ECOPHYSIOLOGY OF PHOTOSYNTHESIS

Impact of radiation regime on CO_2 assimilation of forests

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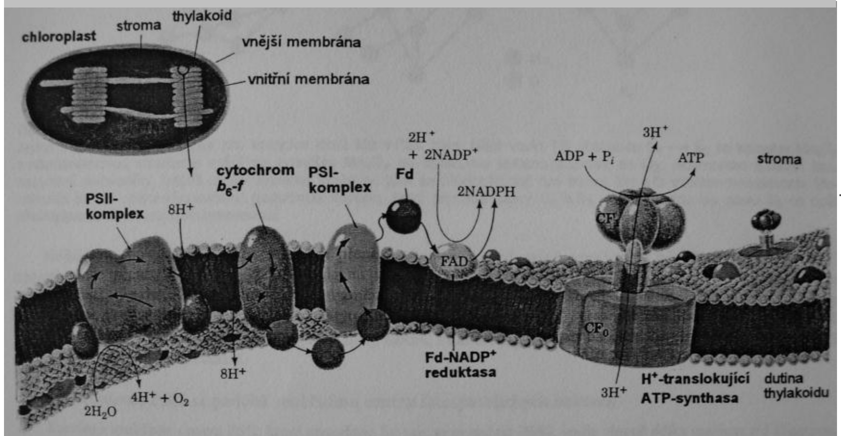
INVESTICE DO ROZVOJE VZDĚLÁVÁNÍ

Methodological approaches

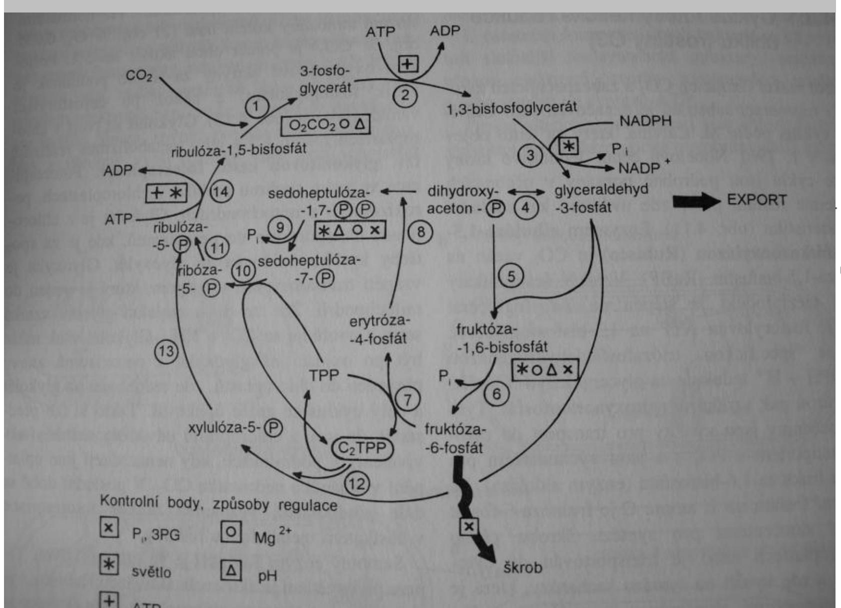
- **analytical approach** – detailed investigation of individual parts of a biological system:
  - chromatography
  - spectroscopy
  - aerodynamic techniques
  - observation of phenology
- **systemic approach** – investigation of processes which precisely describe the whole biological system
  - photosynthesis (C cycle) – crosspoint of matter and energy fluxes
    - connected with basic plants traits,
    - determines and is subject to other processes
    - couplet with s microclimate conditions
      - particularly radiation regime

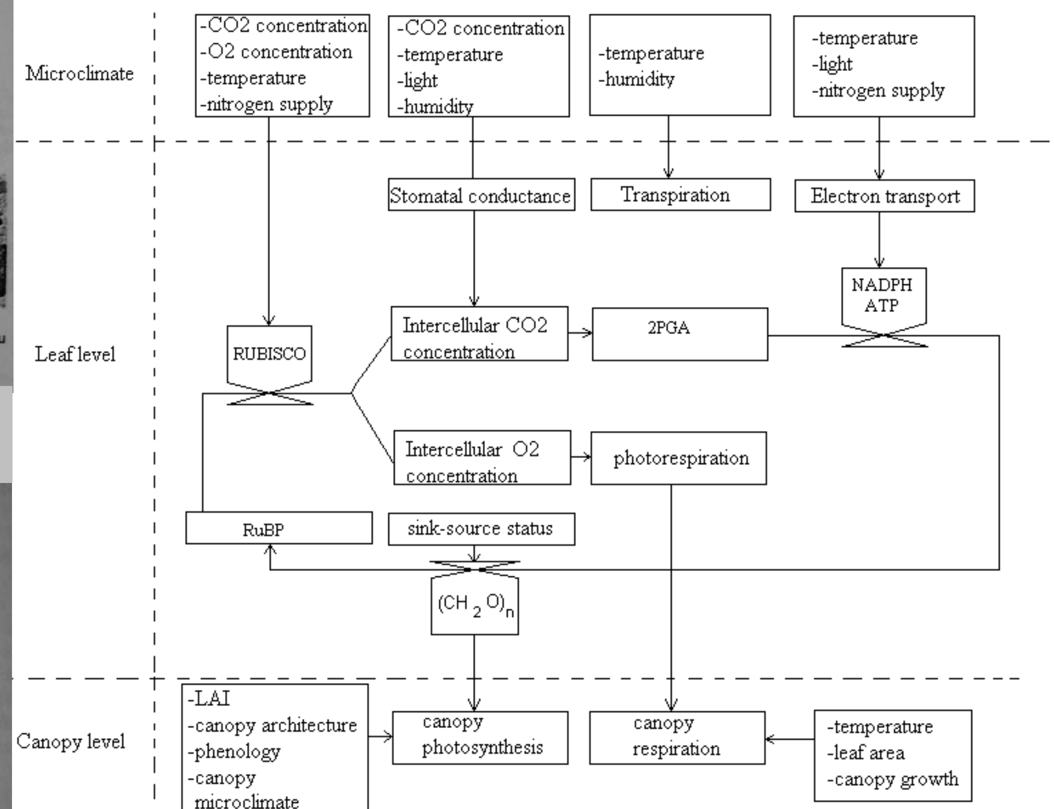
Photosynthesis and microclimate

Primary phase



Secondary phase



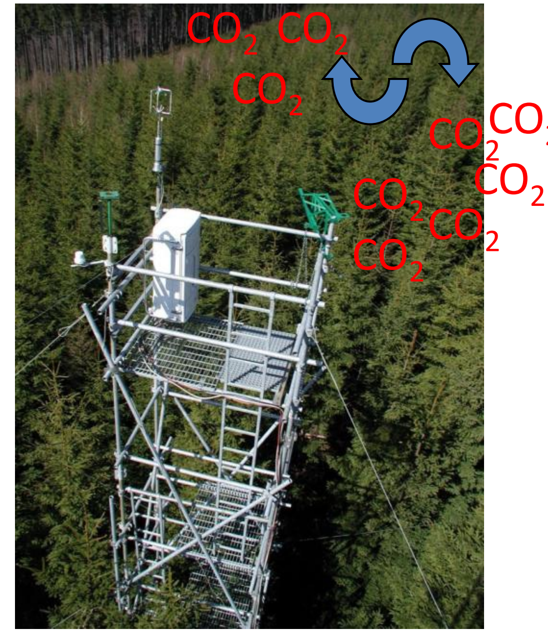


How to study C cycle?

Leaf level (parts of ecosystem)

