Primary production

INVESTICE DO ROZVOJE VZDĚLÁVÁNÍ

Tento projekt je spolufinancován Evropským sociálním fondem a Státním rozpočtem ČR InoBio – CZ.1.07/2.2.00/28.0018

Lesson Content

- Solar energy x water in forest ecosystem
- Solar radiation x energy transfer in forest ecosystem
- Carbon input to the ecosytem and photosynthesis
- Photosynthesis and respiration
- Biomass a nd plant production
- Global climatic change –principles and importance

Premises

- The hydrologic cycle, driven by solar energy, is the master cycle that drives all other biogeochemical cycles
- Water and solar energy are essential for life. Their uneven distribution across Earth´s surface account for the large-scale patterns of ecosystem structure and functioning and are central to an understanding of ecosystem dynamics
- Water and energy cycles are so tightly intertwined that they cannot be treated separately
- **The aim of the lesson** is to describe ecosystem energy budgets and other controls over the hydrologic cycle

Solar energy and water

- Solar energy drives the hydrologic cycle through vertical transfer of water from Earth to the atmosphere via **evapotranspiration**
- **Evapotranspiration** is the sum of surface evaporation and the loss of water from plant leaves – **transpiration**
- Evapotranspiration acounts for 80% of turbulent energy transfer (i.e., latent plus sensibile heat flux) from Earth to the atmosphere
- The hydrologic cycle also controls global biogeochemical cycles by dissolving nutrients and transfering them within and among ecosystems

cont.

- Water enters terrestrial ecosystem as **precipitation** and leaves as **evapotranspiratio**n and **runoff**
- **Available wate**r in the soil moves along a film of liquid water through soil-plant.atmosphere continuum in response to a **gradient in water potential** (driven by **transpiration**=evaporation from cell surface in leaves)
- Evapotranspiration from canopies depends on: (1) the **net radiation** and VPD= **vapor pressure deficit** in the air) and (**2) aerodynamic conductance** of the canopy and **stomatal conductance** of leaves, (3) **soil evaporation**
- **Runoff** is the water that draines from the ecosystem when precipitation exceeds evapotranspiration plus any increase in water storage

Solar radiation x energy transfer

- Net radiation is the balance between incoming and outcoming short and longwave radiation
- Ecosystems affect net radiation primarily through **albedo (shortwave reflectance)**
- **Albedo** is the reflectance of individual leaves and other surfaces (canopy ..)
- Most **absorbed energy is released** to the atmosphere as **latent heat**
- **flux** (evapotranspiration) and **sensibile heat flux**
- **Latent heat flux** *cools* the surface and transfers water vapor to the atmosphere
- **Sensibile heat flux** *warms* surface air
- The ratio of sensibile to latent heat flux determines the strenth of the coupling of the water cycle to the energy budget

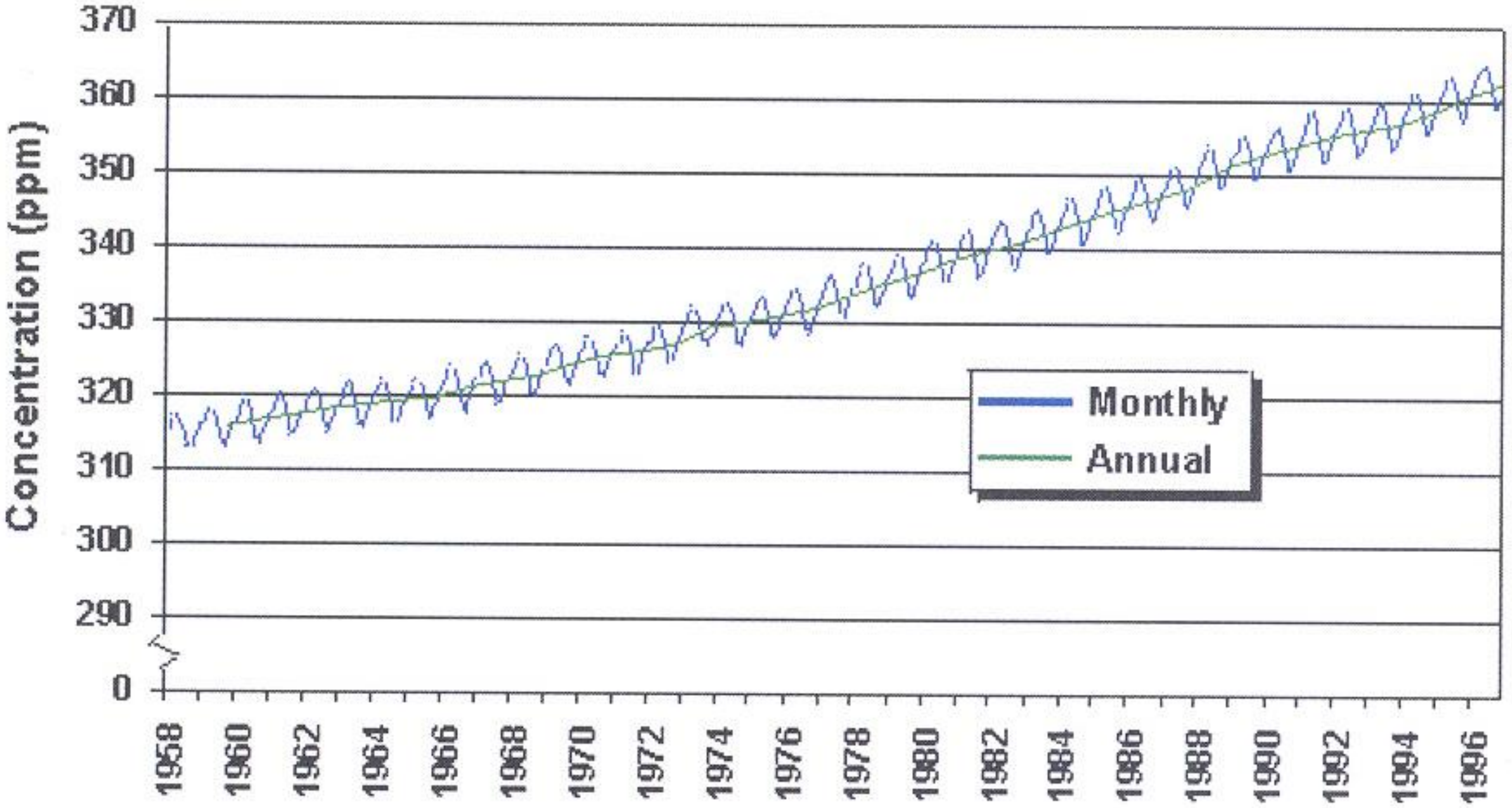
Water movements within ecosystems

- In closed canopy forests are the precipitation *captured* in canopy = **interception** and then are evaporated
- Canopy interception is the fractionthat does not reach the ground – it is commonly about **10-20%** for close close-canopy ecosystem
- Rest of precipitation rich soil surface as **throughfall** or **stemflow**
- **Canopy interception** reduces water input to soil, especially from light rains, also change chemical composition of water (dry deposition). Very often nitrogen increases.
- In contrast **fogs** are responsible to increase inputs water to the soil in mountains area
- **Water balance** of the ecosystem will be will be subject of nexte lesson (see also Chapin F.S. ,2011)

Carbon input to the ecosytem and photosynthesis

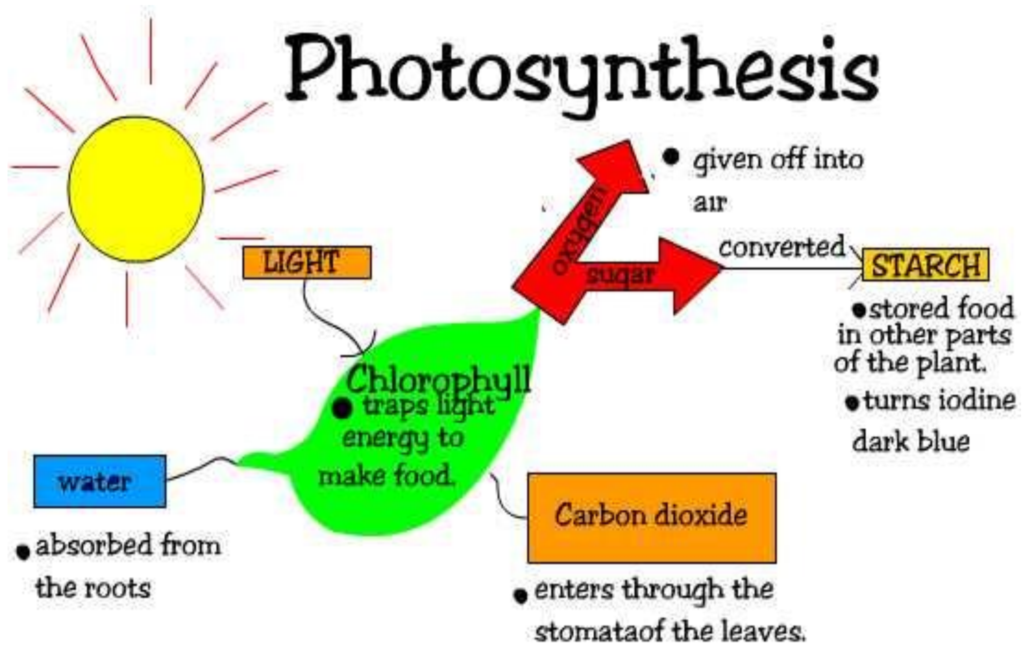
- Most carbon enters the terrestrial ecosystems through **photosynthesis** as CO_2
- **CO_2 and water** exchange through pores (stomata) in the leaf surface
- Open **stomata** maximize carbon gain and productivity when water is transpirated (water lost)
- Partial closure of **stomata** under dry conditions reduces carbon gain but increases the photosynthesis efficiency
- Photosynthesis is **light-harvesting reactions** in which light energy is transformed into chemical energy and CO_2 is convert to sugars.
- The enzymes that carry out these reactions account for about half of the **nitrogen** in photosynthetic cells
- The main environmental facors that explain carbon gain are the **temperature** (lenght of vegetation time) and the soil resources (**water and nutrient**s)
- Environmental stresses (lack of water, extreme temperatures and pollutants reduce the photosynthesis efficiency
- Photosnthesis is primarily subject of Ecophisiology (2nd semester)

Monthly and annual atmospheric concentrations of carbon dioxide (CO_2, ppm) Mauna Loa station (1958-1996)

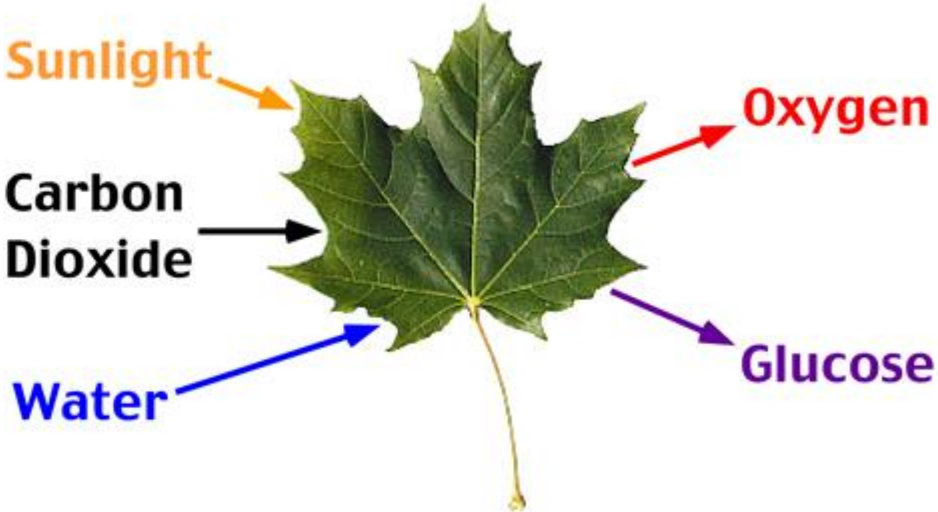


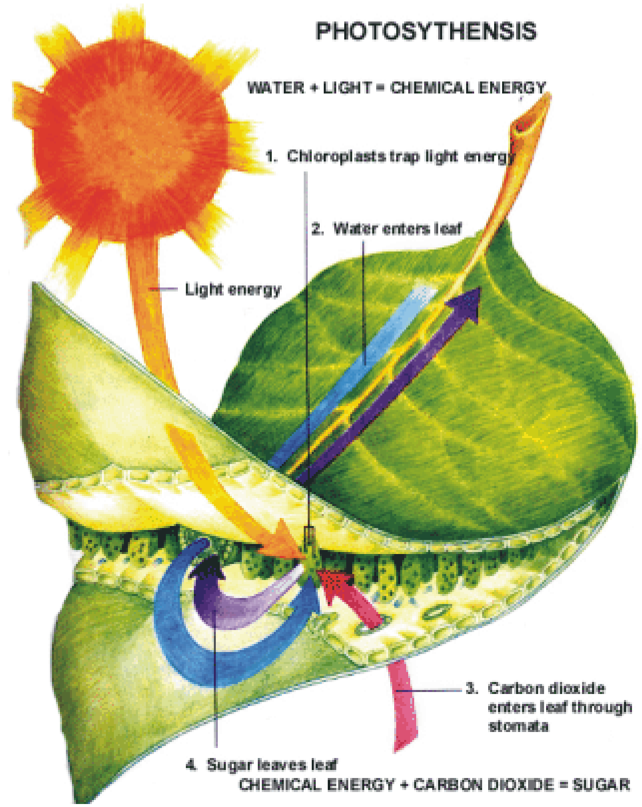
Photosynthesis

- **Photosynthesis** is the process by which plants convert atmospheric CO_2 to carbon products
- Gross (GP) and net photosynthesis (NP)



