4

RADIATION STRESS

PROPERTIES OF RADIATION

- **Properties of electromagnetic radiation**

1a. Intensity (as photon flux density)
Related to the quantity of photons incident on a known surface per unit of time

1b. Intensity (as radiation energy)
Related to the energy of photons incident on a known surface per unit of time

2. Spectral composition(radiation quality)
Expressing the relative distribution of photons in the different spectral regions of the electromagnetic spectrum

PROPERTIES OF RADIATION

- **Properties of electromagnetic radiation**

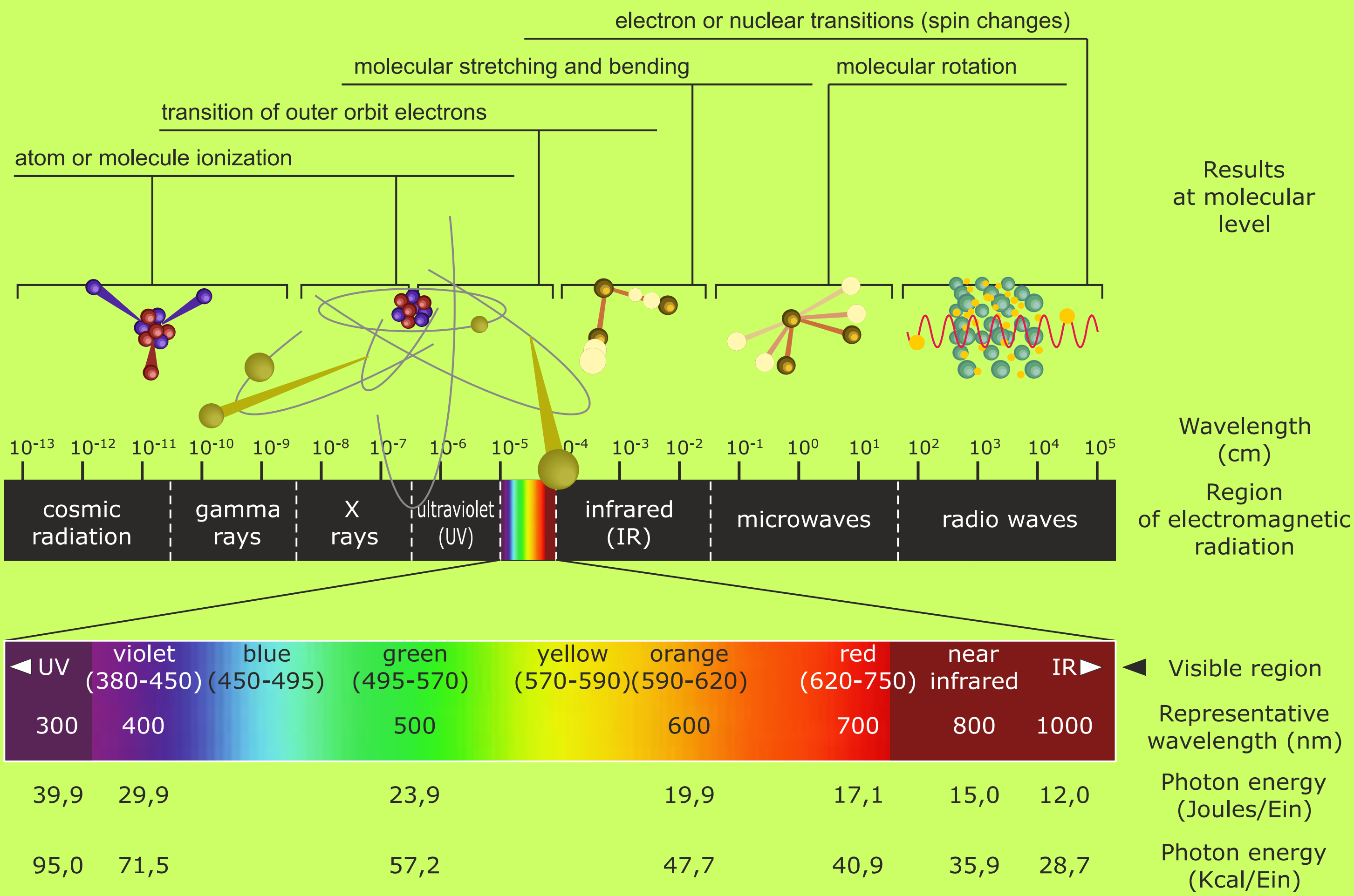
1a. Intensity (as photon flux density)
Measured in µmol photons (quanta) m^{-2} s^{-1}, where 1 mol = 6,023 · 10^{23} (photons). Maximum intensity of visible solar radiation in south European countries ~2000 µmol m^{-2} s^{-1}

1b. Intensity (as radiation energy)
Measured in units of power per unit of surface

2. Spectral composition(radiation quality)
Usually measured as a spectrum (a graphical representation of the quantity of photons per spectral region

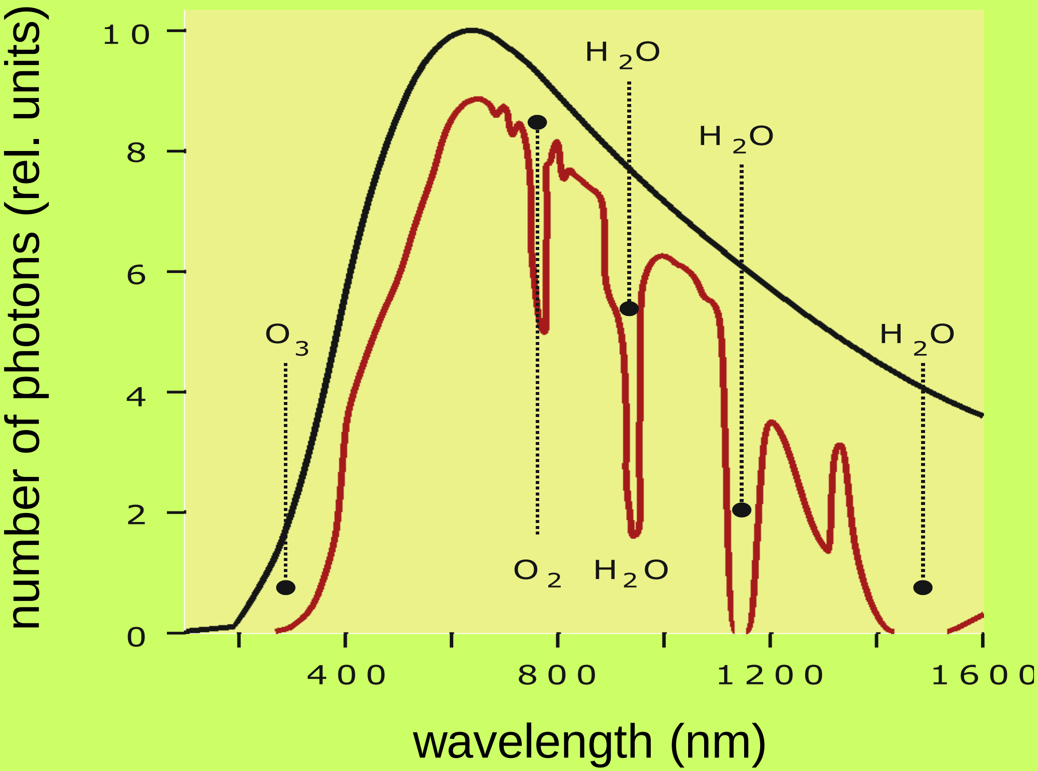
PROPERTIES OF RADIATION

- **Properties of electromagnetic radiation**



PROPERTIES OF RADIATION

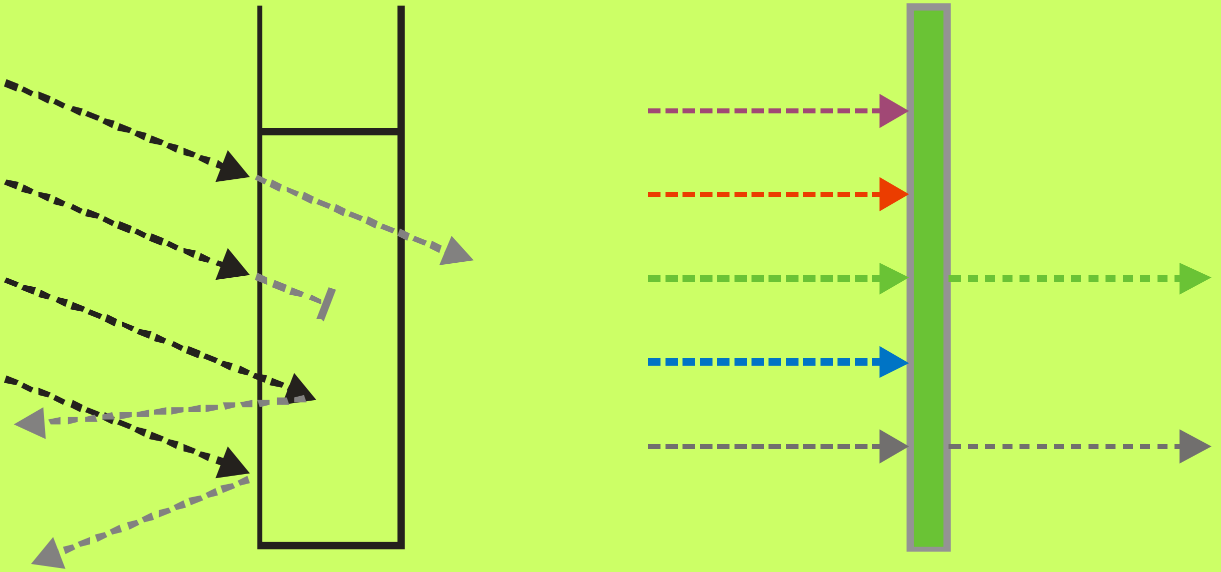
- **Properties of electromagnetic radiation**



PROPERTIES OF RADIATION

- **Interaction between radiation and matter**

  1. Transmission
  2. Diversion of photon course
     a) Reflection
     b) Scattering
  3. Absorption



RADIATION AS A STRESS FACTOR

- **Stress can develop due to low or high intensity**

Low intensity of Photosynthetically Active Radiation (PAR) can cause stress due to inability to perform photosynthesis

High intensity of PAR can cause stress due to accumulation of excess light energy to photosystems with respect to the ability for photochemical quenching of the energy and use of reduced equivalents to the Calvin-Benson cycle

RADIATION AS A STRESS FACTOR

- **High ultraviolet radiation stress**

High intensity of ultraviolet (UV) cause stress due to chemical transformation of sensitive targets such as membrane lipids, proteins, photochemical centers and nucleic acids

SPECIAL LIGHT REGIMES

- **The light regime of 'shadow'**

  Many plants thrive in environments with very low PAR intensity, such as a forest understory. Shadow is characterized from light of very different spectral quality than abundant sunlight.

- **The light regime of 'sun flecks'**

  Sun flecks are produced when local discontinuities in superimposed foliage result in, usually sudden, shaded plant/leaf illuminance with abundant sunlight.