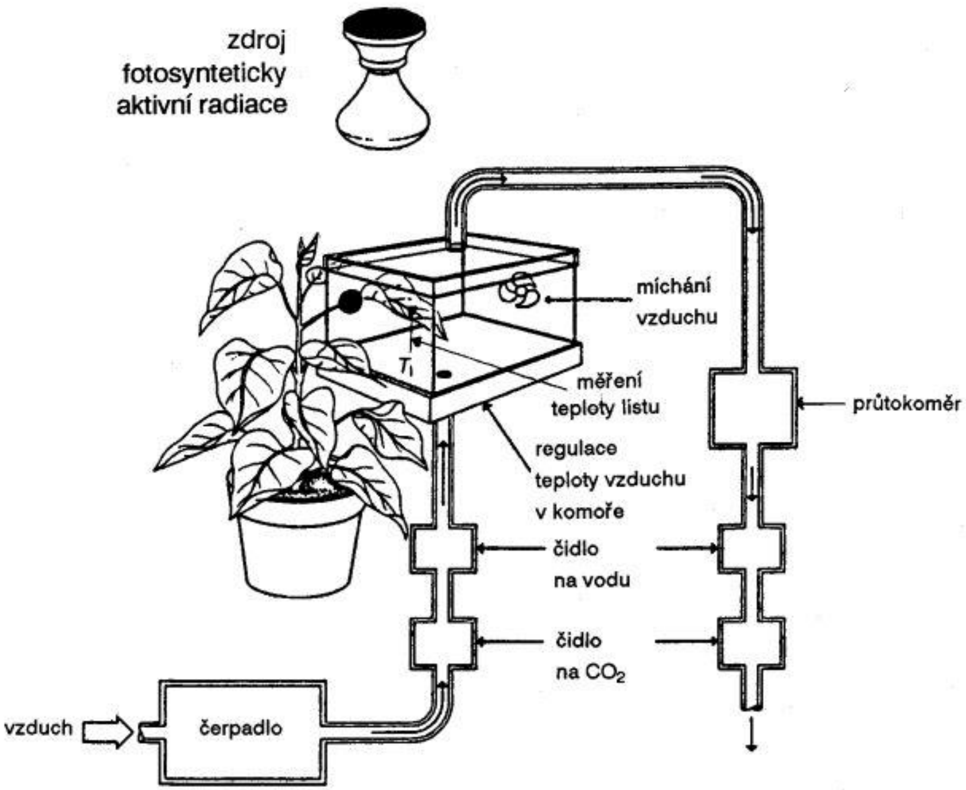
Chamber measurements

Ecosystem level



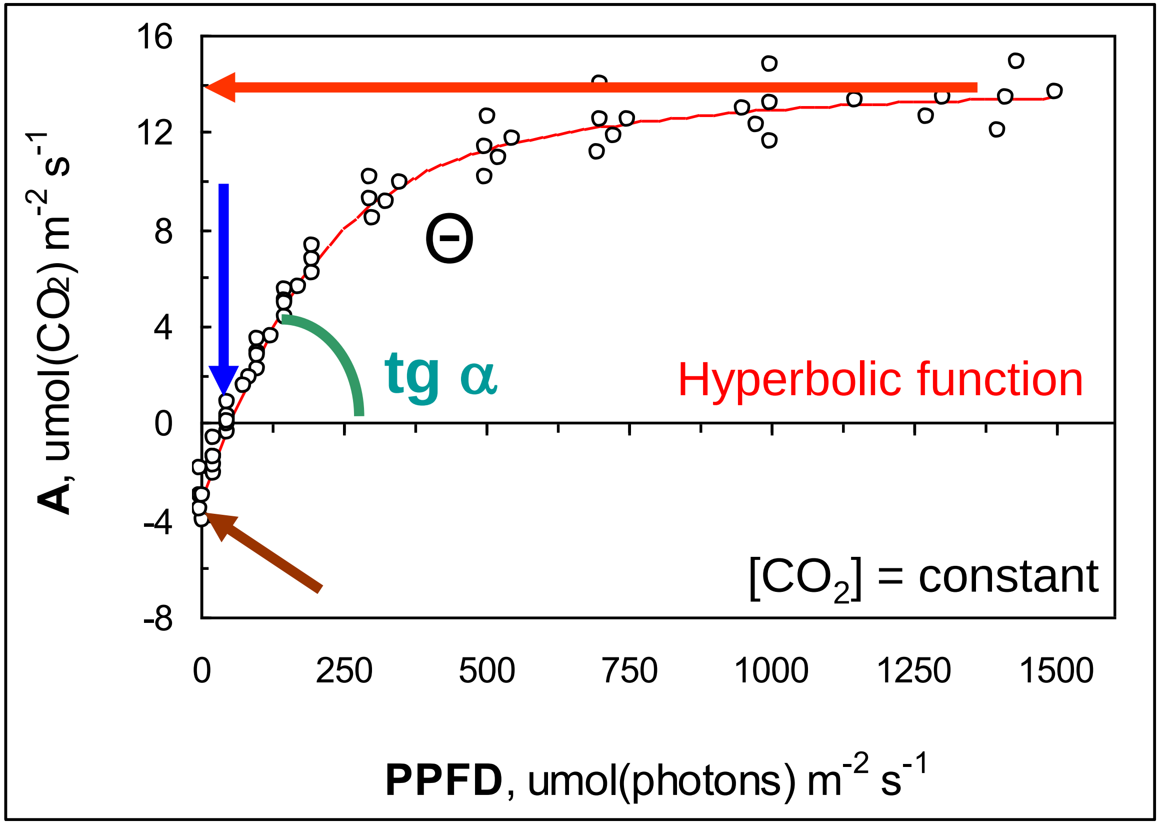
- Gas-exchange technique - exact, continual measurement of **gas** (CO_2, H_2O) **exchange** between plant/ecosystem and atmosphere
- Differences in H_2O a CO_2 concentrations **on input and output** from the assimilation chamber – infrared spectroscopy (**IRGA**)
  - Lambert-Beer law; $a_\lambda = 1\text{-}\exp(-\lambda.M.k_\lambda)$
- eddy-covariance technique
  - sufficient wind speed required for the development of turbulent air movement
  - sonic anemometer – movement air samples in 3D

GAZOMETRICKÉ METODY



- přesné, kontinuální měření **výměny plynů** (CO_2, O_2 a H_2O) mezi rostlinným pletivem a okolní atmosférou
- změny koncentrace H_2O a CO_2 se stanovují pomocí infračervené analýzy plynů (**IRGA**)
- Lambert-Beerův zákon
  - $\mathbf{a_\lambda = 1\text{-}exp(\text{-}l.M.k_\lambda)}$
- **rozsah**: individuální jehlice → celý ekosystém (b.l.m.)

CO_2 assimilation relates to light



R_D – dark respiration
$\mu mol(CO_2)\ m^{-2}\ s^{-1}$

Γ_I – compenzation irradiance
$\mu mol\ (photon)\ m^{-2}\ s^{-1}$

AQE (tg α) – (apparent) quantum efficiency
$mol(CO_2)\ mol^{-1}(photons)$

Θ – curvature (0 – 1)
dimensionless

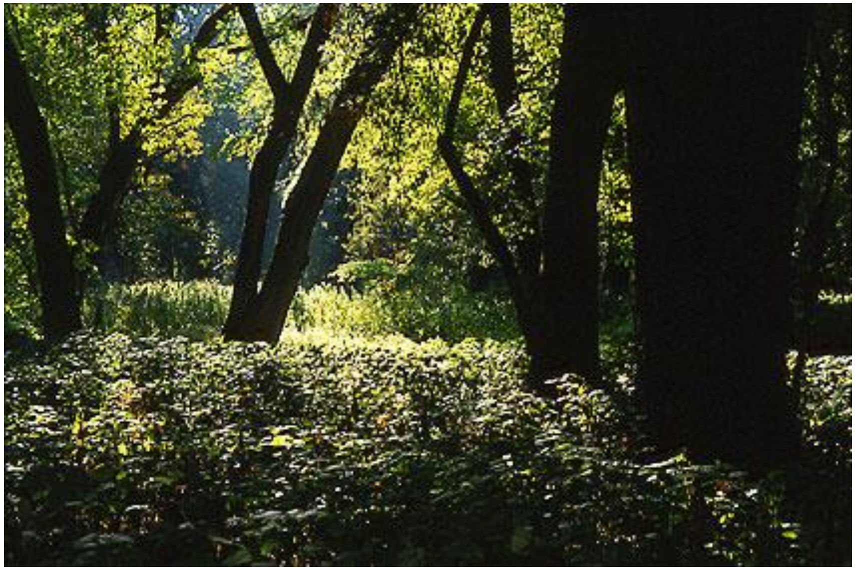
A_{max} – light-saturated rate of CO2 assimilation rate CO2
$\mu mol(CO_2)\ m^{-2}\ s^{-1}$

$$A = \frac{AQE \cdot I + A_{max} - \sqrt{(AQE \cdot I + A_{max})^2 - 4 \cdot AQE \cdot I \cdot \Theta \cdot A_{max}}}{2 \cdot \Theta} - R_D$$

Prioul JL, Chartier P (1977) Annals of Botany, 41, 789–900.

Light and plants

- traditionally – light intensity
  - μmol(photons) m^{-2} s^{-1}
  - photosynthetetically active radiation (PAR; 400-700 nm)
- in plant physiology (photosynthesis)
  - spectral composition
    - ratio UV : PAR : FR
  - **geometrical composition**
    - **direct x diffuse radiation**
  - time variability
    - dynamic light environment

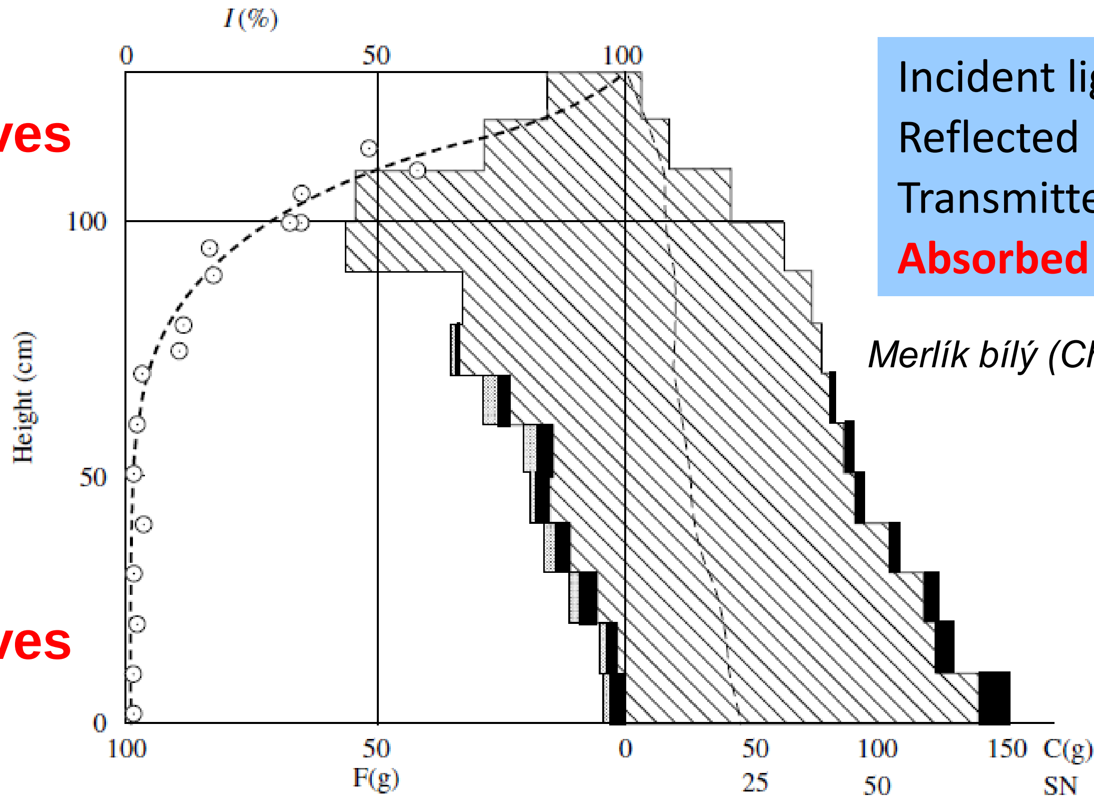


Vertical variability in light intensity

Monsi et Sakei (2005) Annals of Botany 95: 549–567

Sun leaves

Shade leaves



- Incident light
- Reflected light
- Transmitted light
- **Absorbed light**

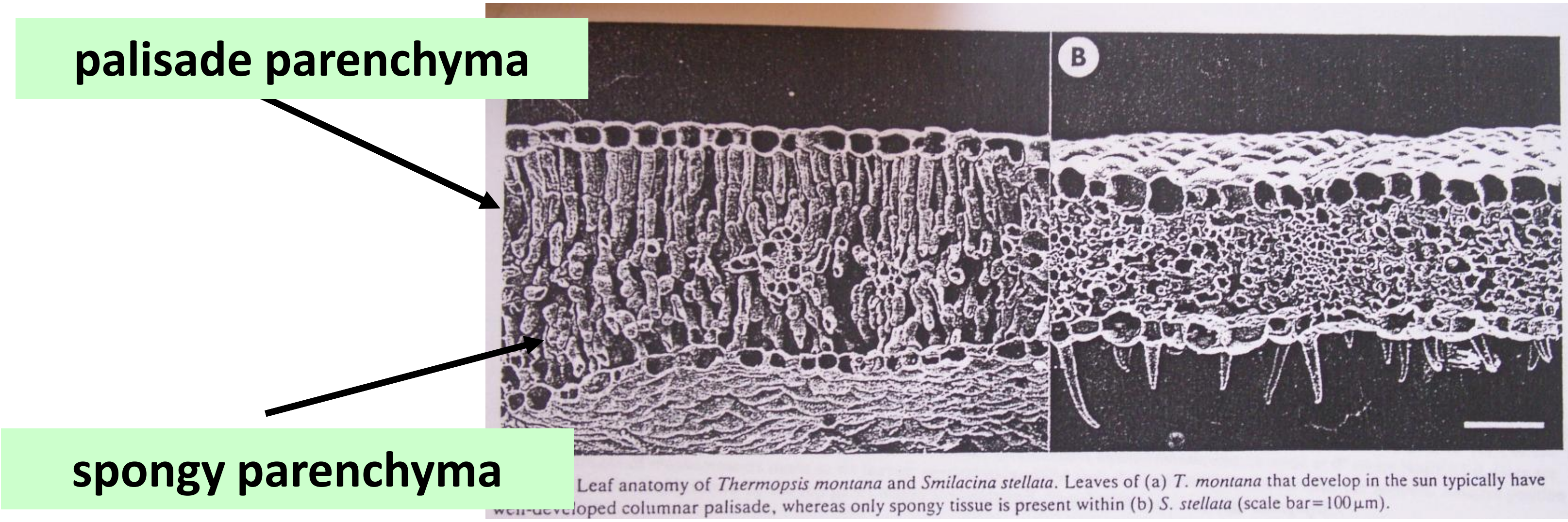
Merlík bílý (Chenopodium album)