Photosynthesis



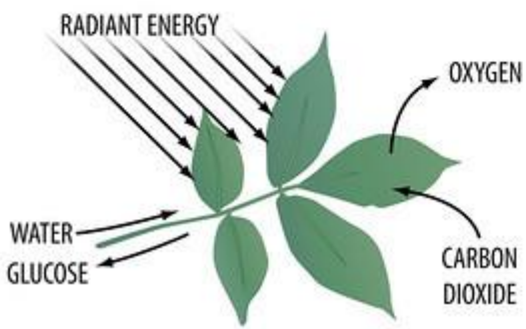


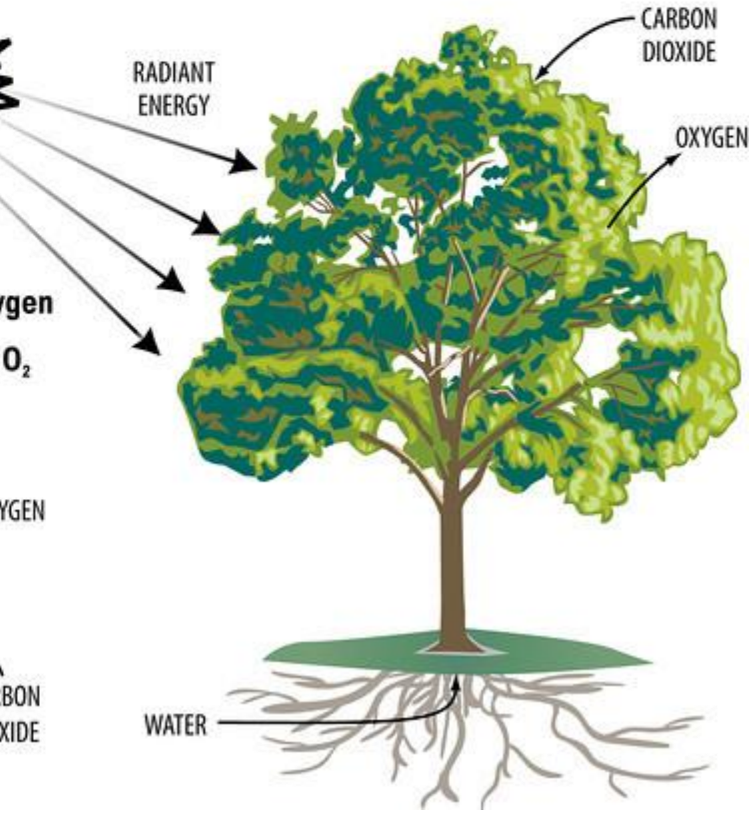
Photosynthesis

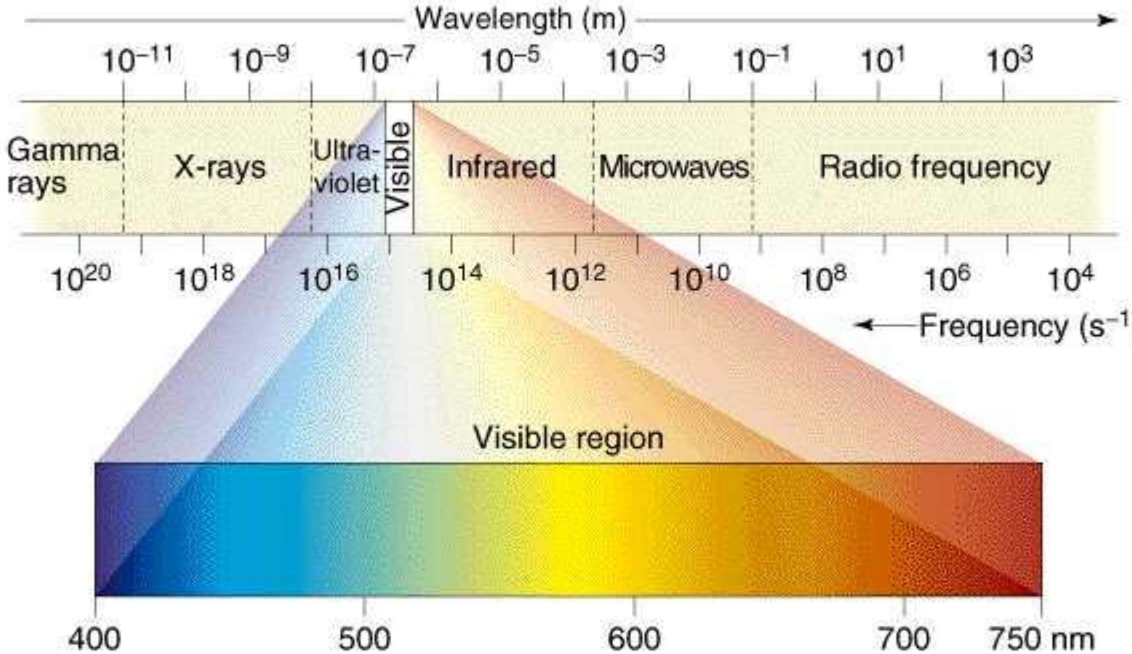
In the process of photosynthesis, plants convert radiant energy from the sun into chemical energy in the form of glucose (or sugar).

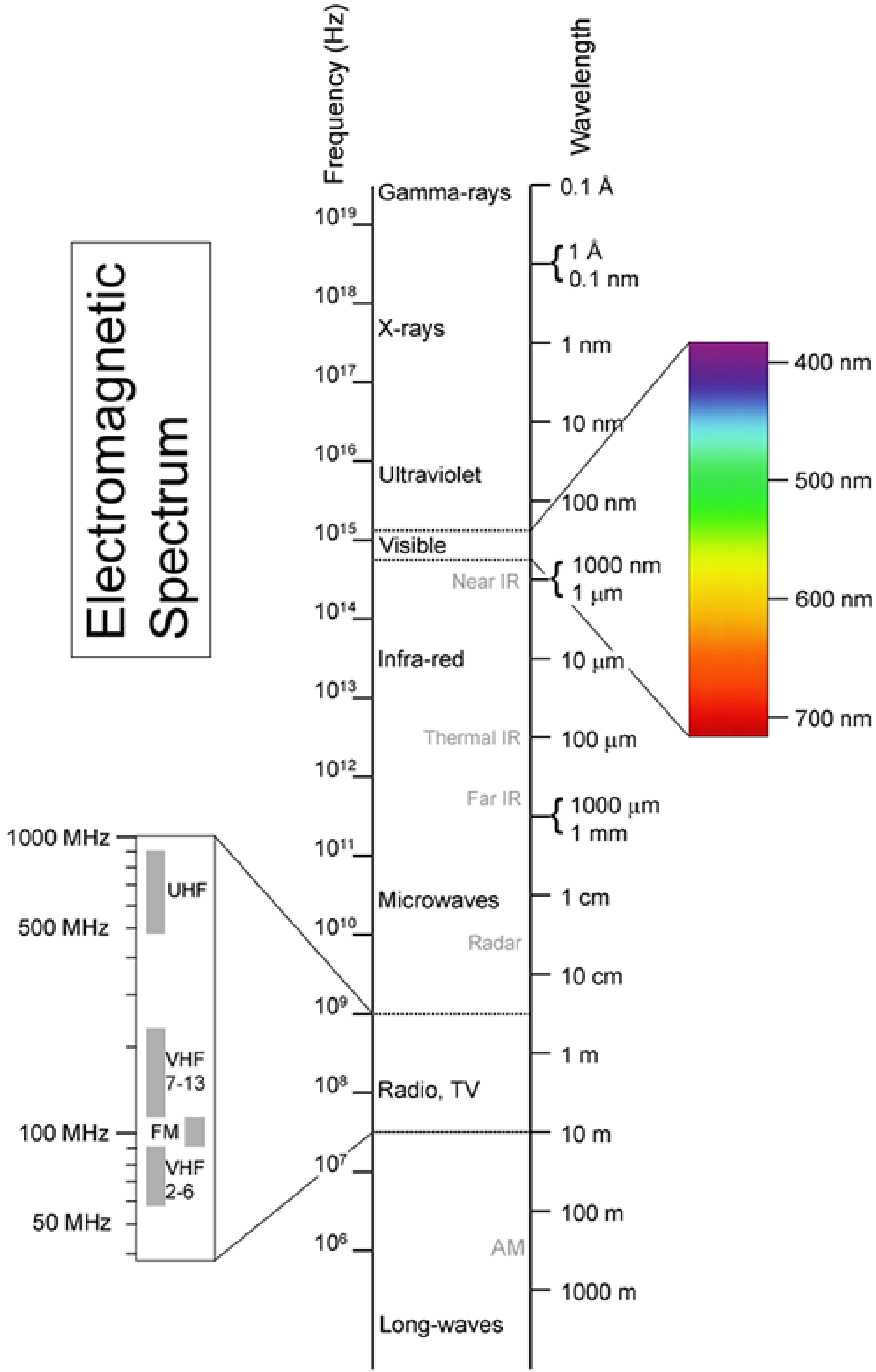
water + carbon dioxide + sunlight ⟶ glucose + oxygen

$$6\,H_2O + 6\,CO_2 + \text{radiant energy} \longrightarrow C_6H_{12}O_6 + 6\,O_2$$

