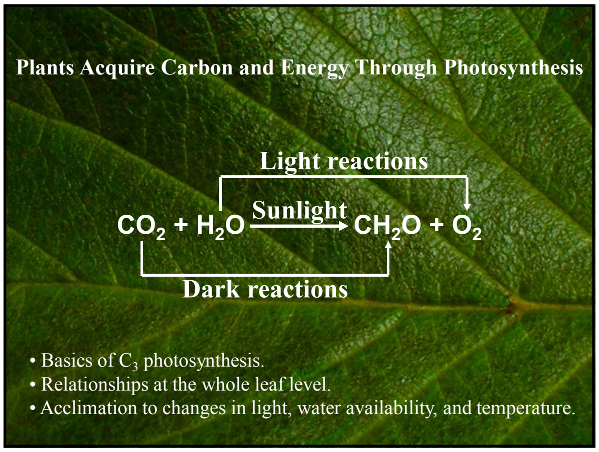


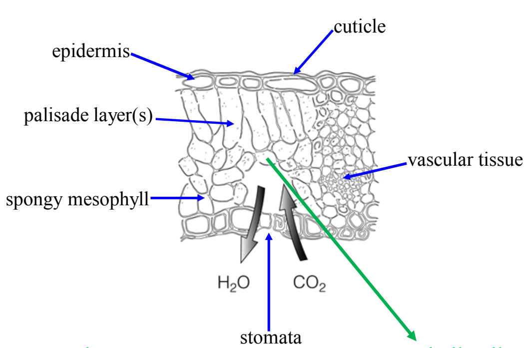
Photosynthesis requires near simultaneous capture of two different resources

- Photons (400-700 nm):
  - Atmospheric conditions, time, orientation, canopy position.
  - Efficiency of light capture apparatus: chlorophyll content, absorptance.

Cannot move photons to different plant parts once absorbed by chlorophyll.

- CO_2:
  - Atmospheric CO_2 concentration.
  - CO_2 diffusion gradient from atmosphere to chloroplast.

Plants don't breathe, must rely on diffusion of CO_2.



In atmosphere:
$CO_2 \approx 390$ µmol mol^{-1}

In mesophyll cell:
$CO_2 \approx 230$ µmol mol^{-1}

CO_2 diffusion barriers

Medium dependent: diffusion constant at 25 °C [$mm^2\ s^{-1}$]

CO_2 in air	15.1
CO_2 in water	0.0016
HCO_3^- in water	0.0014
H_2O in air	24.9
H_2O in H_2O	0.0025

