Chapter 7

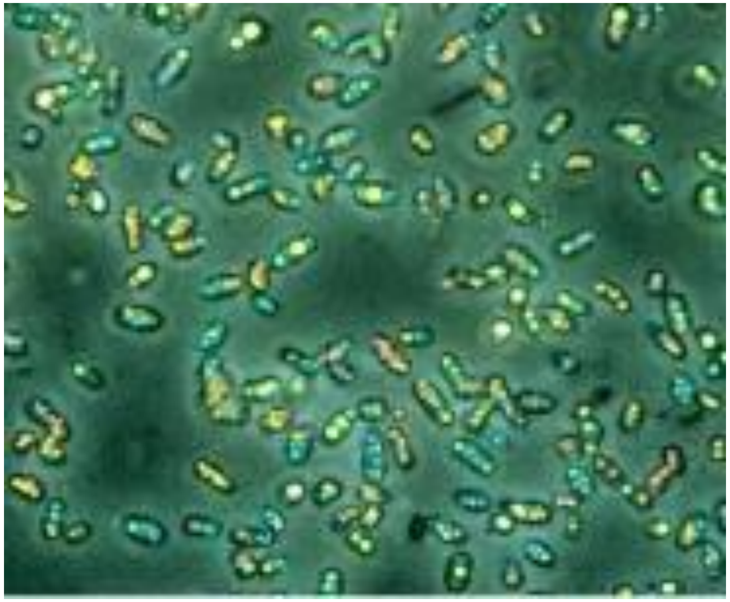
Photosynthesis: The Light Reactions

Outline

- History and intro
- Properties of light and pigments
- Light-dependent reactions
  - photosystem II and I
  - ATP synthesis
- Light-independent reactions
  - Calvin cycle
  - Rubisco and photorespiration
  - CAM and C_4 plants
- Physiological and ecological considerations
  - light
  - plant anatomy
  - plant responses
  - excess light and photoinhibition
  - greenhouse effect and consequences

History

- 1600's van Helmont - soil alone does not nourish plant
- 1700's Priestley - plants restore air from burning candles
- 1700's Ingenhousz - only green parts of plants restore air, suggests CO_2 split to release O_2
- 1931 van Niel - Ps in purple sulfur bacteria produced S_2 instead of O_2 during Ps thus proposed O_2 released from Ps comes from H_2O, not CO_2
- 1937 Hill - isolated chloroplasts produced O_2 w/o CO_2 confirming O_2 released from Ps comes from H_2O, not CO_2
- 1905 Blackman - Ps composed of light-dep. + light-indep. rxns, enzymes involved

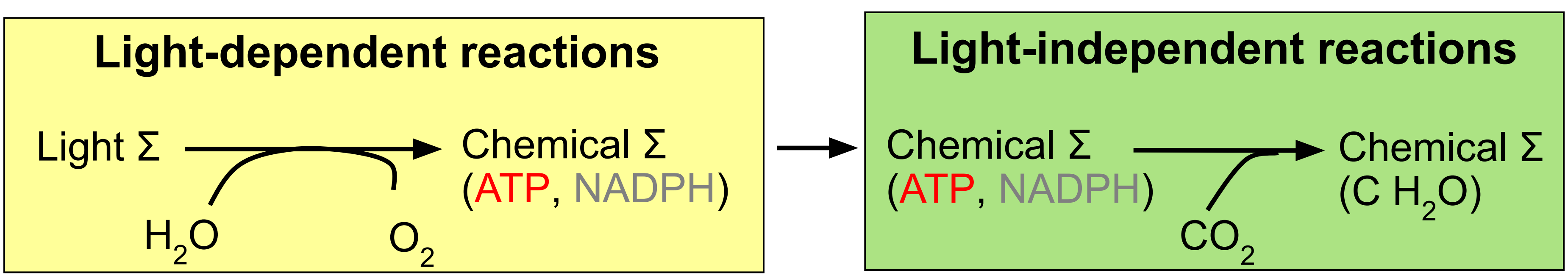


Intro

- Photosynthesis (Ps) = process by which plants convert sunlight into chemical Σ, how Σ enters biosphere
  - chemical Σ used to convert water and CO_2 into sugars, O_2 is produced as byproduct

$$6\ CO_2 + 6\ H_2O \rightarrow C_6H_2O_6 + 6\ O_2$$

- Consists of light-dependent + light-independent rxns



Intro

- Light-dependent rxns (a.k.a) light rxns, thylkoid rxns, light-transduction rxns
  - require light, occur on thylakoid membranes
  - split water (oxidize water to O_2)
  - produce NADPH, ATP (via PMF)
  - uses 2 photosystems
- Light-independent rxns (a.k.a) dark rxns, carbon fixation rxns, stroma rxns, Calvin cycle
  - don't require light, occur in chloroplast stroma
  - use ATP, NADPH
  - produce reduced carbon cmpds (i.e. glucose) from CO_2
- Ps primarily occurs in leaf mesophyll cells
  - mesophyll contains lots of chloroplasts

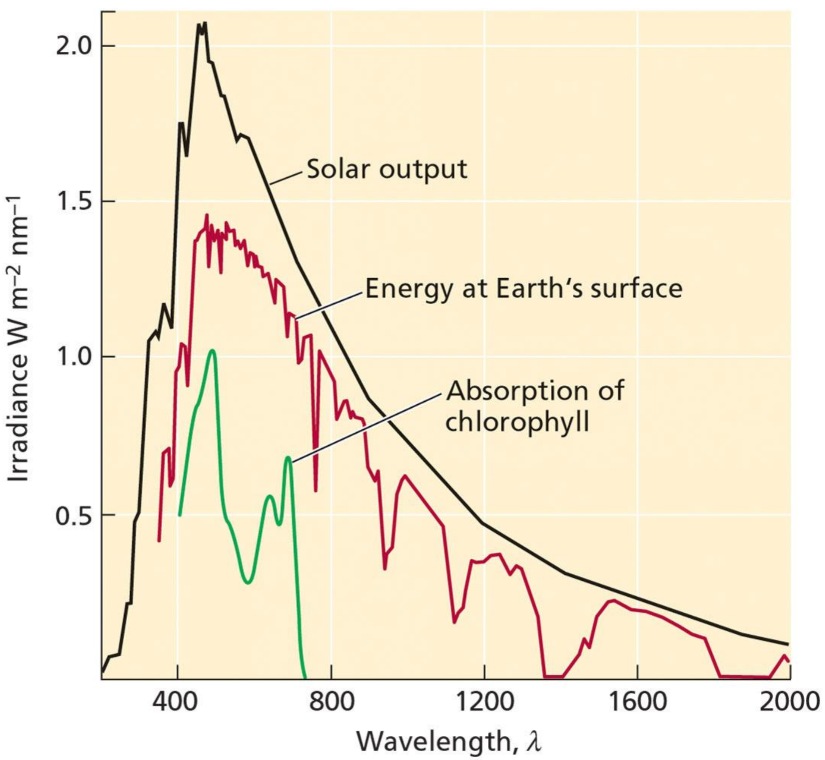
Properties of Light

- Light travels in waves
  - wavelength (λ) = distance btwn 2 crests
  - frequency (v) = # of wave crests that pass a pt in a given time

    $c = \lambda v$ where: c = wave speed, $c_{light} = 3.0 \times 10^8$ m s^{-1}
- Light composed of particles of Σ (photons)
  - Σ contained in discrete packets (quantum)
  - Σ of photon inversely proportional to frequency