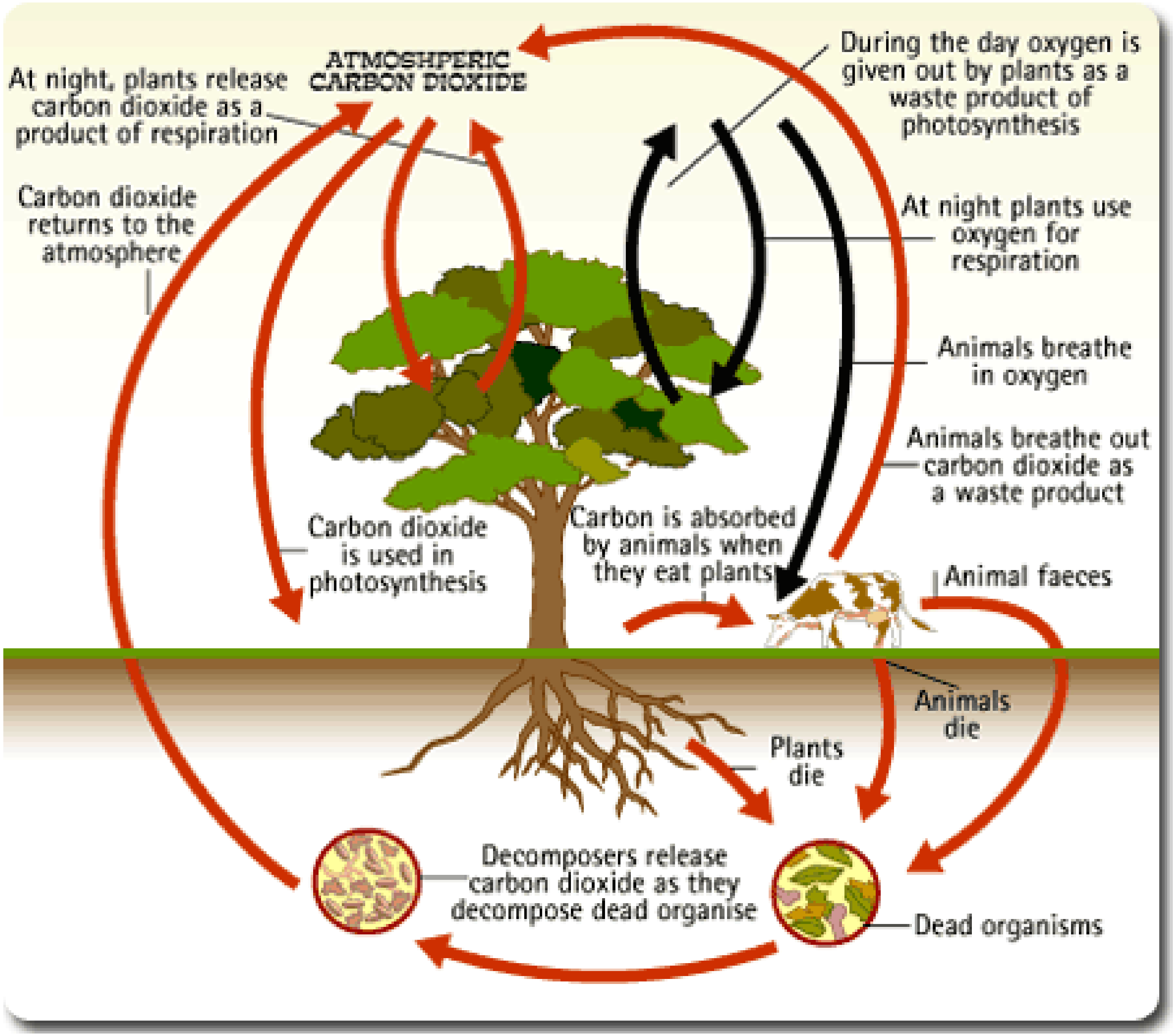


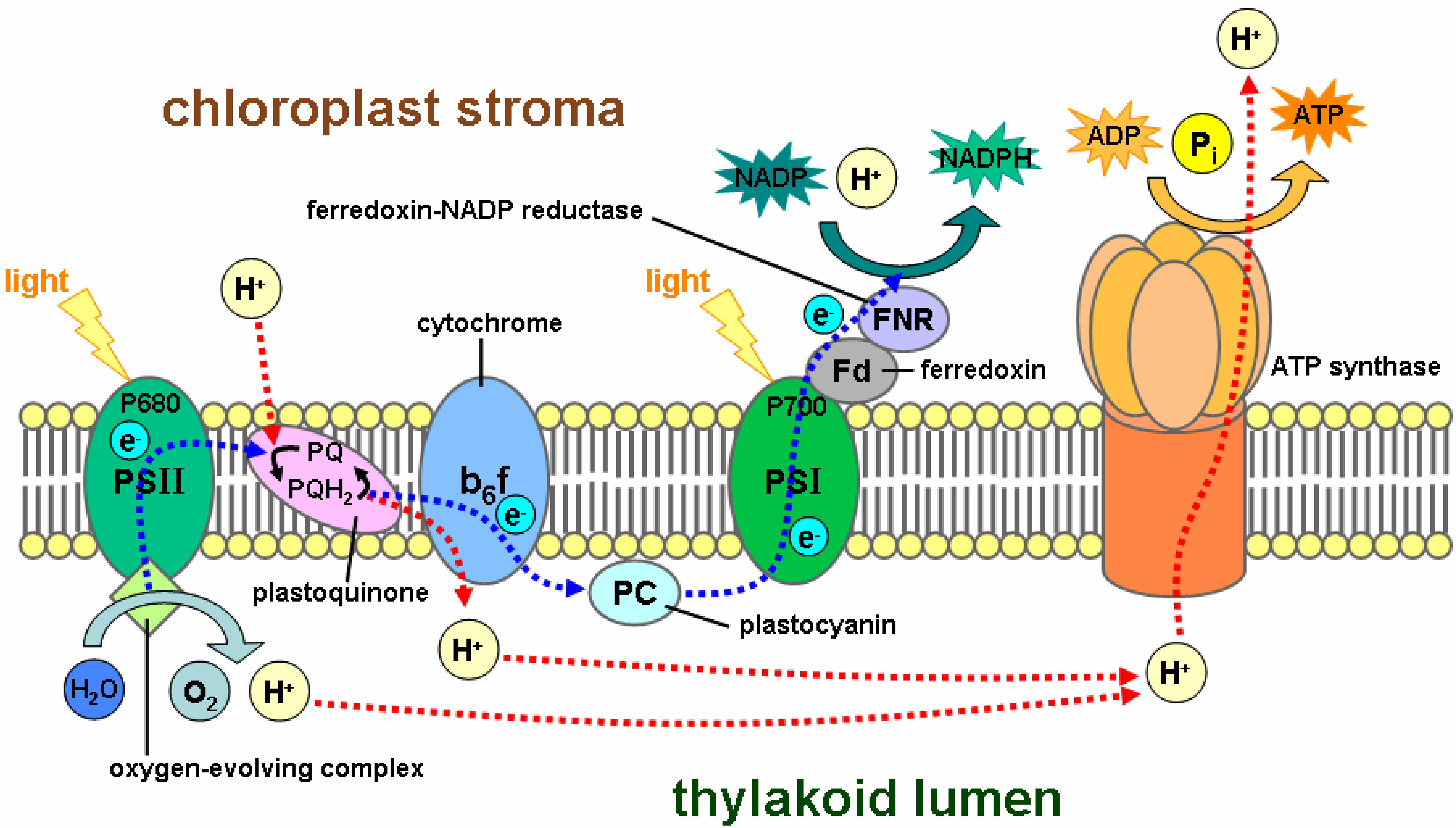


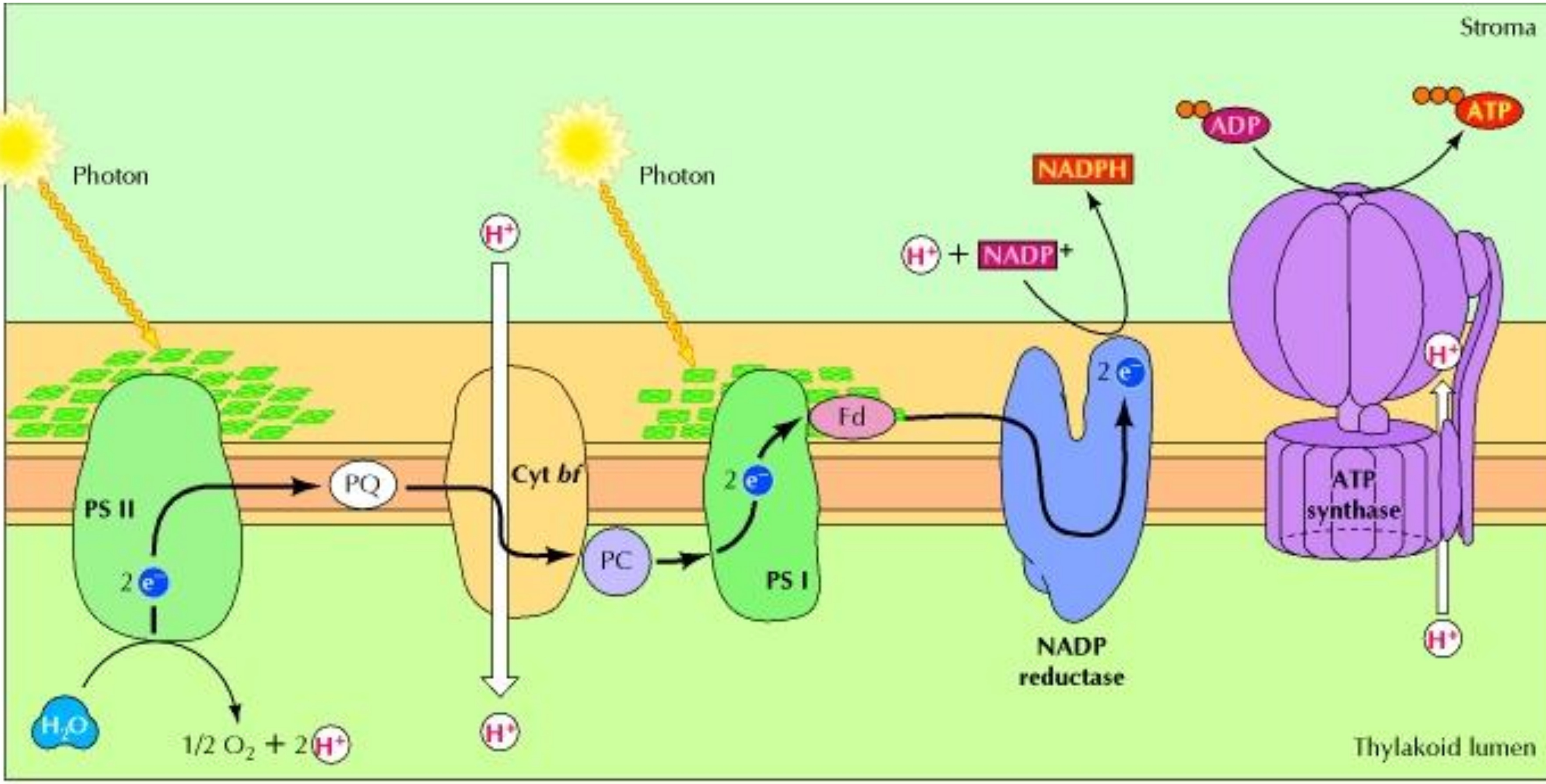

Wavelength (m)
10−11 10−9 10−7 10−5 10−3 10−1 10¹ 10³
Gamma rays
X-rays
Ultra-violet
Visible
Infrared
Microwaves
Radio frequency
10²⁰ 10¹⁸ 10¹⁶ 10¹⁴ 10¹² 10¹⁰ 10⁸ 10⁶ 10⁴
Frequency (s−1)
Visible region
400 500 600 700 750 nm