SUN FLECKS

Sun flexes represent a mechanism for local, transient increase in photosynthetic rate but, also, a possible stressor in leaves of the understory

SPECIAL LIGHT REGIMES

Light intensity and percent (%) of photons per spectral region					
conditions	Photon flux (μmol quanta m^{-2} s^{-1})	blue	green	ref	near IR
ample	1700	23	26	26	25
Below foliage (LAI=4)					
Below 5 mm of soil					
Below 1 m of clear water					

SPECIAL LIGHT REGIMES

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conditions	Photon flux (μmol quanta m^{-2} s^{-1})	blue	green	ref	near IR
ample	1700	23	26	26	25
Below foliage (LAI=4)	60	4	15	11	70
Below 5 mm of soil					
Below 1 m of clear water					

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ample	1700	23	26	26	25
Below foliage (LAI=4)	60	4	15	11	70
Below 5 mm of soil	0,002	1	5	17	76
Below 1 m of clear water					

SPECIAL LIGHT REGIMES

Light intensity and percent (%) of photons per spectral region					
conditions	Photon flux (μmol quanta m^{-2} s^{-1})	blue	green	ref	near IR
ample	1700	23	26	26	25
Below foliage (LAI=4)	60	4	15	11	70
Below 5 mm of soil	0,002	1	5	17	76
Below 1 m of clear water	700	30	39	36	5

TWO PLANT GROUPS CAN BE DISTINGUISHED

- **Shade plants (scyophytes)**

  These plants show adaptive traits and wide acclimation ability to shade. Exposure to high PAR intensities causes radiation stress

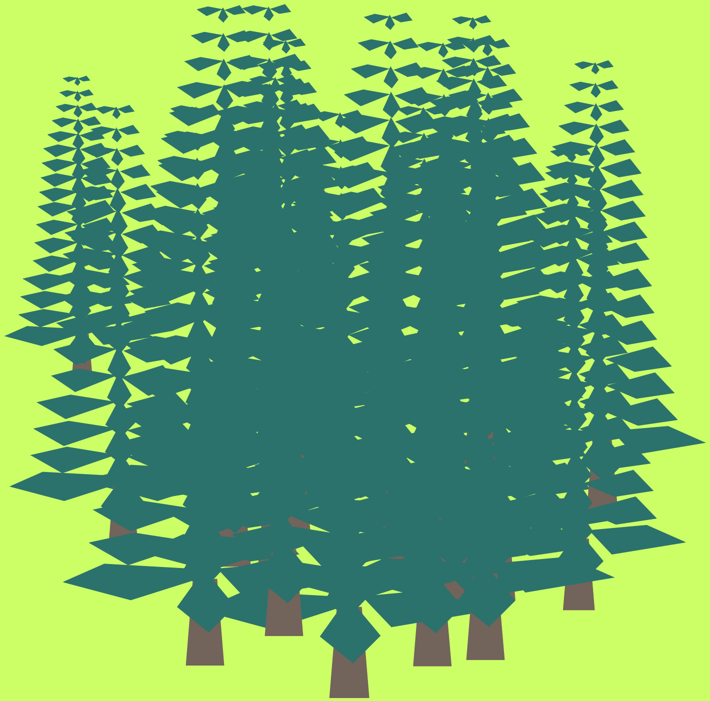
- **Sun plants (or heliophytes)**

  These plants only grow properly under ample light. They develop energy deficiency under low light. Light plants show adaptive and acclimation characteristics that contribute to light damage avoidance and/or resistance

TWO PLANT GROUPS CAN BE DISTINGUISHED

- **Distribution of shade and sun plants**

  Their distribution to the same habitat usually is distinguished spatially or temporally



TWO PLANT GROUPS CAN BE DISTINGUISHED

- **Distribution of shade and sun plants**

  Their distribution to the same habitat usually is distinguished spatially or temporally

THREE DIFFERENT STRATEGIES

- **Escape**

  Annuals, ephemeral plant organisms. These plants complete their life cycle within the narrow limits of the favorable period during which there is no superimposed foliage

THREE DIFFERENT STRATEGIES

- **Avoidance**

  Sun plants have avoidance mechanisms based on perception of quality of light through which the increase of internode intervals is controlled

THREE DIFFERENT STRATEGIES

- **Avoidance**

  Some small seeds of herbs (usually) only germinate in the presence of red enriched light. There seeds do not germinate in the dark or in light regimes which are enriched in Far Red (FR)

THREE DIFFERENT STRATEGIES

- **Resistance**

This strategy is followed by plants that thrive in dim light environments without however developing any low light stress. βιοχημικών χαρακτηριστικών των φύλλων.
Resistance is due to proper anatomical, morphological, biochemical and physiological traits

THREE DIFFERENT STRATEGIES

- **Resistance**

As a genetically determined adaptation includes **obligate shade plants**.
As a phenotypic acclimation, it includes **facultative shade plants** whose leaves posses enough plasticity to be able to acclimate to different light regimes.

THREE DIFFERENT STRATEGIES

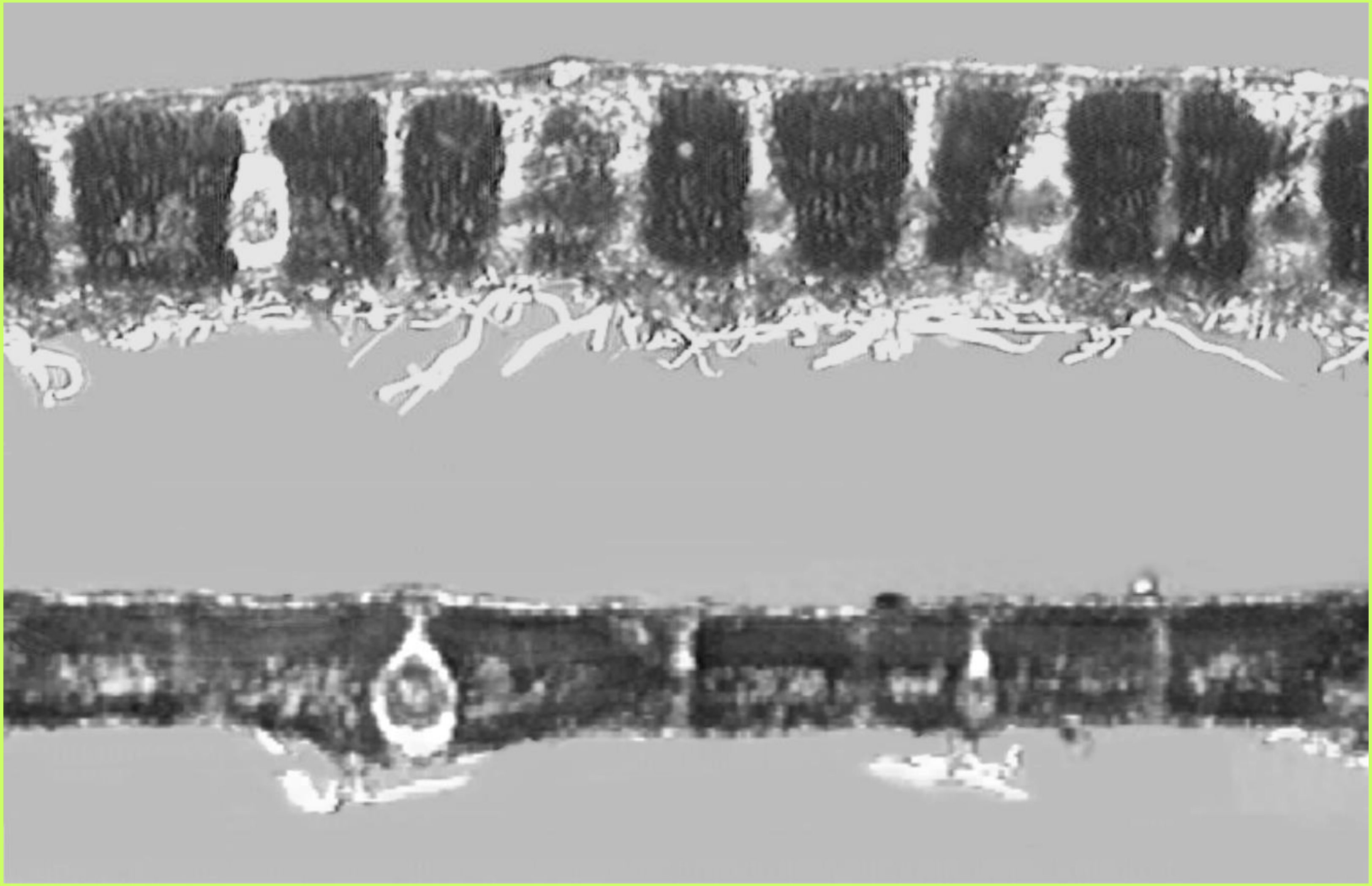
- **Resistance mechanisms - Anatomy**

  The peculiar anatomy of shade leaves aims in the optimization of light penetration in the mesophyll while light transmittance is reduced. This results in large light harvesting of the leaves. These photons will eventually be absorbed resulting in higher absorptivity.

DIFFERENCES BETWEEN SHADE AND SUN LEAVES

Leaf trait	Shade plants/leaves	Sun plants/leaves
morphoanatomical traits		
leaf thickness	low	high
leaf surface	high	low
leaf arrangement	horizontal	vertical
epidermal cells	idiomorphic	usual
stomatal localization	abaxial	both adaxial and abaxial
leaf mesophyll asymmetry	common	possible
leaf lamina bicoloring	apparent	usually absent
lignin deposition	low	high
chloroplast arrangement	near the outer epiclinic cell wall	variable, usually near the anticlinic cell walls
chloroplast fine structure		
chloroplast size	large	small
stroma volume	low	high
grana volume	high	low
biochemical traits		
photosystem concentration	low	high
antenna size	large	low
Chl concentration per mass	high	low
Chl*a*/*b* ratio	low	high
Chl(*a*+*b*)/VAZ ratio	high	low
RubisCO concentration	low	high
***A*max**	low	high
light compensation point	low	high