- ↓UV:FAR
- ↓R:FR
- ↓B:R

$$I = I_0 e^{-k*LAI}$$

- I_0 – intenzita dopadající sluneční radiace
- I – intenzita prošlé (transmitované) sluneční radiace
- LAI – index listové plochy ($m^2\ m^{-2}$)
- k – extinkční koeficient
  - vlnová délka světla
  - geometrická kompozice

Sun- x shade-acclimated leaves



Vogelmann T.C. and G. Martin: PCE (1993) 16, 65-72

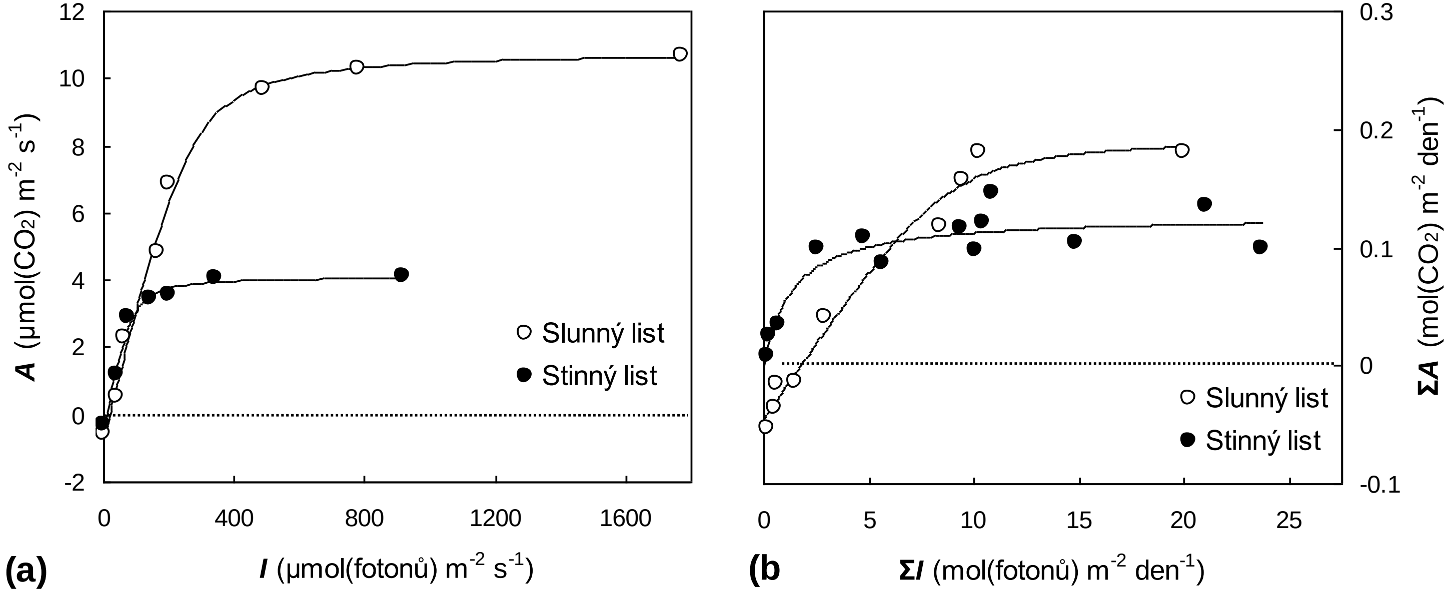
Shade-acclimated leaves:

- thinner leaves but larger area (higher specific leaf area – SLA; $cm^2\ g^{-1}$)
- lower number of stomata per unit leaf area (stomata are bigger)
- bigger chloroplasts with irregularly oriented granna
- higher chlorophyll and carotenoids content per unit mass (mg g_{DW}^{-1})
- lower conductance to CO2 in the mesophyll
- lower Nitrogen content – lower Rubisco content

investments into the protein structures connected with the efficient photochemical reactions (primary phase of photosynthesis)

Functional differences

Sims et Pearcy (1994) Plant, Cell and Environment, 17, 881–887.



Shade-acclimated leaves/plants:

- lower mitochondrial resp. (R_D)
- lower compensation irrad. (Γ_I)
- higher quantum effic. (AQE)
- lower light-saturated rate of CO_2 assimilation (A_{max})

Shade-acclimated leaves/plants:

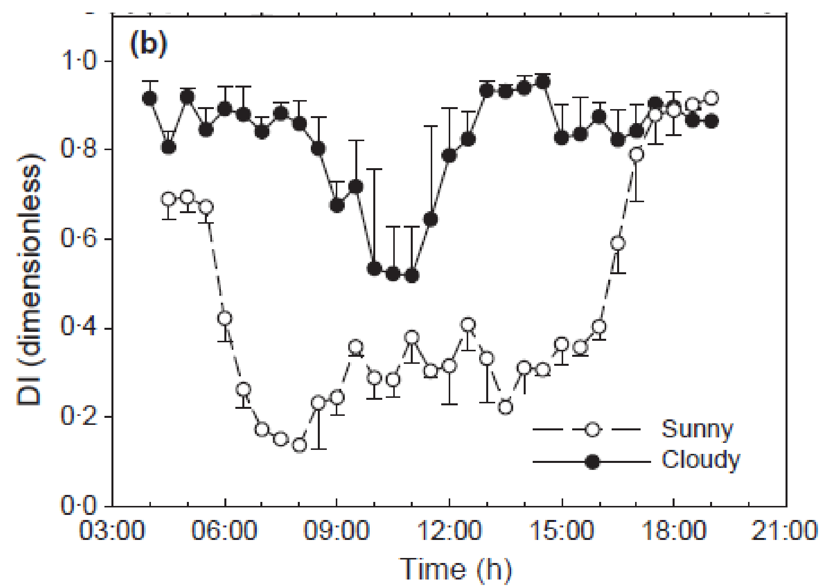
- higher sum of assimilated CO_2 (ΣA) at lower amount of daily irradiance (ΣI)
- more effective in dynamic light environment
  - faster induction, slower deactivation of photosynthesis

Assimilation of a canopy depends on its structure (sun/shade leaves ratio)

Incident solar radiation

- global radiation (Q)
- direct (I)
  - beam of parallel rays
  - passes through the atmosphere unaffected
- diffuse (isotropic; D)
  - scattering on particles in atmosphere
  - molecules (Rayleigh)
  - aerosols (Mie)
- diffuse index; DI = D/Q
  - clear (sunny) sky: 0.2 – 0.3
  - cloudy sky: 0.9 – 1.0

Solarimeter Kipp-Zonnen – measurement of diffuse radiation



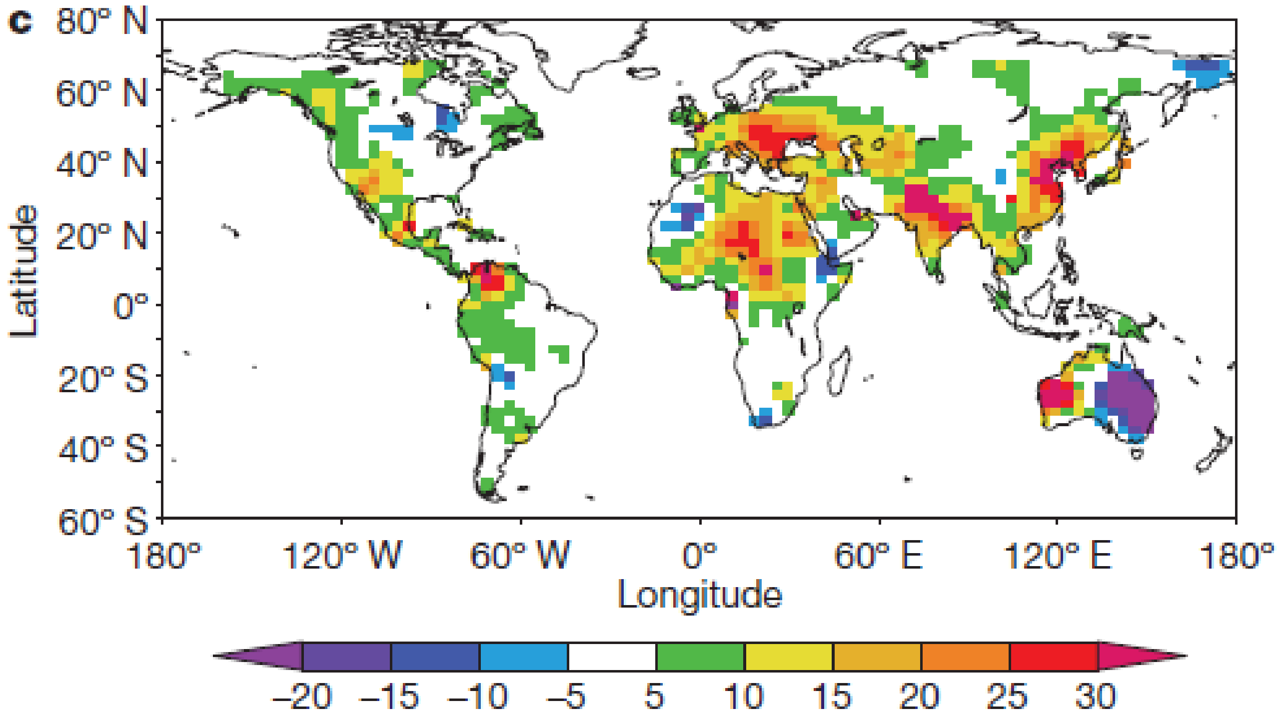
Daily course of DI; Urban et al. (2012) Func.Ecol. 26, 46-56.