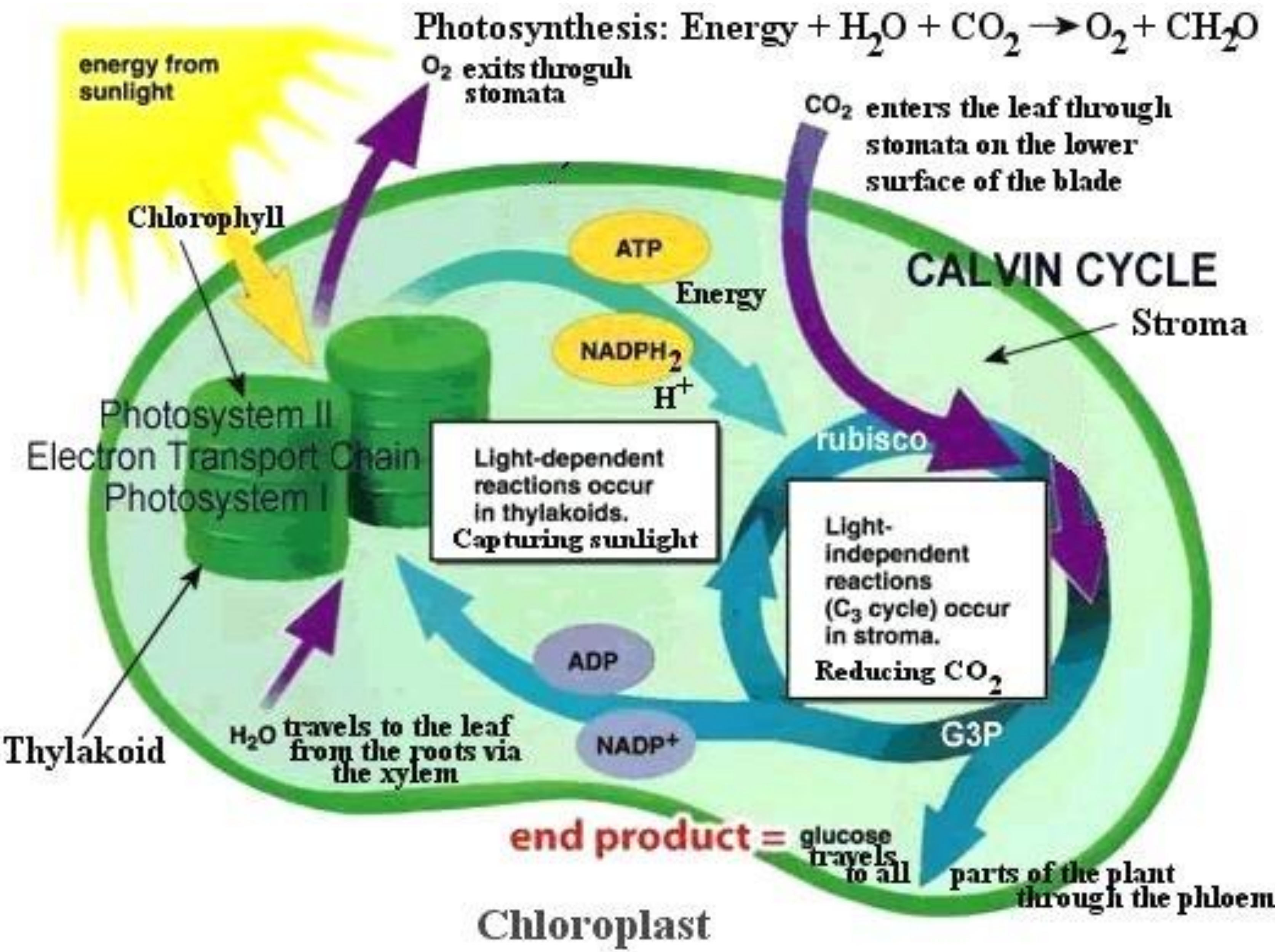


Electromagnetic Spectrum
Frequency (Hz)
Wavelength
Gamma-rays
X-rays
Ultraviolet
Visible
Near IR
Infra-red
Thermal IR
Far IR
Microwaves
Radar
Radio, TV
AM
Long-waves
10^{19}
10^{18}
10^{17}
10^{16}
10^{15}
10^{14}
10^{13}
10^{12}
10^{11}
10^{10}
10^{9}
10^{8}
10^{7}
10^{6}
0.1 Å
1 Å
0.1 nm
1 nm
10 nm
100 nm
1000 nm
1 µm
10 µm
100 µm
1000 µm
1 mm
1 cm
10 cm
1 m
10 m
100 m
1000 m
400 nm
500 nm
600 nm
700 nm
1000 MHz
500 MHz
100 MHz
50 MHz
UHF
VHF
7-13
FM
VHF
2-6

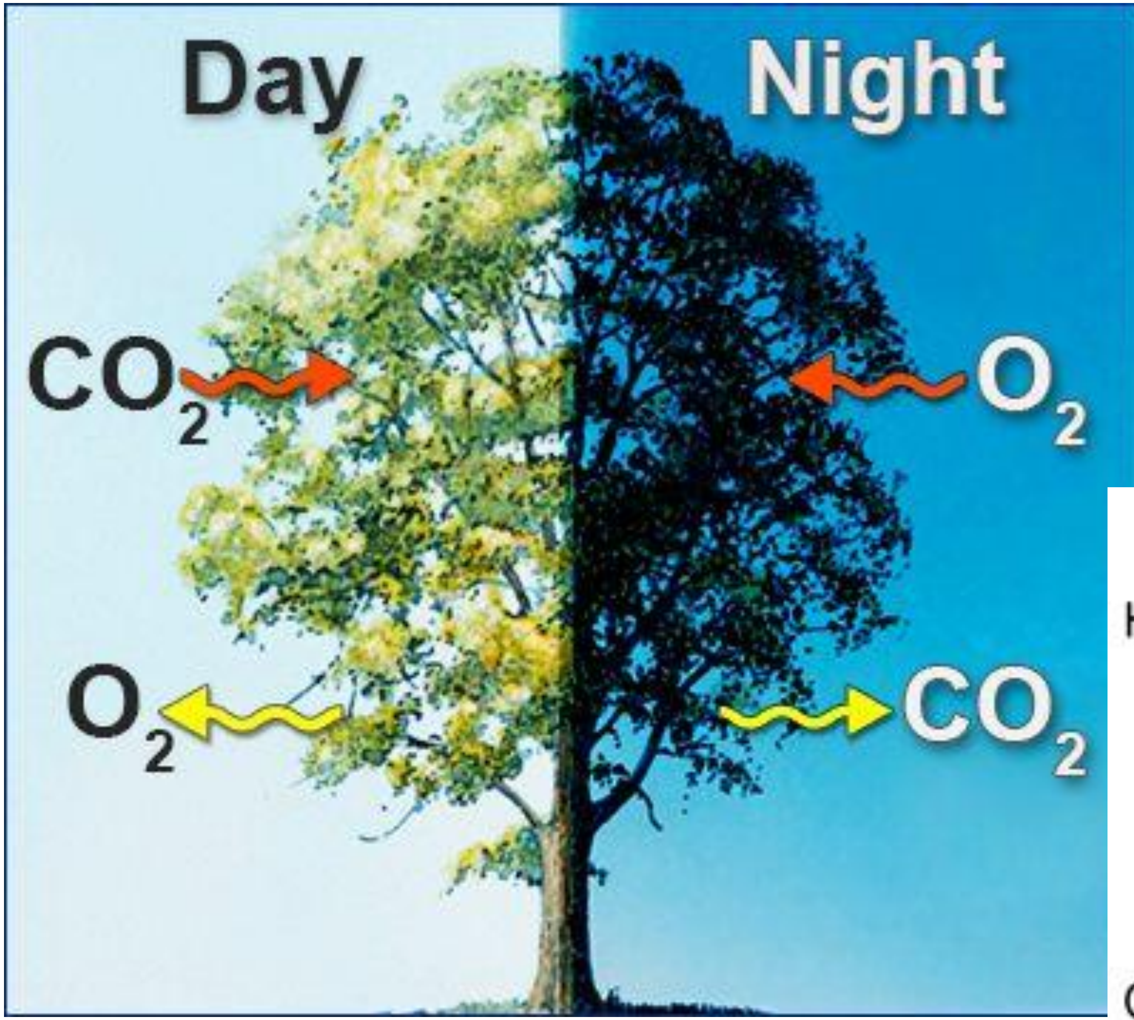

ATMOSHPERIC CARBON DIOXIDE
At night, plants release carbon dioxide as a product of respiration
During the day oxygen is given out by plants as a waste product of photosynthesis
Carbon dioxide returns to the atmosphere
At night plants use oxygen for respiration
Animals breathe in oxygen
Animals breathe out carbon dioxide as a waste product
Carbon dioxide is used in photosynthesis
Carbon is absorbed by animals when they eat plants
Animal faeces
Animals die
Plants die
Decomposers release carbon dioxide as they decompose dead organise
Dead organisms

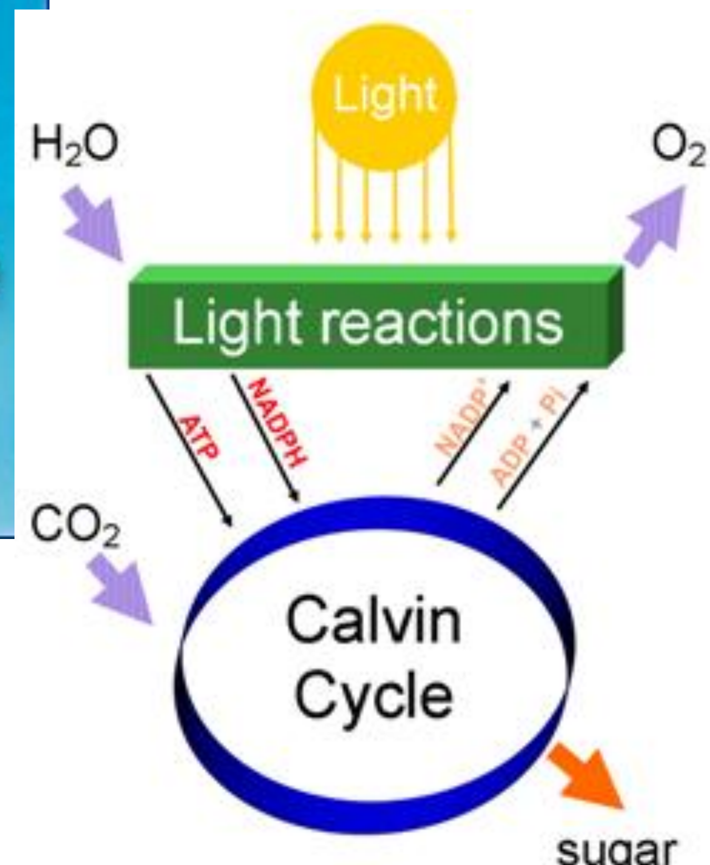

chloroplast stroma
H+
ATP
ADP
Pi
NADP
H+
NADPH
ferredoxin-NADP reductase
light
H+
light
e-
FNR
cytochrome
Fd
ferredoxin
ATP synthase
P680
P700
e-
PQ
PSII
PQH2
b6f
PSI
e-
e-
plastoquinone
PC
plastocyanin
H+
H+
H2O
O2
H+
oxygen-evolving complex
thylakoid lumen


Stroma
Photon
Photon
H+
NADPH
H+ + NADP+
ADP
ATP
PQ
Cyt bf
PS II
2 e−
PC
2 e−
PS I
Fd
2 e−
ATP synthase
H+
H+
NADP reductase
H2O
1/2 O2 + 2 H+
H+
Thylakoid lumen



Photosynthesis: Energy + H_2O + CO_2 → O_2 + CH_2O
energy from sunlight
O_2 exits throguh stomata
CO_2 enters the leaf through stomata on the lower surface of the blade
Chlorophyll
ATP
Energy
NADPH2
H+
CALVIN CYCLE
Stroma
Photosystem II
Electron Transport Chain
Photosystem I
Light-dependent reactions occur in thylakoids.
Capturing sunlight
rubisco
Light-independent reactions (C_3 cycle) occur in stroma.
Reducing CO_2
ADP
NADP+
G3P
Thylakoid
H_2O travels to the leaf from the roots via the xylem
end product = glucose travels to all parts of the plant through the phloem
Chloroplast


Day
Night
CO2
O2
O2
CO2


Light
H2O
O2
Light reactions
ATP
NADPH
NADP+
ADP + Pi
CO2
Calvin
Cycle
sugar

Biomass

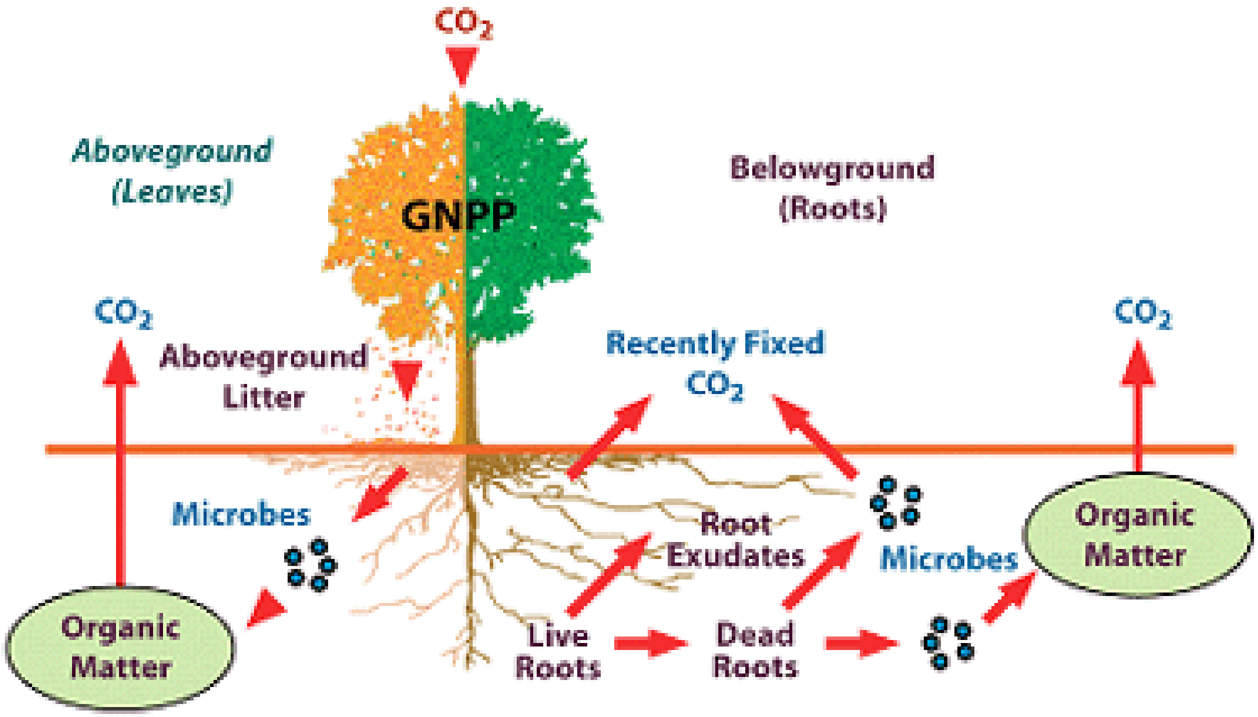
- The **biomass** of a forest is defined as the mass of living organisms normally expressed in mass of wet or dry substance (g/m^2, kg per hectare, g/m^3, or other measures) or in units proportional to it (mass of carbon or nitrogen of body organic matter or J/m2).
- **GPP** of terrestrial ecosystems integrates the effect of environmental factors and leaf photosynthetic propperties through the canopy
- GPP is the sum of the net photosynthesis by all photosynthetic tissue measured at the ecosystem scale
- The **balance between carbon inputs** through **gross primary production (GPP)** and carbon losses through **plant respiration** and tissue turnover govern the **carbon balance** of plants
- **Plants lose carbon** also through several pathways (plants death, herbivores consumption, volatilization, fire, human harvest…)

Biomass cont.