DIFFERENCES BETWEEN SHADE AND SUN LEAVES



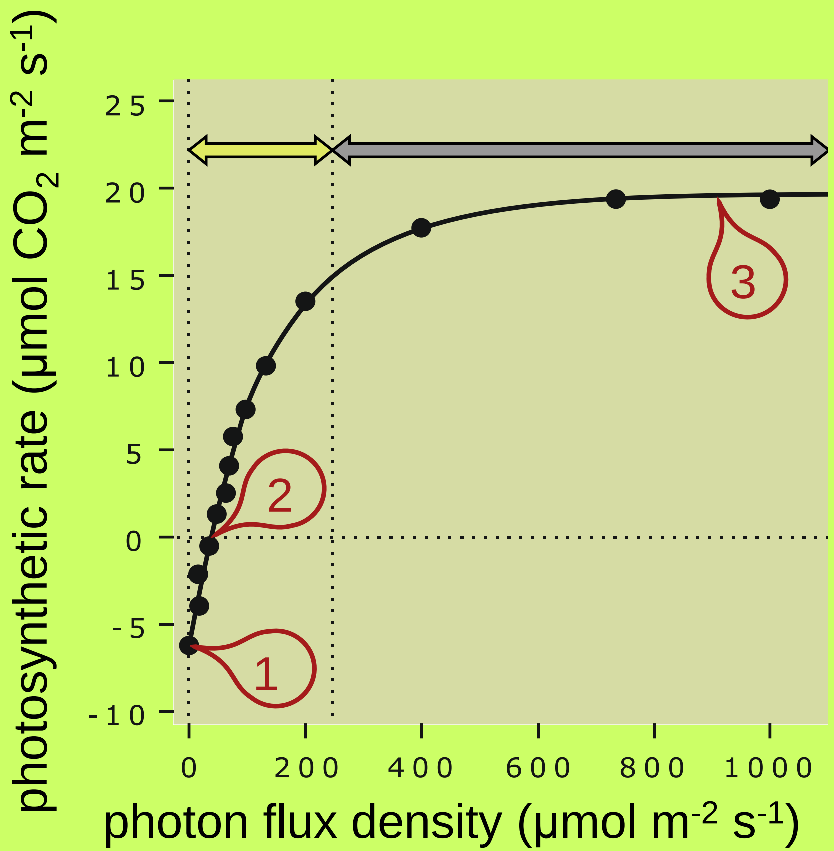
PROPERTIES OF SHADE LEAVES

- **Resistance physiological mechanisms**

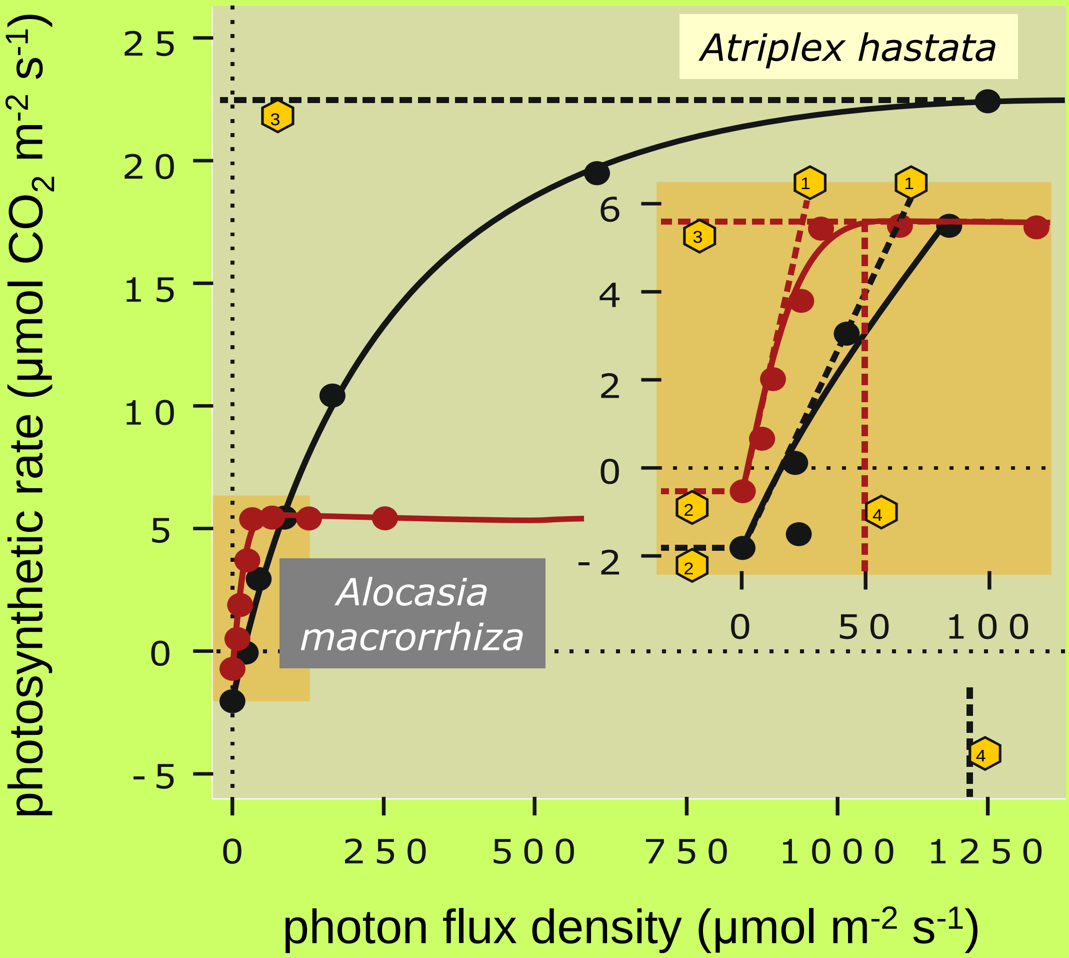
Chloroplasts of **shade** leaves are **very efficient** in capturing the **scarce photons** that will reach their light harvesting complexes even if these belong to the **green** spectral region

Light harvesting complexes are large and have a special pigment composition. The participation of chlorophyll *b* and carotenoids is increased. This shifts the **Chl *a/b* ratio** to lower values in shade leaves

PROPERTIES OF SHADE LEAVES



PROPERTIES OF SHADE LEAVES



LIGHT UTILIZATION EFFICIENCY OF SUN LEAVES

- **The large photosynthetic capacity of sun leaves is due to a series of traits:**

1. High stomatal and mesophyll conductance CO_2
2. High CO_2 exchange surface
3. Suitable mesophyll architecture that permits light penetration and homogenization of light microenvironment
4. High photosystem density per chloroplast
5. High concentration of Calvin-Benson cycle enzymes

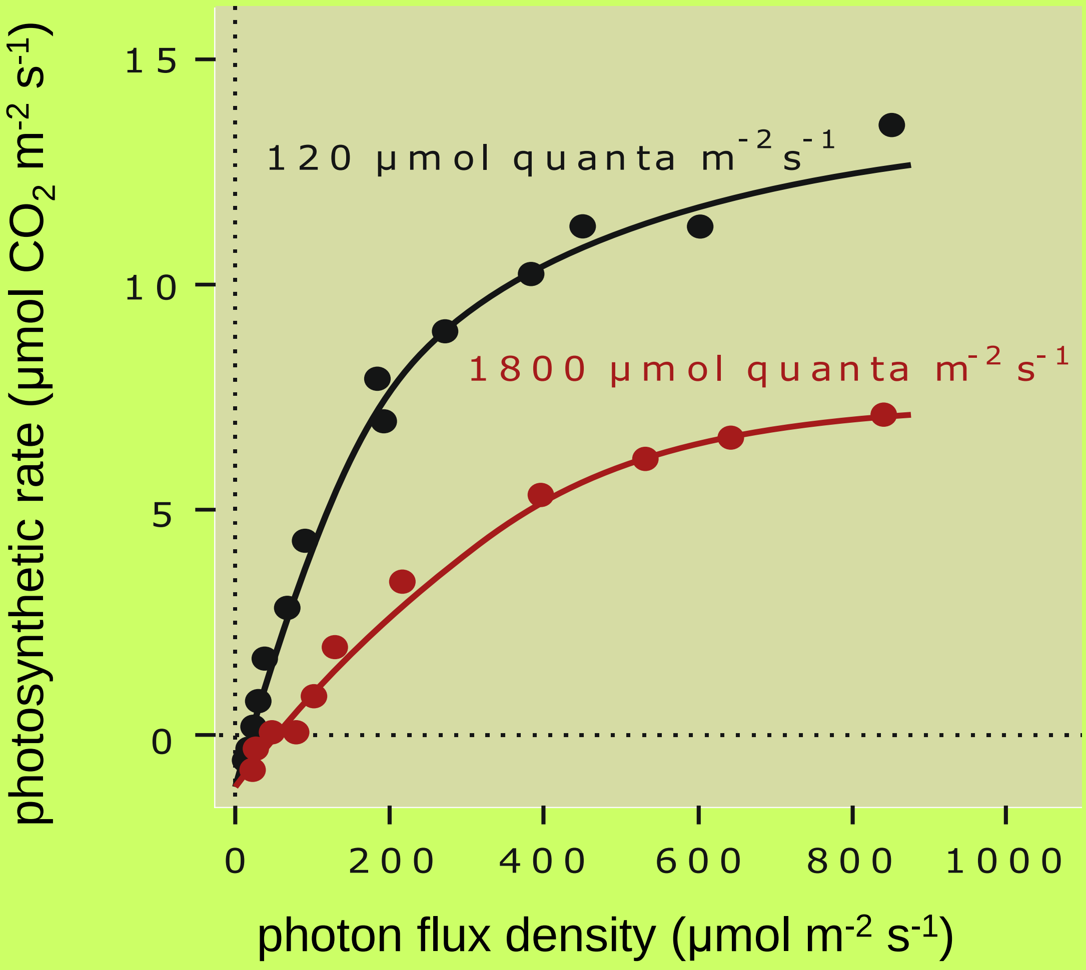
HIGH LIGHT INTENSITY STRESS

- **High light intensity stress**

  1. Considerably reduces photosynthetic capacity and photon efficiency (quantum yield)
  2. Causes photobleaching
  3. Causes extensive damage due to oxidative stress

HIGH LIGHT INTENSITY STRESS

- **High light intensity stress**



HIGH LIGHT INTENSITY STRESS

- **High light intensity stress**

  1. Appears in plants not previously adapted or acclimated to high irradiance
  2. Appears seasonally in plants in the understory of deciduous forests or transiently due to superimposed foliage or earth movements
  3. Outer cell chloroplasts are particularly susceptible to light damage (photoinhibition)
  4. According to the **action spectrum** of photoinhibition, stress accumulates due to both the PAR and the UV spectral region

