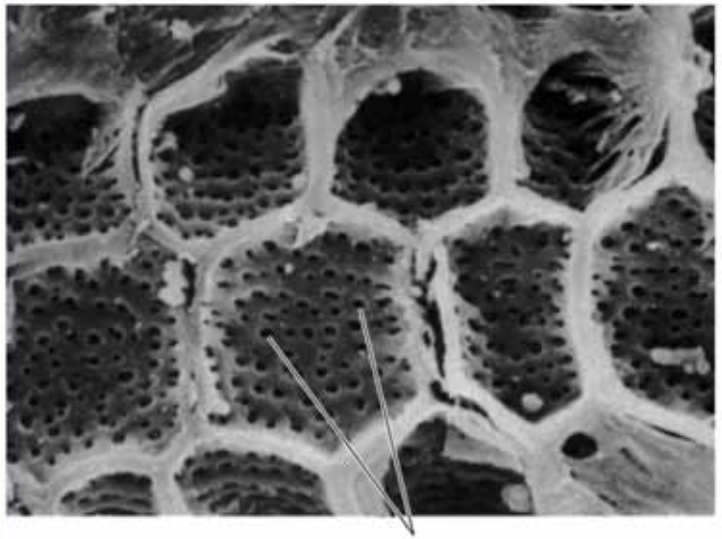


(C)

C4 dvouděložná



(E)