Biomass is a complex **mixture of organic materials**, such as carbohydrates, fats, and proteins, along with small amounts of minerals, such as sodium, phosphorus, calcium, and iron.

- The main components of plant biomass are **carbohydrates** (approximately 75%, dry weight) and **lignin** (approximately 25%), which can vary with plant type.
- The carbohydrates are mainly **cellulose or hemicellulose fibers**, which impart strength to the plant structure, and lignin, which holds the fibers together.
- Some plants also store **starch** (another carbohydrate polymer) and **fats** as sources of energy, mainly in seeds and roots.
- The biomass is **largest in forests** (500 tons/ha or more in **tropical forests**, about 300 tons/ha in broad-leaved forests of the **temperate zones**). Among the heterotrophic organisms feeding on plants, the **microorganisms** - bacteria, fungi, actinomycetes, and others-have the largest biomass. Their biomass in productive forests is **several tons per hectare.**
- **The soil fauna** (such as earthworms, insect larvae, nematodes, myriapods…) account for a large part of the total animal biomass in the temperate zone. This fauna **amounts to hundreds of kg/ha** in the forest zone, mainly produced by earthworms (300 to 900 kg/ha). The average biomass of **vertebrate** animals is 20 kg/ha or more, but it often ranges from 3 to 10 kg/ha.

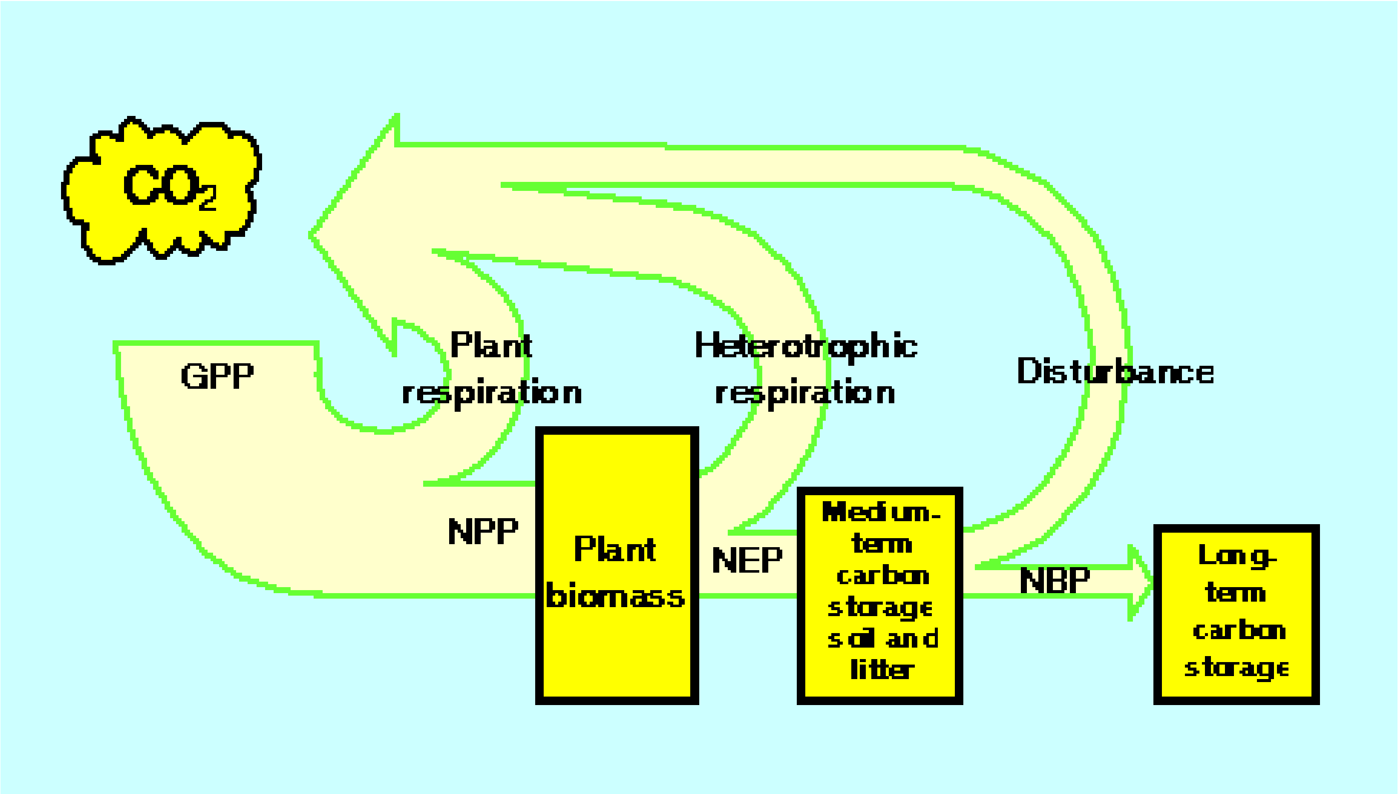
Carbon cycle and productivity



Productivity

- **Biomass production (productivity)** is the rate at which biomass is accrued per unit area **over a fixed interval, usually one year.**
- If **wildlife populations** are the focus of management, managers may choose to measure biomass or numbers of individual animals.
- Ecologists interested in the general responses of forest ecosystems, measure **net primary production** (NPP), usually expressed as gross primary production (GPP) minus the respiration of autotrophs (Ra)
- Another response commonly of interest is **net ecosystem production** (NEP) or Net ecosystem exchange (**NEE**)usually expressed as NEP=GPP-(Ra+Rh) where R is respiration of autotrophs and heterotrophs

Scheme of primary production



Review questions

1. Characterize photosynthesis and their limiting factors in forest ecosystem
2. Explain diferences between primary and secondary productivity
3. Define Net primary productivity and biomass allocation in different forest type
4. Explain how climate change will influence the NPP of forest ecosytem
5. What are the main principles and explanations for global climatic changes

Literature

Basic reading list:

WARING, R H. - RUNNING, S W. ***Forest ecosystems : analysis at multiple scales.*** 3. ed. Amsterdam: Elsevier/Academic Press, 2007. 420 s. ISBN 978-0-12-370605-8.

CHAPIN, F.S. ,Matson,P.A.,Vitousek P.M..,*Principles of terrestrial Ecosystem Ecology*: Springer 2011, 529 p. ISBN 1-4419-9502-5.

AGREN, G I. - ANDERSSON , F O. ***Terrestrial Ecosystem Ecology***. Cambridge University Press, New York, USA: Cambridge University Press, 2012. 330 s. ISBN 978-1-107-64825-8.

PERRY, David A, Ram OREN a Stephen C HART. ***Forest ecosystems***. 2nd ed. Baltimore: Johns Hopkins University Press, c2008. ISBN 978-0-8018-8840-3.

SCHULZE, Ernst-Detlef, Erwin BECK a Klaus MÜLLER-HOHENSTEIN. ***Plant ecology***. Berlin: Springer, c2005, 702 s. ISBN 3-540-20833-x.

VALENTINI, R. ***Fluxes of carbon, water, and energy of European forests***. Berlin: Springer, c2003, 270 s. ISBN 3-540-43791-6.

Book: Ecology of Woodlands and Forests: Description, Dynamics and Diversity (Thomas et al. 2007) -
http://books.google.cz/books?id=0Ntvos9aaC8C&printsec=frontcover&dq=Ecology+of+Woodlands&hl=cs&sa=X&ei=Lvk_UrTHLYKctQa0oICICg&ved=0CDMQ6AEwAA#v=onepage&q=Ecology%20of%20Woodlands&f=false

Figures

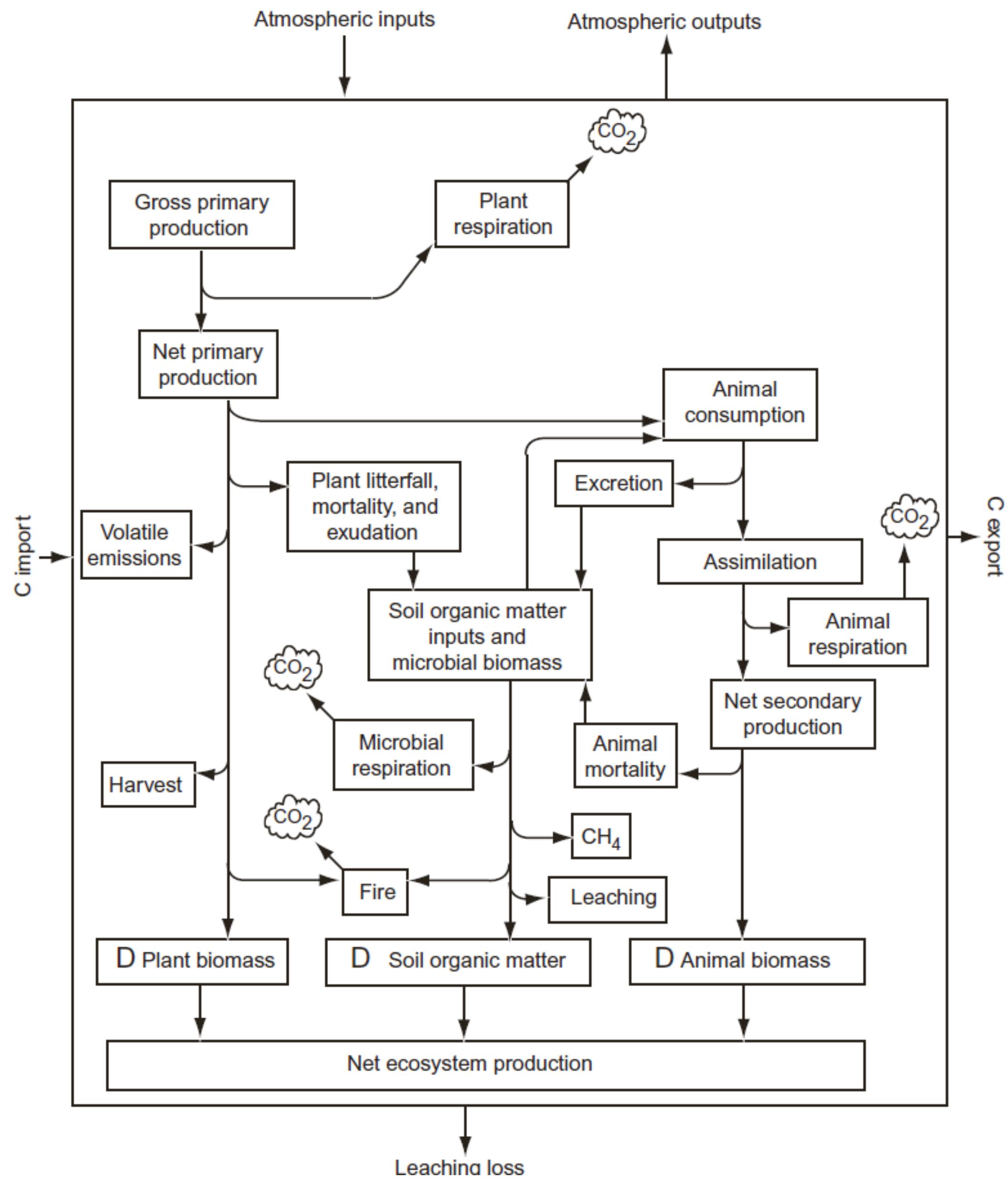
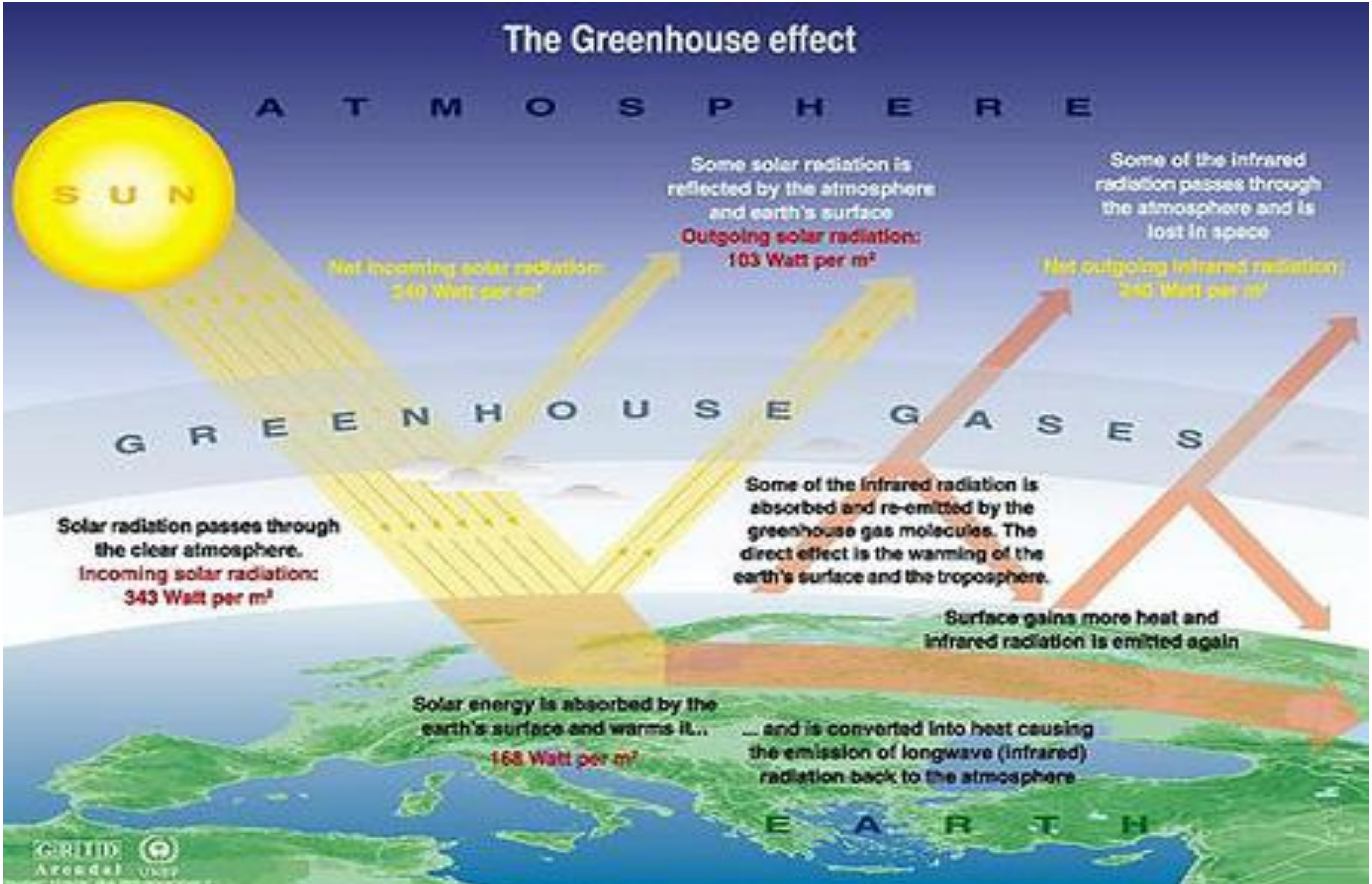