$CO_2 + H_2O \longleftrightarrow HCO_3^- + H^+$

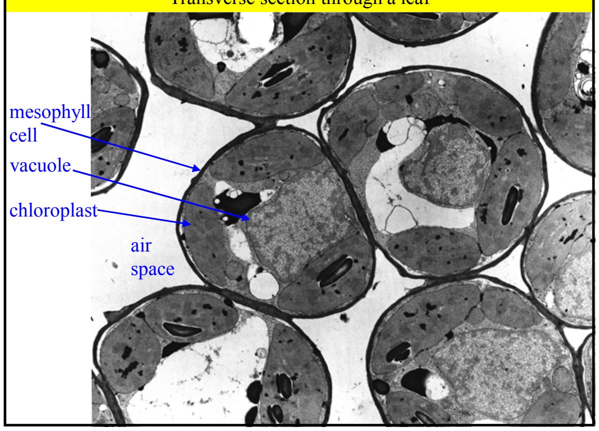
Carbonic Anhydrase

Solubility dependent: CO_2 solubility in water [$mm^3\ m^{-3}$] is low

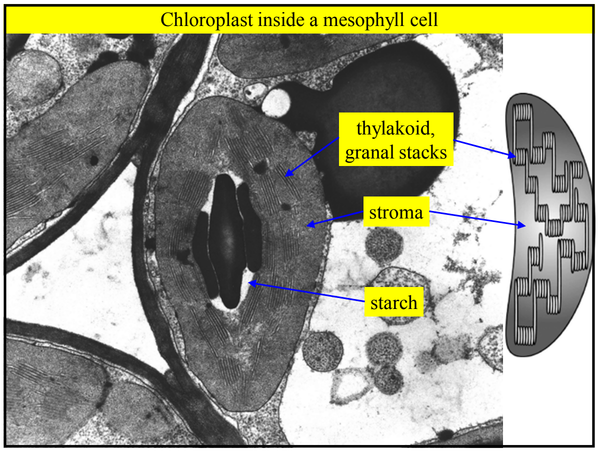
10 °C	1.194
20 °C	0.878
30 °C	0.665

Structure dependent: diffusion inside leaves

Transverse section through a leaf



Chloroplast inside a mesophyll cell

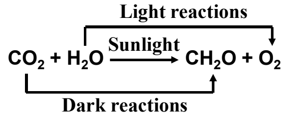


C_3 photosynthesis

1. Absorption of photons by chlorophyll.
2. Energy from photons splits H_2O, electrons transported along an electron transport chain: produces ATP and NADPH
3. ATP and NADPH are used in the photosynthetic carbon reduction cycle (Calvin cycle) to synthesize 3-carbon compounds from CO_2.

Light reactions (1–2)

Dark reactions (3)



Light reactions in the thylakoids suspended in the stroma of the chloroplast: Energy capture and transfer

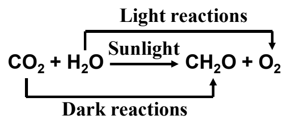
Light harvesting complex (structure of chlorophyll molecules) absorbs photons and transfers the excitation energy to the reaction center of one of the photosystems.

Photosystem II (pigment and protein unit) uses excitation energy is to split water; source of electrons, H^+ ions, and O_2.

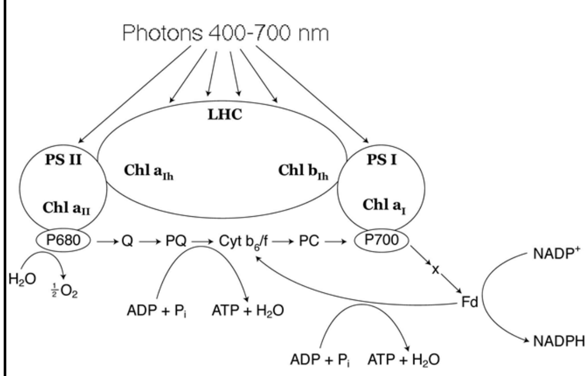
Photosystem I (pigment and protein unit) transfers excitation energy to an electron.

Excited electrons and H^+ ions from the photosystems drive the synthesis of ATP and NADPH.

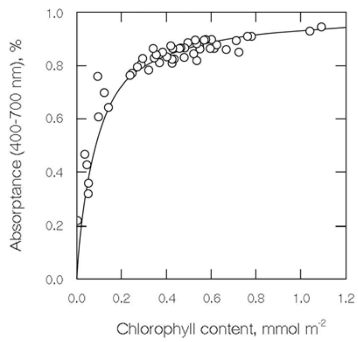
- At high PPFD, the initial carboxylation step by Rubisco is limiting.
- At low PPFD, production of ATP and NADPH for regeneration of RuPB is limiting.



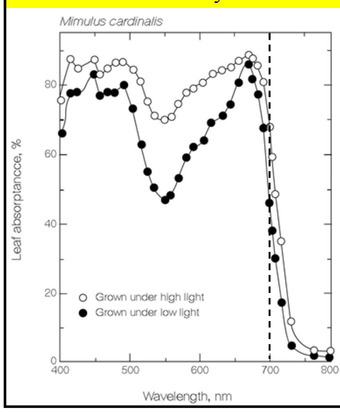
Light harvesting complex and photosystems in thylakoids



Most leaves absorb 80-85% of all PPFD, even at low chlorophyll concentrations



Leaves absorb very little radiation outside 400-700 nm



- Chlorophyll reaches the same excitation state independent of the wavelength (energy content) of an absorbed photon.
- Plants are photon counters: total number of absorbed photons drives photosynthesis, not total energy.
- Not all absorbed photons drive photosynthesis: excited chlorophyll can convert absorbed energy into heat and excited chlorophyll can emit a photon (fluorescence).