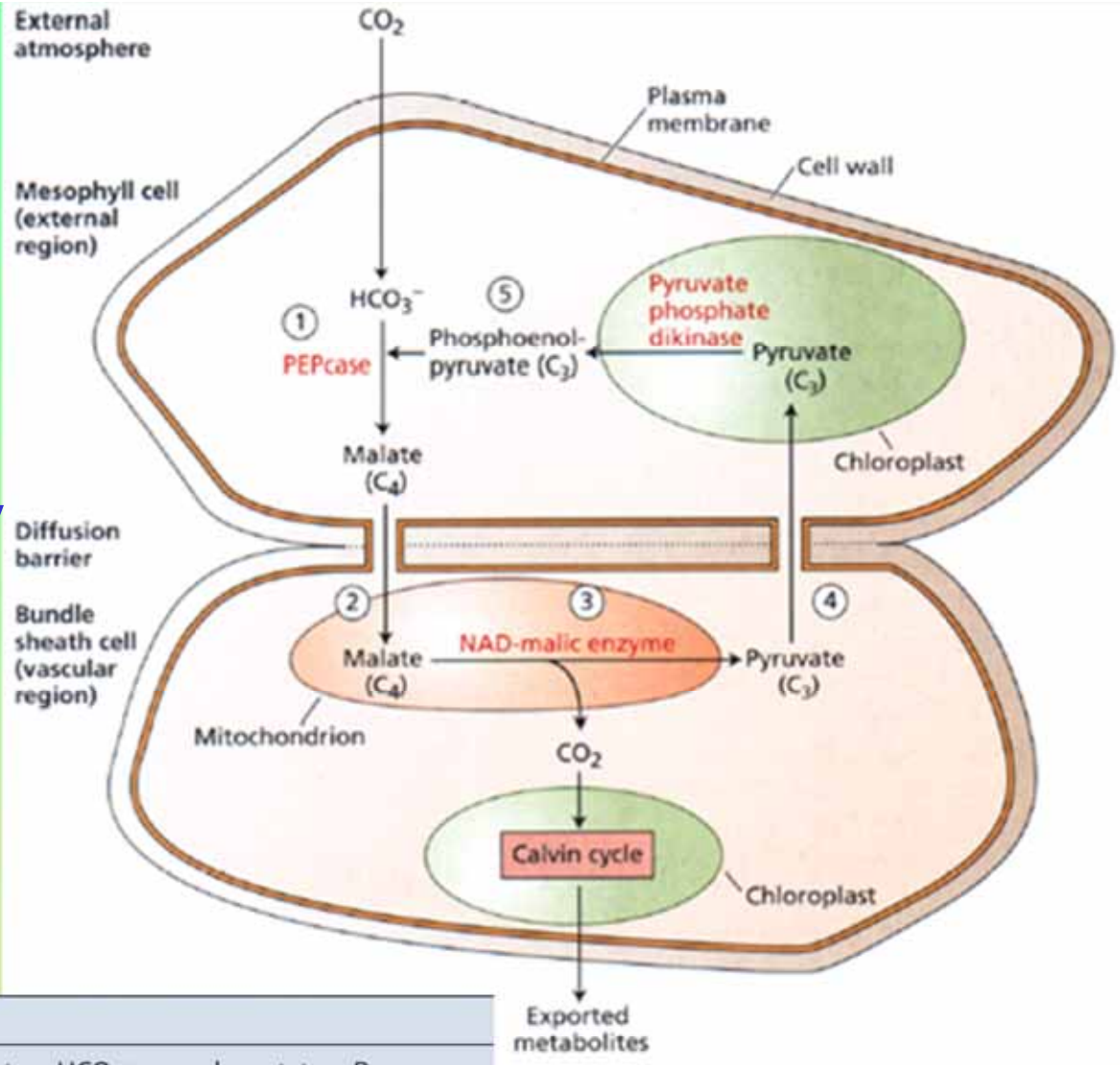
C4 cyklus

mesofilní buňky
buňky pochev cévních svazků

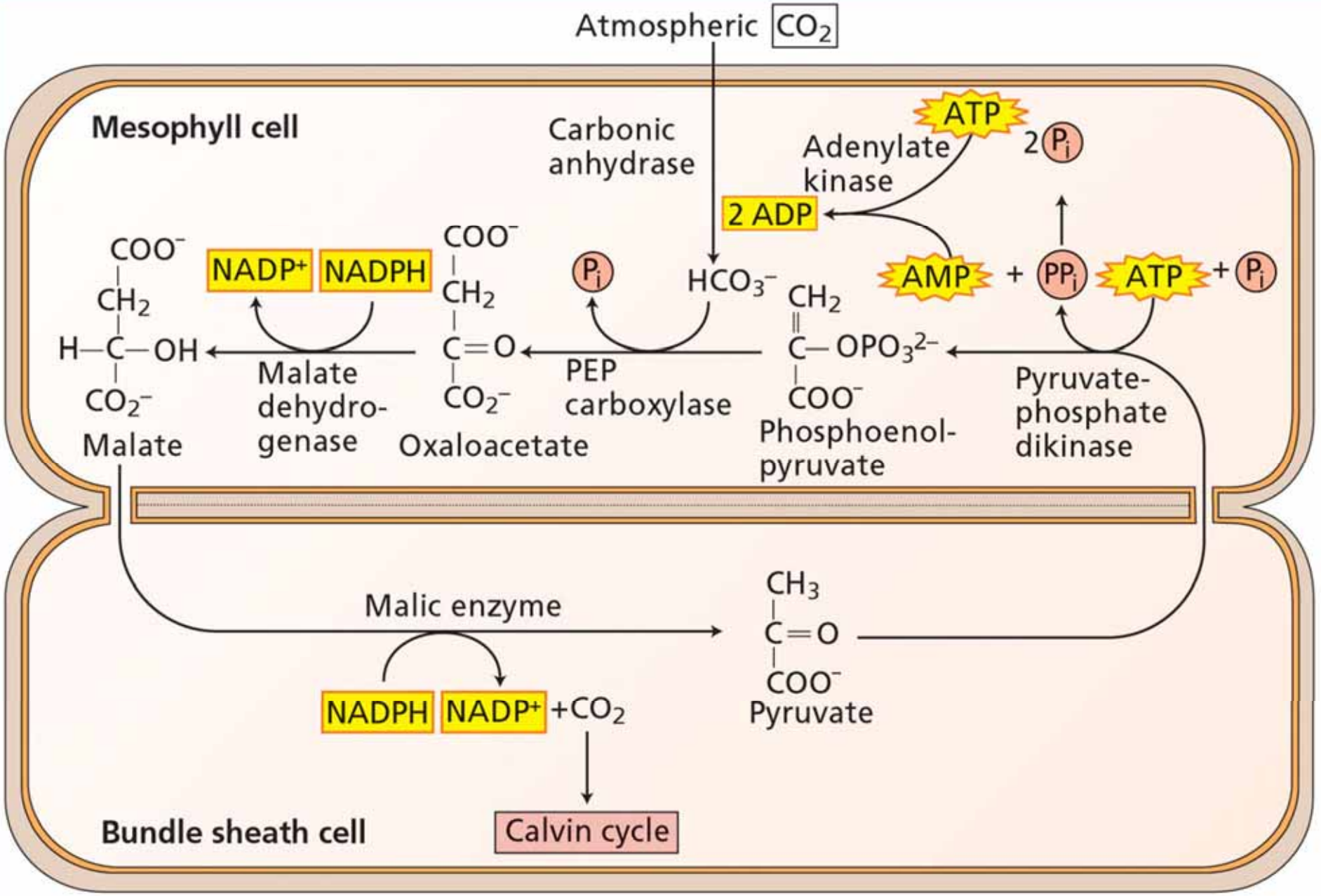
eliminace oxygenázové aktivity

koncentrace CO_2 ~ 15x

z 5 na 70 μM



Enzyme	Reaction
1. Phosphoenolpyruvate (PEP) carboxylase	Phosphoenolpyruvate + HCO_3^- → oxaloacetate + P_i
2. NADP:malate dehydrogenase	Oxaloacetate + NADPH + H^+ → malate + $NADP^+$
3. Aspartate aminotransferase	Oxaloacetate + glutamate → aspartate + α-ketoglutarate
4. NAD(P) malic enzyme	Malate + $NAD(P)^+$ → pyruvate + CO_2 + NAD(P)H + H^+
5. Phosphoenolpyruvate carboxykinase	Oxaloacetate + ATP → phosphoenolpyruvate + CO_2 + ADP