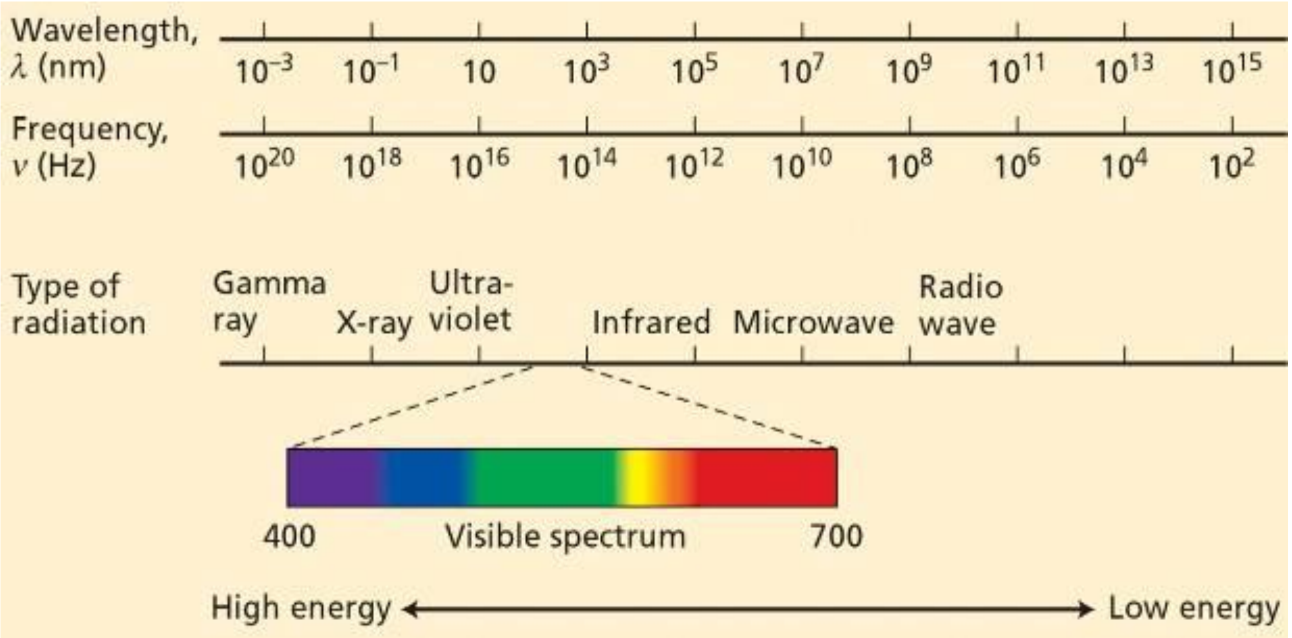
    $E = hv$ where: v = frequency of light

    h = Planck's constant = 6.626 x 10-34 J s



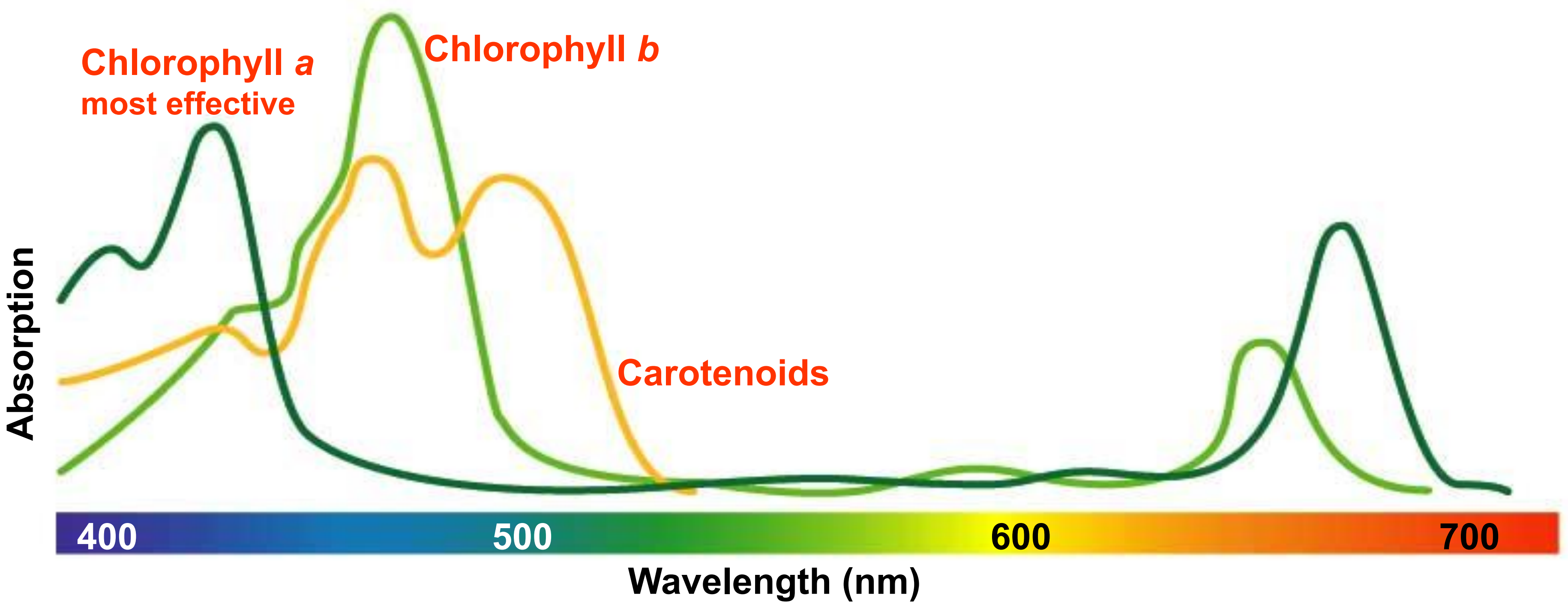
Properties of Light

- Electromagnetic spectrum = entire range of radiation
  - visible spectrum = what we can see
  - each wavelength has particular amnt Σ
    - shorter wavelength = ↑ Σ (violet)
    - longer wavelength = ↓ Σ (red)
    - UV has ↑ Σ, infared has ↓ Σ



Properties of Light

- Absorption spectrum = amount of light Σ absorbed by a substance as a func. of wavelength
  - chlorophyll a absorbs blue (430 nm) and red (660 nm) portion of spectrum
  - other pigments extend Ps useful portion of spectrum



Quantum Efficiency vs Energy Efficiency

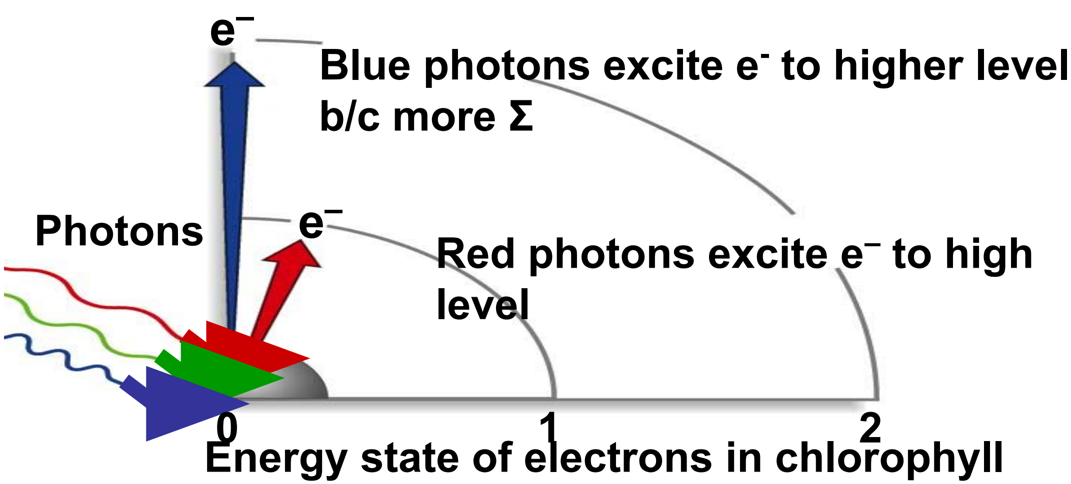
- Quantum efficiency = fraction of absorbed photons that engage in photochemistry = 100%
  - energy efficiency = fraction of absorbed Σ that is stored as chemical products = 27%
    - other 73% converted to heat
    - of the 27%, most is used for R_m

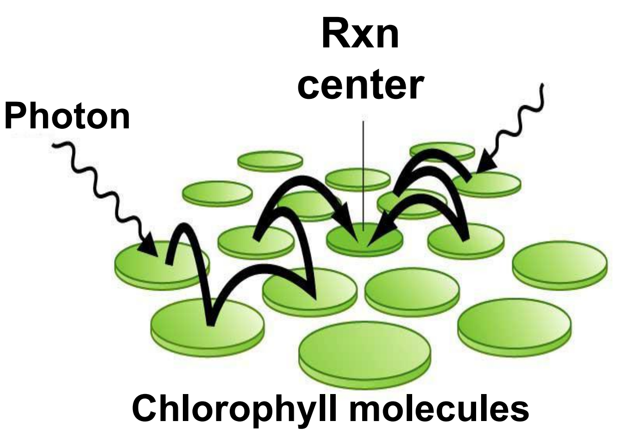
Pigments

- Pigment = substance that absorbs photons of light
  - photon hits pigment it can be absorbed, transmitted or reflected
  - we see transmitted or reflected
  - pigments absorb specific wavelengths of light = absorption spectrum
    - pigment absorbs all wavelengths in visible spectrum = black
    - pigment absorbs green and blue wavelengths but transmits or reflects red wavelengths = red (750 nm)
    - chlorophyll = reflects green, absorbs violet, blue and red
- Action spectrum = effectiveness of wavelengths