Dark reactions in the stroma of the chloroplast: Photosynthetic carbon reduction (PCR) cycle (Calvin cycle)

Rubisco: CO_2 + RuBP ⟶ 2 phosphoglyceric acid (PGA)

Rubisco (Ribulose-1,5-bisphospate carboxylase/oxygenase): Enzyme that catalyzes the primary step in the Calvin cycle.

2 PGA + ATP + NADPH ⟶ RuBP + CH_2O

- At high PPFD, the initial carboxylation step by Rubisco is limiting.
- At low PPFD, production of ATP and NADPH for regeneration of RuPB is limiting.

Light reactions

$CO_2 + H_2O \xrightarrow{\text{Sunlight}} CH_2O + O_2$

Dark reactions

Rubisco can function as a carboxylase and oxygenase: Photosynthetic carbon oxygenation (PCO) in addition to PCR

Rubisco: O_2 + RuBP ⟶ PGA + phosphoglycolate (PG)

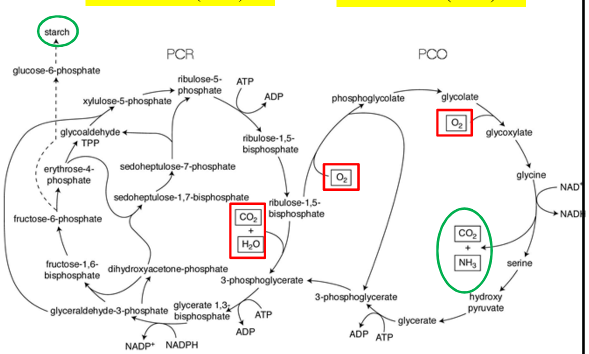
Photorespiration: consumes O_2 and releases CO_2.

- Dependent on ratio of CO_2 to O_2 and temperature.
- High CO_2 relative to O_2: favors carboxylation.
- Low temperature: favors carboxylation.
- Distinct from mitochondrial respiration.

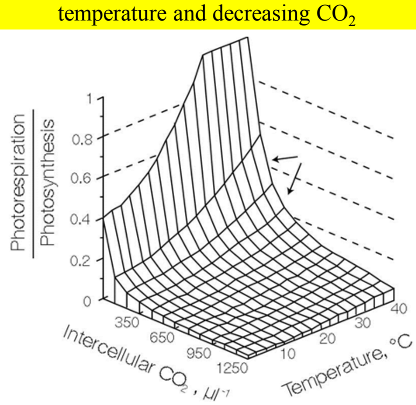
Climate change has the potential to significantly influence the ratio of photorespiration to photosynthesis.

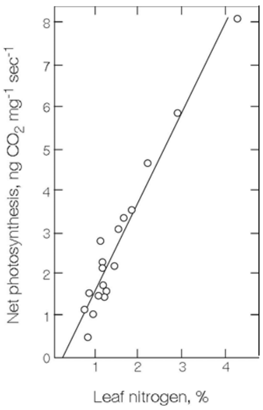
Photosynthetic carbon reduction (PCR)

Photosynthetic carbon oxidation (PCO)



Photorespiration increases with increasing temperature and decreasing CO_2





Photosynthetic machinery accounts for more than half of the nitrogen in leaves.

Changes in leaf nitrogen content reflect changes in protein content, particularly changes in the amount of Rubisco (photosynthetic enzyme).

Less Rubisco = lower photosynthetic capacity.

Similar relationship between phosphorus and photosynthesis.

Less ATP = lower photosynthetic capacity.