ACTION SPECTRUM

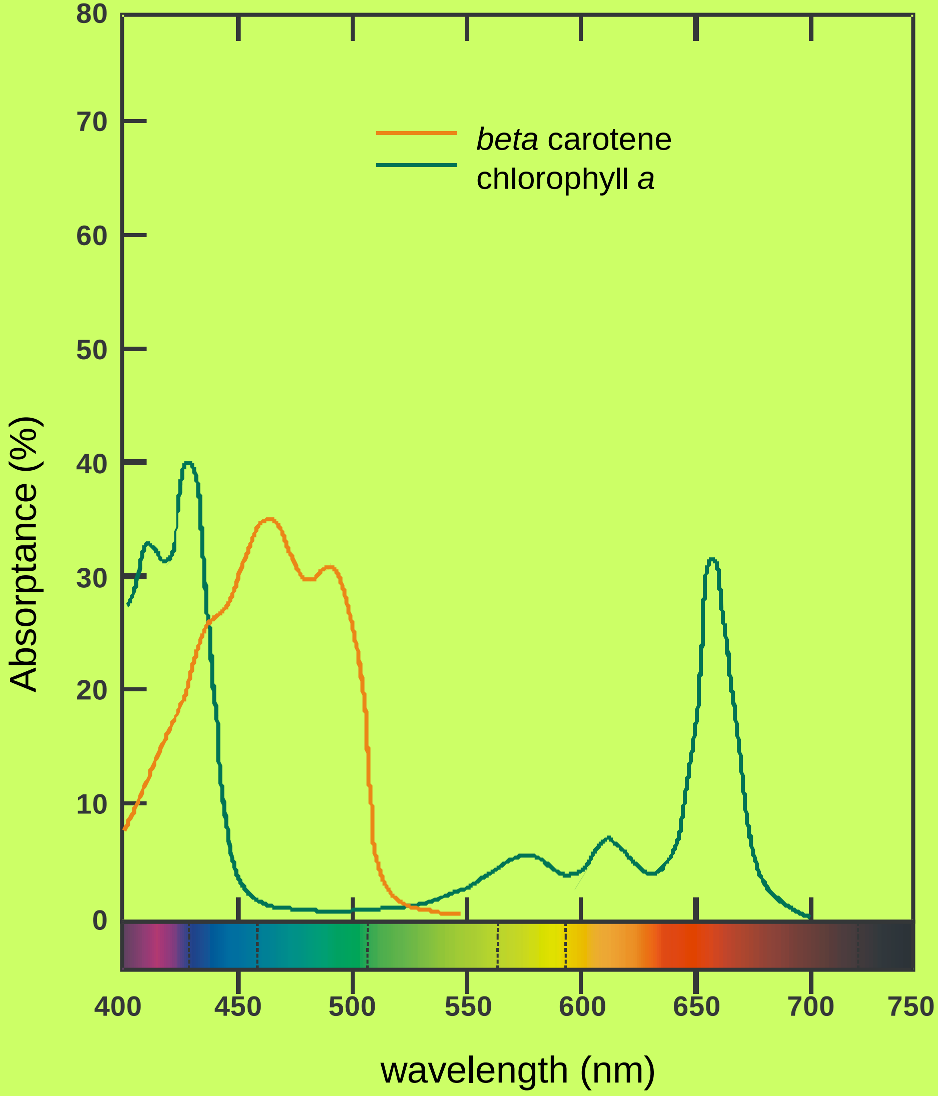
- **Absorbance (absorptance) spectrum**

  Describes how matter absorbs photons belonging in different spectral regions

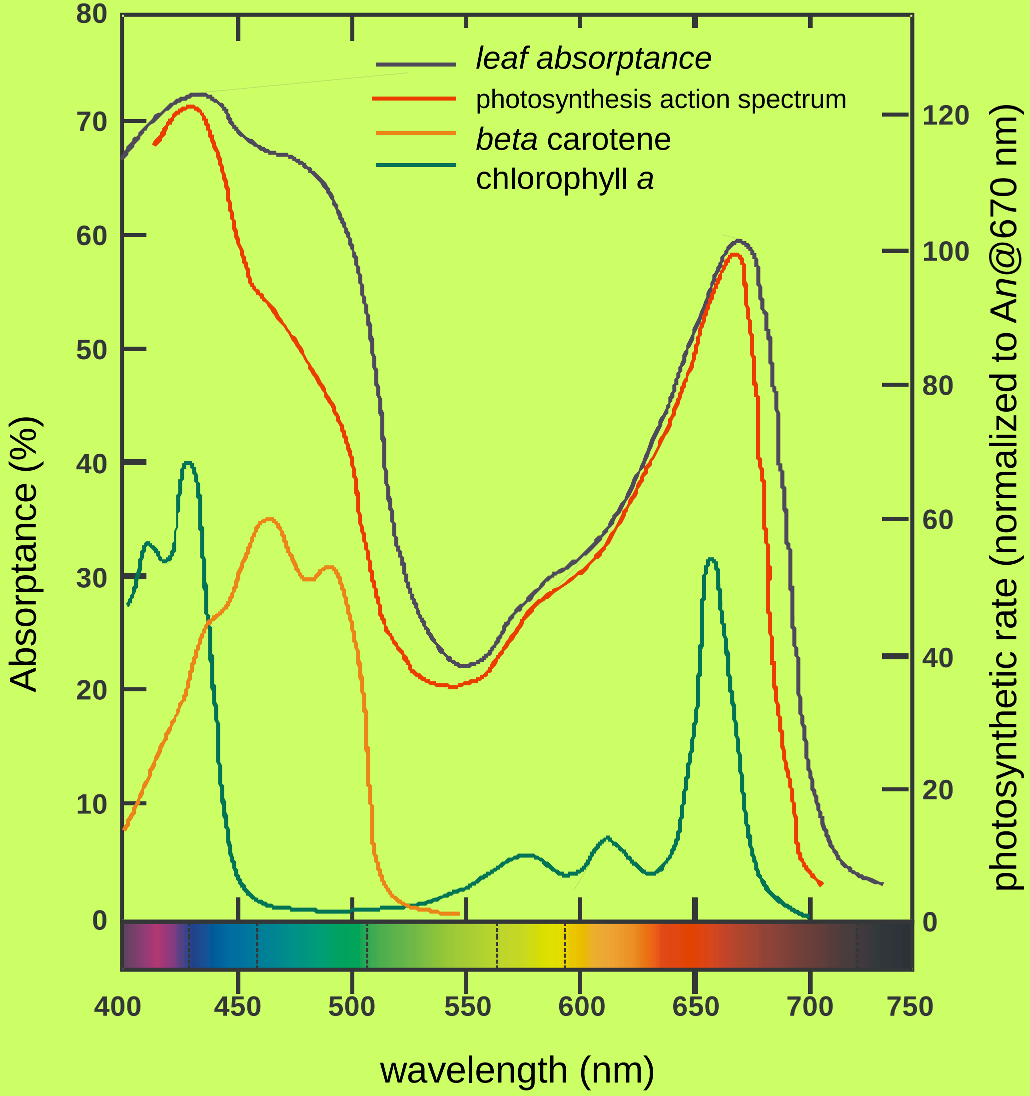
- **Φάσματα δράσης**

  Describes the effect of photons belonging to different spectral regions based on their ability to promote a biological activity

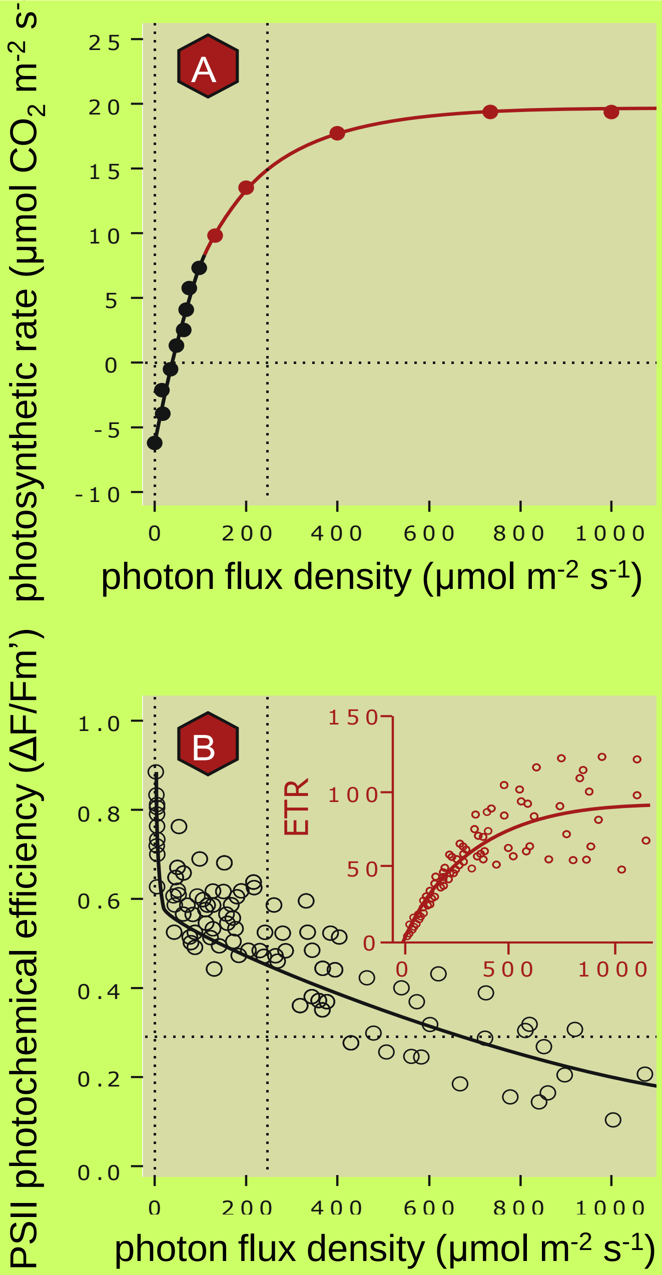
ACTION SPECTRA vs ABSORPTION SPECTRA



ACTION SPECTRA vs ABSORPTION SPECTRA



HIGH LIGHT INTENSITY STRESS



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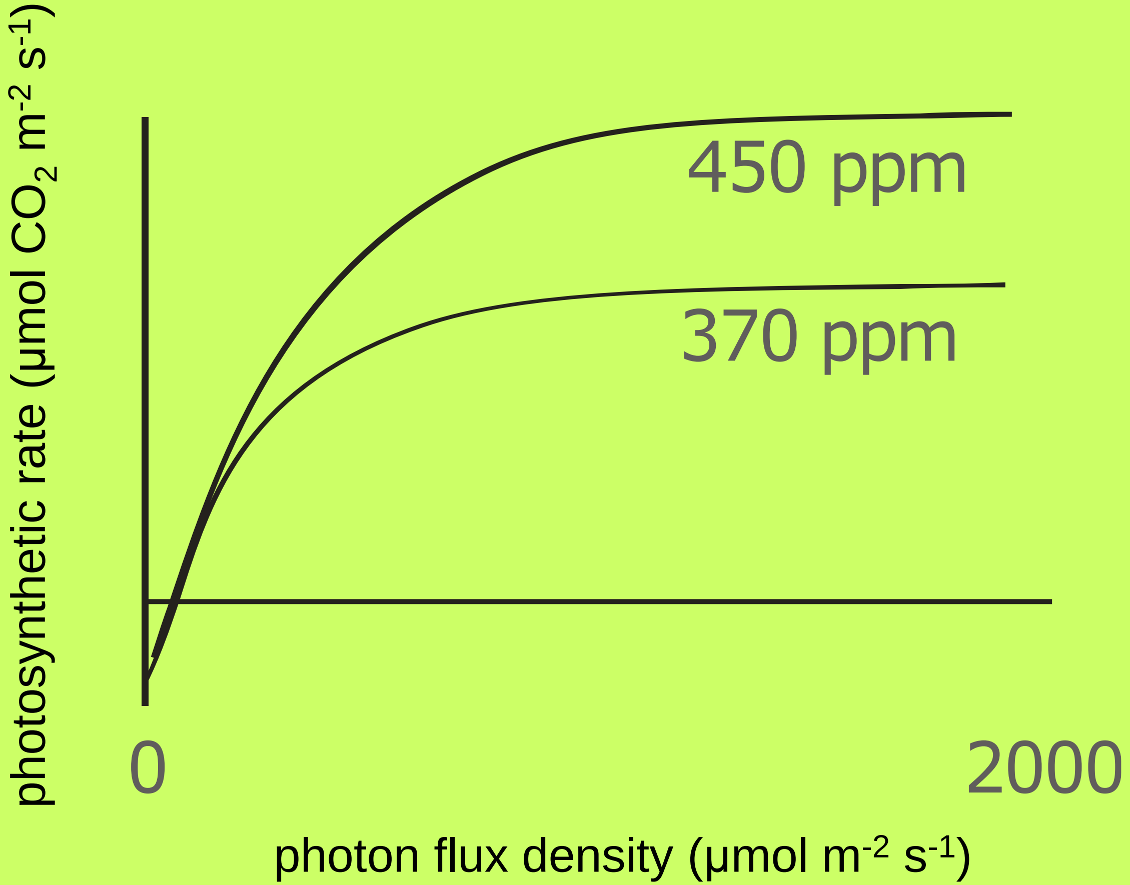

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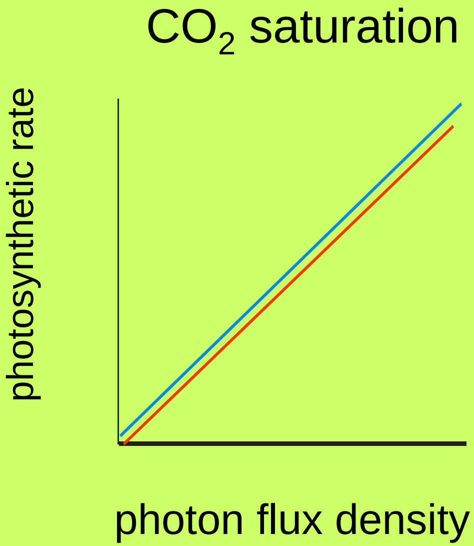

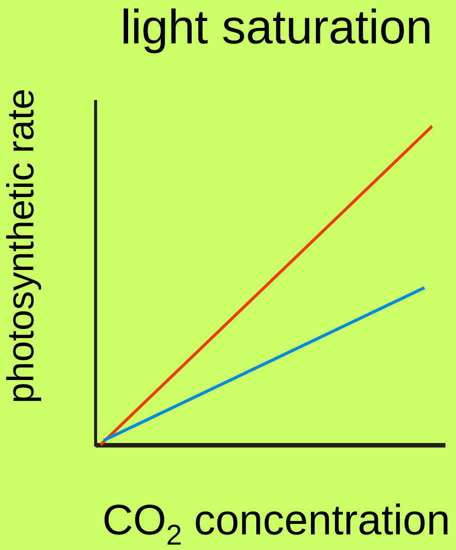

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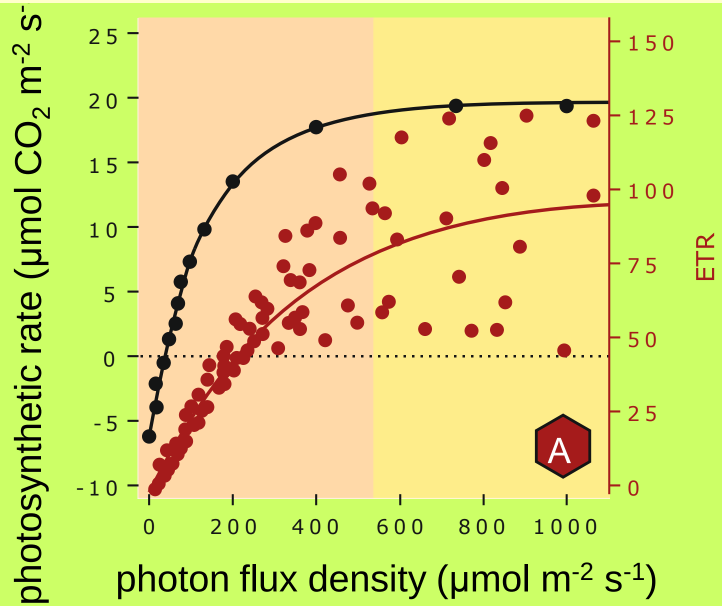