Pigments

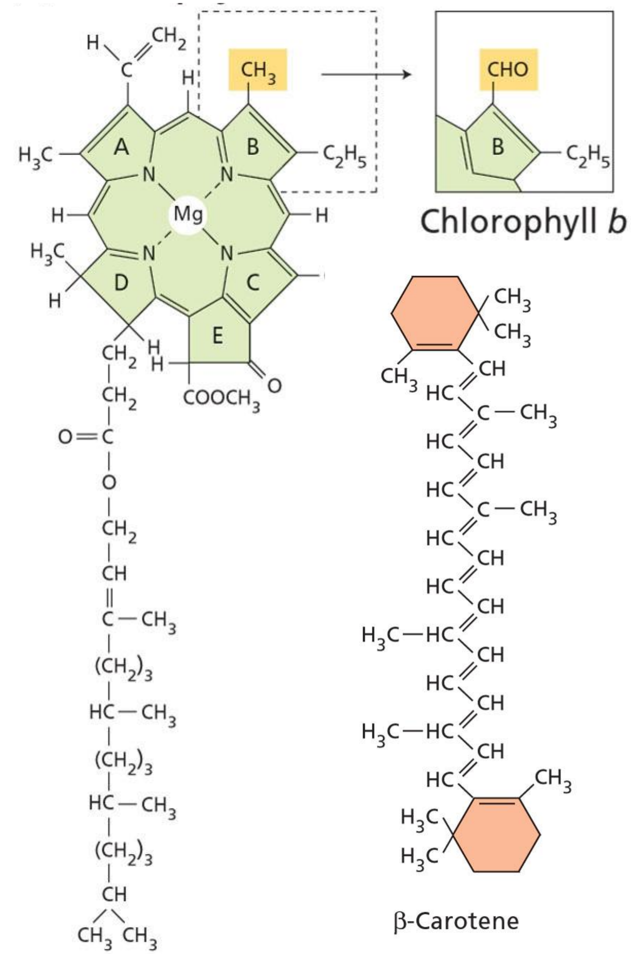
- When photon hits pigment, e^- bumped to higher orbital (↑ potential Σ b/c further from nucleus) (excited state)
  - once e^- in higher orbital (unstable) it has 4 fates
    - re-emit photon and fall back to original position (florescence and heat)
    - convert Σ to heat
    - transfer Σ to another chlorophyll until reaches reaction center (a.k.a. resonance energy transfer)
    - transfer Σ to other chemical rxns in ETS





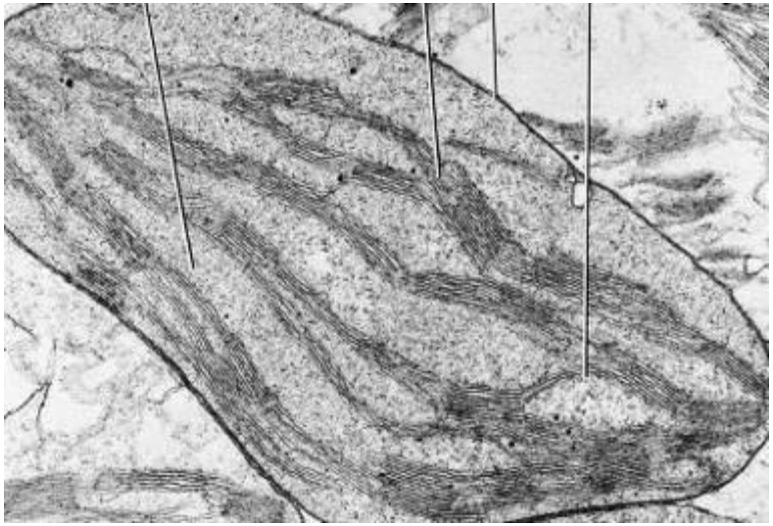
Pigments

- All Ps pigments found in chloroplast
  - primary photosynthetic pigment = chlorophyll *a*
    - must have chl. *a*
    - ring structure w/ Mg
    - similar to hemoglobin
    - hydrophobic tail embedded in thylakoid membrane
  - chl. *b*, carotenoids and phycobilins are accessory pigments
    - accessory pigments = not directly involved in Σ transduction, pass Σ to chl. *a* which transforms it to chemical Σ, extend useful spectrum, antioxidant func.
    - carotenoids = red/orange/yellow, embedded in thylakoid, fall color
      - 2 types carotenoids - carotene and xanthophyll

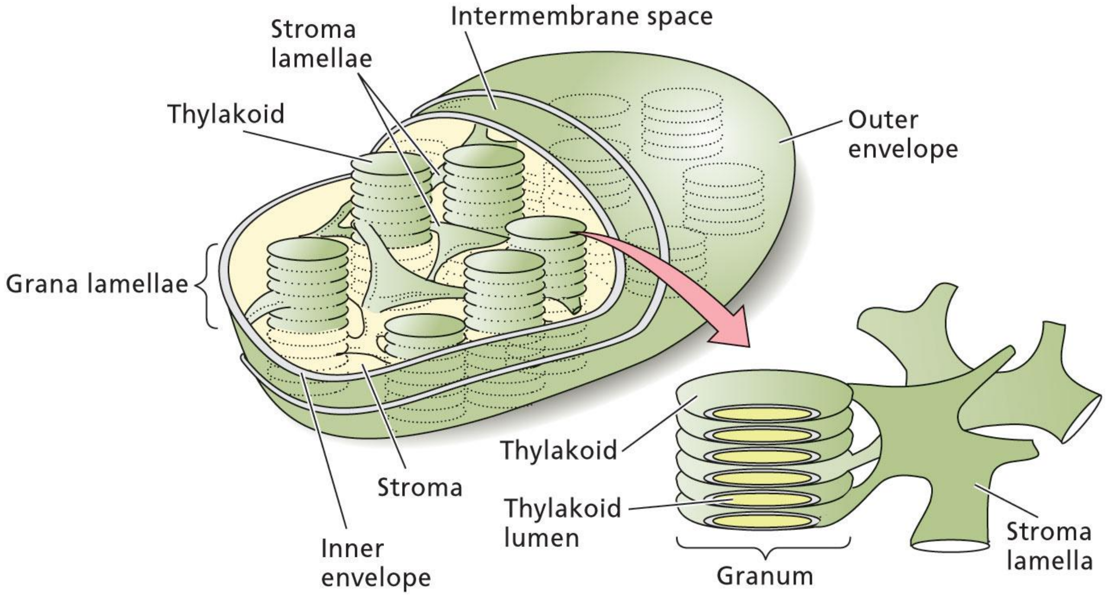


Chlorophyll *a*

Anatomy

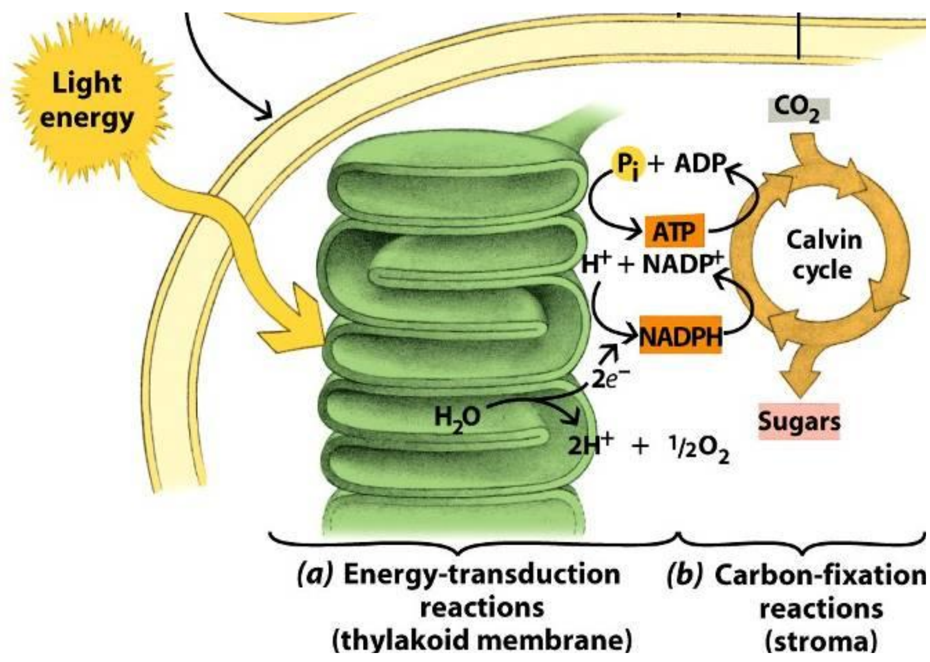


- Ps occurs in chloroplast
  - double-membrane, DNA, RNA, ribosomes
  - extensive 3rd membrane = thylakoid membrane
    - chlorophyll embedded (light-dep. rxns)
  - stroma (light-indep. rxns)
  - grana lamellae (PS II)
  - stroma lamellae (PS
  - granum
  - lumen