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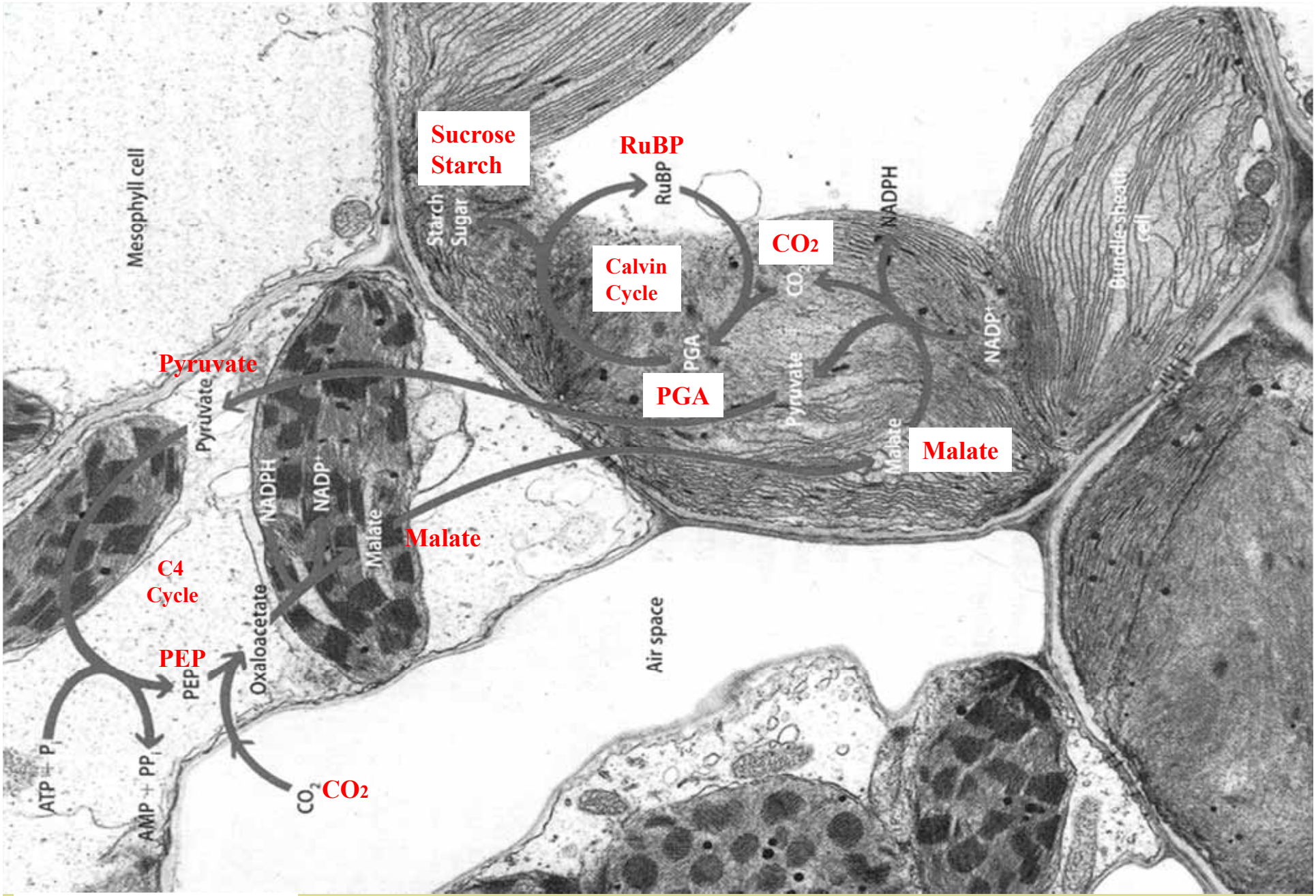
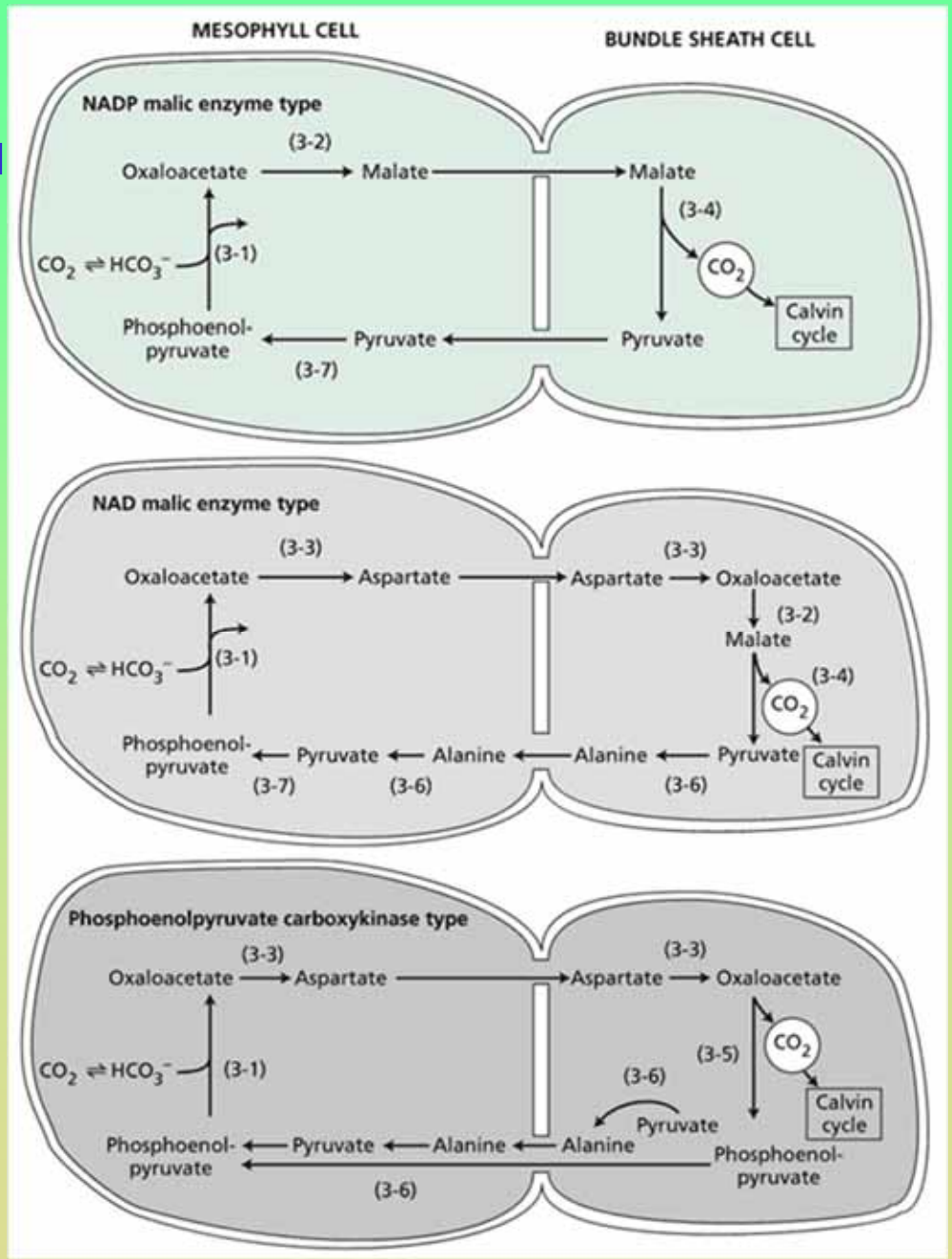

Sucrose
Starch
RuBP
Calvin
Cycle
CO2
Pyruvate
PGA
Malate
Malate
C4
Cycle
PEP
Oxaloacetate
CO2
Mesophyll cell
Bundle-sheath cell
Air space
NADPH
NADP+
ATP
AMP + PPi

Figure 7-24

3 varianty C4 metabolismu

liší se podle C4 kyseliny, která přenáší C do věnčitých buněk a podle dekarboxylaní reakce

NADP- malát
NAD malát
PEP karboxykináza



C4 cykly mají větší spotřebu energie než C3

TABLE 8.4
Energetics of the C_4 photosynthetic carbon cycle

Phosphoenolpyruvate + H_2O + NADPH + CO_2 (mesophyll)	→	malate + $NADP^+$ + P_i (mesophyll)
Malate + $NADP^+$	→	pyruvate + NADPH + CO_2 (bundle sheath)
Pyruvate + P_i + ATP	→	phosphoenolpyruvate + AMP + PP_i (mesophyll)
PP_i + H_2O	→	2 P_i (mesophyll)
AMP + ATP	→	2ADP
Net: CO_2 (mesophyll) + ATP + 2 H_2O	→	CO_2 (bundle sheath) + 2ADP + 2 P_i

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

	NADP-ME	NAD-ME	PEPCK
ATP Required			
C4 Cycle	2	2	3
PCR Cycle	3	3	3
Total ATP	5	5	6
NADPH Required			
C4 Cycle	1	0	0
PCR Cycle	1	2	2
Total NADPH	2	2	2

C4 metabolismus i u rostlin a řas bez věnčité anatomie!!