Changes in incident radiation

- continuous reduction of solar radiation intensity (from 1960) - 0.51 ± 0.05 W m^{-2} per year
  - i.e. 2.7 % per decade
  - *dimming effect*
- reasons of global dimming
  - increase of air pollution (dust, aerosols)
  - increase of water vapour content
    - clouds ≈ increase in temperature
  - volcano eruption
  - stratospheric „geoengineering“
- increase in diffuse radiation

- *Stanhill G, Cohen S (2001) Agricultural and Forest Meteorology, 107, 255–278.*
- *Wild M (2009) Journal of Geophysical Research, 114, D00D16, doi:10.1029/2008JD011470.*
- *Berry ZC, Smith WK (2012) Agricultural and Forest Meteorology, 162, 27-34.*

Changes in diffuse radiation



- percentage change
  - proportion of diffuse radiation in the years 1950-1980
  - *Merkado L.M. et al.: Nature 458: 1014-1018, 2009.*

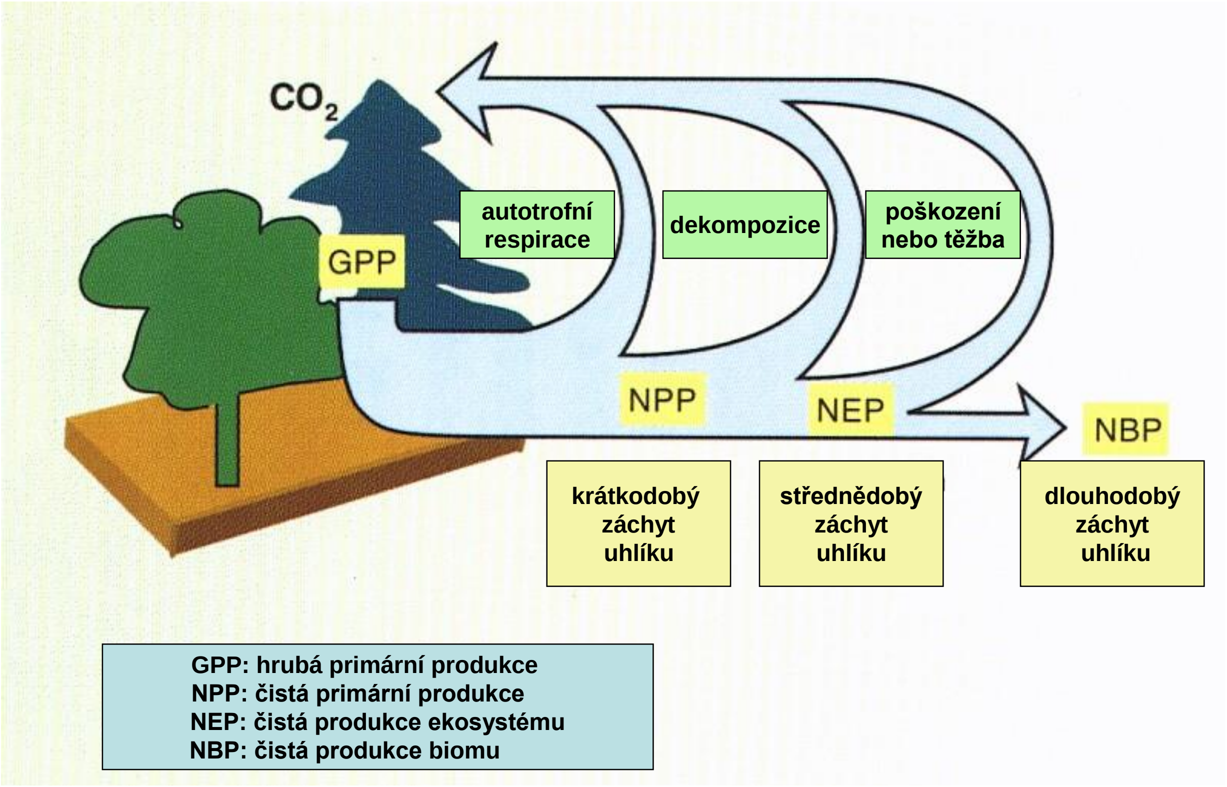
Impact of diffuse light on ecosystems

- eruption of Mt. Pinatubo volcano
  - Philippines, Manila (1991)
  - 20 Gt SO_2
  - decrease in global temperature by 0.5°C
  - increase in diffuse radiation by 50%

- atmospheric CO_2 concentration
  - slow increase between 1992 and 1993
  - carbon stock up to 2Gt(C) $year^{-1}$
  - increase in biomass production of tropical ecosystems

- *Farquhar GD Roderick ML (2003) Science 299: 1997–1998, 2003.*
- *Gu LH, Baldocchi DD, Wofsy SC et al. (2003) Science, 299, 2035–2038.*

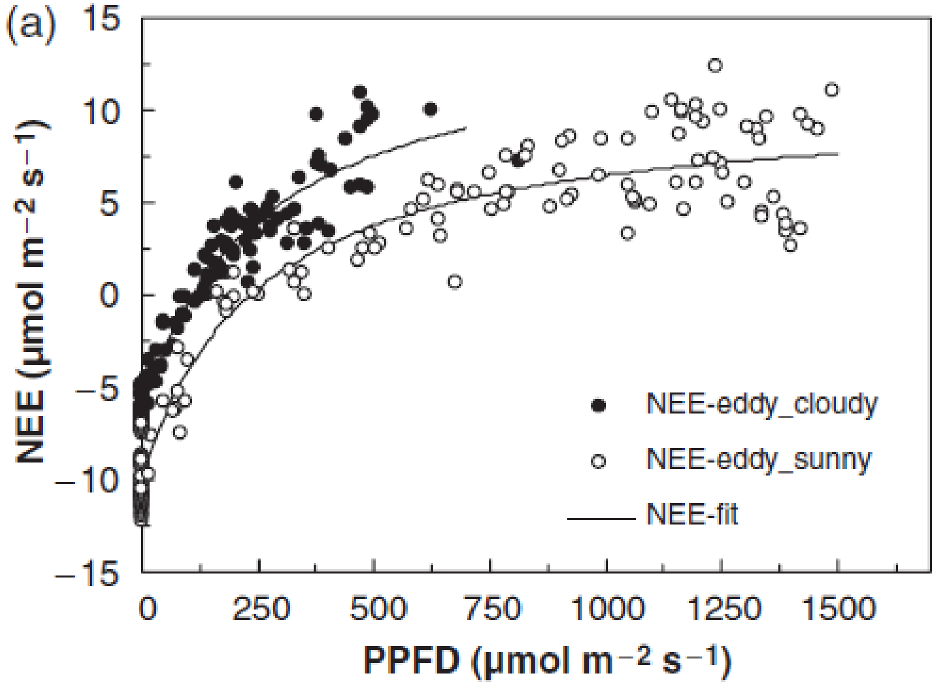
Carbon cycle in ecosystems



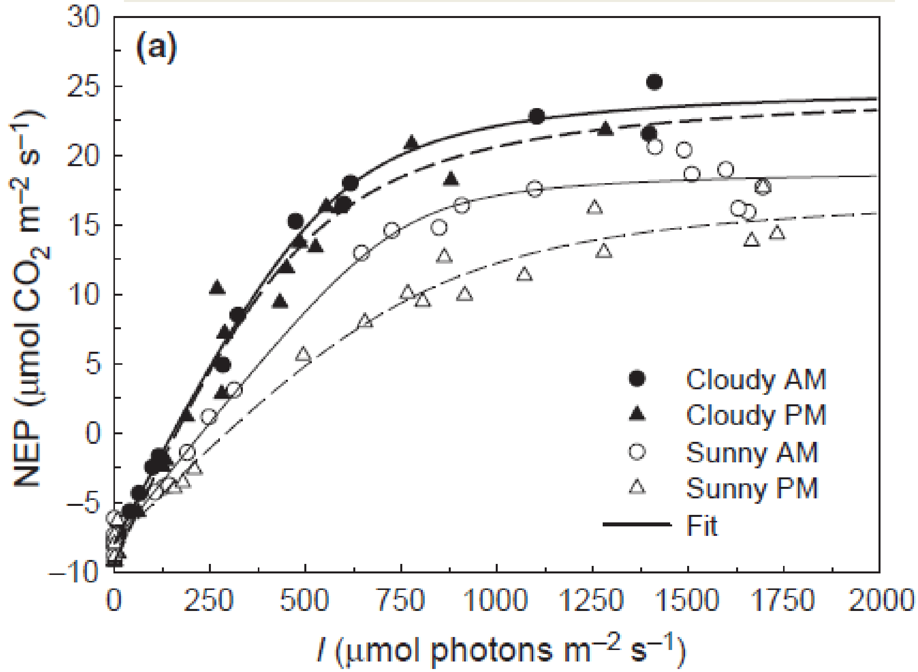
- reasons of increased (stimulated) C sequestration
  - (1) increase of photosynthesis rate **(C uptake)**
  - (2) reduction of respiration and decomposition **(C release)**

C assimilation under clear x cloudy sky

Urban O. et al.: GCB 13: 157-168, 2007.



Urban O. et al.: Func.Ecol. 26: 46-55, 2012



- cloudy sky conditions - predominant diffuse radiation (DI > 0.8),
- NEE was relatively higher compared to sunny days,
  - NEE was higher up to 150% at irradiance 400 μmol m^{-2} s^{-1},
  - AQE higher by 20%,
  - Γ_I lower by 50% $\Rightarrow$ **better use of the low light intensities**.
- hysteretic response curves of assimilation in sunny days