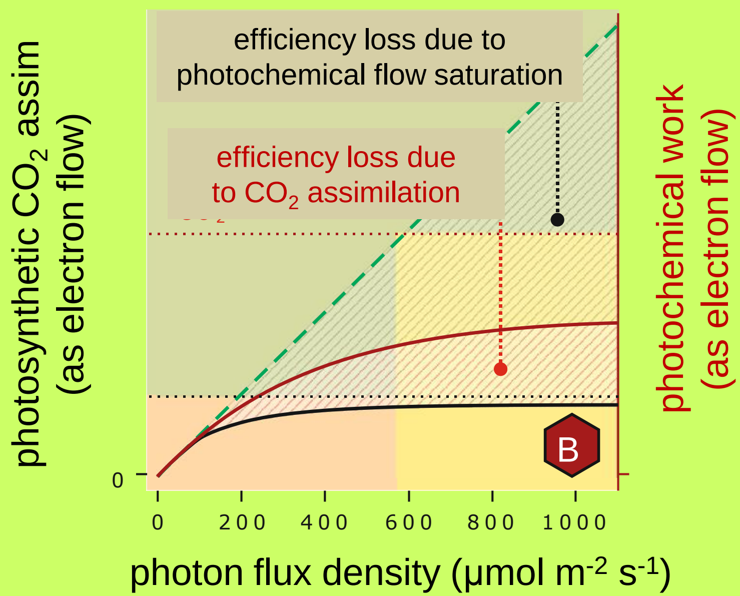

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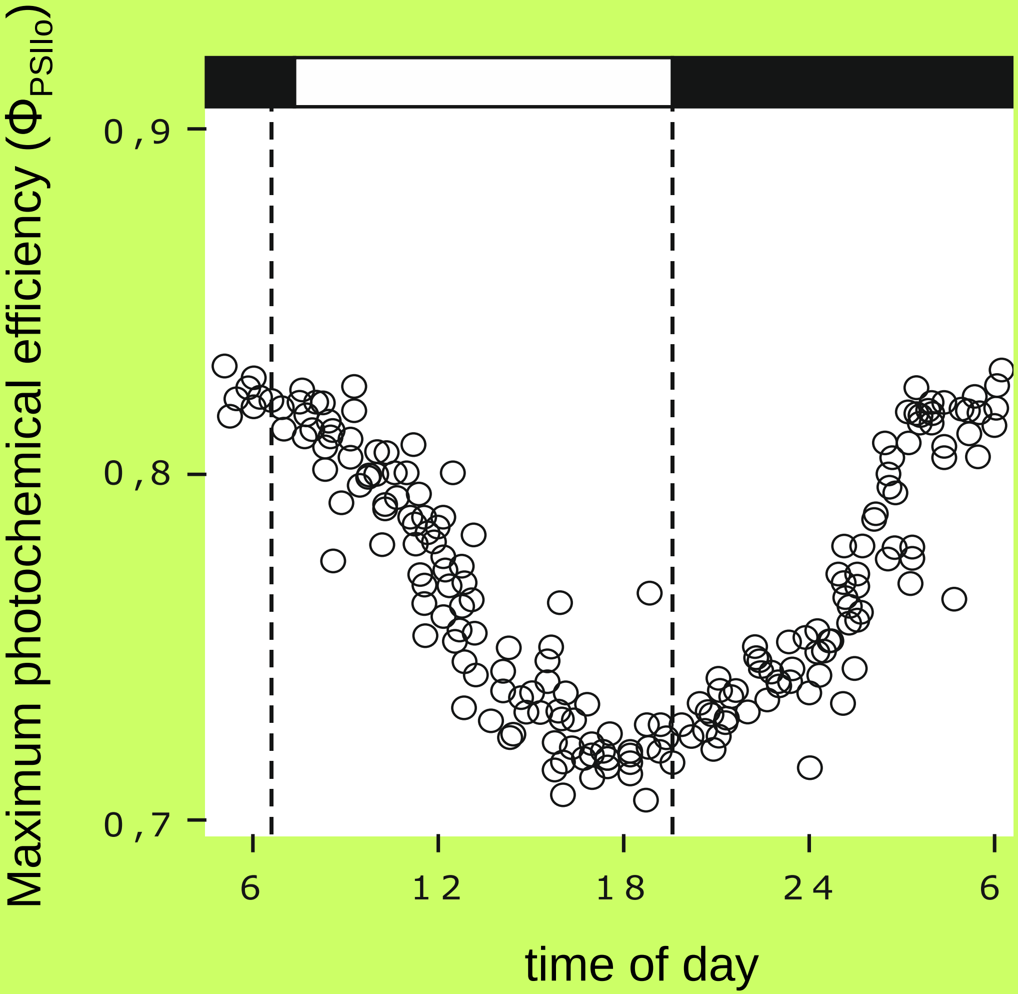


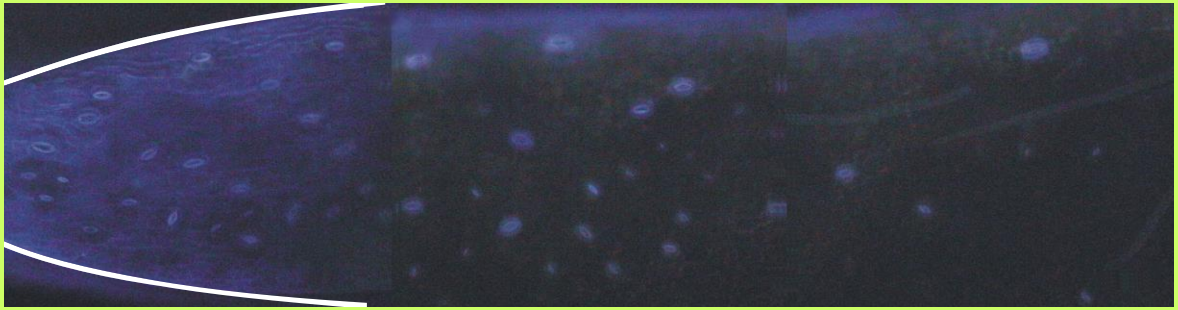
HIGH LIGHT INTENSITY STRESS

- **Environmental parameters increasing light stress**

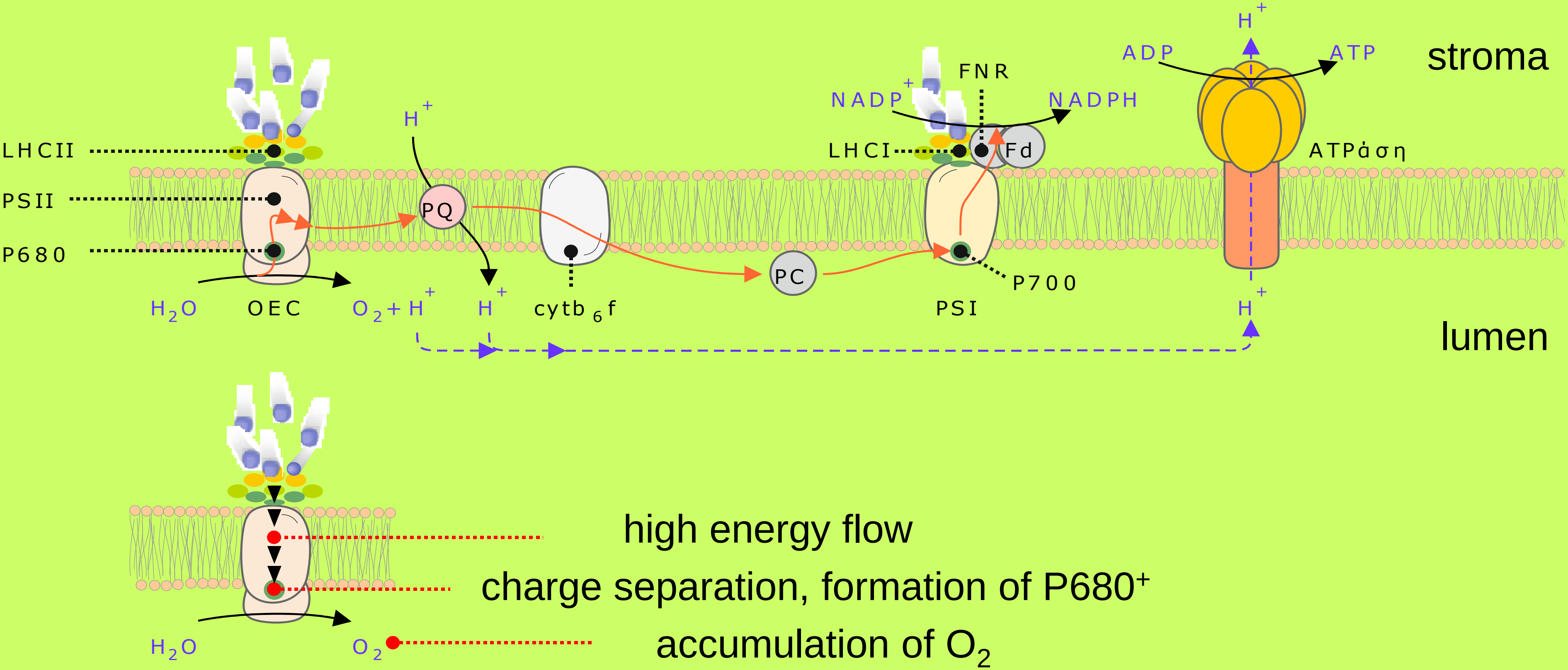
  1. Extreme temperatures
  2. Water and salt stress
  3. Polution
  4. Nutrient deficiencies

- **Physiological parameters increasing light stress**

  5. Developmental stage



HIGH LIGHT INTENSITY STRESS



HIGH LIGHT INTENSITY STRESS

Y_z	**D1 protein tyrosine 161**
$P680$	**PSII reaction center**
Q_A Q_B	**Quinnones A and B**
Ph	**Pheophytin**

Y_z $P680$ Ph Q_A Q_B	PSII open
Y_z $P680$ Ph Q_A Q_B	photon absorption
Y_z $^1P680^*$ Ph Q_A Q_B	PSII P680 excitation
Y_z $P680^+$ Ph^- Q_A Q_B	charge separation
Y_z $P680^+$ Ph Q_A^- Q_B	e^- transfer
Y_z^+ $P680$ Ph Q_A Q_B^-	P680 reduction

low energy pressure, energy flow compensated with photosynthetic anabolism

Y_z $P680$ Ph Q_A Q_B	e^- flow towards PSI
Y_z $P680$ Ph Q_A Q_B	PSII open
Y_z $P680$ Ph Q_A Q_B	photon absorption

repetition of the process

high energy pressure, inability of e^- flow towards the PSI, electron acceptors reduced

Y_z $P680$ Ph Q_A Q_B^-	PSII open
Y_z $P680^*$ Ph^- Q_A^- Q_B^-	photon absorption
Y_z $^1P680^*$ Ph Q_A Q_B^-	PSII P680 excitation
Y_z $P680^+$ Ph^- Q_A Q_B^-	charge separation
Y_z $P680^+$ Ph Q_A^- Q_B^-	e^- transfer, quinnone pair reduced (PSII closed)
Y_z^+ $P680$ Ph^- Q_A^- Q_B^-	P680 reduction
Y_z $P680$ Ph^- Q_A^- Q_B^-	e^- flow inability
Y_z $P680$ Ph^- Q_A^- Q_B^-	photon absorption
Y_z $^1P680^*$ Ph^- Q_A^- Q_B^-	PSII P680 excitation, inability for charge separation
Y_z $^1P680^*$ Ph^- Q_A^- Q_B^-	P680 remains in singlet excited state

internal conversion of ^{1}Chl*a to ^{3}Chl*a***

$^3P680$	$^3O_2$	P680 deexcitates by exciting triplet oxygen
$P680$	$^1O_2$	ROS creation (conversion to singlet excited oxygen)