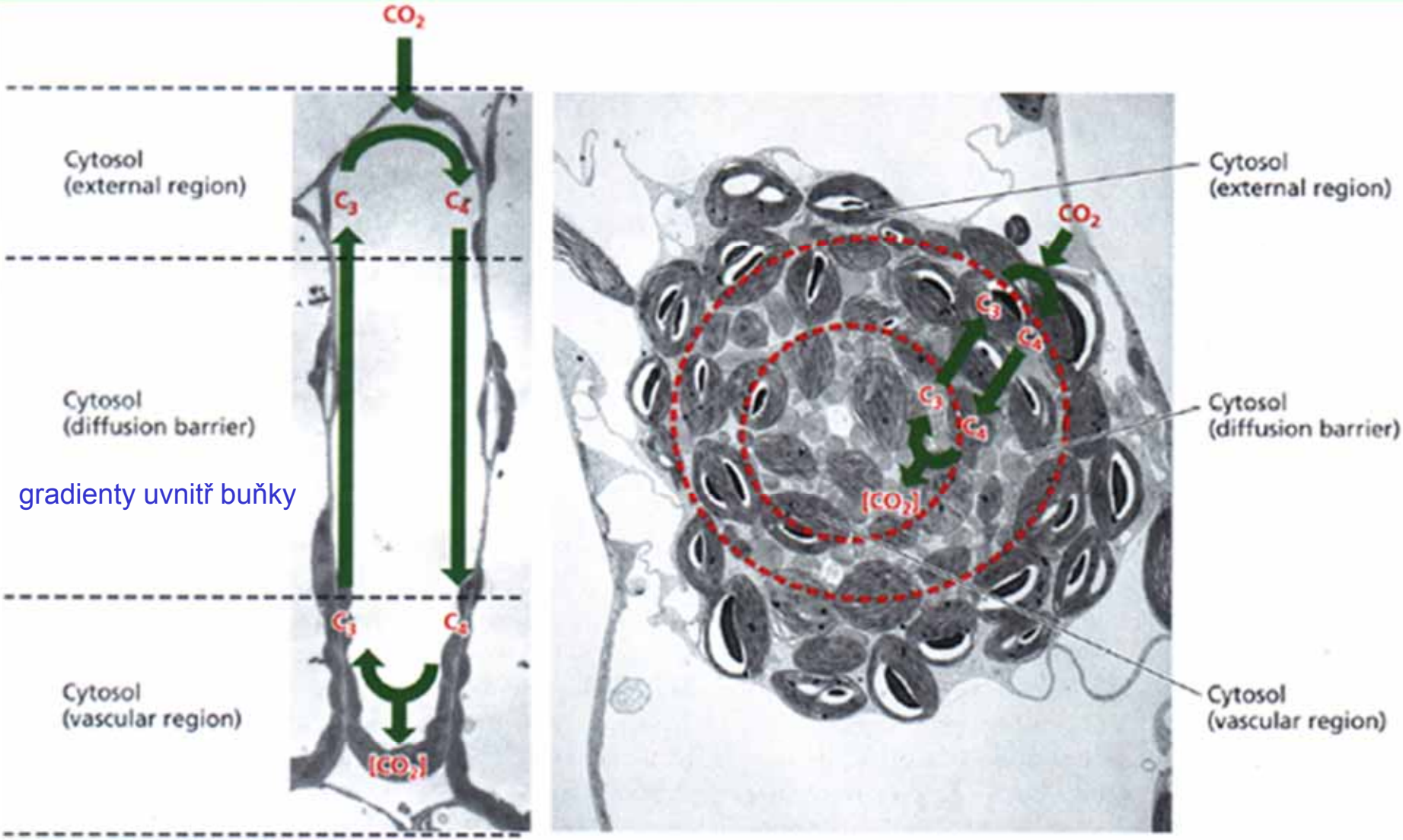
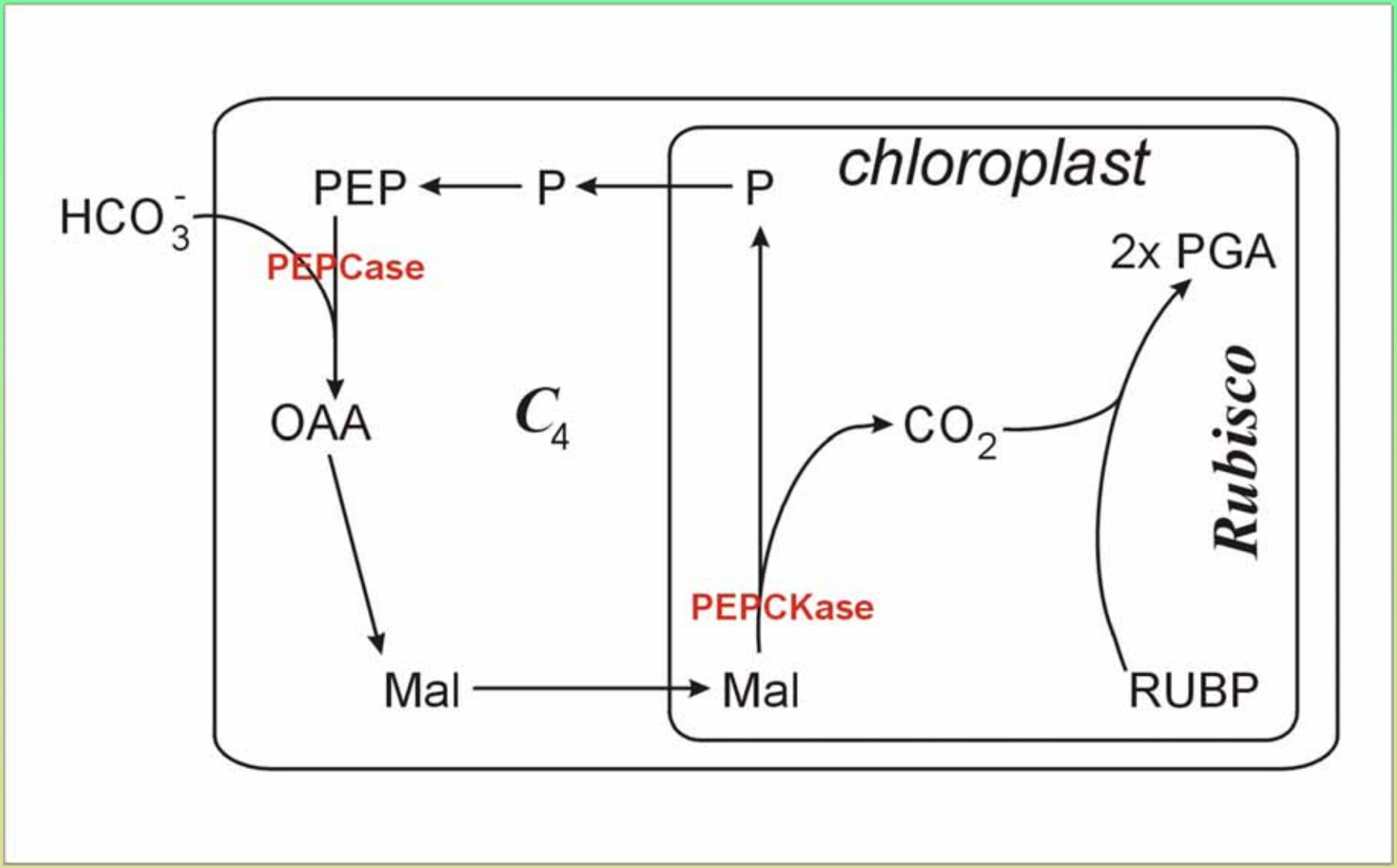