Leaf transpiration rate: Ohm's law analogy

Leaf latent heat flux [W m^{-2}]:

$$\lambda E = g_{wv}\lambda(e_{leaf} - e_{air}) / P_b$$

Leaf transpiration rate [mol m^{-2} s^{-1}]:

$$E = g_{wv}(e_{leaf} - e_{air}) / P_b$$

e_{leaf} = water vapor pressure inside leaf [kPa]
e_{air} = water vapor pressure of air [kPa]
g_{wv} = water vapor conductance [mol m^{-2} s^{-1}] → boundary layer and stomatal
λ = heat of vaporization (44,000 J mol^{-1} at 25 °C)
P_b = barometric pressure (101.3 kPa at sea level)

Leaf photosynthesis rate: Ohm's law analogy

Leaf photosynthesis rate [μmol m^{-2} s^{-1}]:

$$A_n = g_{CO2}(C_a - C_c)$$

A_n = net assimilation (photosynthesis – respiration)
g_{CO2} = carbon dioxide conductance [mol m^{-2} s^{-1}]
C_a = CO_2 mole fraction in atmosphere [μmol mol^{-1}]
C_c = CO_2 mole fraction in chloroplast [μmol mol^{-1}]

g_{CO2} is three conductors in series:

1. boundary layer
2. stomatal → $g_{sH2O} = 1.6 g_{sCO2}$
3. internal (mesophyll)

A boundary layer develops as air flows across a leaf

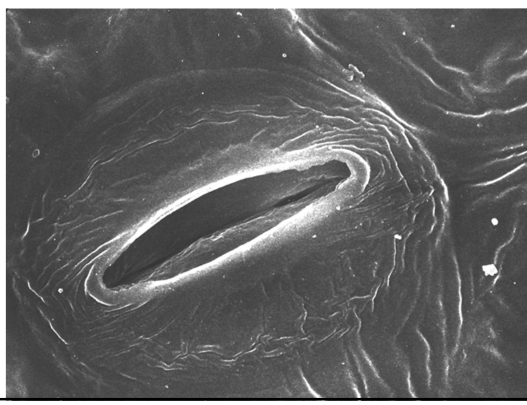
$$g_h = 0.135(u / d)^{0.5}$$

$$\delta = 4(d / u)^{0.5}$$

δ = boundary layer thickness [mm]
d = mean leaf length [m]
u = wind speed [m s^{-1}]

Boundary layer impedes the transfer of heat, H_2O, and CO_2 between the leaf and surrounding air.

Stomatal conductance quantifies degree of stomatal opening



Water use efficiency (WUE): A_n / E

Leaf transpiration rate [mol m^{-2} s^{-1}]:

$$E = g_{sH2O}(e_{leaf} - e_{air}) / P_b$$

Leaf photosynthesis rate [mol m^{-2} s^{-1}]:

$$A_n = g_{sCO2}(C_a - C_c)$$

$$g_{sH2O} = 1.6 g_{sCO2}$$

WUE [mol mol^{-1}]:

$$A_n / E = (C_a - C_c) / 1.6(e_{leaf} - e_{air})$$

Examples of water use efficiency

$A_n / E = (C_a - C_c) / 1.6(e_{leaf} - e_{air})$

Humid: $(e_{leaf} - e_{air}) \approx$ 0.5-1.0 kPa

Arid: $(e_{leaf} - e_{air}) \approx$ 3.0-4.0 kPa

$(C_a - C_c) \approx$ 100-200 µmol mol^{-1}

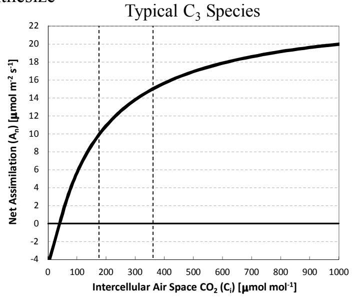
$(C_a - C_c) \approx$ 0.01-0.02 kPa

WUE [mol mol^{-1}]:

Humid: WUE ≈ 1 / 50-1 / 100

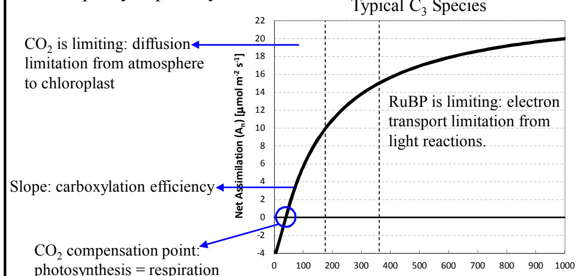
Arid: WUE ≈ 1 / 300-1 / 400

A_n-C_i curve: Leaf net photosynthesis response to intercellular CO_2: Leaf's capacity to photosynthesize