Experimental site – Bílý Kříž

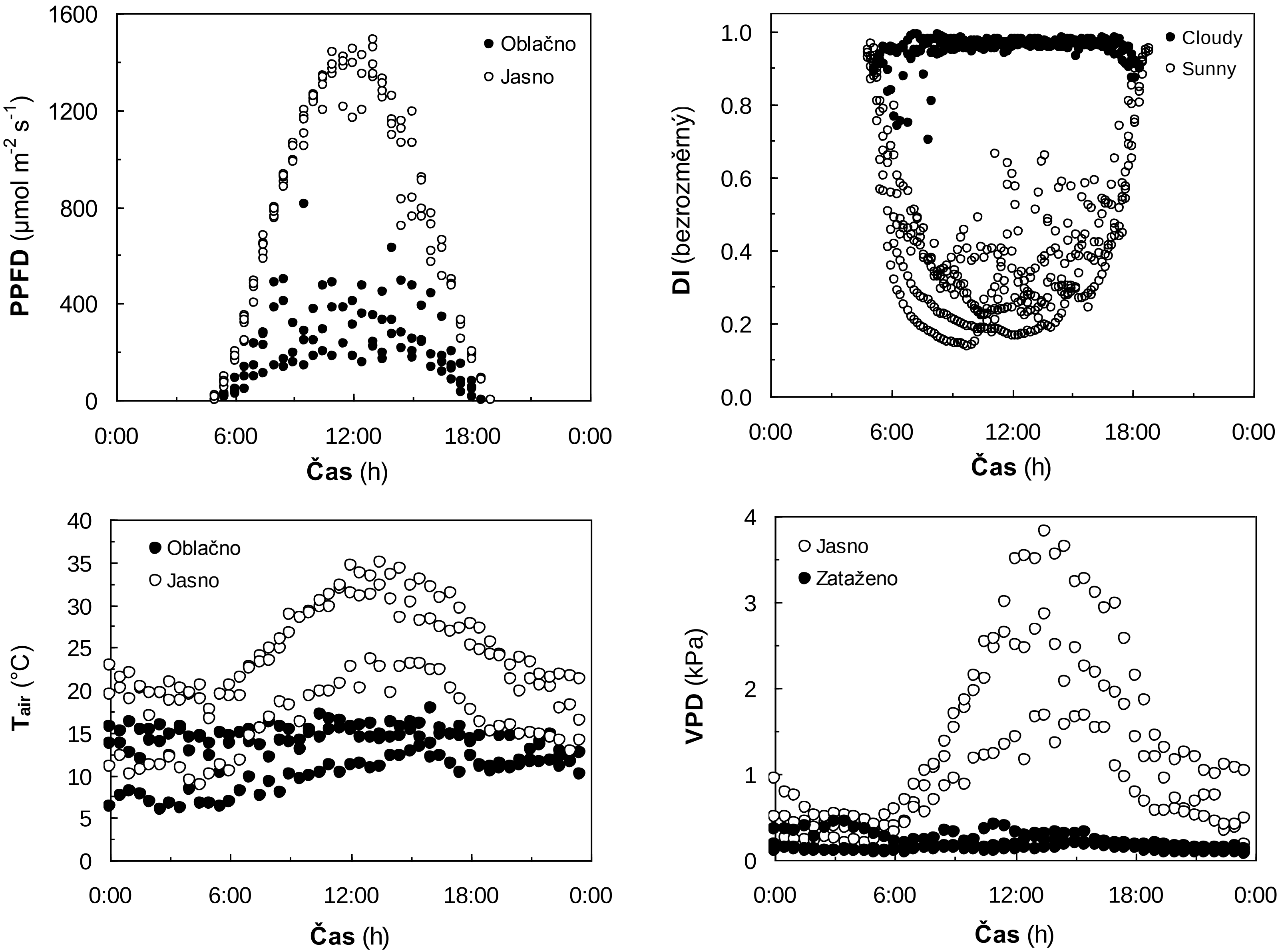
Experimental forest

- Beskydy Mts. (Czech Republic)
- 49°33´ N, 18°32´ E
- slope 11-16° SSW orientation
- Norway spruce monoculture
- 30-year-old; 1428 trees ha^{-1}
- LAI 9.5 ± 0.2 m^2 m^{-2}
- trees height 13.4 ± 0.1 m
- stem diameter 15.8 ± 0.2 cm

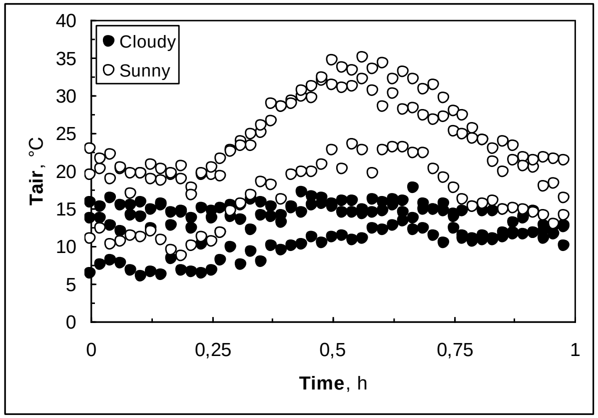
foot-print area: 0.5km^2

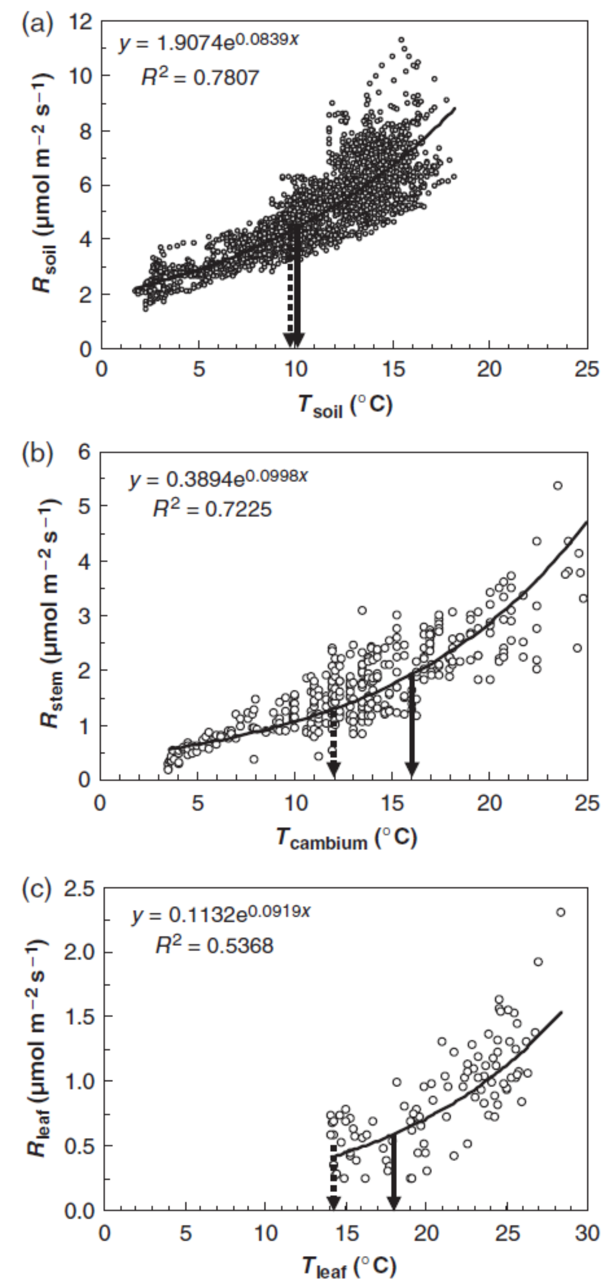
What are the reasons of higher NEE?

Microclimatic conditions



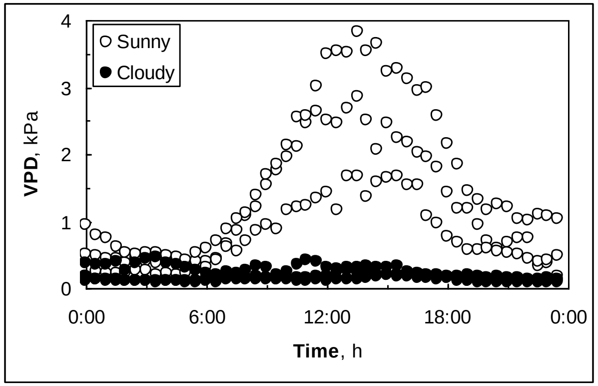
I. reduced ecosystem respiration – lower temperature



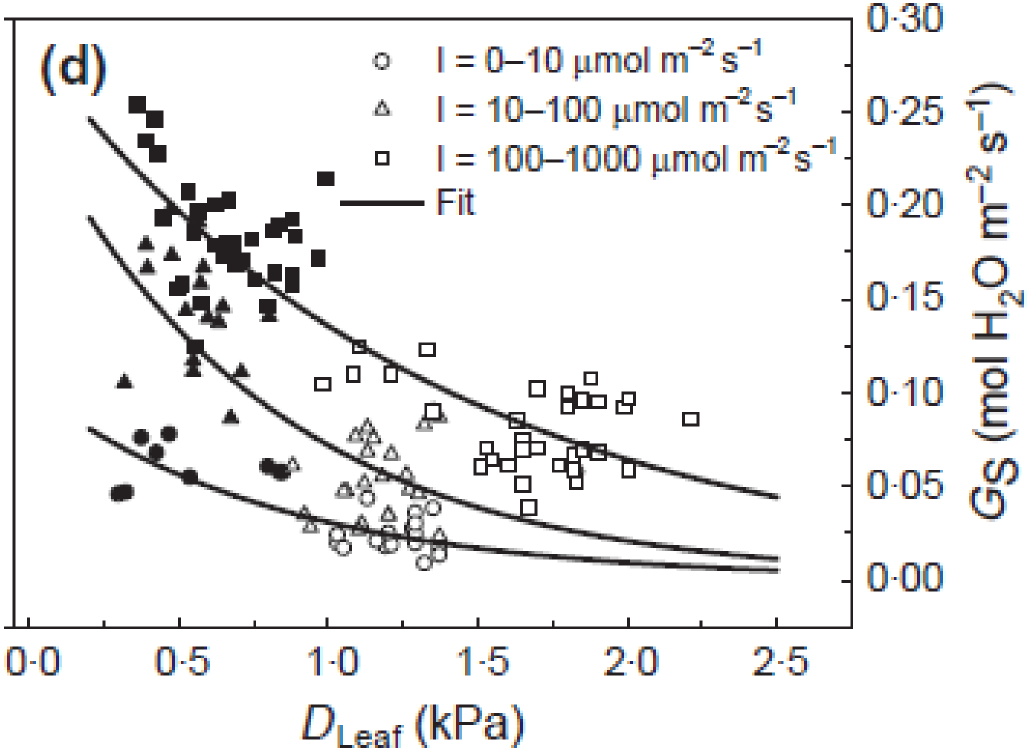


- respiration of individual ecosystem parts correlates with temperature
  - chamber measurements
  - SAMTOC/SAMTOL
- **exponential relationship**
- **dominant CO_2 source – soil – soil temperature is stable in short-terms**
  - **relationship with soil water content**