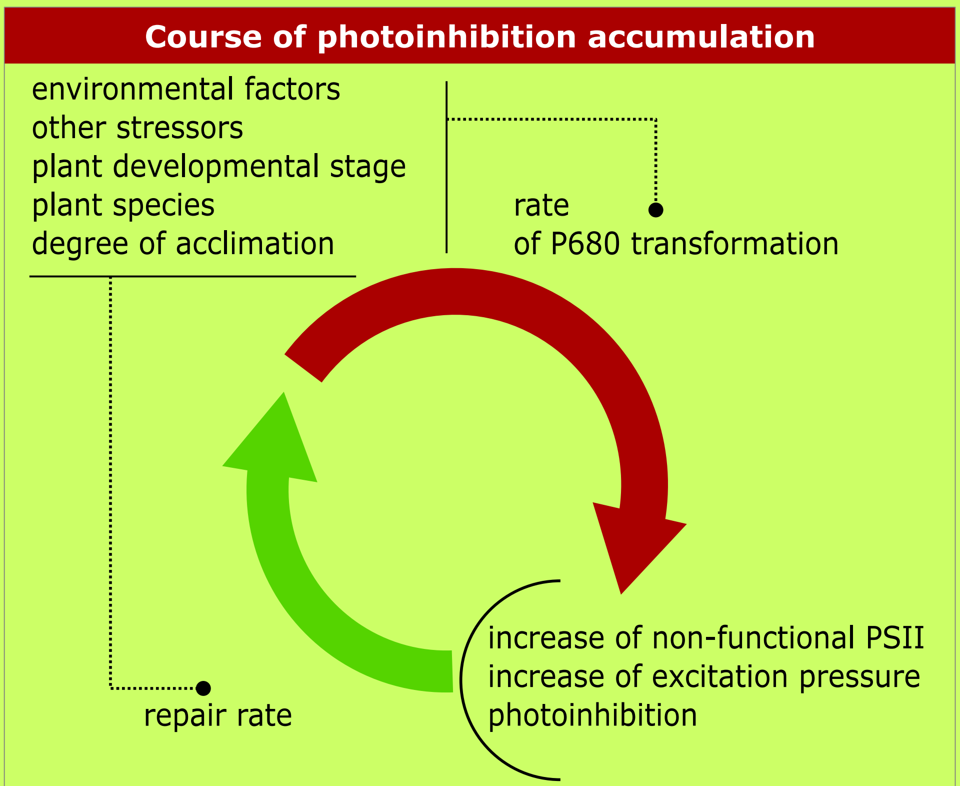
low energy pressure,
energy flow compensated
with photosynthetic anabolism

Y_z P680 Ph Q_A Q_B — e^- flow towards PSI

Y_z P680 Ph Q_A Q_B — PSII open

Y_z P680 Ph Q_A Q_B — photon absorption

repetition of the process



Y_z P680 Ph^- Q_A^- Q_B^- — e^- flow inability

Y_z P680 Ph^- Q_A^- Q_B^- — photon absorption

Y_z $^1P680^*$ Ph^- Q_A^- Q_B^- — PSII P680 excitation, inability for charge separation

Y_z $^1P680^*$ Ph^- Q_A^- Q_B^- — P680 remains in singlet excited state

internal conversion of ^{1}Chl*a * **to ^{3}Chl*a** ***

^{3}P680 — $^3O_2$ — P680 deexcitates by exciting triplet oxygen

P680 — $^1O_2$ — ROS creation (conversion to singlet excited oxygen)

P680 — $^1O_2$ — P680 attacked by ROS

[P680] — O_2 — transformed P680 (non-functional PSII)

repair

disassembly of PSII

D1 PSII protein degradation

de novo biosynthesis

reassembly of PSII

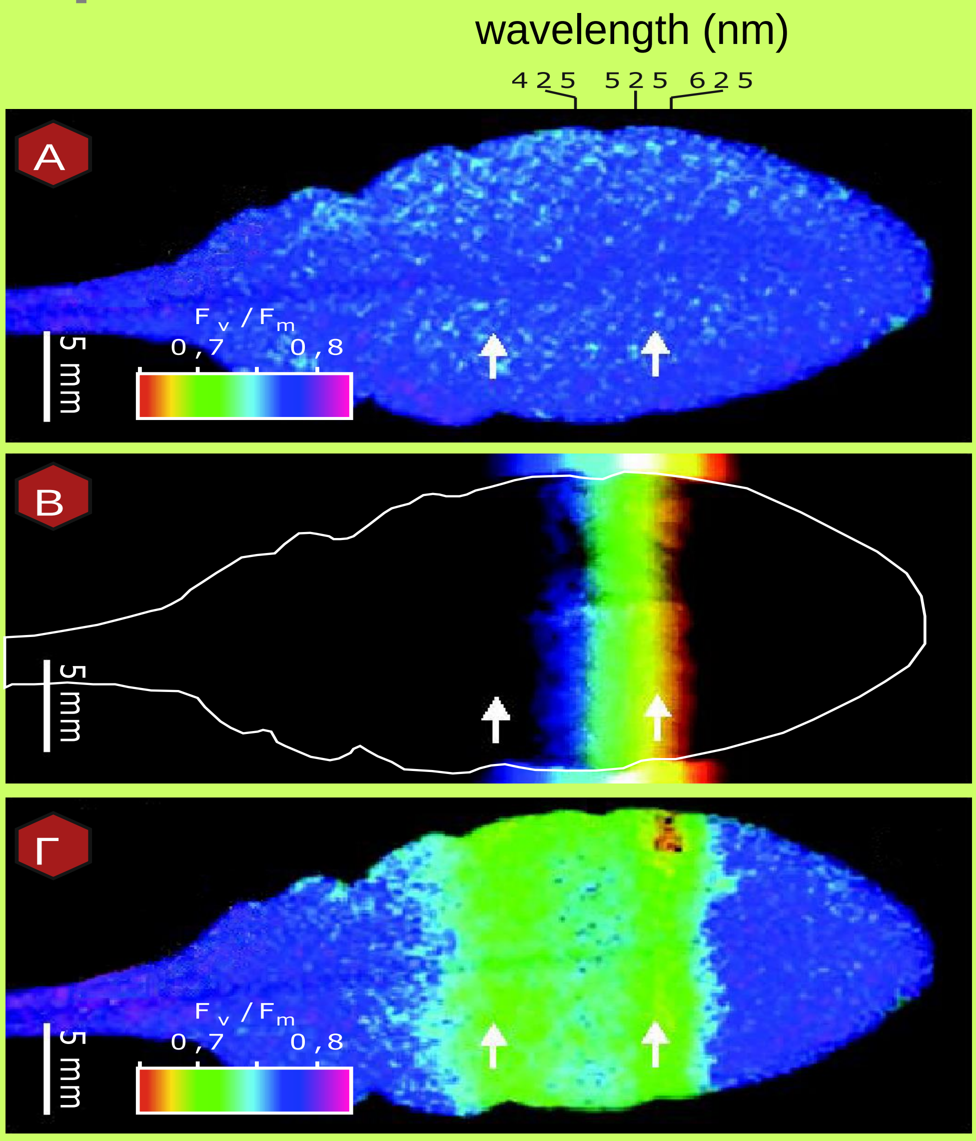
HIGH LIGHT INTENSITY STRESS

- **Causes of photoinhibition**

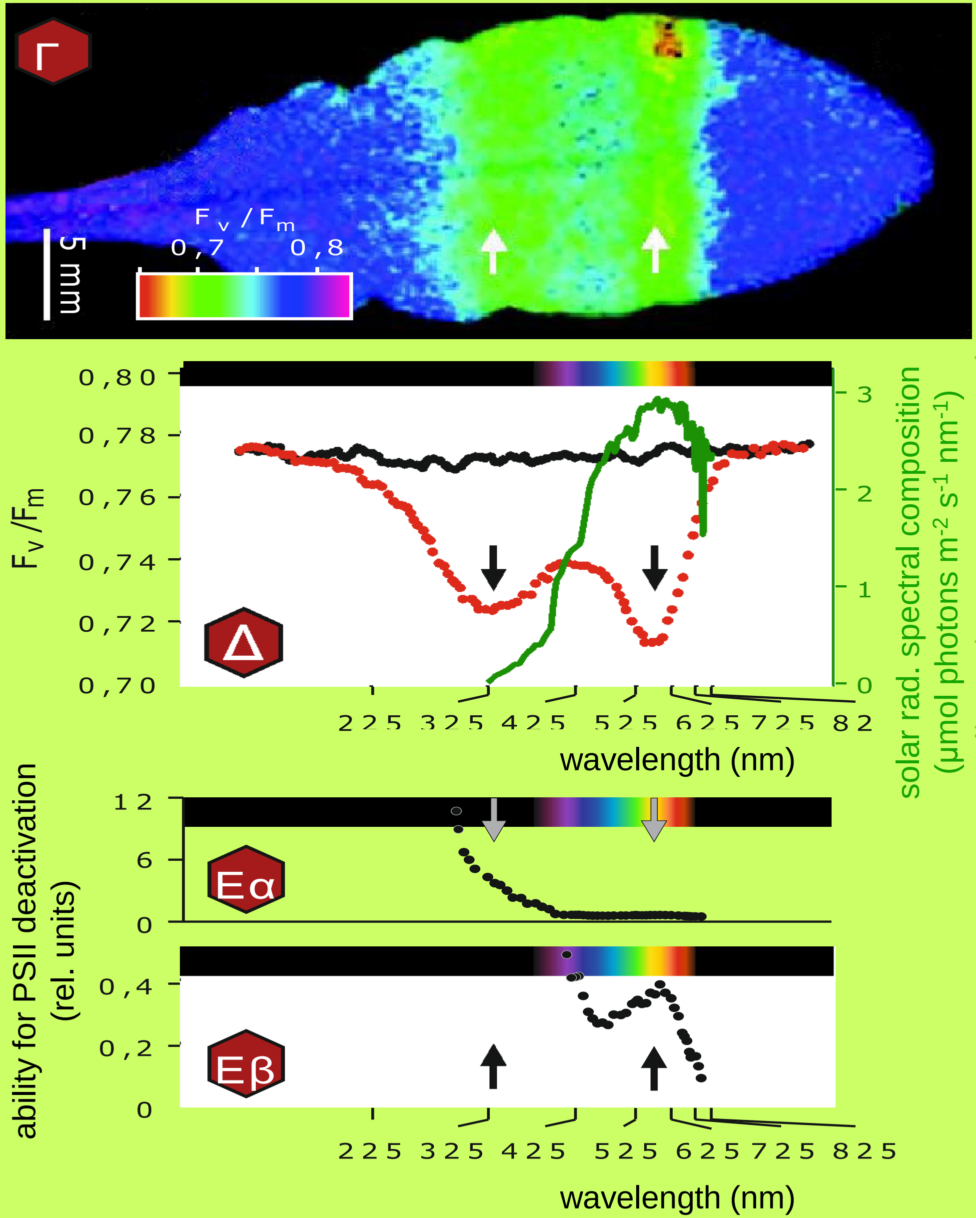
1. The photosynthetic anabolic Calvin-Benson cycle **is not enough to quench all light energy** collected under high light intensity
2. Low CO_2 conductance **maximizes** the effect
3. Photochemical **electron flow will slow down** if all electron acceptors are reduced
4. D1 protein of PSII will be transformed to non-functional and **repair rate may have lower capacity than required**

HIGH LIGHT INTENSITY STRESS

- **Causes of photoinhibition**



HIGH LIGHT INTENSITY STRESS



HIGH LIGHT INTENSITY STRESS

- **Final end of photoinhibition**

    1. Overexcitation of reaction centers lowers photochemical efficiency evidenced by increased chlorophyll fluorescence emission (F_o or F_s basal fluorescence levels increase)
    2. ROS accumulate due to the increase of side photochemical reactions other than electron flow to photochemical chain
    3. ROS load overtakes the capacity of chloroplast’s antioxidant metabolism

THREE DIFFERENT STRATEGIES

- **Escape**

  Chosen by annual ephemeral plant species. They complete their life cycle within the favorable period whereat superimposed foliage provides enough shade

THREE DIFFERENT STRATEGIES

- **Avoidance**

Plants **avoid to harvest** too much light energy. They are equipped with **optical barriers** or filters that scatter, reflect or absorb part of PAR resulting in **lessening of the overexcitation** of photochemical centers.

Other mechanisms arrange leaf lamina and chloroplasts in such a way to **reduce light absorption** by lessening exposure to incident radiation

THREE DIFFERENT STRATEGIES

- **Resistance**

These plants **absorb excessive amounts** of light energy that cannot be compensated by energy consumption by photosynthesis. Hence, **chloroplasts are under a high energy pressure**.

Resistance is accomplished by an array of efficient **photoprotective mechanisms** that **safely dissipate excessive energy**.
They also have a **high repair capacity** and **strong antioxidative protection**.