(Assumes high internal conductance: $C_c \approx C_i$)

A_n-C_i curve: Leaf net photosynthesis response to intercellular CO_2: Leaf's capacity to photosynthesize



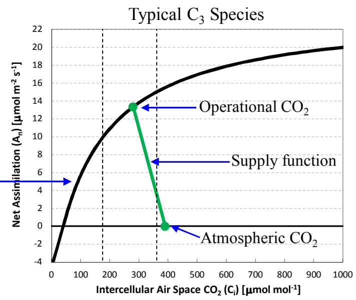
- Photosynthetic rate is determined by supply of and demand for CO_2.
- Plants tend to operate in the range where CO_2 and RuBP co-limit A_n: optimization of light and dark reactions.

Actual A_n is determined by supply of and demand for CO_2

Intersection of supply and demand functions is operational point:

$C_i / C_a \approx 0.6\text{-}0.8$

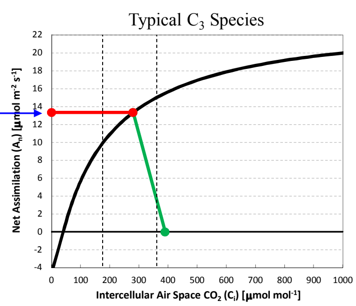
Demand function



- Supply → diffusion of CO_2 from atmosphere to chloroplast (g_{CO2}).
- Demand → radiation, CO_2 processing by enzymes, plant demand for energy.

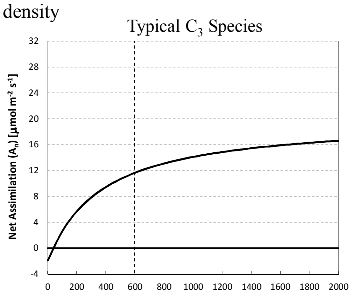
Actual A_n is net photosynthesis rate at C_i (the operational point)

A_n for current conditions



- Deviation from operation at $C_i / C_a \approx 0.6\text{-}0.8$ (CO_2 supply and demand are co-limiting) occurs when plants are under stress or growing in an extreme environment.

A_n-PPFD curve (light response curve): Leaf net photosynthesis response photosynthetic photon flux density



(Should be absorbed PPFD, often incident PPFD)

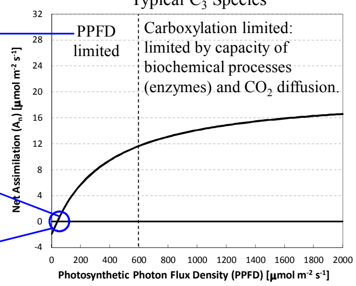
A_n-PPFD curve (light response curve): Leaf net photosynthesis response photosynthetic photon flux density

Typical C_3 Species

Limited by capacity of light-harvesting pigments and conversion of light energy to ATP and NADPH.

Slope: quantum yield (light use efficiency)

Light compensation point: photosynthesis = respiration

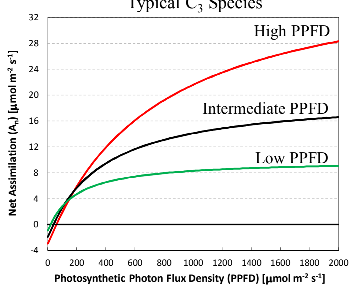


- Quantum yield is near 0.05 under natural conditions (20 photons reduce 1 CO_2).
- Quantum yield varies with temperature, CO_2, and O_2 (reflects photorespiration).

A_n-PPFD curve (light response curve): Leaf net photosynthesis response photosynthetic photon flux density

Typical C_3 Species

Leaves are acclimated to their environments.



- Sun leaves: higher A_n rates, higher light compensation point.
- Shade leaves: lower A_n rates, lower light compensation point.