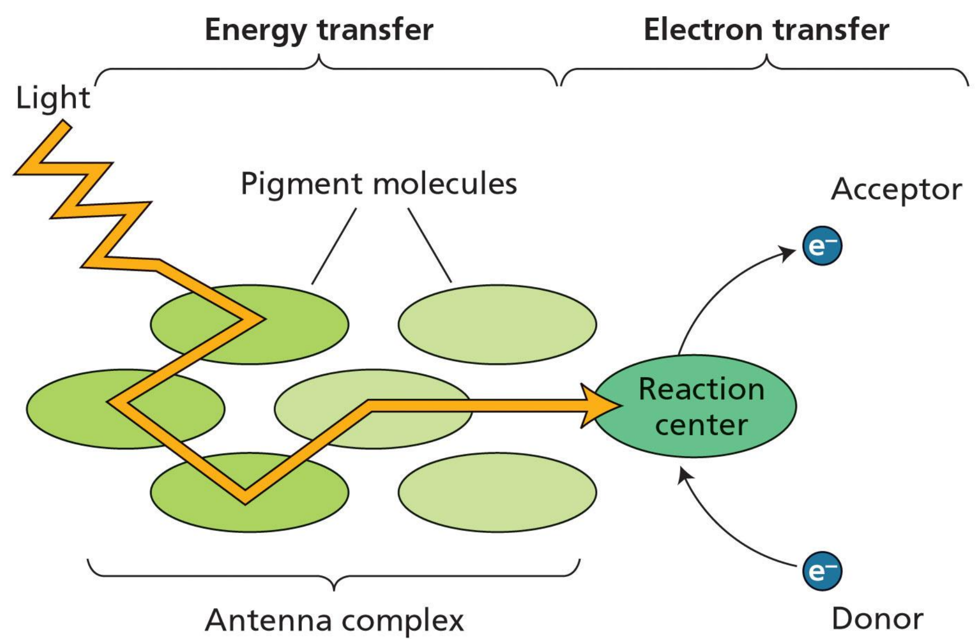
Overview of Photosynthesis

- 2 main events of Ps (+50 rxn steps in Ps discovered)
  - light-dependent rxns
    - light Σ transferred to chemical bond in ADP and reduction of $NADP^+$, forming ATP and NADPH
    - thylakoid membranes
  - light-independent rxns
    - ATP used to link CO_2 to organic molecule
    - NADPH used to reduce to simple sugar
    - carbon or CO_2 fixation = conversion of CO_2 into organic cmpds
    - stroma



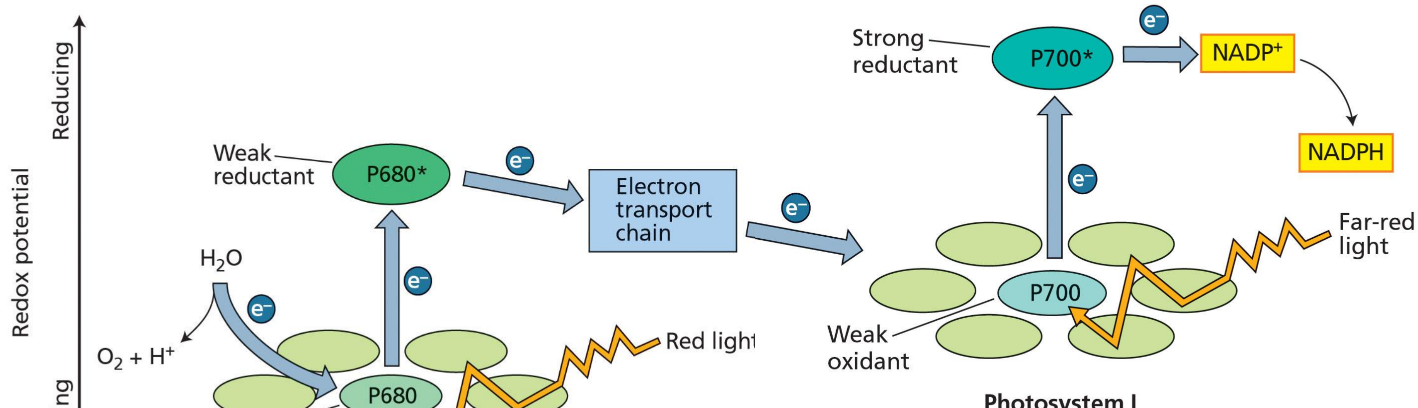
Antenna Complex and Reaction Center

- Most pigments serve as antenna
  - antenna collect light and transfer its Σ to reaction center
    - antenna complex = group of antenna molecules
    - means of increasing efficiency
    - integral proteins
  - reaction center complex = Σ is stored by transferring e^- from chlorophyll to e^- acceptor (REDOX rxns)
    - e^- boosted to higher orbital
    - integral proteins



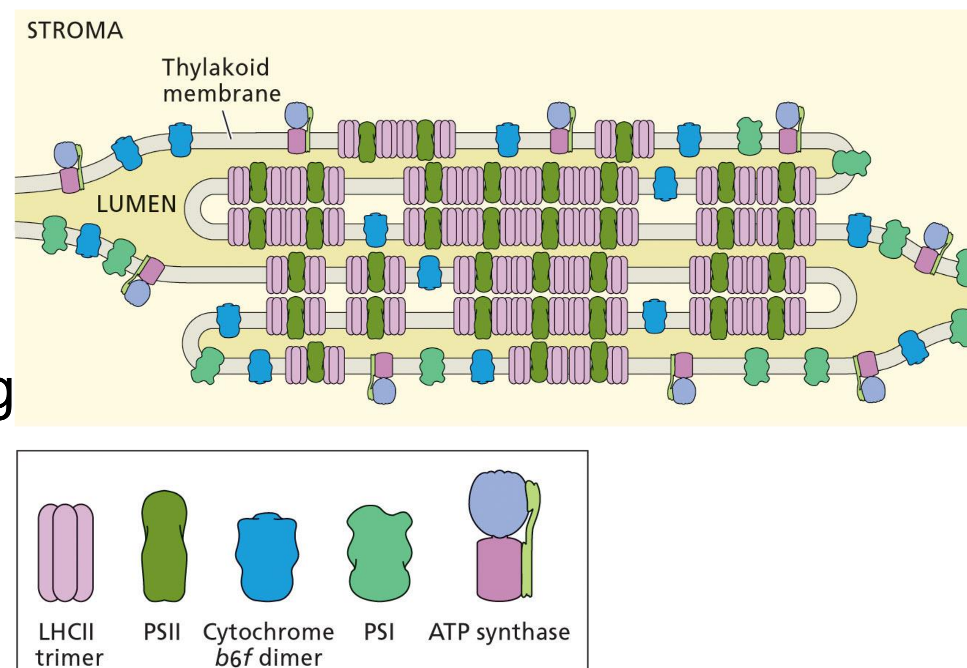
Photosystems I and II

- Enhancement effect = Ps rate greater w/ red and far-red light together than w/ each separate
  - due to 2 photochemical complexes (photosystem I and II)
  - work in conjuction, independent antenna and rxn centers
  - linked by electron transport chain
- e^- flow = H_2O → PS II → PS I → $NADP^+$ (Z scheme)
- PSII chl. *a* = P_{680} (red) vs PSI chl. *a* = P_{700} (far-red)