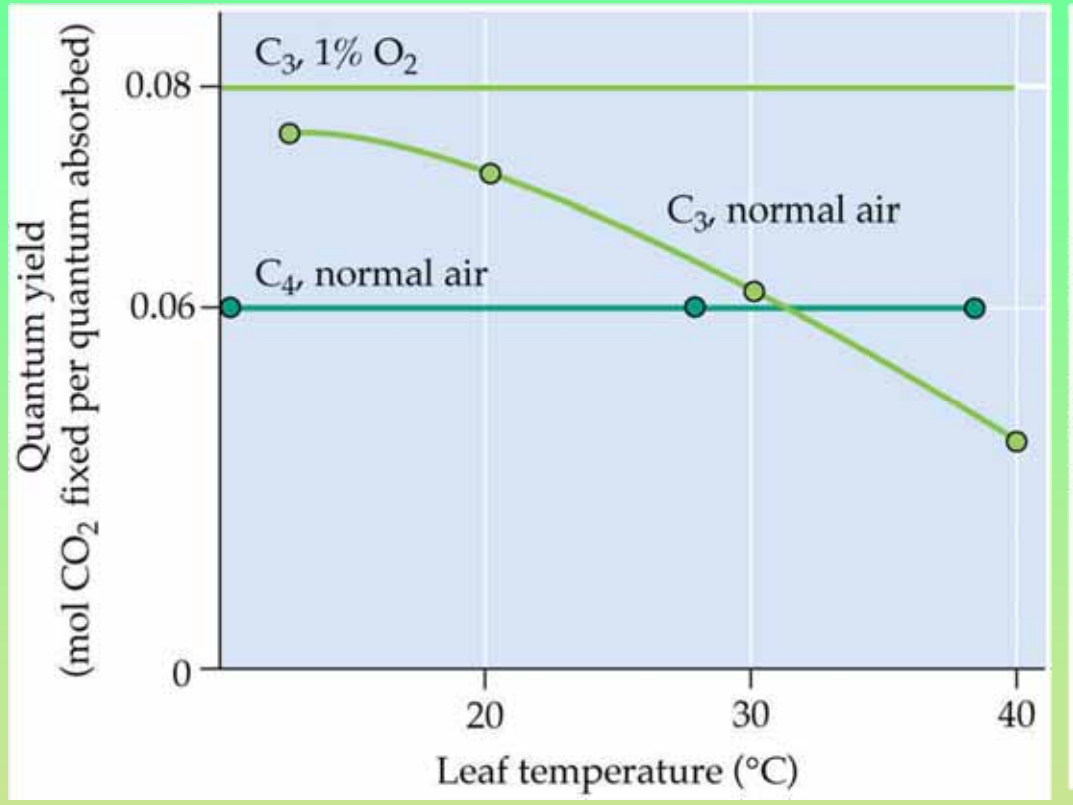
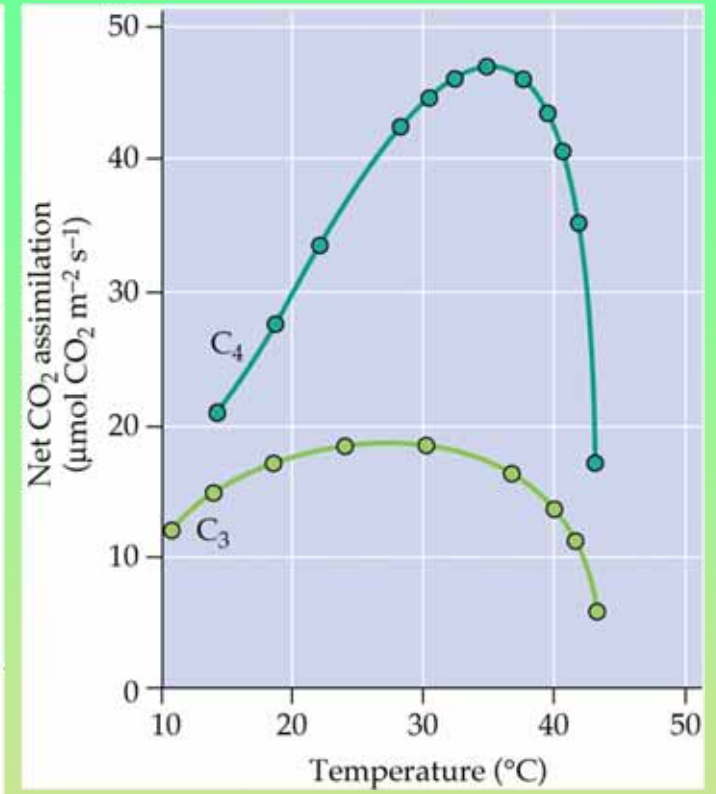