STRATEGY OF AVOIDANCE

- **Adaptive traits**

Optical filters / barriers:

1. Pigments (antho- and beta-cyanins)
2. Epicuticular waxes
3. Trichome

Anatomical traits and optical properties:

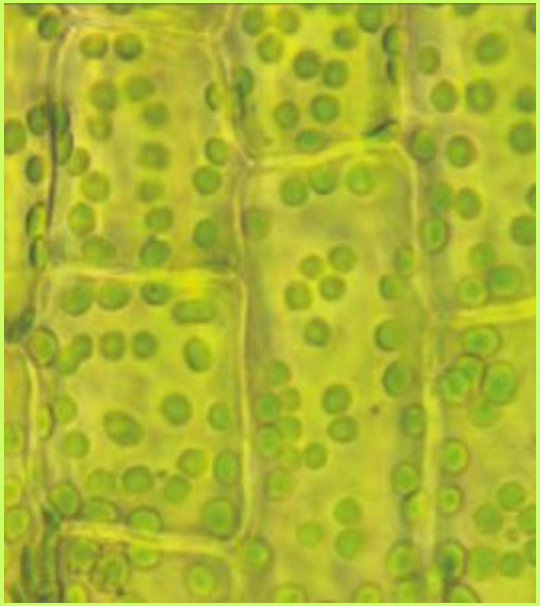
4. Leaf lamina angle
5. Leaf lamina geometry and petiole mechanics
6. Anatomical features for light guidance
    - 6α. Sclereids and fibers
    - 6β. Bundle sheath extensions

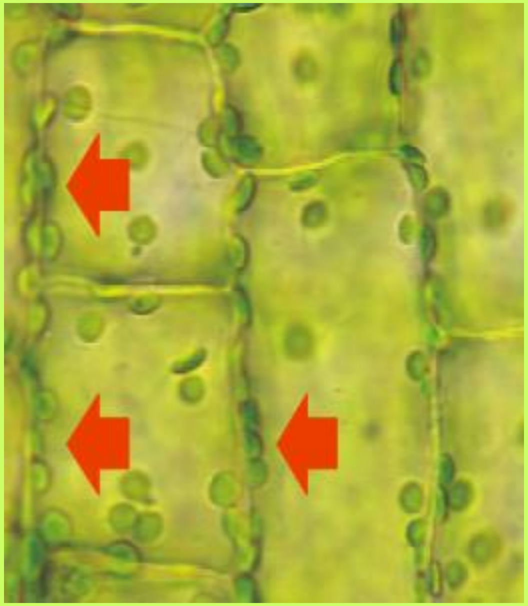
STRATEGY OF AVOIDANCE

- **Acclimation characteristics**

Movements:

1. Paraheliotropic lamina movements
2. Growth movements
3. Chloroplastic movements





STRATEGY OF RESISTANCE

- **Alternative paths for energy dissipation**

Dissipation at light harvesting level (photon quenching)

A. Non-photochemical quenching

1. Energy-dependent thermal quenching (qE)

Dissipation at electron flow level (metabolic quenching)

B. Photochemical, photosynthetic quenching

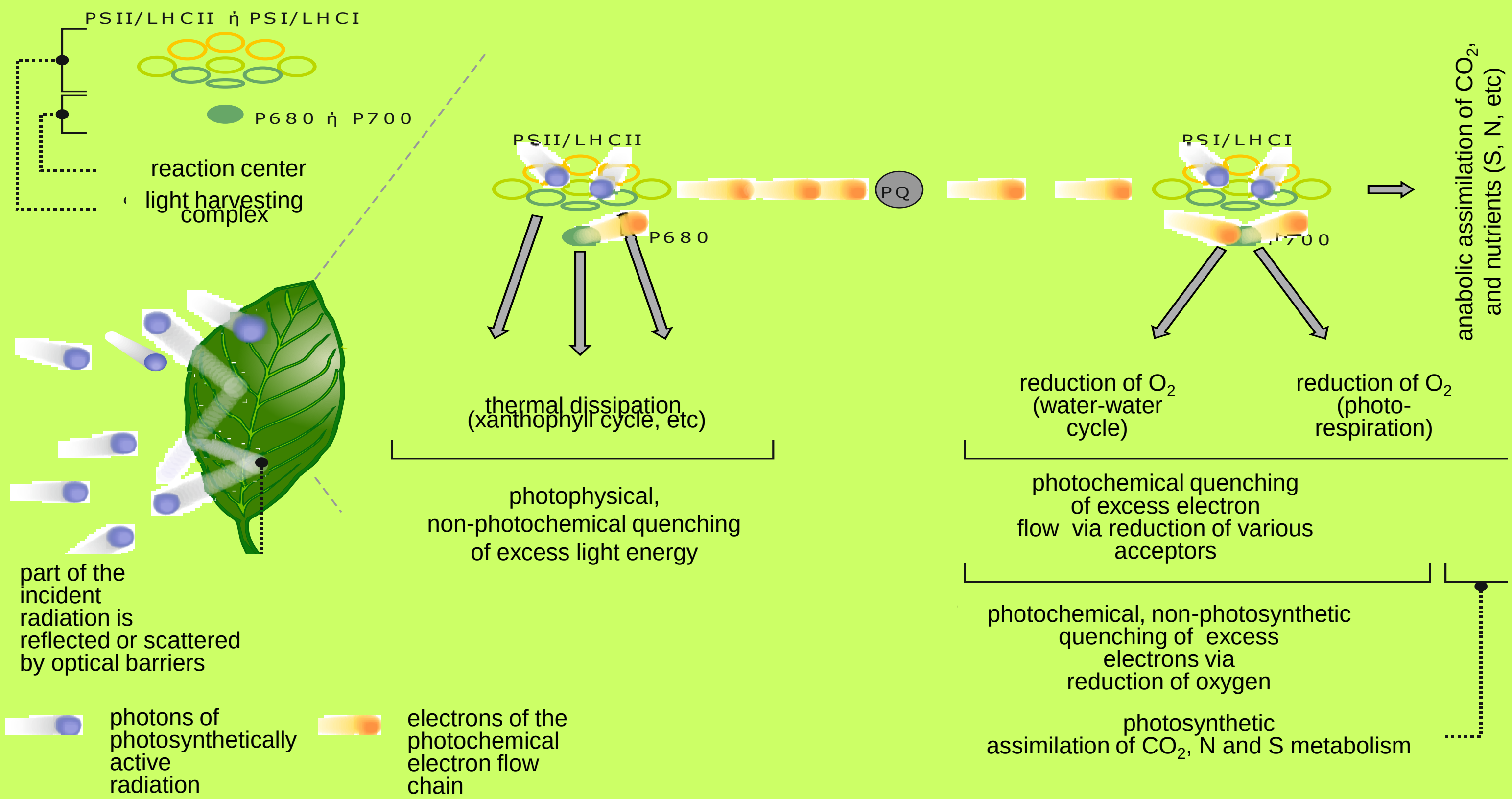
2. CO_2 assimilation via the consumption of reduced molecules ($NADPH_2$) and ATP

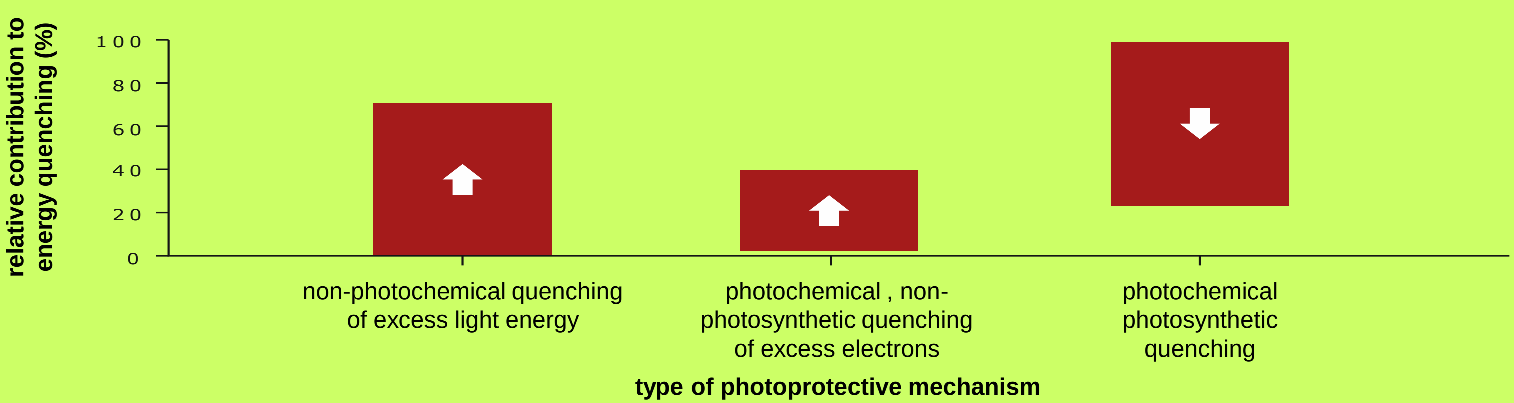
Γ. Photochemical, non-photosynthetic quenching

3. Photorespiration

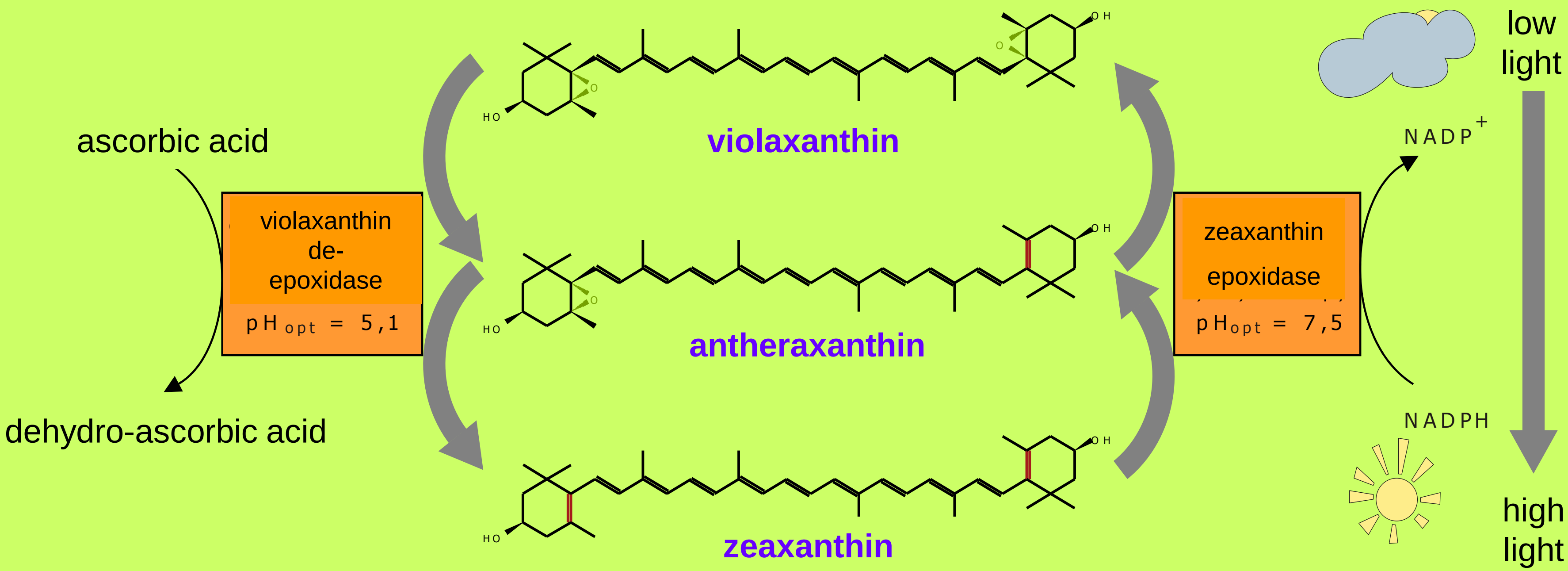
4. Mehler reaction (water-water cycle)