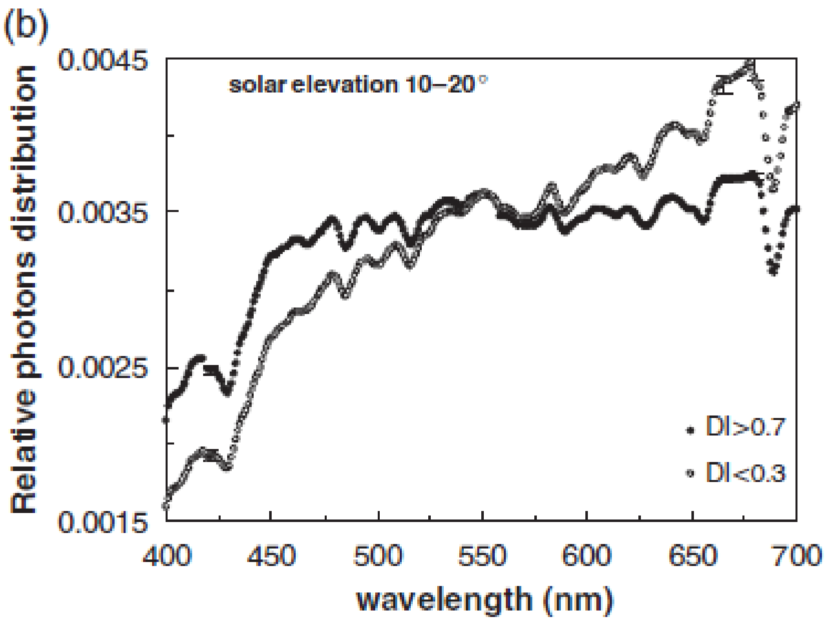
II. low vapour pressure deficit

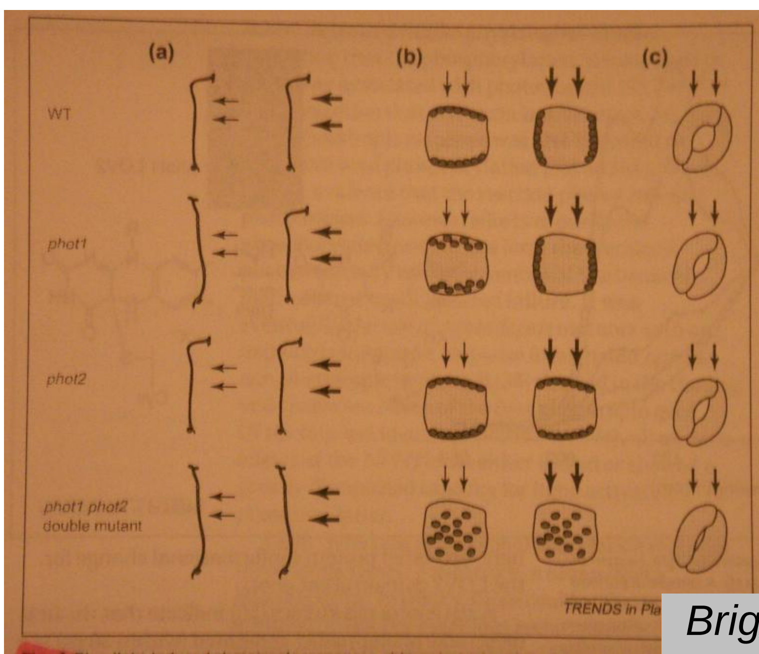


- high VPD (D) values lead to closure of stomata and reduction of stomatal conductance to CO_2 diffusion
- **reduction of intercellular CO_2 concentration**



III. changes in spectral composion of light

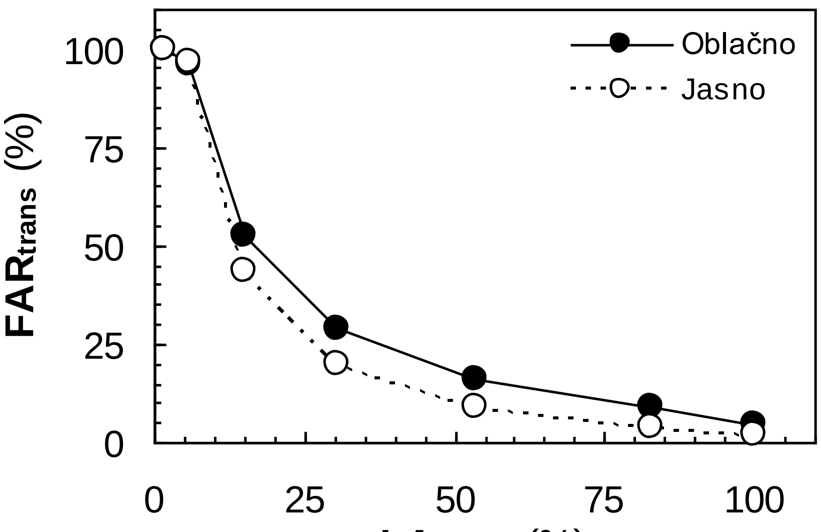




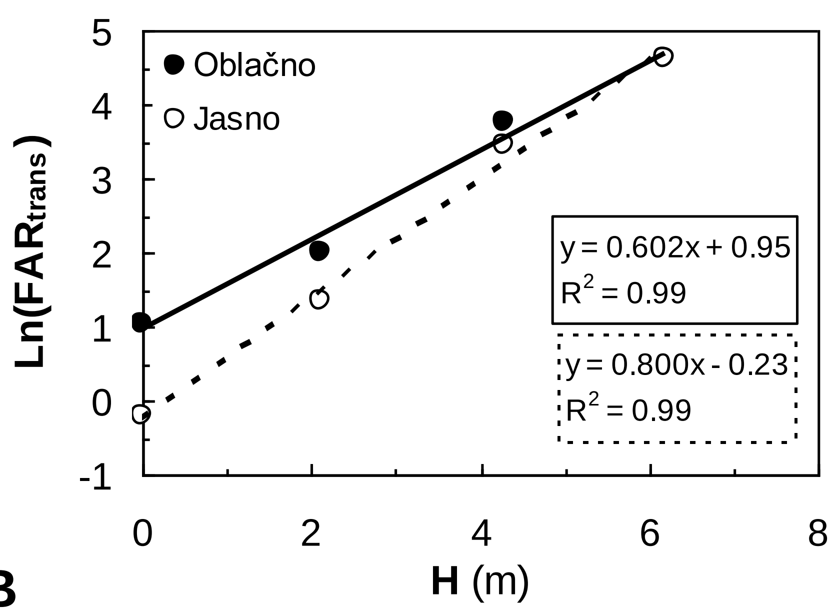
- increase in relative representation of blue light λ ≈ 450-500 nm
  - increase of B/R ratio
- absorption maxima for chlorophylls and carotenoids
- facilitates opening of stomata ⇒ increase of intercellular [CO_2] concentration
- optimization of photosynthesis due to phototropins (photoreceptors)
  - absorptance in UV-A and blue light region of solar spectrum
  - phototropism
  - migration of chloroplasts
  - opening of stomatal aperture
- *generally, minor effect*

Briggs and Christie: Trends in Plant Science 7: 204- 210, 2002

IV. effective penetration of diffuse radiation



A



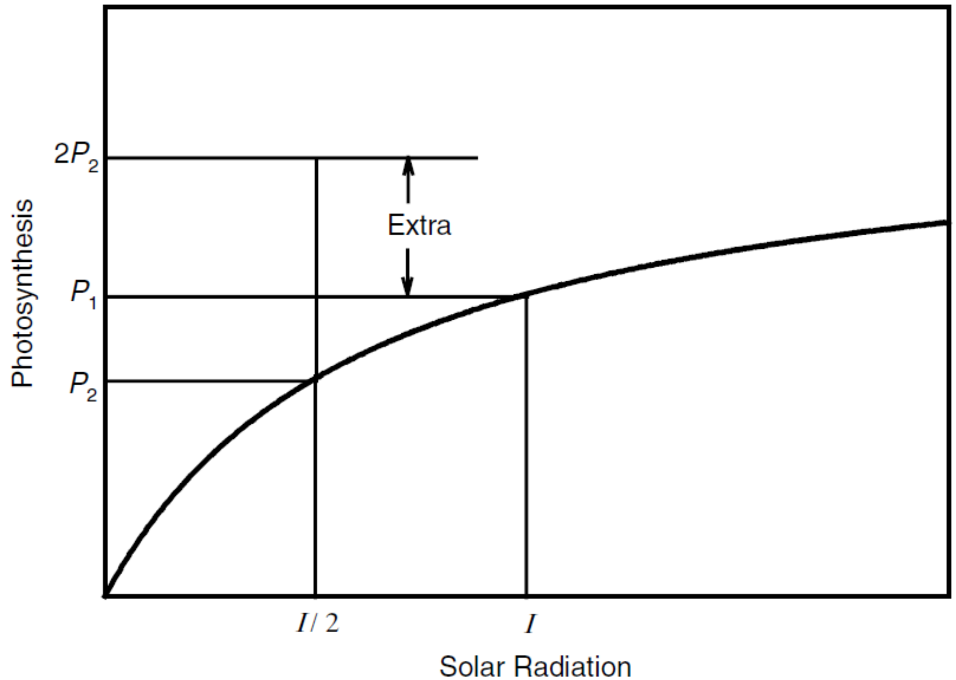
B

- main reason of higher NEE
- diffuse radiation penetrates better to lower parts of the canopy
- lower coefficients of extinction
  - ≈ 25% (c. 0.6 x 0.8)
- bigger part of leaf area is productive (photosynthetically active)
  - 30 – 40 μmol m^{-2} s^{-1} (Γ_l)
- during sunny days up to ≈ 70% LA may be a potential source of CO_2

Fig. 9A,B: Relationship between cumulative leaf area (LA_{cumul}) and transmitted photosynthetic photon flux density ($PPFD_{trans}$) estimated during sunny (empty circles) and cloudy (full circles) days (**A**). Slopes of linear relationship between logarithmic $PPFD_{trans}$ and canopy height (*H*) represent the extinction coefficients (small graph). Calculation was done on the basis of PPFD transmittance measurements and foliage distribution (Pokorný *et al.*, 2004) within the canopy. Distribution of solar equivalent leaf area (SELA) within vertical canopy profile (**B**). SELA was calculated for incident PPFD 400 μmol m^{-2} s^{-1}. Empty columns, sunny days; Filled columns, cloudy days.