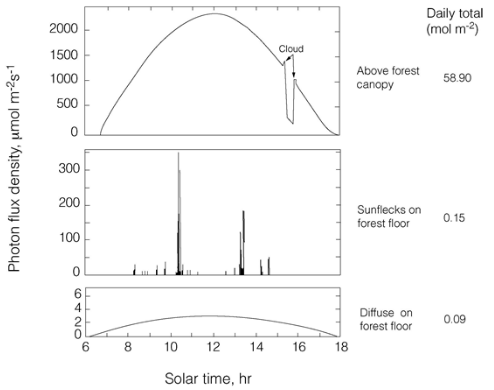
All leaves in a canopy do not experience the same environment

The physical environment can differ in:

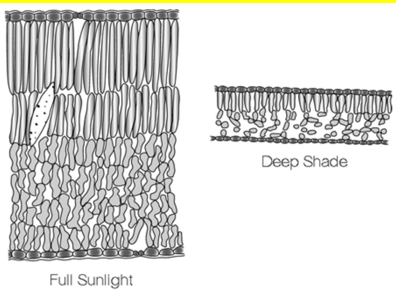
- Sunlight intensity (PPFD):
  daily, seasonal, positional variability.
- Soil water content:
  seasonal variability.
- Air temperature:
  daily, seasonal, episodic variability.

In order to maintain a positive net carbon balance, the structural and physiological features of a leaf often adjust to changes in the environment through a process known as acclimation.

Sun and shade PPFD environments are variable and differ dramatically



A sensor in the apical meristem assesses light quality of the environment and determines the structure of the leaf that soon develops



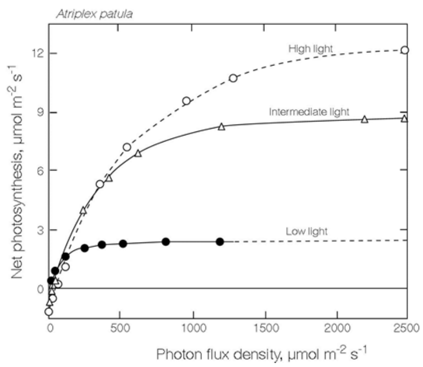
Biochemical and gas exchange characteristics develop as leaves acclimate to differences in the PPFD levels of the environment.

Tradeoff: High maximum A_n requires lots of resources.

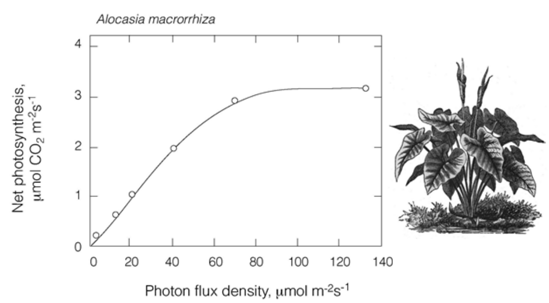
Generalized differences in characteristics: sun versus shade leaves

Structural:	**Sun Leaf**	**Shade Leaf**
Stomatal density	high	low
Leaf dry mass per area	high	low
Mesophyll thickness	high	low
Chloroplast per area	high	low
Thylakoids per stroma volume	low	high
Biochemical:		
Chlorophyll per chloroplast	low	high
Chlorophyll a / b ratio	high	low
Light harvesting complex per area	low	high
Electron transport components per area	high	low
Rubisco per area	high	low
Nitrogen per area	high	low
Xanthophylls per area	high	low
Gas exchange:		
Photosynthetic capacity (maximum A_n) per area	high	low
Mitochondrial respiration per area	high	low
Carboxylation capacity per area	high	low
Electron transport capacity per area	high	low
Quantum yield	similar	similar

Photosynthesis acclimates to changes in the PPFD growth environment



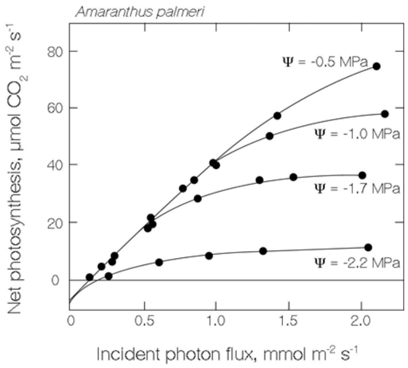
In shade plants, photosynthesis is often light saturated at 5-10 % full sunlight