FIGURE 8.13 Single-cell C_4 photosynthesis. Diagrams of the C_4 cycle are superimposed on electron micrographs of *Borszczowia aralocaspica* (A) and *Bienertia cycloptera* (B). Studies on the localization of key photosynthetic enzymes also indicate two dimorphic chloroplasts located at different cytoplasmic compartments having photosynthetic functions analogous to mesophyll and bundle sheath cells in Kranz NAD-malic enzyme-type C_4 plants. (From Edwards et al. 2004.)

Fotosyntéza rozsivek







Díky substrátové specificitě PEPC pro HCO_3^- nedochází ke kompetici s O_2 (oxygenaci) za vyšších teplot

Obsah přednášky

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- C4 metabolismus
- CAM metabolismus
- Syntéza cukrů a škrobu

CAM = crassulacean acid metabolism

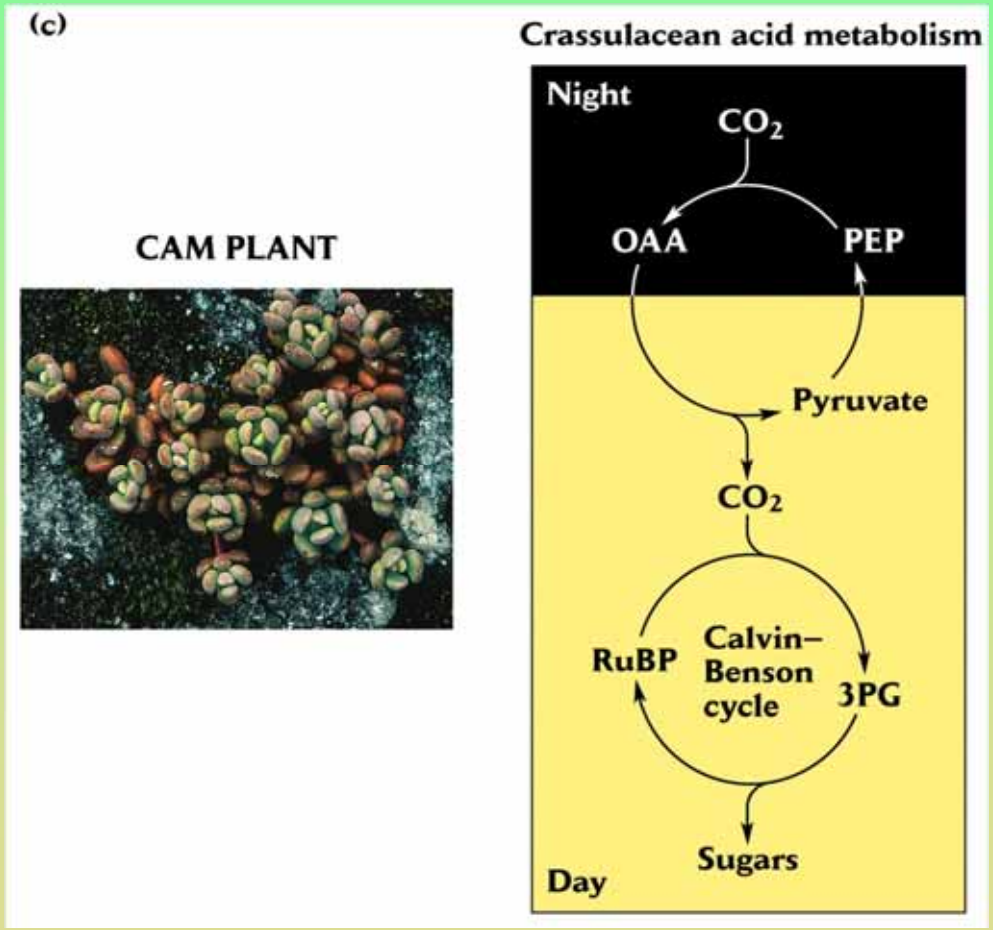
metabolismus kyselin u tučnolistých

aridní rostliny „rostliny CAM“
charakteristické jsou silné kutikuly, velké vakuoly, malá stomata