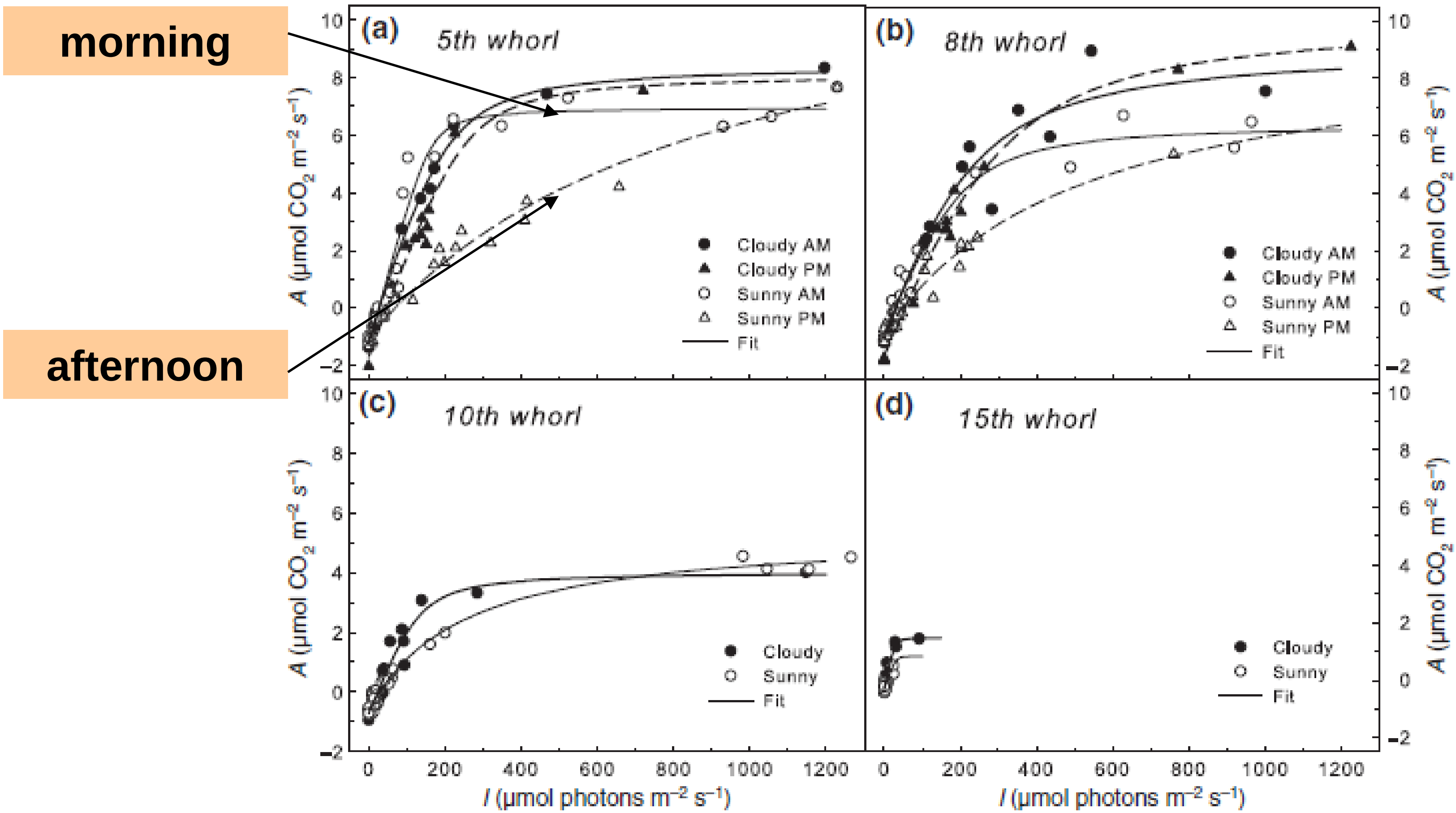
Even distribution of solar irradiance is better

Gu L. et al. (2003) Science, 299, 2035–2038.



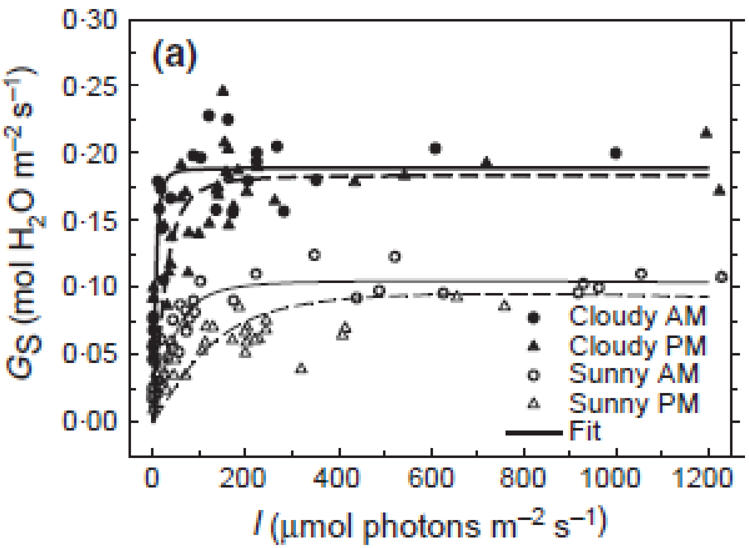
- result of saturation shape of light response curve
- for forest it is better when:
  - two leaves are half-illuminated than
  - one over illuminated and second exposed to dark

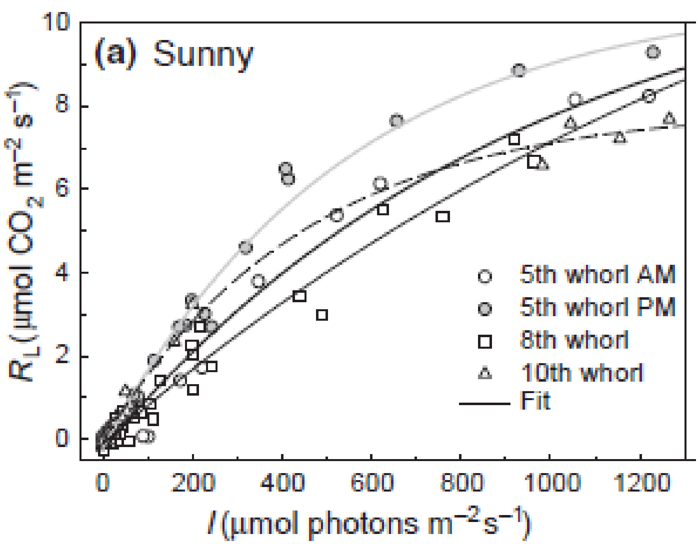
Distribution of assimilation activity



- light response curve of CO_2 assimilation
- hysteresis shape of LRC in upper layer under clear sky conditions
  - negative (lower A values in the afternoon hours)

Reasons of hysteresis response



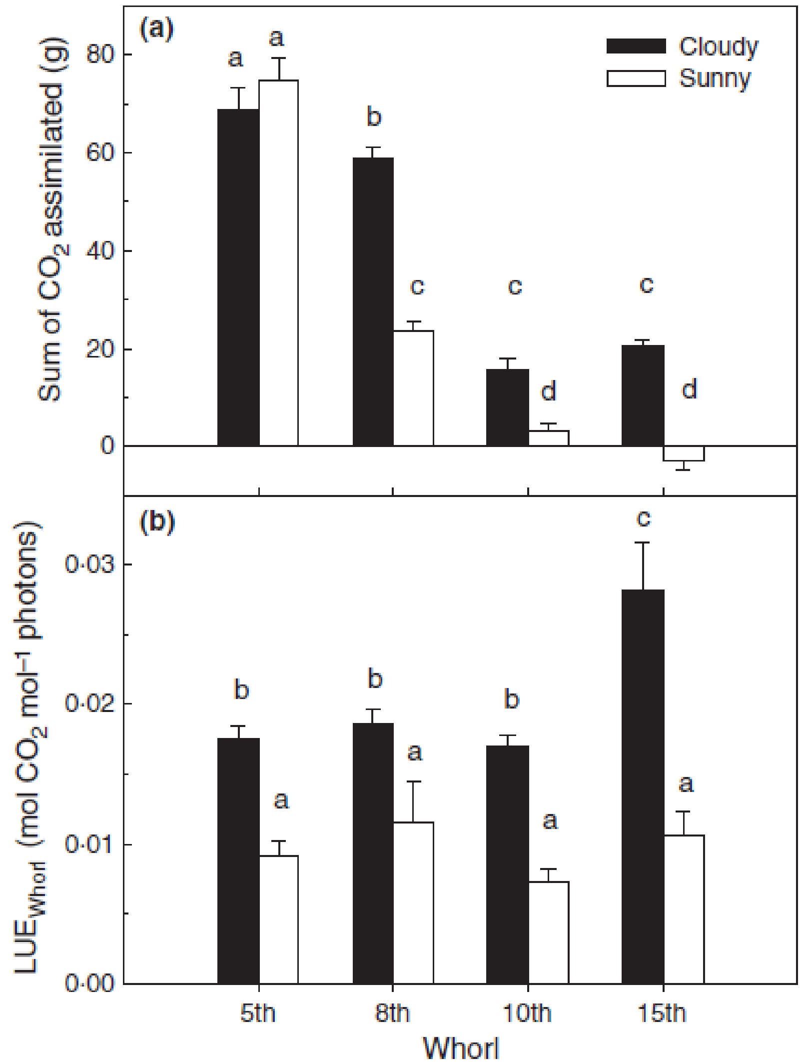


- closure of stomata in afternoon hours due to high VPD
- reduction of intercellular (chloroplastic) CO_2 concentration
  - increase of O_2/CO_2
  - higher leaf temperature in afternoon
- → higher C losses due to photorespiration (*minor*)
- → reduced assimilation rate
- photoinhibition

Modelling of C assimilation

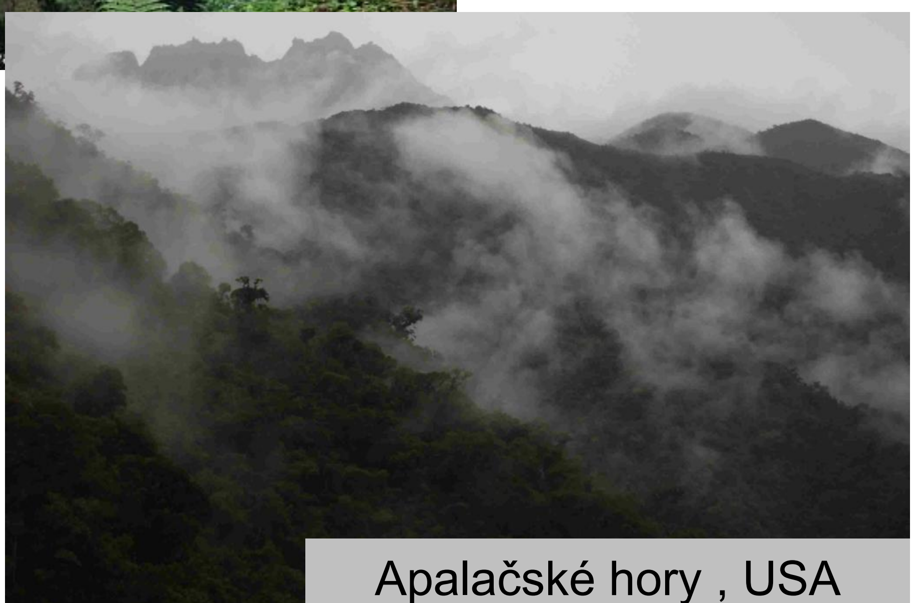
$$A = \frac{AQE \cdot I + A_{max} - \sqrt{(AQE \cdot I + A_{max})^2 - 4 \cdot AQE \cdot I \cdot \Theta \cdot A_{max}}}{2 \cdot \Theta} - R_D$$