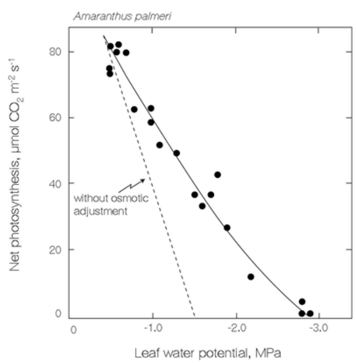
Excess radiation absorption can damage photosystems and reduce photosynthesis, especially if plant is water or temperature stressed

- All photons absorbed by chlorophyll result in excitation, but beyond the light-limited range of the light response curve not all excited chlorophyll results in photosynthesis.
- Excess energy damages photosystems and leads to reduced photosynthesis: photoinhibition.
- Plants can dissipate excess energy through absorption by a group of non-photosynthetic pigments: carotenoids.
- Specific carotenoids called xanthophylls are particularly important in dissipating excess energy through the xanthophyll cycle in order to minimize photoinhibition.

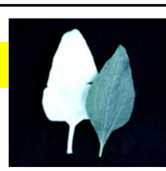
Photosynthesis in higher plants exhibits an acclimation response, responding to both PPFD and water stress changes

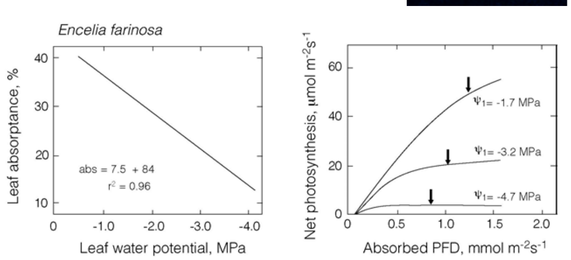


Shifts in leaf water relations properties (osmotic adjustment) in response to water stress occur at the same time as photosynthetic adjustments

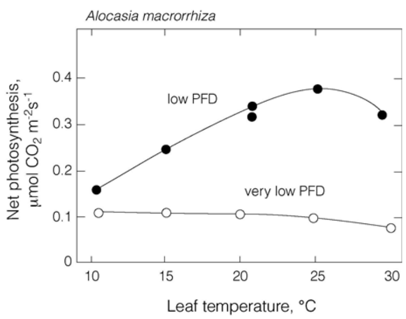


Photosynthetic rate declines significantly in *Encelia farinosa* as leaf absorptance declines in response to drought

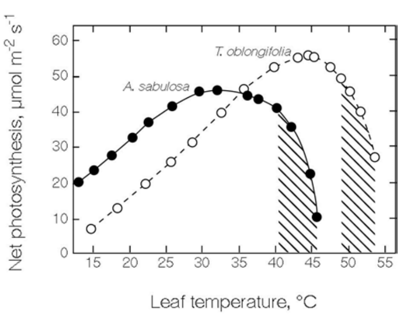




Photosynthesis is temperature insensitive in a low PPFD environment

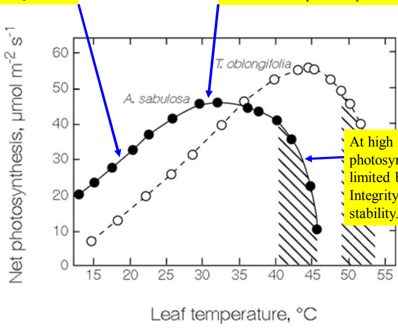


Photosynthesis can be temperature sensitive in a high PPFD environment



At low temperatures, photosynthesis is limited by enzyme activity.

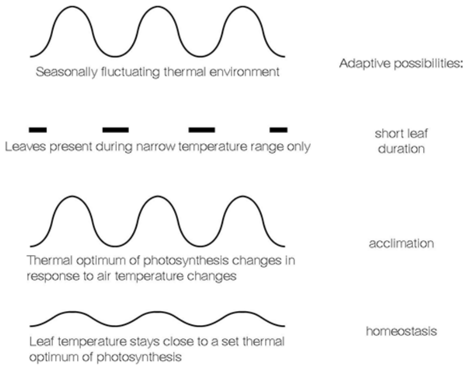
At intermediate temperatures, photosynthesis is limited by CO_2 diffusion and photorespiration.