CAM rostliny:
50 -100 g H_2O na 1 g fixovaného CO_2

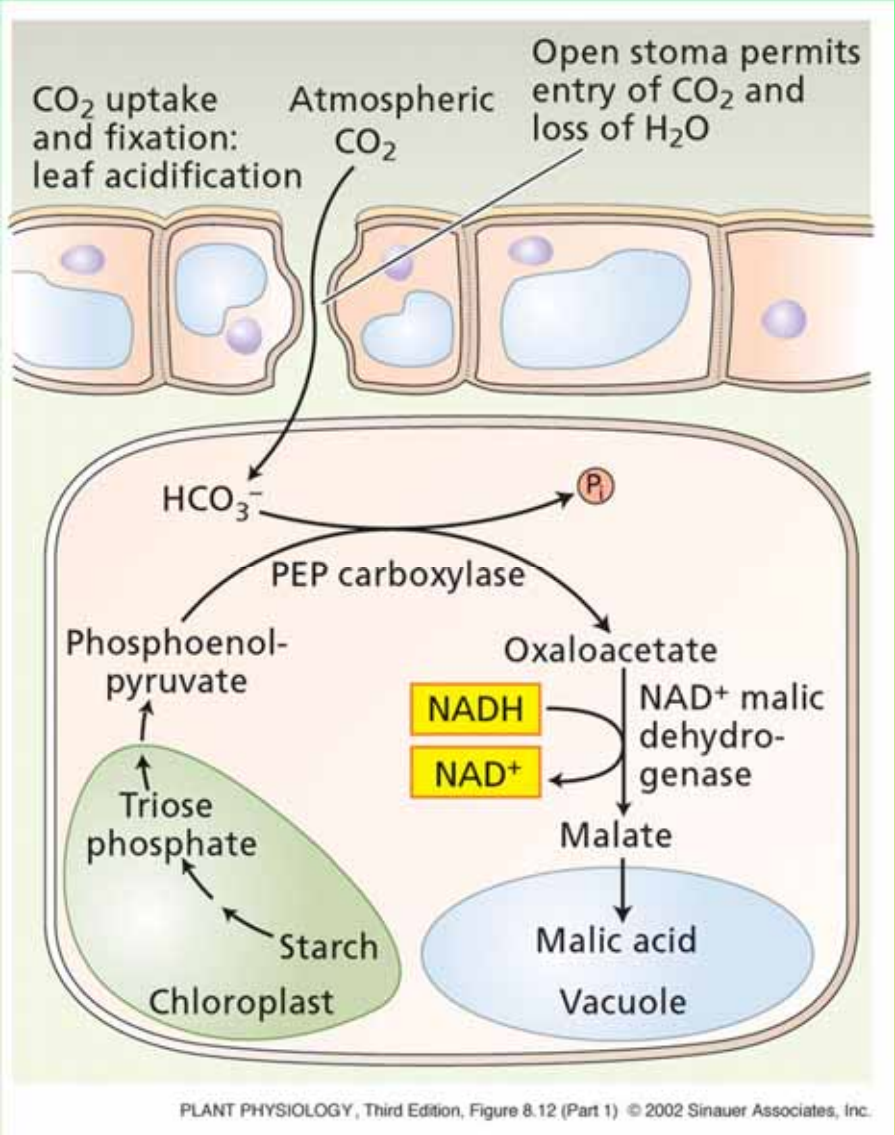
C4 rostliny
250 – 300 g H_20

C3 rostliny
400 - 500 g H_20

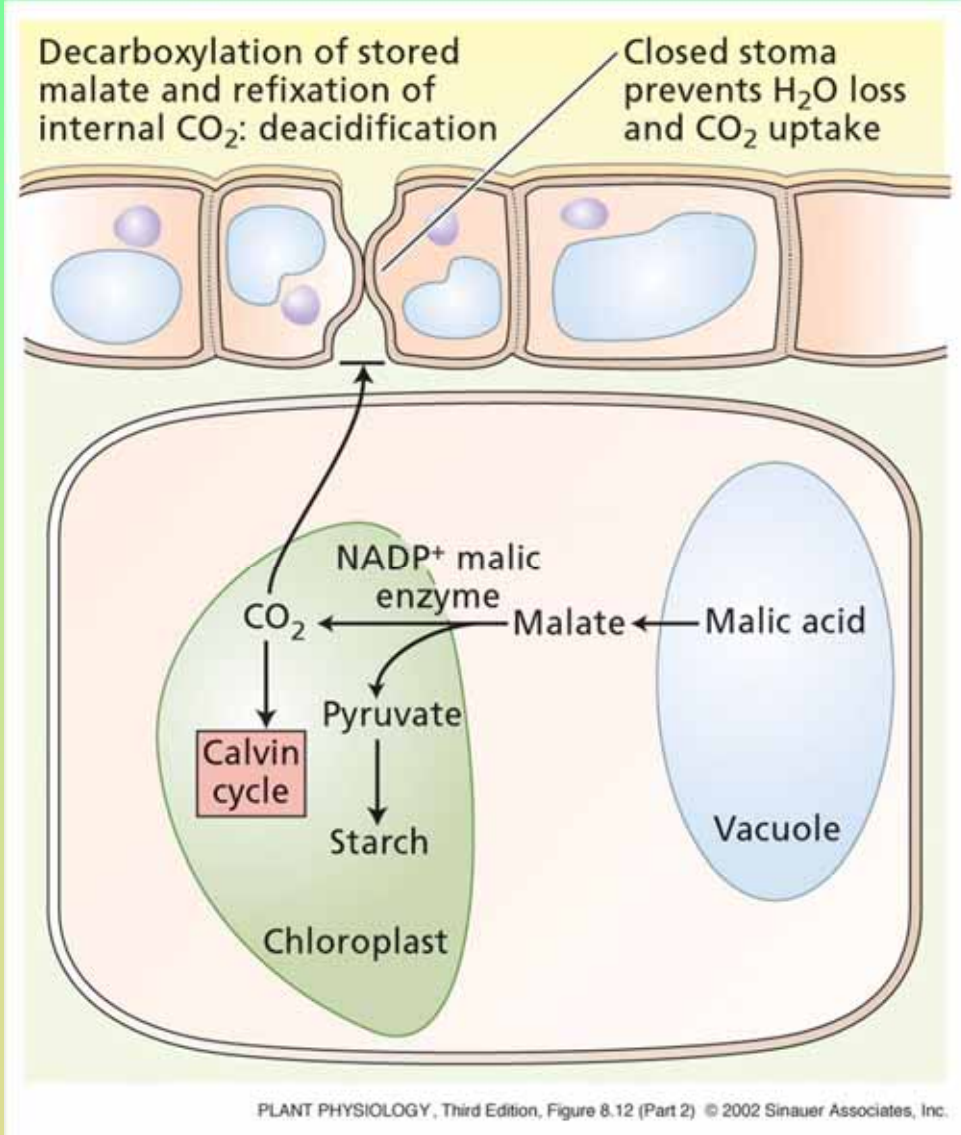


CAM metabolismus

tma



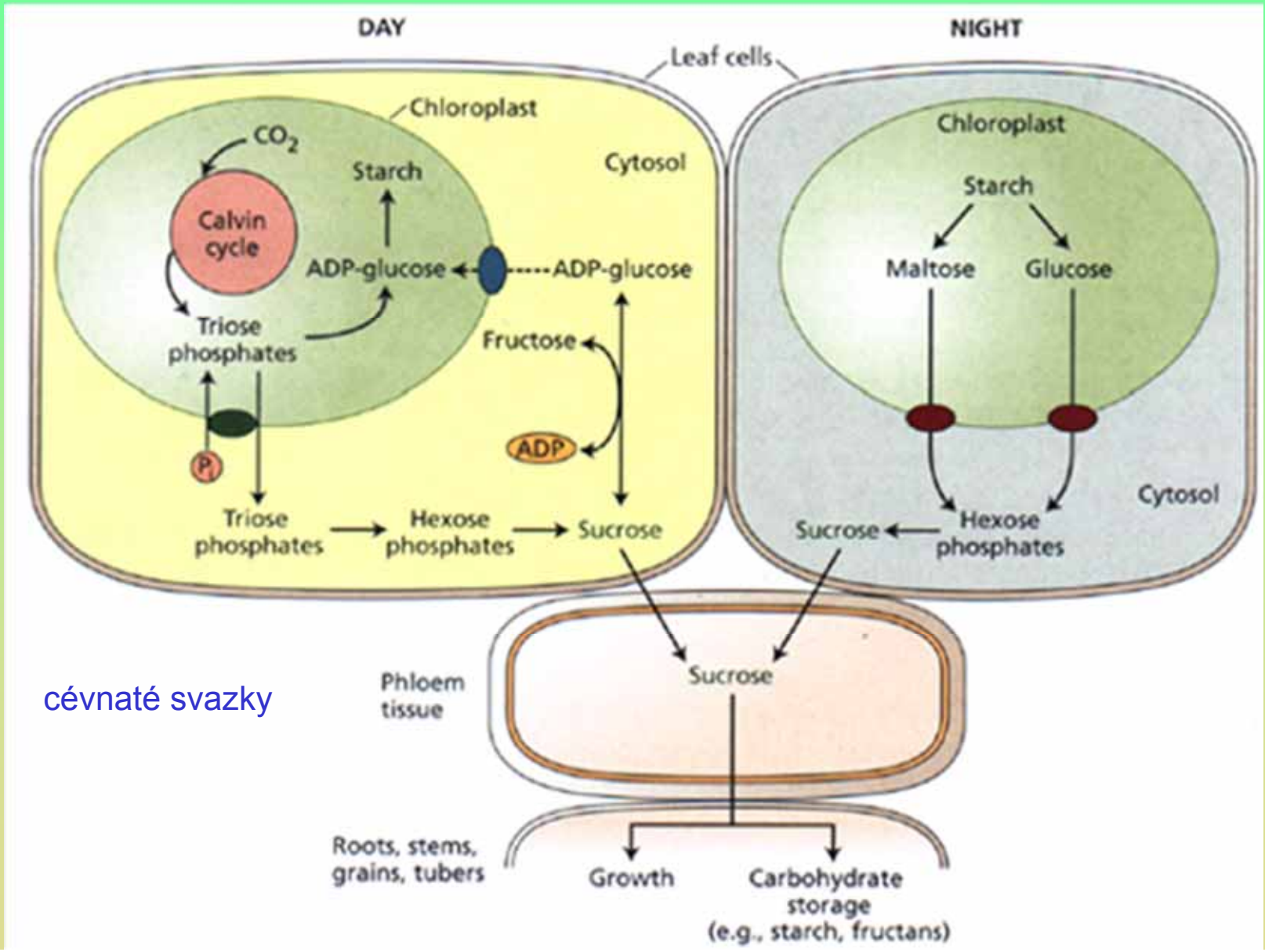
světlo



Obsah přednášky

- fixace a redukce CO_2
- fotorespirace
- mechanismy koncentrace CO_2
- C4
- CAM
- Syntéza cukrů a škrobu