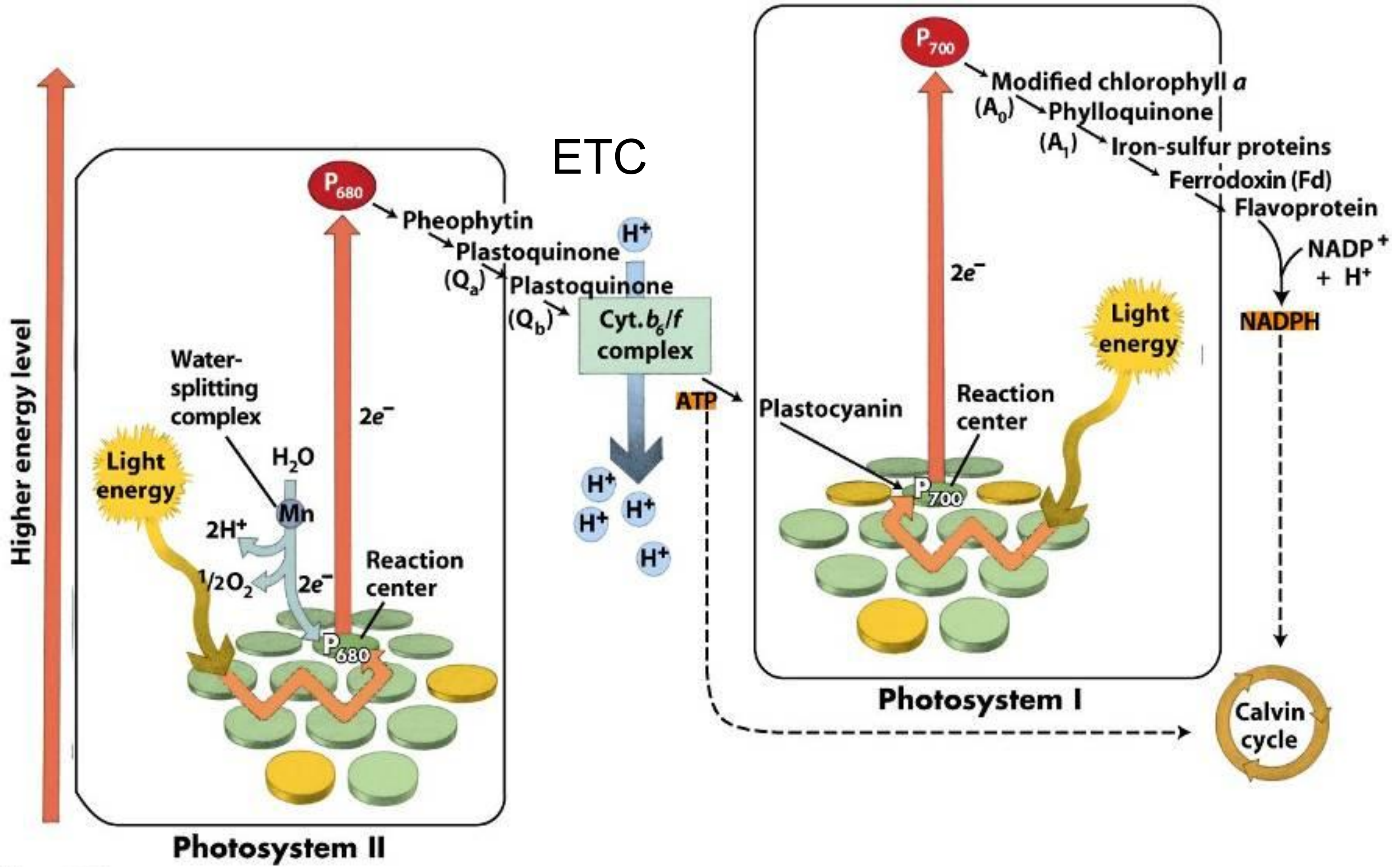


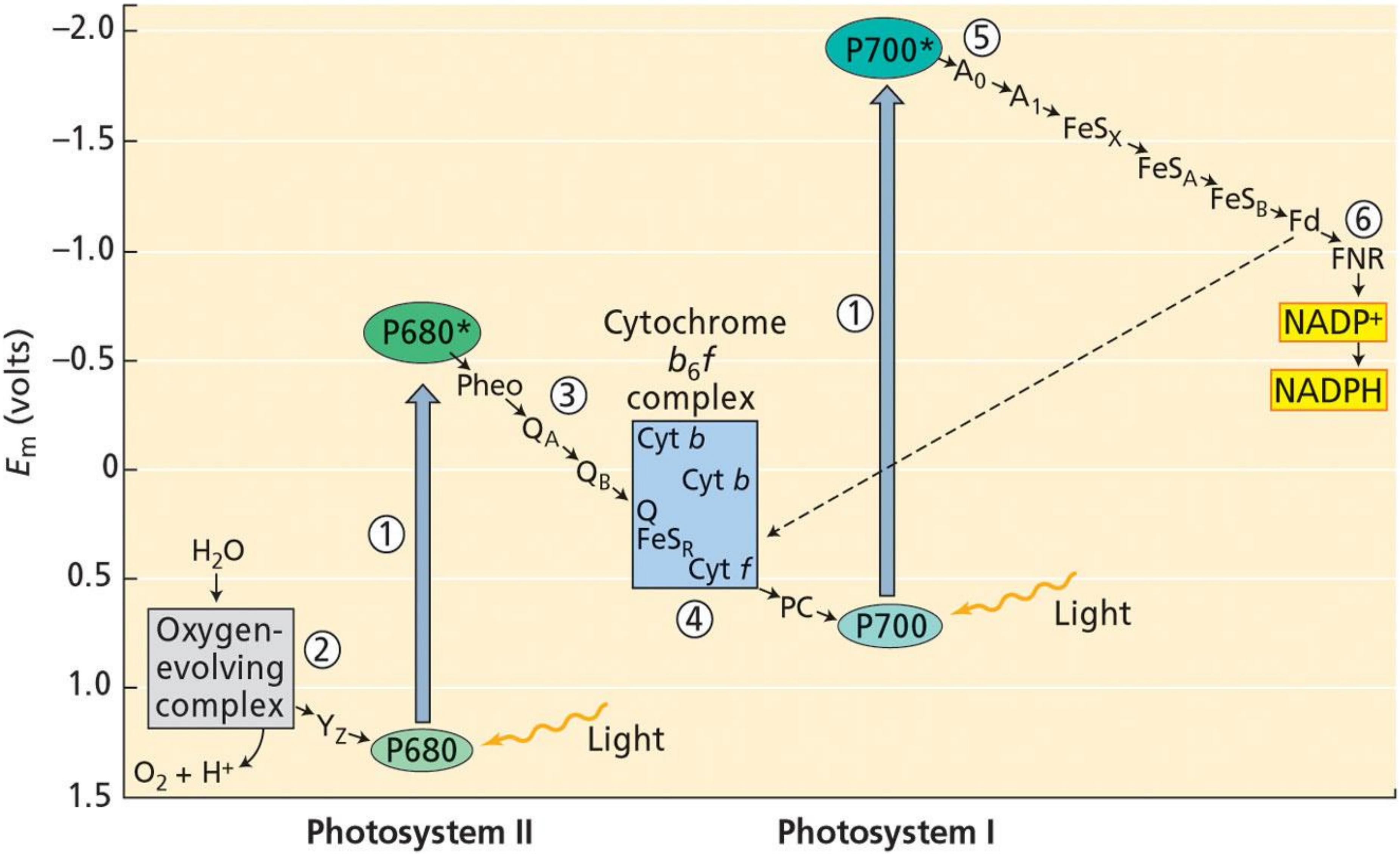
Photosystems I and II

- PS I and II spatially separated on thylakoid membrane
  - PS II on grana lamellae
  - PS I on stroma lamellae
  - ETC that connects PSII to PSI found throughout
  - PSII produces
    - 4 photons + $2H_2O \rightarrow 4\,H^+ + 4e^- + O_2$ (photolysis)
  - H^+ released in lumen (H^+ gradient)
  - increases efficiency b/c pool of reducers vs having to associate w/ single PS