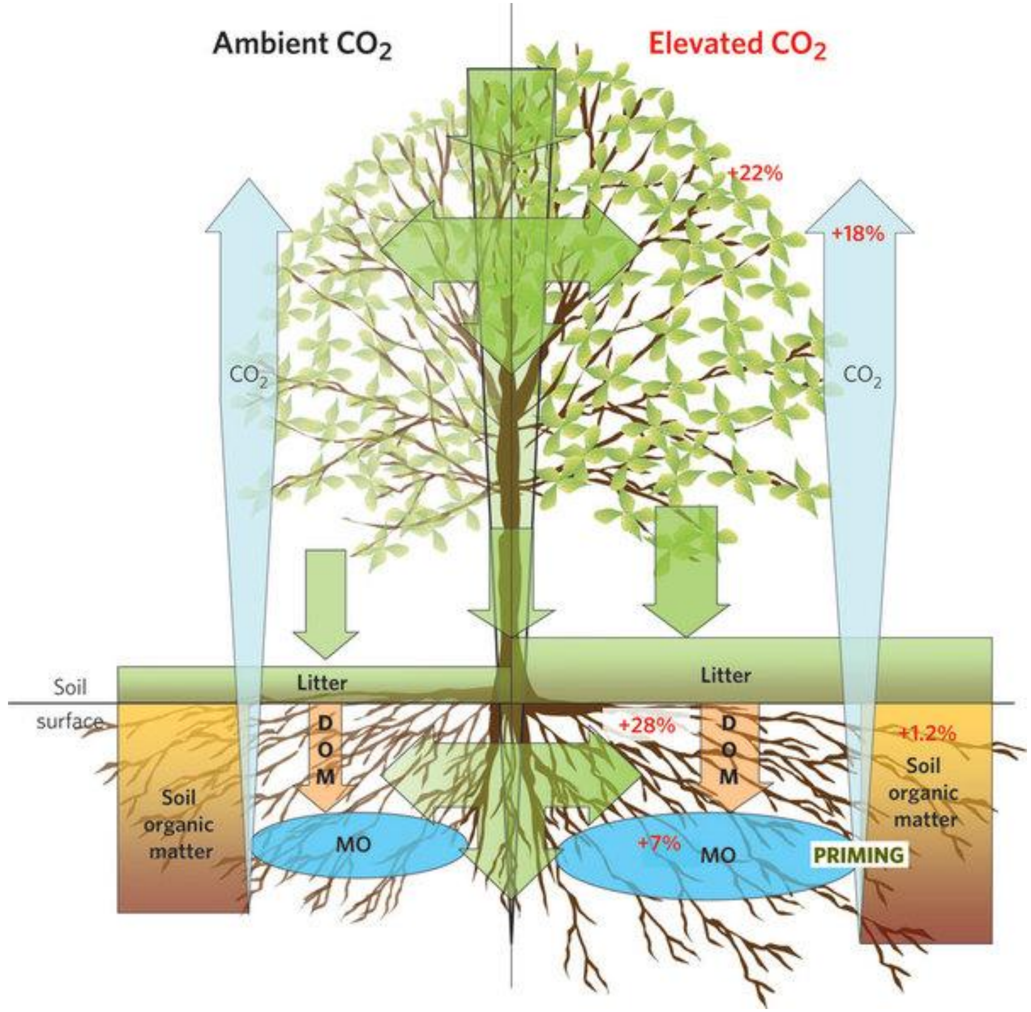
FIGURE 6.8. Overview of the carbon fluxes of an ecosystem. The large box represents the ecosystem, which exchanges carbon with the atmosphere, other ecosystems, and groundwater.

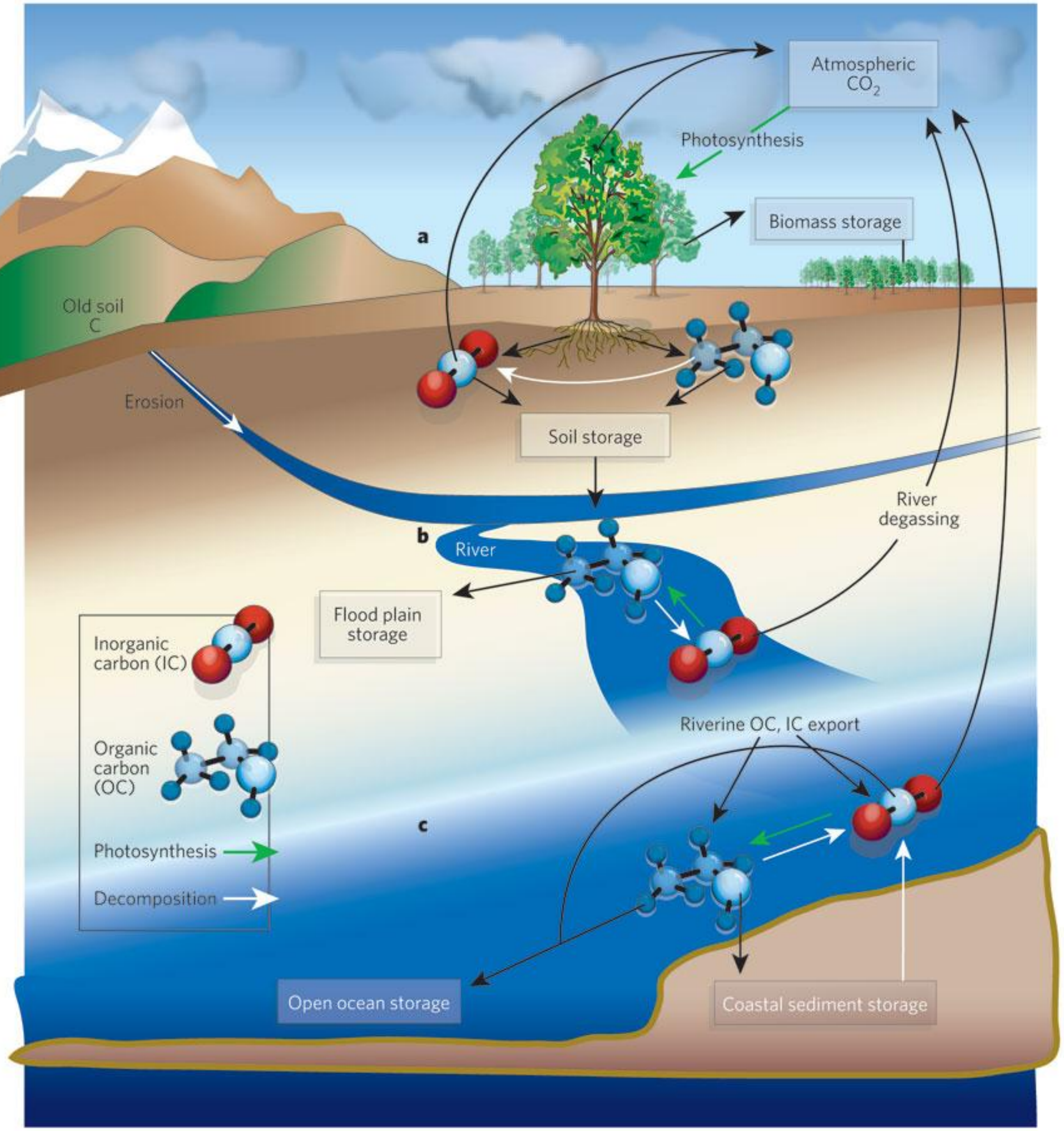
Scheme of Greenhouse effect



Sources: Okanagan university college in Canada, Department of geography, University of Oxford, school of geography; United States Environmental Protection Agency (EPA), Washington; Climate change 1995, The science of climate change, contribution of working group 1 to the second assessment report of the intergovernmental panel on climate change, UNEP and WMO, Cambridge university press, 1996.