- modelling – parameters of LRCs in individual canopy layers
- detailed measurement of radiation regime (CANFIB)
- during cloudy sky conditions
  - lower parts of canopy have positive C balance (24h)
  - higher light use efficiency (LEU)



Effect on forest structure

Deštný prales, Guatemala



Apalačské hory , USA

- diffuse radiation is key for maintenance of shade leaves
- forest canopies are adapted to the most common light conditions that they receive
  - sites where conditions are predominantly cloudy – forests with high LAI
- MCF – mountain cloud forests
  - temperate zone
- endemic tree species
  - *Abies fraseri*

Take Home Message

- efficiency CO_2 assimilation is higher under cloudy sky conditions (coniferous/broadleaf forests)
- reasons
  - (1) favourable microclimatic conditions under cloudy days
    - reduced temperatures lead to lower respiration,
    - lower VPD results in lower stomatal conductance,
    - blue-light effect
  - (2) effective penetration of diffuse light into lower depths of the canopy and more even distribution of solar radiation between sun and shade leaves.
- during cloudy sky conditions the lower parts of canopy have positive C balance

Refferences

1. Brodersen C.R. et al.: A new paradigm in leaf-level photosynthesis: direct and diffuse lights are not equal. Plant Cell Environ. 31, 159-164, 2008.
2. Farquhar GD Roderick ML: Pinatubo, diffuse light, and the carbon cycle. Science 299: 1997–1998, 2003.
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4. Christie JM, Briggs WR: Blue light sensing in higher plants. Journal of Biological Chemistry 276 (15): 11457-11460, 2001.
5. Merkado L.M. et al.: Impact of changes in diffuse radiation on the global land carbon sink. Nature 458: 1014-1018, 2009.
6. Stanhill G, Cohen S: Global dimming: a review of the evidence for a widespread and significant reduction in global radiation with discussion of its probable causes and possible agricultural consequences. Agricultural and Forest Meteorology, 107, 255–278, 2001.
7. Urban O., Janouš D., Acosta M., et al.: Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. Global Change Biology 13: 157-168, 2007.
8. Urban O., Klem K., Ač., et al.: Impact of clear and cloudy sky conditions on the vertical distribution of photosynthetic CO2 uptake within a spruce canopy. Functional Ecology 26: 46–55, 2012.
9. Wild M.: Global dimming and brightening: A review. Journal of Geophysical Research, 114, D00D16, 2009.

Thank You for Attention!

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Asimilace CO_2 na úrovni listu

- C.R. Brodersen et al.: Plant Cell Environ. (2008) 31, 159-164: **A new paradigm in leaf-level photosynthesis: direct and diffuse lights are not equal**
- fotosyntéza **slunných listů** (C_3 i C_4 rostlin) může být o 10-15% vyšší za přímého radiace v porovnání s radiací difúzní téže intenzity
- **stinné listy** obvykle nevykazují rozdíl mezi při osvětlení přímou a difúzní radiací

Slunný

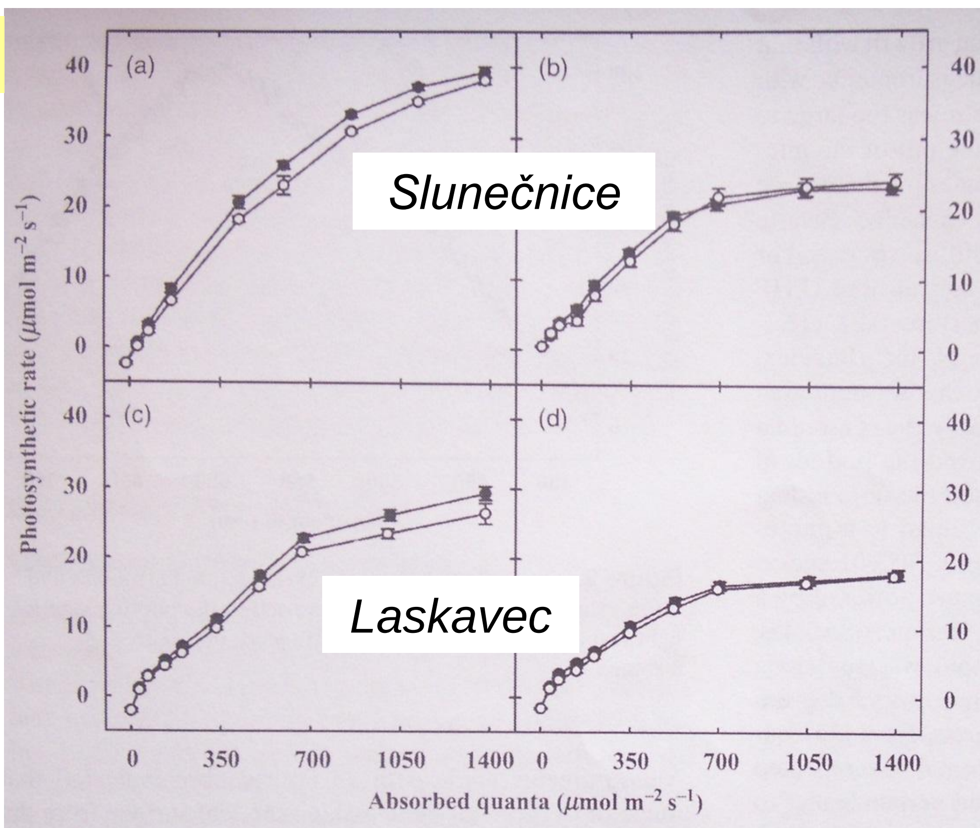

Figure 3. Photosynthetic response to direct and diffuse light for (a) *Helianthus annuus* under direct (closed symbols) and diffuse (open symbols) light grown with supplemental lighting; (b) *H. annuus* under direct (closed symbols) and diffuse (open symbols) light grown without supplemental lighting; (c) *Amaranthus retroflexus* under direct (closed symbols) and diffuse (open symbols) light grown with supplemental lighting; (d) *A. retroflexus* under direct (closed symbols) and diffuse (open symbols) light grown without supplemental lighting. All error bars – SE, $n = 6$.

Proč?

Vogelmann T.C. and G. Martin: PCE (1993) 16, 65-72

- difúzní záření proniká hlouběji do prostoru listu než záření přímé
- kolimovaný zdroj: gradient strmější u listů s houbovým parenchymem,
- difúzní zdroj: gradienty obou typů listů byly obdobné

- cylindrické palisádové buňky napomáhají průniku rovnoběžných paprsků
- utváření palisádového parenchymu je úměrné množství přímé sluneční radiace

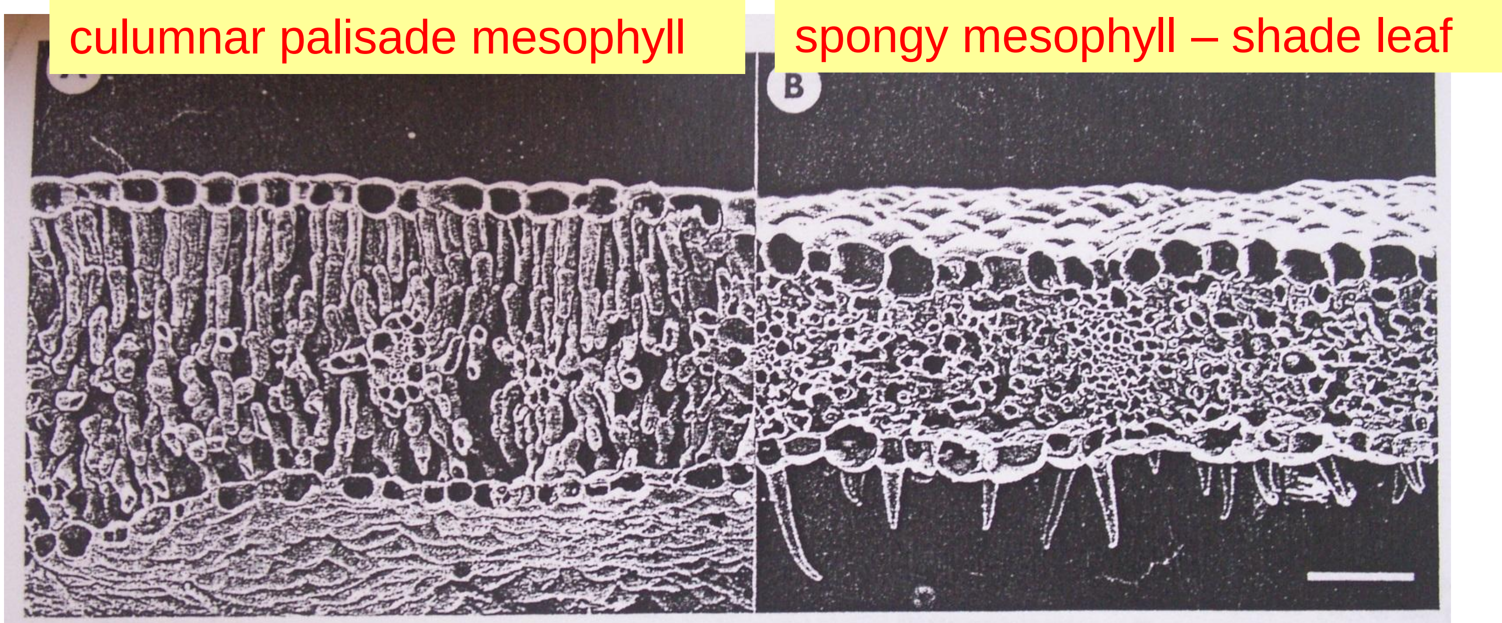

Figure 2. Leaf anatomy of *Thermopsis montana* and *Smilacina stellata*. Leaves of (a) *T. montana* that develop in the sun typically have well-developed columnar palisade, whereas only spongy tissue is present within (b) *S. stellata* (scale bar=100 µm).

Další vlivy difúzního záření

- efektivitu využití vody vzrůstá s rostoucím podílem difúzní radiace
  - WUE = okamžitá rychlosti fotosyntézy / evapotranspirace
  - fotosyntéza porostů reaguje na působení difúzní radiace výrazněji, než jejich transpirace
- vliv difúzní radiace na produkci isoprenu
  - isopren = nenasycený uhlovodík emitovaný různými druhy dřevin temperátní zóny v průběhu metabolické fixace uhlíku (Fuentes *a kol.* 2000)
  - isopren přispívá k produkci ozónu (v troposféře silně toxický)
  - za růstových podmínek, kdy převládá difúzní radiace, dochází k poklesu emise těchto volatilních látek
  - příčina: snížená intenzita globálního záření za oblačných dnů vede k ochlazování aktivního povrchu ekosystému, což následně vede ke snížení biologické produkce isoprenu dřevinami

- *Knohl A, Baldocchi DD (2008) Effects of diffuse radiation on canopy gas exchange processes in a forest ecosystem. Journal of Geochemical Research, 113, G02023.*