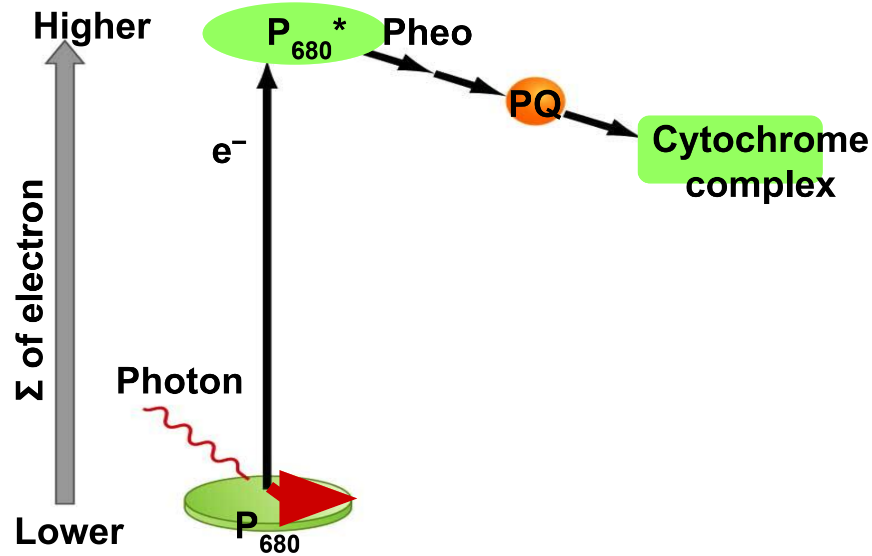
ETC


Higher energy level
P680
Pheophytin
Plastoquinone
(Qa)
Plastoquinone
(Qb)
H+
Cyt. b6/f
complex
H+
H+
H+
H+
ATP
Water-
splitting
complex
H2O
Mn
2H+
1/2O2
2e−
2e−
Light
energy
Reaction
center
P680
Photosystem II
P700
Modified chlorophyll a
(A0)
Phylloquinone
(A1)
Iron-sulfur proteins
Ferrodoxin (Fd)
Flavoprotein
NADP+
+ H+
NADPH
2e−
Light
energy
Plastocyanin
Reaction
center
P700
Photosystem I
Calvin
cycle



−2.0
−1.5
−1.0
−0.5
0
0.5
1.0
1.5
E_m (volts)
P700*
5
A0
A1
FeSX
FeSA
FeSB
Fd
6
FNR
NADP+
NADPH
1
P680*
Cytochrome
b6f
complex
Pheo
3
QA
QB
Cyt b
Cyt b
Q
FeSR
Cyt f
4
PC
P700
Light
1
H2O
Oxygen-
evolving
complex
2
YZ
P680
Light
O2 + H+
Photosystem II
Photosystem I

Photosystem II



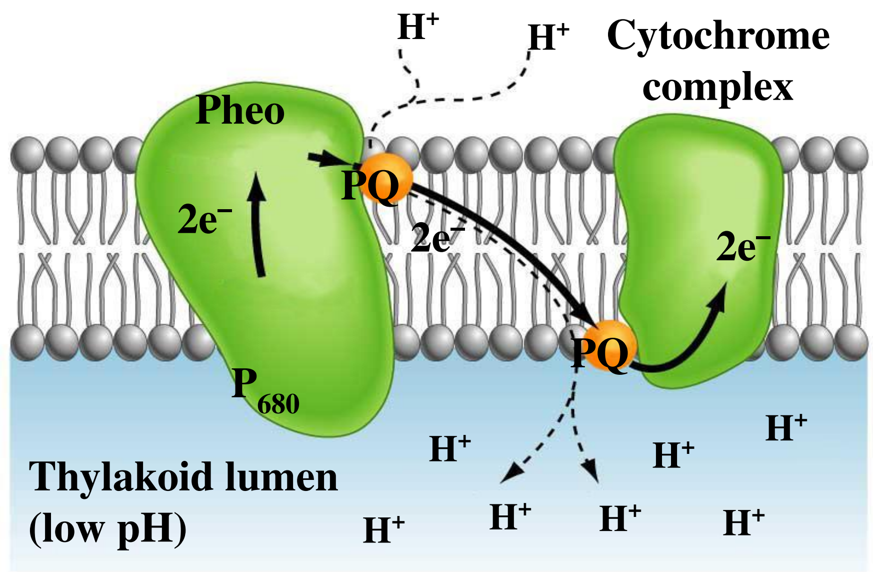
- Photon absorbed by PS II
- e^- in P_{680} (chlorophyll) gets excited (P_{680}*)
- e^- passed from P_{680}* to Pheo (pheophytin)
  - e^- acceptor similar to chlorophyll but lacks a Mg, instead 2 H
  - P_{680} is oxidized as looses e^- to pheophytin
  - ***NOTE:*** P_{680} re-reduced by Y_z who got e^- from splitting (oxidation) water *this is where O_2 comes from!!!*

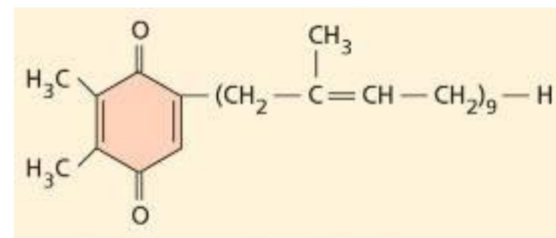
    $4 \text{ photons} + 2H_2O \rightarrow 4\,H^+ + 4e^- + O_2$ (photolysis)

    - occurs in lumen (contributes to H^+ gradient (PMF) across thylakoid membrane)

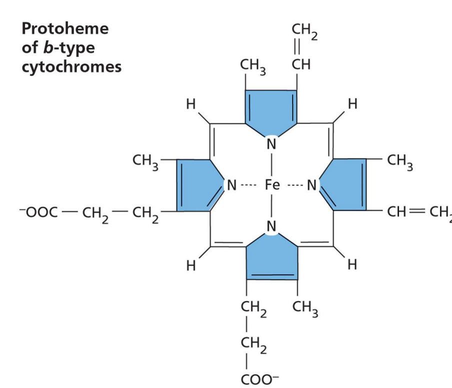
Photosystem II

- e^- passed from Pheo to Q_A and Q_B (plastoquinones/PQ)
  - as e^- passed by Q_A and Q_B, H^+ pumped into thylakoid lumen thereby creating H^+ gradient (PMF) across thylakoid membrane
- e^- passed from PQ to cytochrome b_6f complex
  - large multisubunit protein w/ heme groups
- e^- passed from b_6f complex to plastocyanin (PC)
  - protein w/ copper
- e^- passed from PC to P_{700} (PS II)