Applications in ecology and forestry „simulation“




Atmospheric CO_2
Photosynthesis
Biomass storage
a
Old soil C
Erosion
Soil storage
River degassing
b
River
Flood plain storage
Inorganic carbon (IC)
Organic carbon (OC)
Photosynthesis
Decomposition
Riverine OC, IC export
c
Open ocean storage
Coastal sediment storage

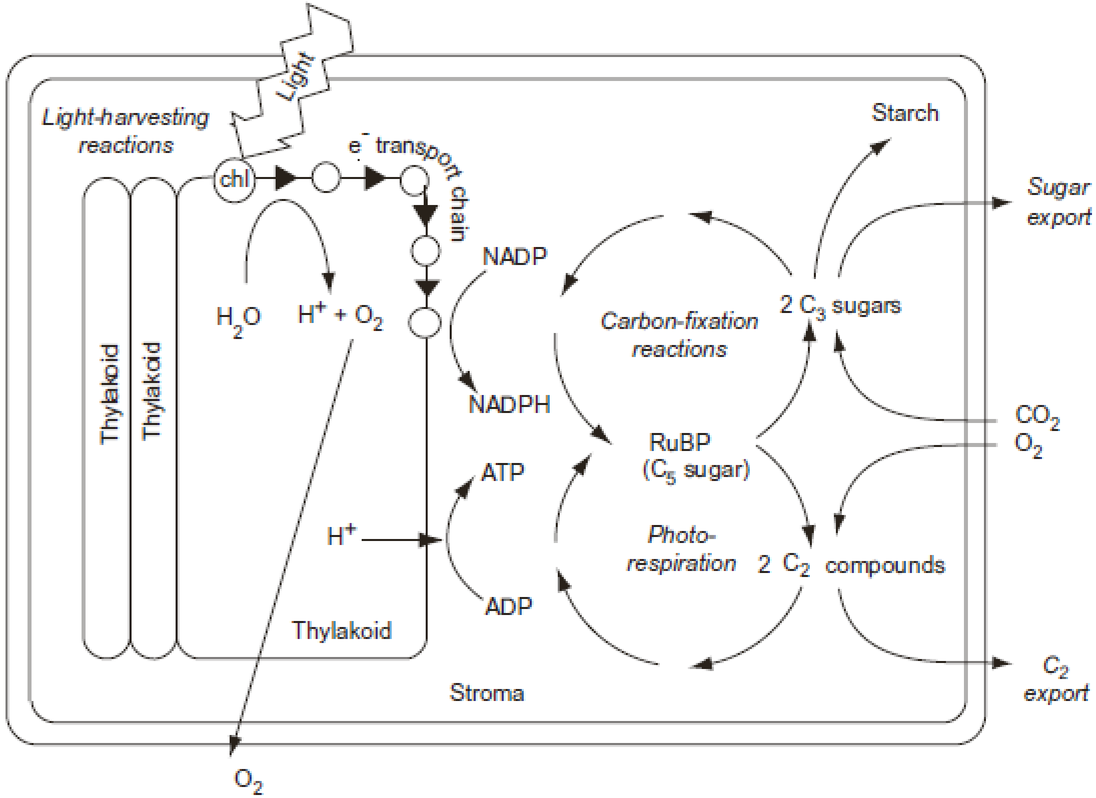


FIGURE 5.3. A chloroplast showing the location of the major photosynthetic reactions. The light-harvesting reactions occur in the **thylakoid** membranes; chlorophyll (chl) absorbs visible light and funnels it to reaction centers (Photosystems I and II). In Photosystem II, water is split to H^+ and O_2, and the resulting electrons are then passed down an electron-transport chain inside the thylakoid, ultimately to NADP, producing NADPH. During this process, protons move across the thylakoid membrane to the stroma, and the proton gradient drives the synthesis of ATP. ATP and NADPH provide the energy to regenerate ribulose-bisphosphate (RuBP) within the carbon fixation reactions. RuBP reacts either with CO_2 to produce sugars and starch (carbon-fixation reactions of photosynthesis) or with O_2 to produce two-carbon intermediates (photorespiration). These two-carbon intermediates are exported from the chloroplast to mitochondria or peroxisomes, where they are again converted to sugars, with loss of CO_2 and ATP. Through either carbon fixation or photorespiration, ADP and NADP again become reactants available to produce additional ATP and NADPH. The net effect of photosynthesis is to convert light energy into chemical energy (sugars and starches) that is available to support plant growth and maintenance.

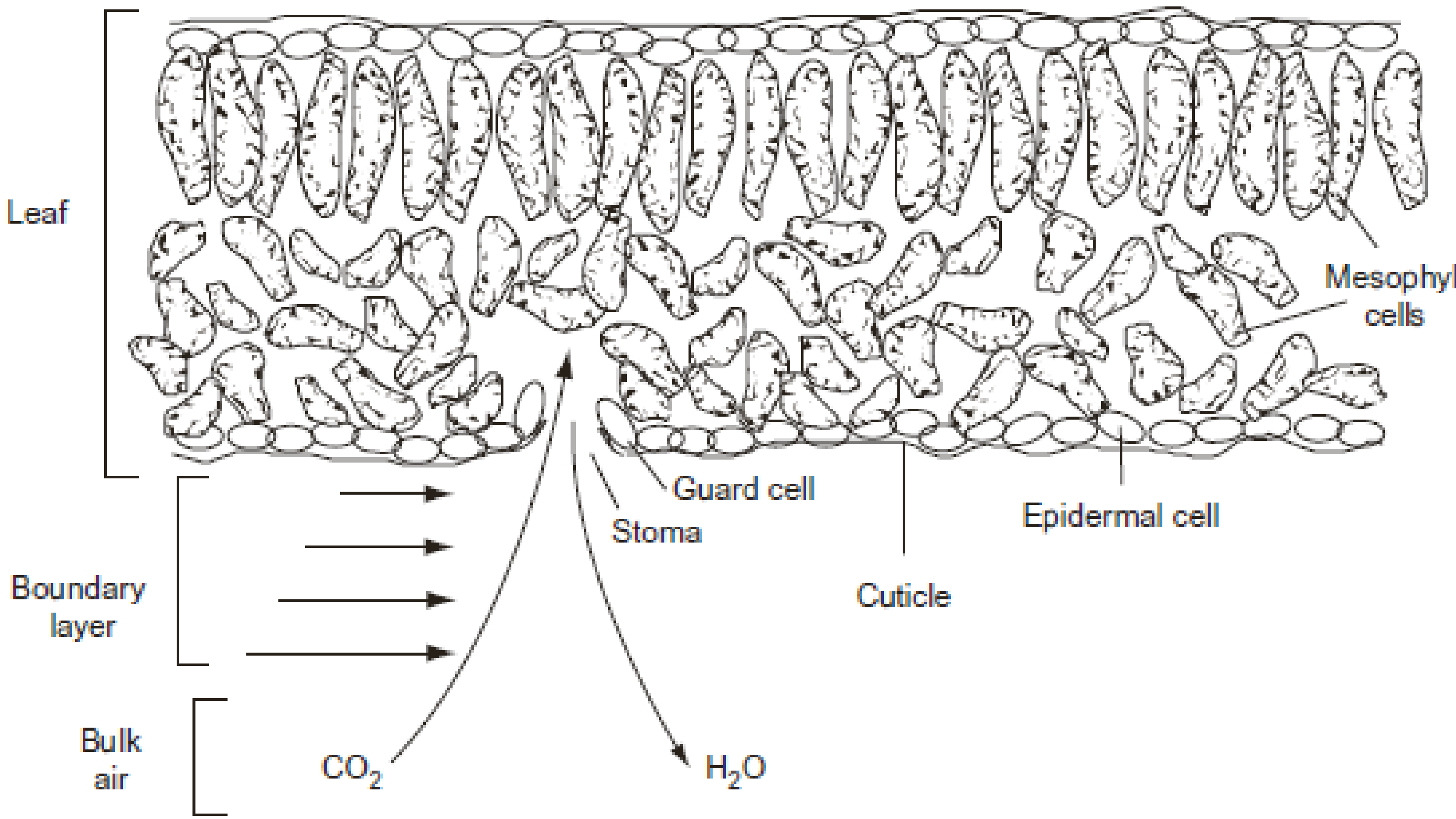


FIGURE 5.4. Cross-section of a leaf showing the diffusion pathways of CO_2 and H_2O into and out of the leaf, respectively. Length of the horizontal arrows outside the leaf is proportional to wind speeds in the boundary layer.

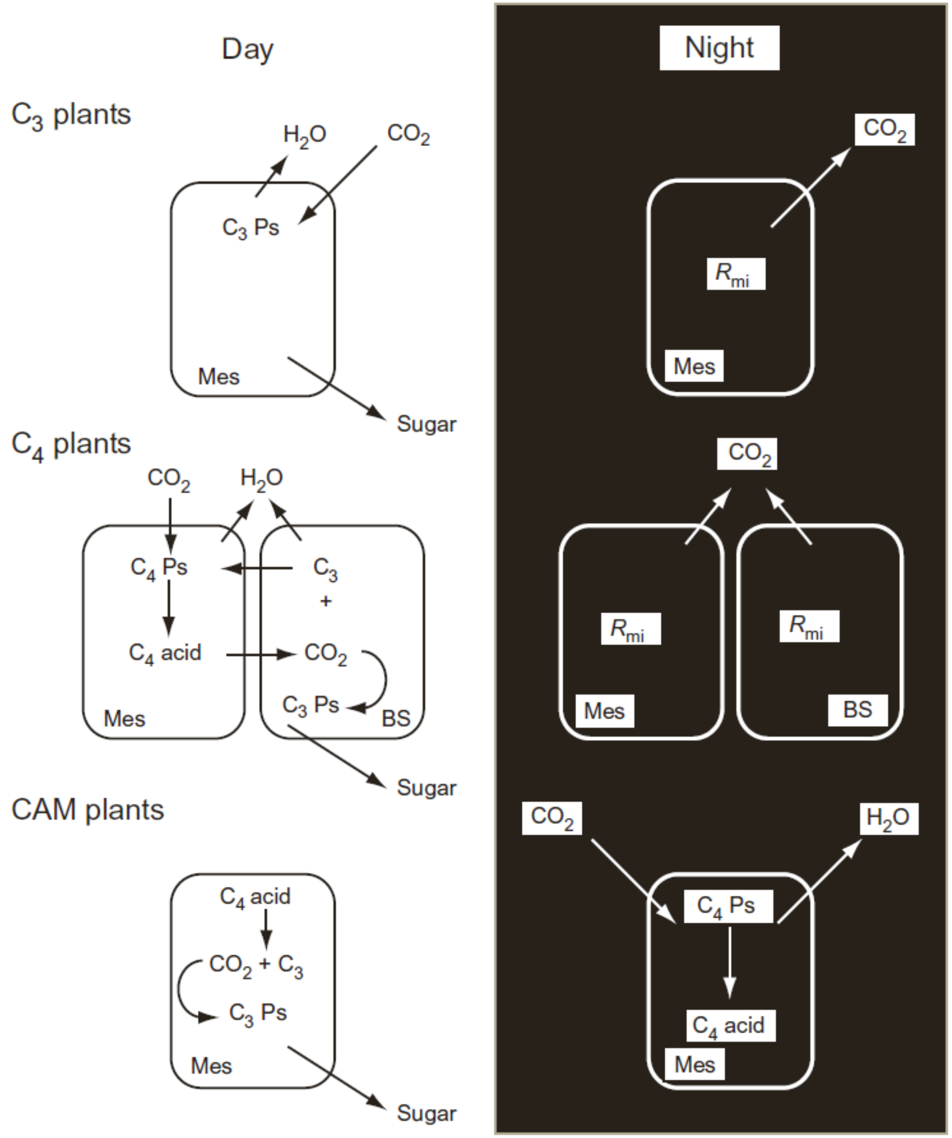


FIGURE 5.5. Cellular location and temporal cycle of CO_2 fixation and water exchange in leaves with C_3, C_4, and CAM photosynthetic pathways. In C_3 and CAM plants, all photosynthesis occurs in mesophyll (Mes) cells. In C_4 plants, C_4 carbon fixation (C_4 Ps) occurs in mesophyll cells and C_3 fixation (C_3 Ps) occurs in bundle sheath (BS) cells. Mitochondrial respiration (R_{mi}) occurs at night. Exchanges of CO_2 and water vapor with the atmosphere occur during the day in C_3 and C_4 plants and at night in CAM plants.