STRATEGY OF RESISTANCE





STRATEGY OF RESISTANCE



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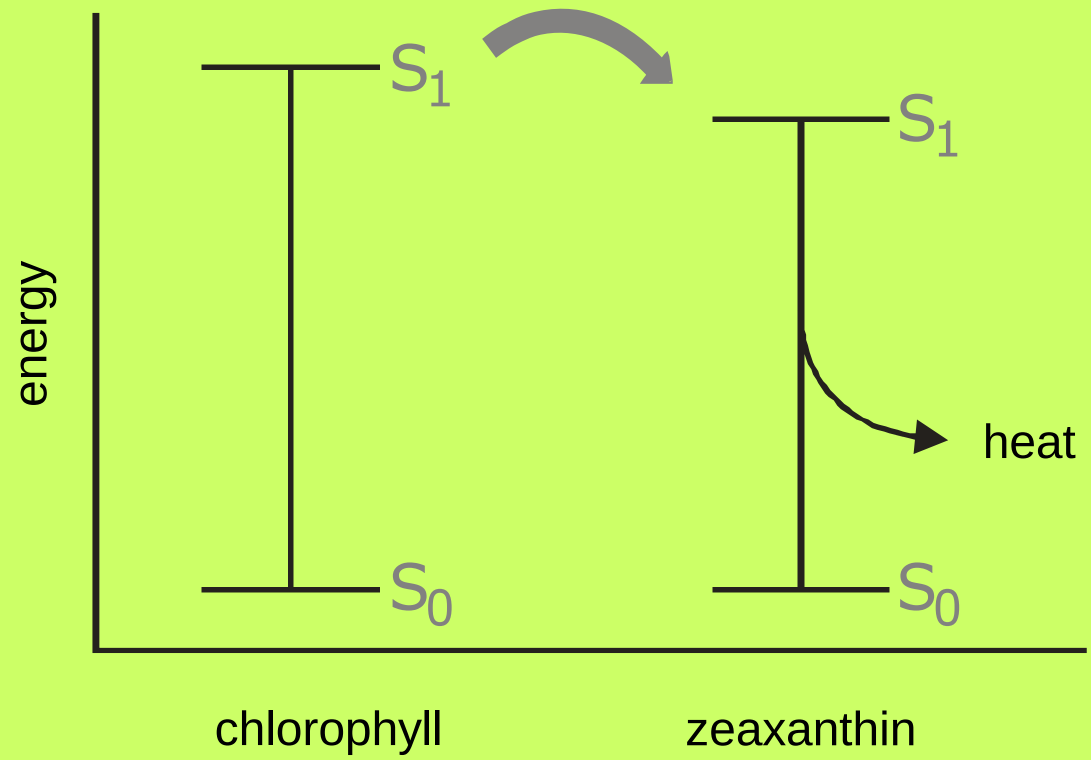

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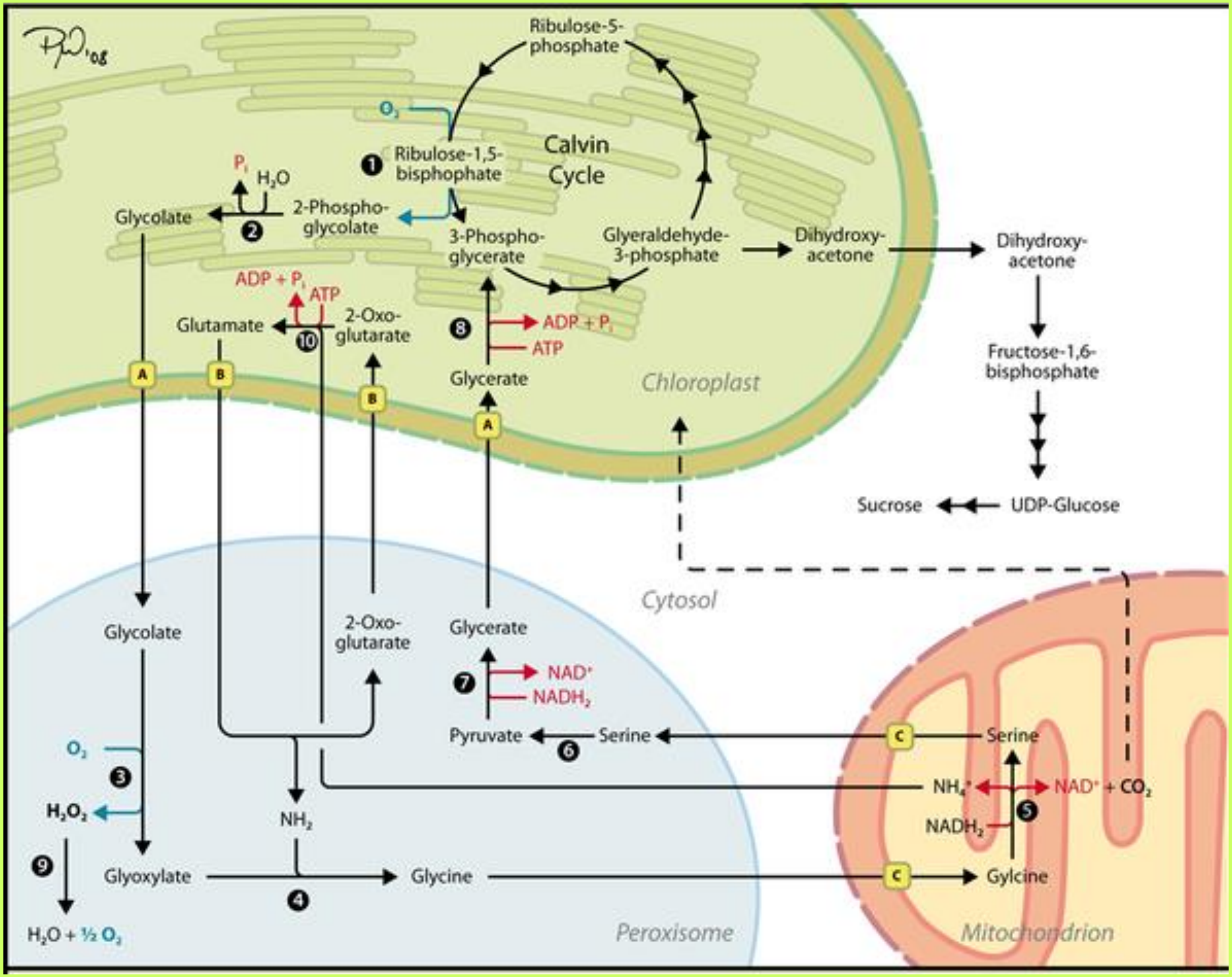

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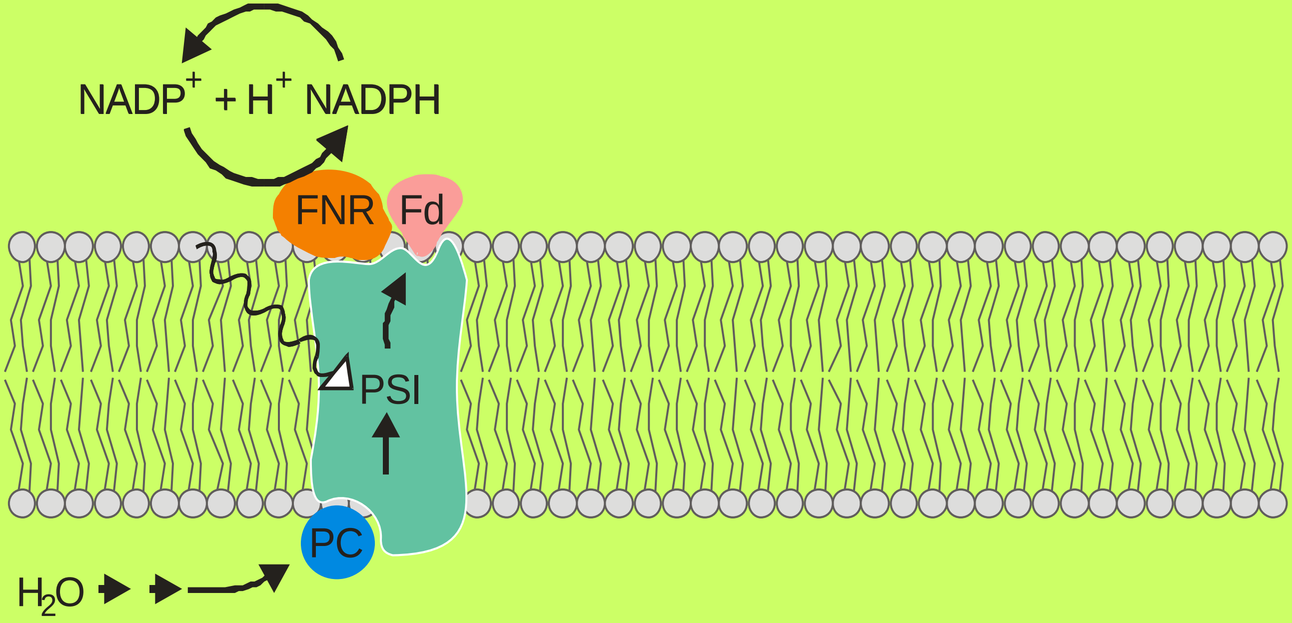
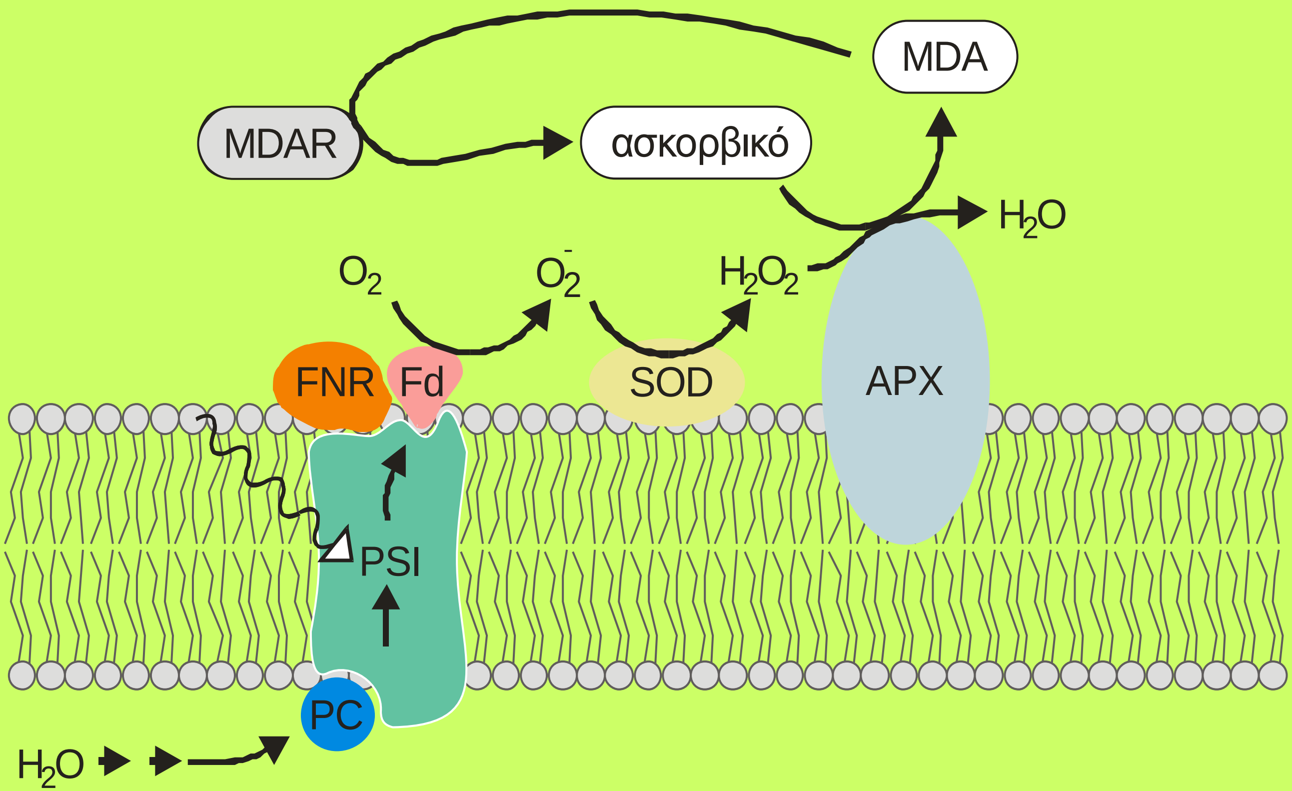


STRATEGY OF RESISTANCE



STRATEGY OF RESISTANCE