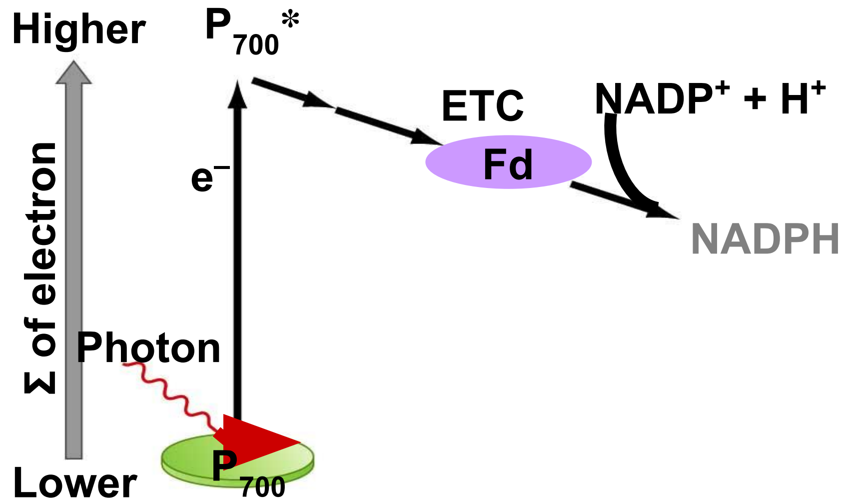




Plastoquinone



Photosystem I



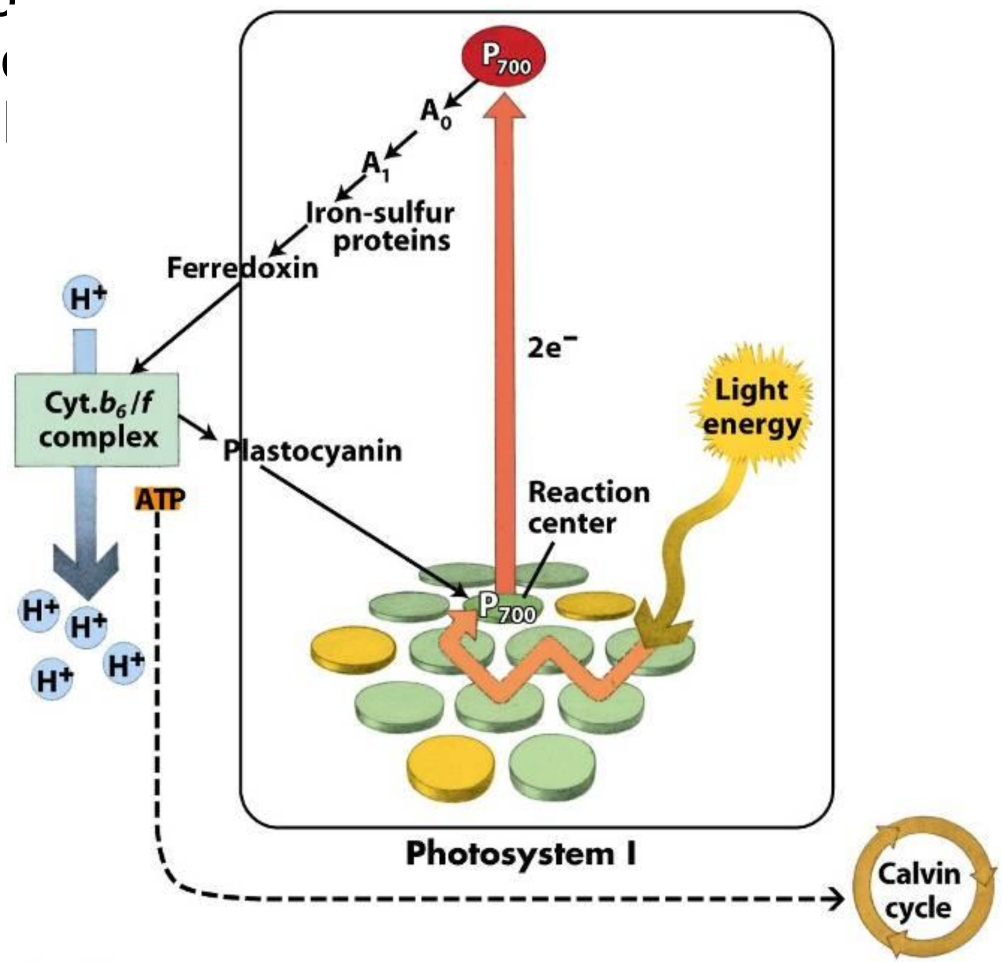
- e^- passed to P_{700} (reduced) from PC in PS II
- Photon absorbed by reduced P_{700}
- e^- in P_{700} gets excited (P_{700}*)
- e^- passed from P_{700}* to A_0 (chlorophyll?) to A_1 (phylloquinone, a.k.a. vitamin A)
- e^- passed from A_1 to FeS_x to FeS_A to FeS_B (Fe-S proteins)
- e^- passed from FeS_B to Fd (ferredoxin) (Fe-S protein)
- Ferredoxin/$NADP^+$ reductase (FNR) txf e^- and H^+ to $NADP^+$ to form NADPH
  - NADPH highly reduced, used to reduce CO_2 in Calvin Cycle
  - occurs in stroma

Noncyclic Photophosphorylation

- Z-scheme used to describe how PS I and II interact
- Noncyclic photophosphorylation (uses light to produce ATP)
  - what we've covered so far
  - 2 photons from each photosystem = 1 NADPH and 1O
  - products go to Calvin Cycle
    - $H_2O + NADP^+ \rightarrow NADPH + H^+ + ½ O_2$
    - $6 e^- = 6 ATP + 6 NADPH$

Cyclic Photophosphorylation

- Cyclic photophosphorylation when extra ATP needed
  - PS I donates e^- to back to PS II resulting in producti additional ATP (no NADP
    - e^- txf via PQ
  - PS II generates ATP only
  - PS I generates NADPH

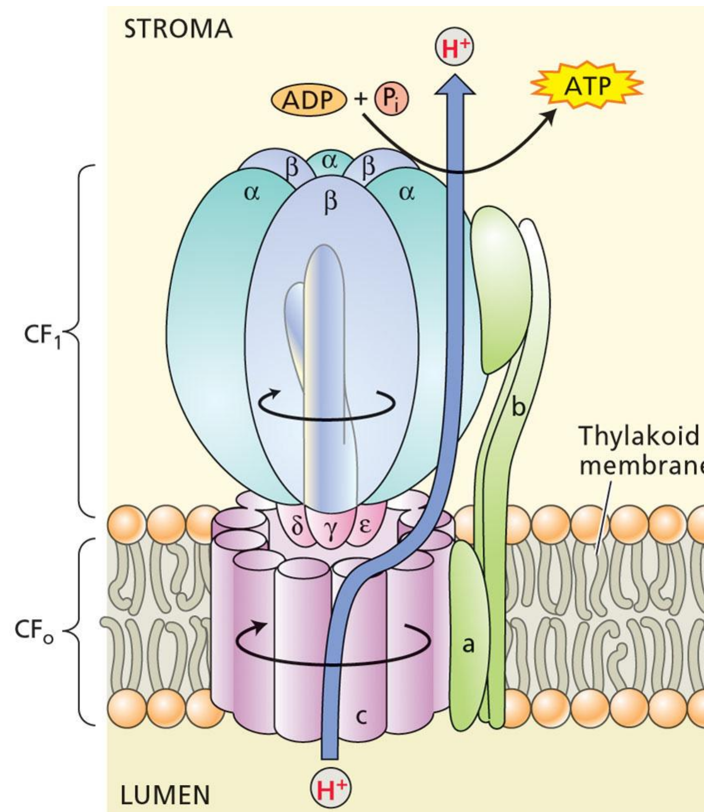


ATP Synthesis

- ATP produced via chemiosmosis = ion conc. differences and electric potential differences across membrane are source of free Σ that can be harnessed to do work
  - 2^{nd} law of thermodynamics = any nonuniform distribution of matter or Σ represents a source of Σ
- ATP synthase (a.k.a. ATPase, CF_0-CF_1) uses PMF to generate ATP
  - H^+ in thylakoid lumen = electrochemical gradient
    - due to splitting of H_2O, cytochrome b_6f complex
    - pH in stroma = alkaline, pH in lumen = acidic
  - gradient drives ATP synthesis via ATP synthase complex

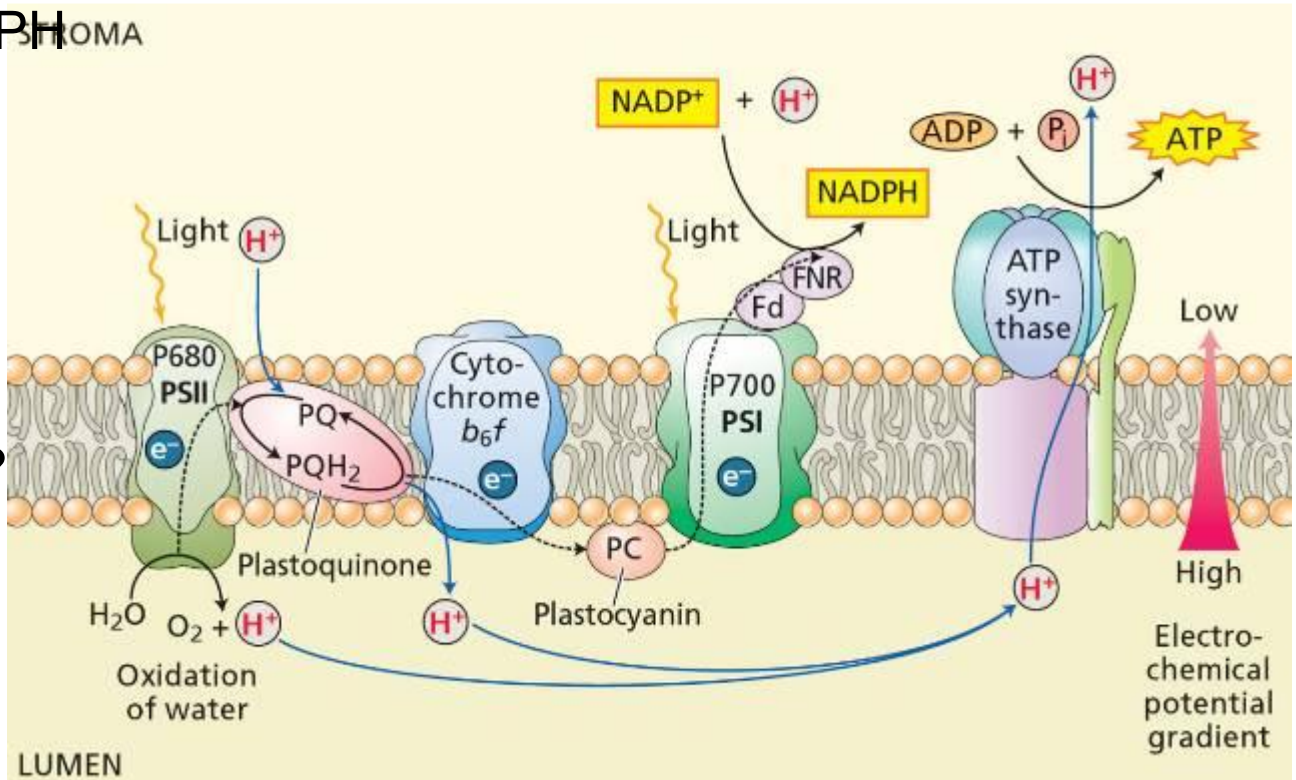
ATP Synthesis

- ATP synthase consists of hydrophobic portion CF_0 (in membrane) and CF_1 (sticks out in stroma)
  - found on stroma lamellae and edge of grana of thylakoid membrane
  - CF_0 contains channel which H^+ pass
    - rotates along w/ internal stalk
  - CF_1 where ATP synthesized
  - when H^+ pass potential energy converted to kinetic
  - kinetic Σ converted to chemical bond
- 4 H^+ translocated per ATP