Konečné produkty fotosyntetické asimilace CO_2: sacharóza a škrob



cévnaté svazky

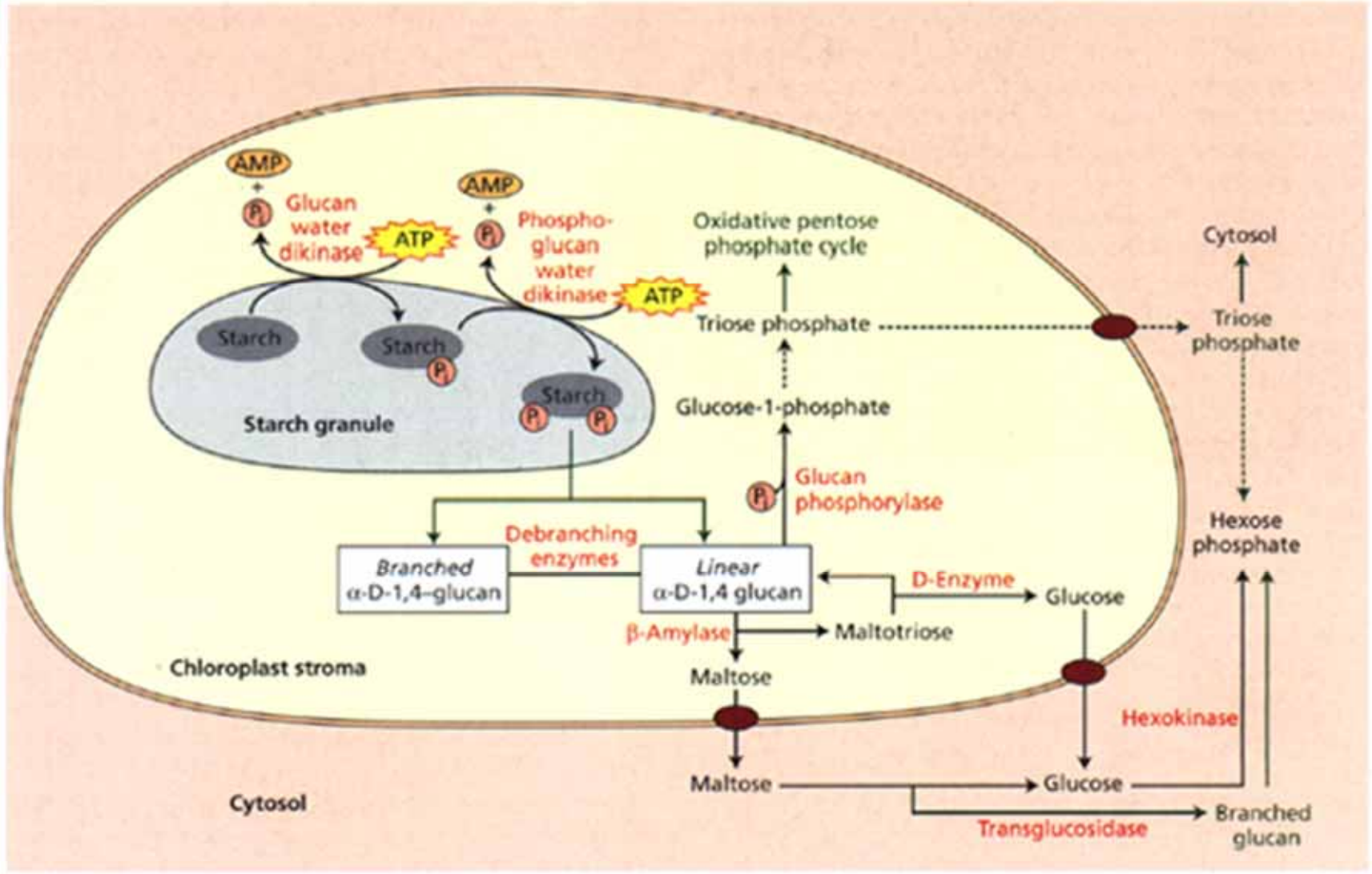


FIGURE 8.16 Nocturnal starch degradation in *A. thaliana* leaves. The release of soluble glucans from the starch granule at night requires the prior phosphorylation of the polysaccharide via a glucan–water dikinase and a phosphoglucan–water dikinase. At this stage, debranching enzymes transform the branched starch into linear glucans, which in turn can be converted into maltose via the β-amylolysis catalyzed by the chloroplastic β-amylase. Residual maltotriose is transformed to maltopentaose and glucose via the disproportionating enzyme (D-enzyme). Two pumps in the chloroplast envelope, one for maltose and another for glucose, facilitate the flow of these products of starch degradation to the cytosol. The utilization of maltose in the leaf cytosol proceeds via a transglucosidase that transfers one glucosyl moiety to a branched glucan, concurrently releasing a glucose. The cytosolic glucose can be phosphorylated via a hexokinase to glucose-6-phosphate for incorporation into the pool of hexose phosphates.

1. The term "dark reactions" was used for many years to describe the reactions for incorporating CO_2 in photosynthesis. Why was this term considered appropriate at the time and why is it considered inappropriate now?
2. Photorespiration is generally considered to be a wasteful process that decreases the yield of C_3 plants. What experiment would you propose to minimize the role of photorespiration in plants?
3. What would be the consequence in each of the following if the thioredoxins in chloroplasts were reduced not by ferredoxin but by NADPH as is the case for their cytosol counterparts? Assume NADPH is constant. Explain your answer.
   A. Rate of starch synthesis.
   B. Hexose monophosphate pool in chloroplasts in the dark.
   C. Synthesis of malate in C_4 plants.
   D. Synthesis of malate in CAM plants assuming an adequate supply of phosphoenolpyruvate.
   E. Activity of Rubisco.
4. There is current concern that the level of CO_2 is increasing in the biosphere due to the burning of fossil fuels. If the level of atmospheric CO_2 were to double, how would the following be affected? Explain your answer.
   A. Rate of oxaloacetate synthesis in C_4 plants.
   B. Rate of 3-phosphoglycerate synthesis in C_3 plants.
   C. Rate of photorespiration in C_3 plants.
   D. Yield of wheat in Kansas.
   E. Temperature of San Francisco Bay.
5. It has been known for many years that the cytosolic concentration of Pi in leaves increases when plants are shifted from light to dark. What effect does this change on each of the following?
   A. The concentration of fructose-1,6-bisphosphate.
   B. Synthesis of sucrose-6-phosphate from a fixed amount of fructose-6-phosphate.
   C. Synthesis of sucrose from fructose-6-phosphate
   D. Pool of dihydroxyacetone phosphate in chloroplasts.

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