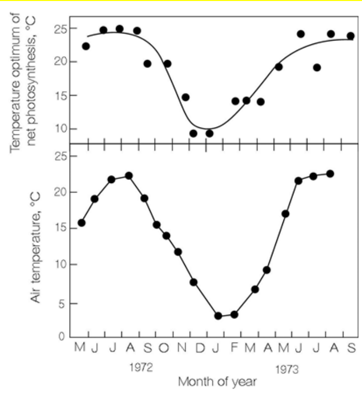
At high temperatures, photosynthesis is limited by membrane Integrity and enzyme stability.

Stomatal conductance typically decreases at high temperatures, decreasing net photosynthesis and flattening the temperature response.

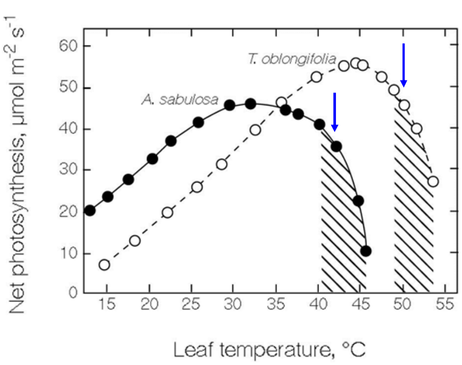
Both biochemical and morphological changes occur as leaves acclimate to temperature changes in a habitat



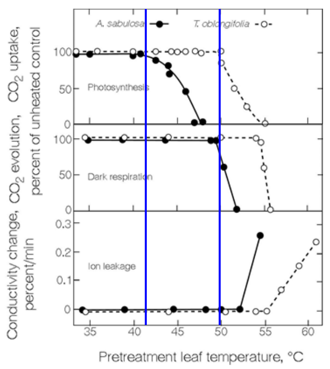
Most species exhibit biochemical adjustments to temperature changes



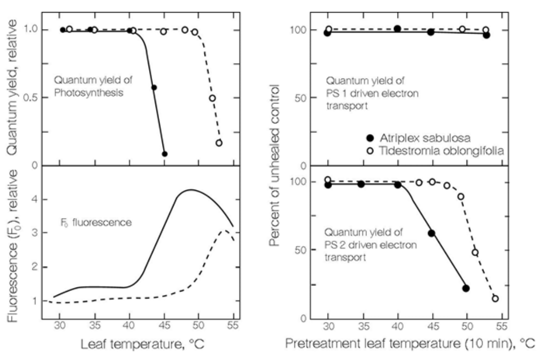
Why does photosynthesis become unstable at high leaf temperatures?



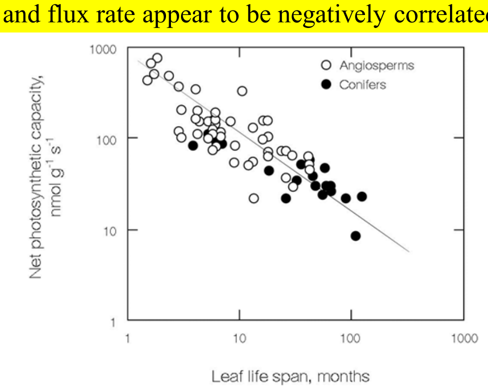
Changes in respiration rate or ion leakage do no contribute to photosynthetic decline



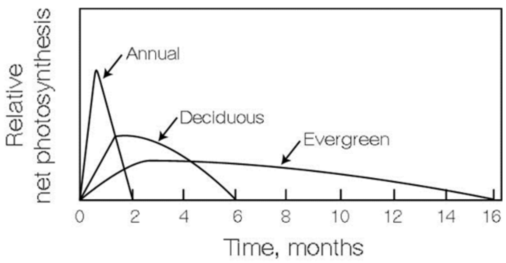
Photosynthesis decline with temperature is associated with PS II



Across a wide range of species, leaf life expectancy and flux rate appear to be negatively correlated



Across a wide range of life forms, leaf life expectancy and flux rate appear to be negatively correlated



Tradeoff between traits that maximize photosynthesis and traits that maximize leaf longevity: investment in photosynthetic machinery versus investment in defenses (water or temperature stress, pathogens, herbivores).