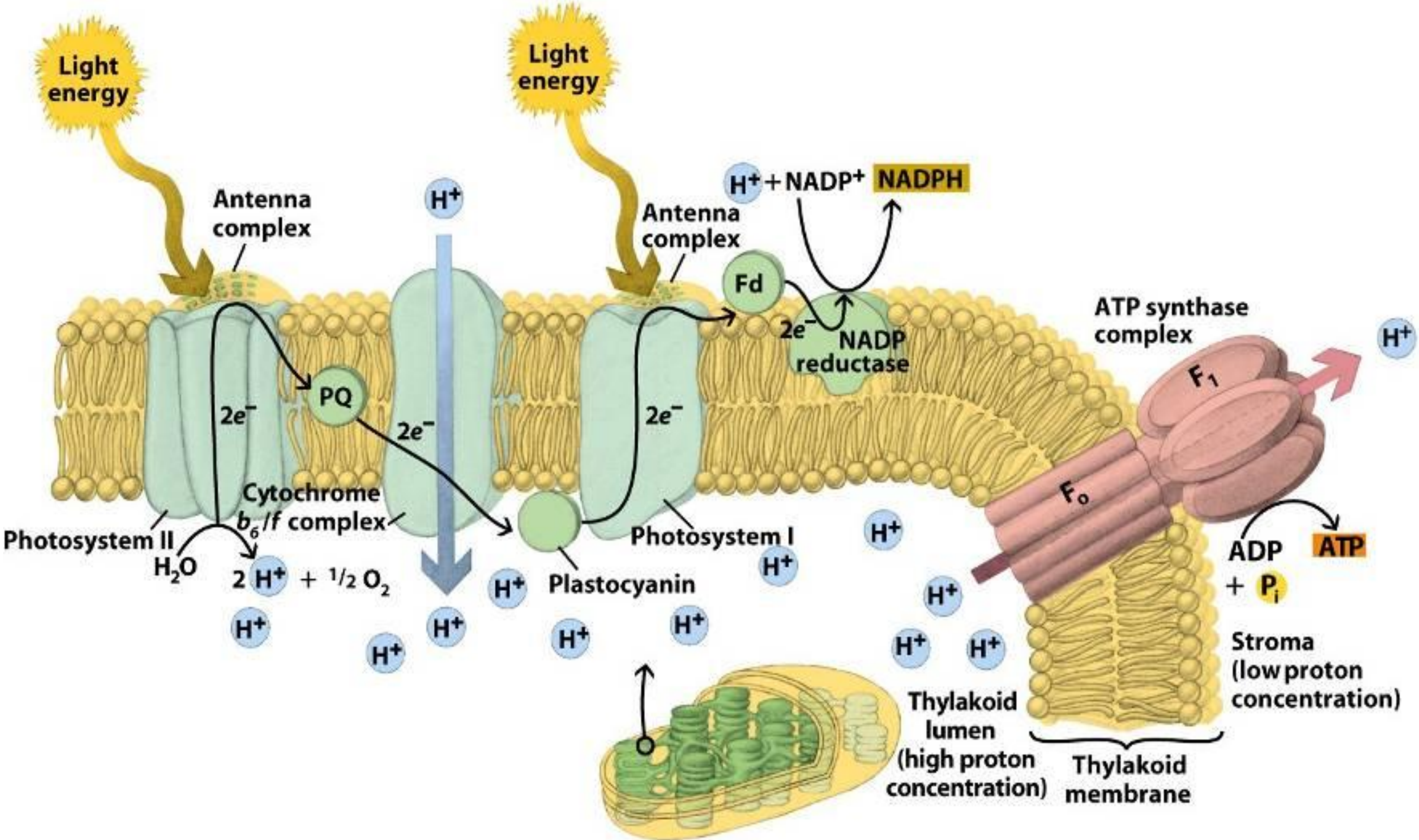
Summary

- 4 major protein complexes
  - PS II oxidizes H_2O, releases H^+ into lumen
  - b_6f complex pumps additional H^+ into lumen
  - PS I reduces $NADP^+$ to NADPH
  - ATP synthase produces ATP

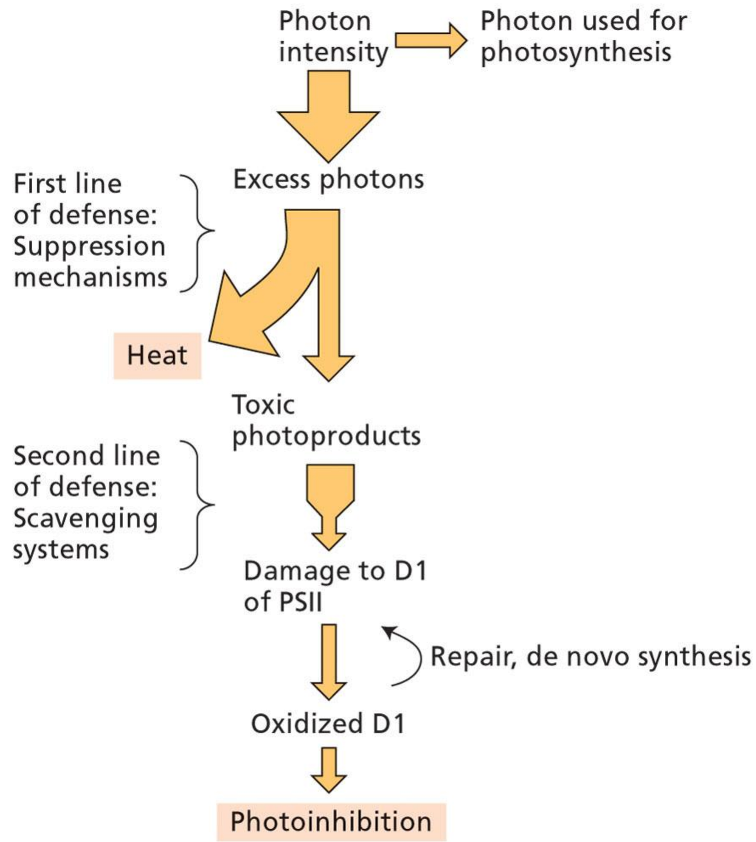


  - initial acceptor?
  - final donor??

Summary II


Light energy
Light energy
Antenna complex
Antenna complex
H+
H+ + NADP+ NADPH
Fd
2e−
NADP reductase
ATP synthase complex
H+
F1
PQ
2e−
2e−
2e−
Fo
Cytochrome b6/f complex
Photosystem II
Photosystem I
H2O
2 H+ + 1/2 O2
H+
H+
H+
H+
Plastocyanin
H+
H+
H+
H+
H+
H+
H+
H+
ADP + Pi
ATP
Stroma (low proton concentration)
Thylakoid lumen (high proton concentration)
Thylakoid membrane

Repair and Regulation



- Regulatory and repair mechanisms needed to safely dissipate excess Σ or repair if damaged
  - carotenoids dissipate excited state of chlorophyll
    - excited state can react w/ O_2 to produce singlet oxygen (extremely reactive, damaging to lipids)
  - xanthophylls (type of carotenoid) also help dissipate Σ and heat
  - prolonged photoinhibition (inhibition of Ps by excess light) = damage to PS II rxn center, esp. D1 protein
    - D1 protein removed and replaced

Chloroplast Genetics

- Chloroplast have their own DNA, mRNA, ribosomes
  - import some genes from nucleus
  - circular DNA
- Reproduce via division
  - chloroplasts divided btwn daughter cells
  - chloroplasts come from female plant
    - non-Mendelian genetics, maternal inheritance

Endosymbiosis

- Chloroplast is semiautonomous
  - own DNA, mRNA, ribosomes
  - descendant of symbiotic relationship btwn cyanobacteria and nonphotosynthetic eukaryotic cell (endosymbiosis)
  - genetic information lost thus needs host