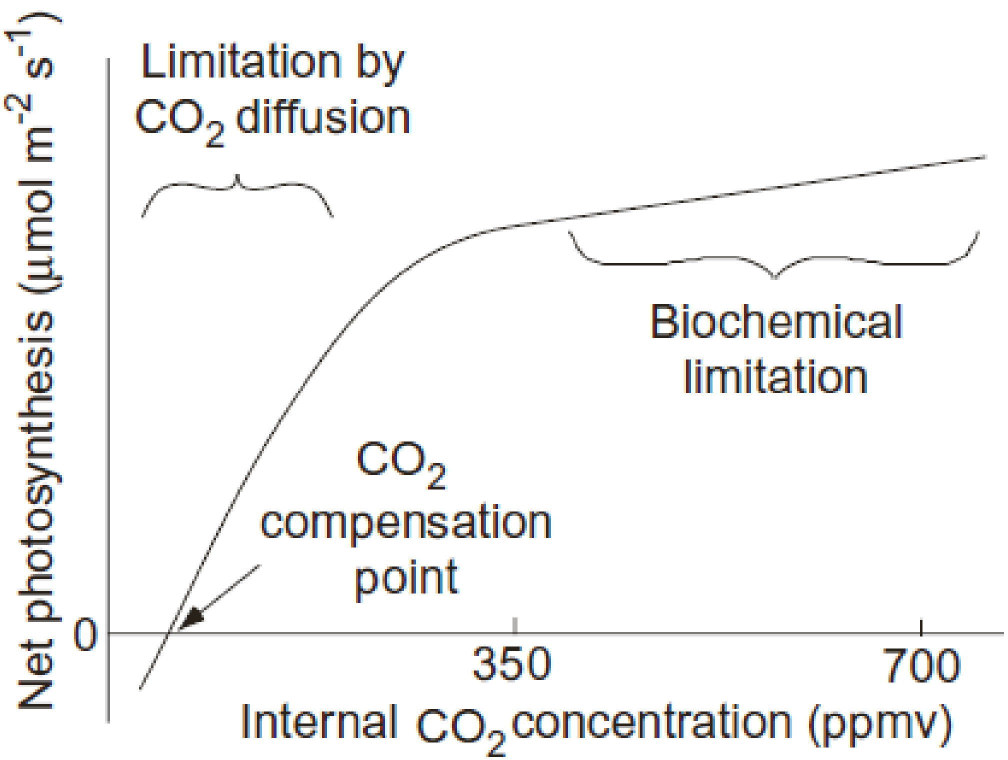


FIGURE 5.6. Relationship of the net photosynthetic rate to the CO_2 concentration inside the leaf. Photosynthetic rate is limited by the rate of CO_2 diffusion into the chloroplast in the linear portion of the CO_2-response curve and by biochemical processes at higher CO_2 concentrations. The CO_2 compensation point is the minimal CO_2 concentration at which the leaf shows a net gain of carbon.

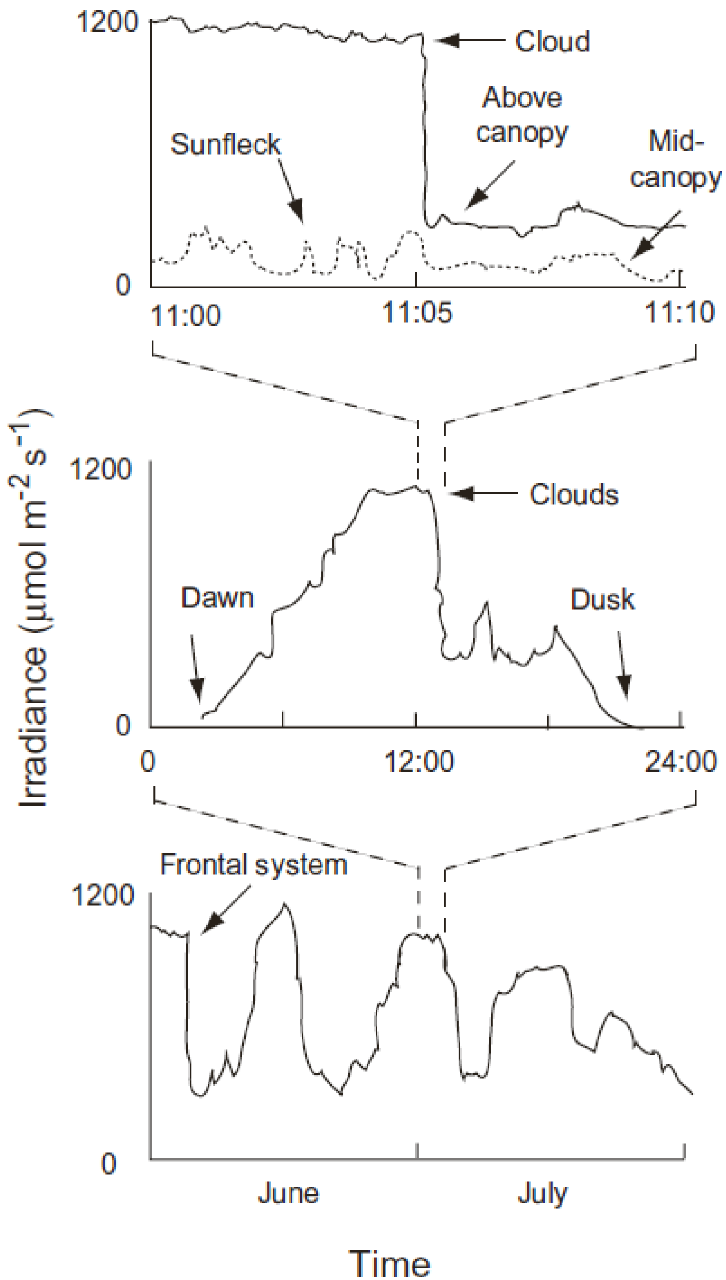


FIGURE 5.7. Hypothetical time course of photosynthetically active radiation above and below the canopy of a temperate forest over minutes, hours, and months. Over the course of a few minutes, light at the top of the canopy varies with cloudiness. Below the canopy, light also varies due to the presence of sunflecks of direct irradiance, which can last tenths of seconds to minutes. During a day, there are large changes in light due to changes in solar angle, with smaller fluctuations caused by passing clouds. Convective activity often increases cloudiness in the afternoon. During the growing season, the major causes of variation in light are seasonal changes in the solar angle and the passage of frontal systems. Some times of year have greater frequency of cloudiness than others due to changes in directions of the prevailing winds and the passage of frontal systems.

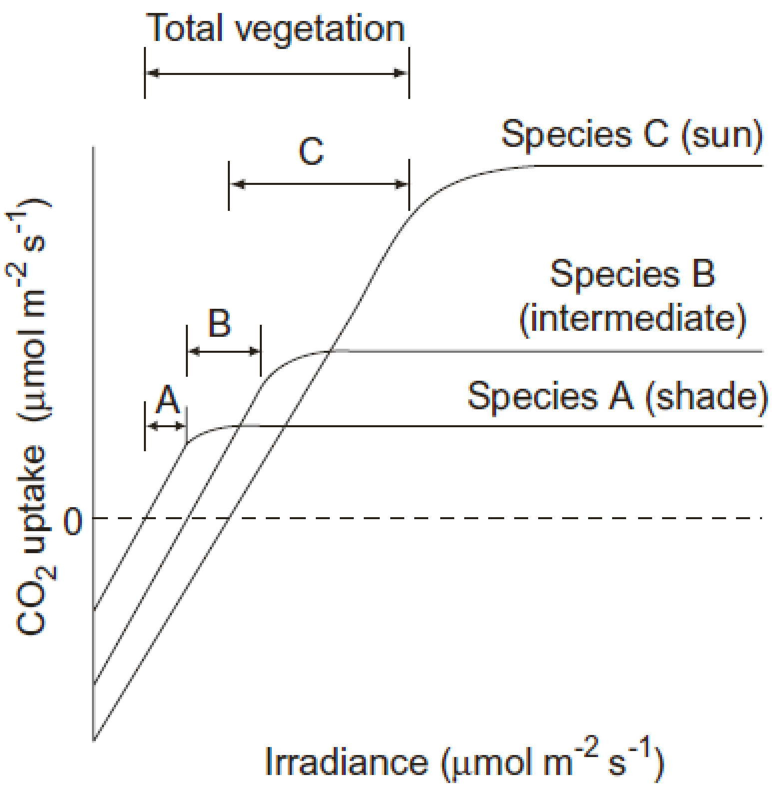


FIGURE 5.9. Light-response curves of net photosynthesis in plants acclimated to low, intermediate, and high light. Horizontal arrows show the range of irradiance over which net photosynthesis is positive and responds linearly to irradiance for each species and for the vegetation as a whole. Acclimation increases the range of irradiance over which net photosynthesis responds linearly to light (i.e., has a constant LUE).

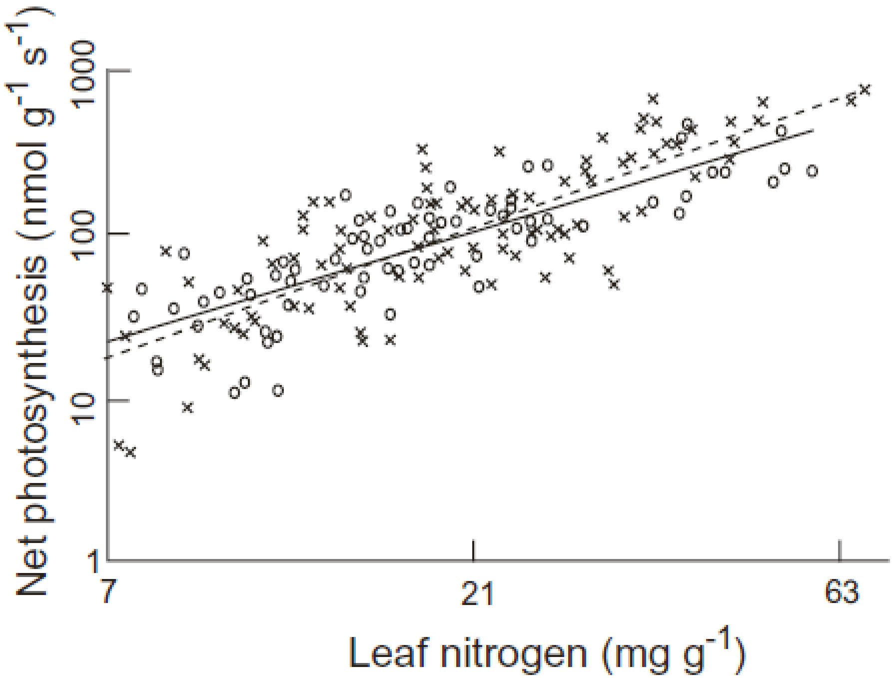


FIGURE 5.10. Relationship between leaf nitrogen concentration and maximum photosynthetic capacity for plants from Earth's major biomes. Open circles and the solid regression line are for 11 species from six biomes using a common methodology. Exes and the dashed regression line are data from the literature. (Redrawn with permission from *Proceedings of the National Academy of Sciences U. S. A.*, Vol. 94 © 1997 National Academy of Sciences, USA; Reich et al. 1997.)

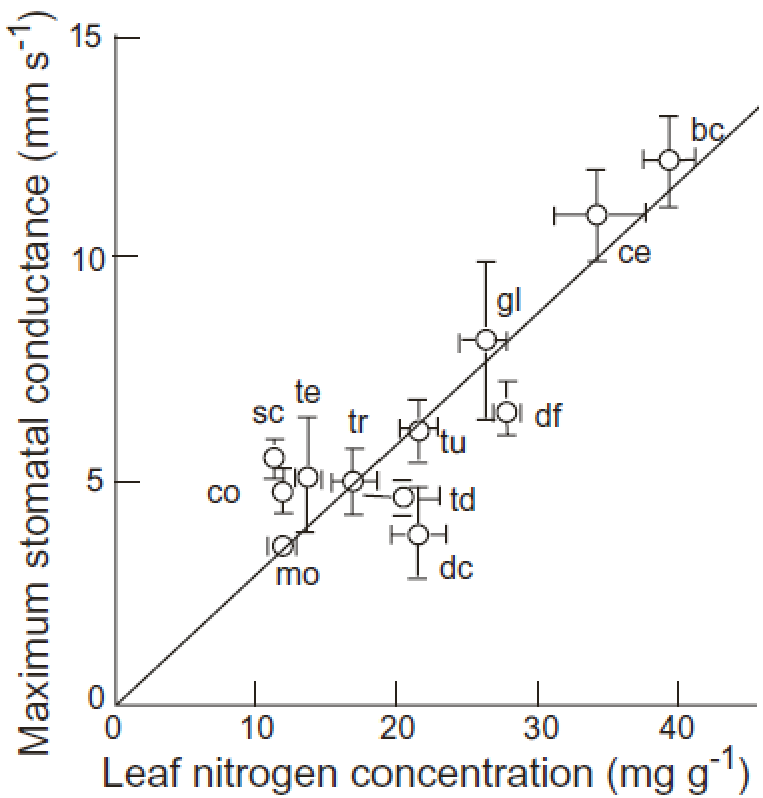


FIGURE 5.11. Relationship between leaf nitrogen concentration and maximal stomatal conductance of plants from Earth's major biomes. Each point and its standard error represent a different biome. bc, Broad-leaved crops; ce, cereal crops; co, evergreen conifer forest; dc, deciduous conifer forest; df, tropical deciduous forest; gl, grassland; mo, monsoonal forest; sc, sclerophyllous shrub; td, temperate deciduous broad-leaved forest; te, temperate evergreen broad-leaved forest; tr, tropical rain forest; tu, herbaceous tundra. (Redrawn with permission from the *Annual Review of Ecology and Systematics*, Vol. 25 © 1994 by Annual Reviews, www.AnnualReviews; Schulze et al. 1994.)

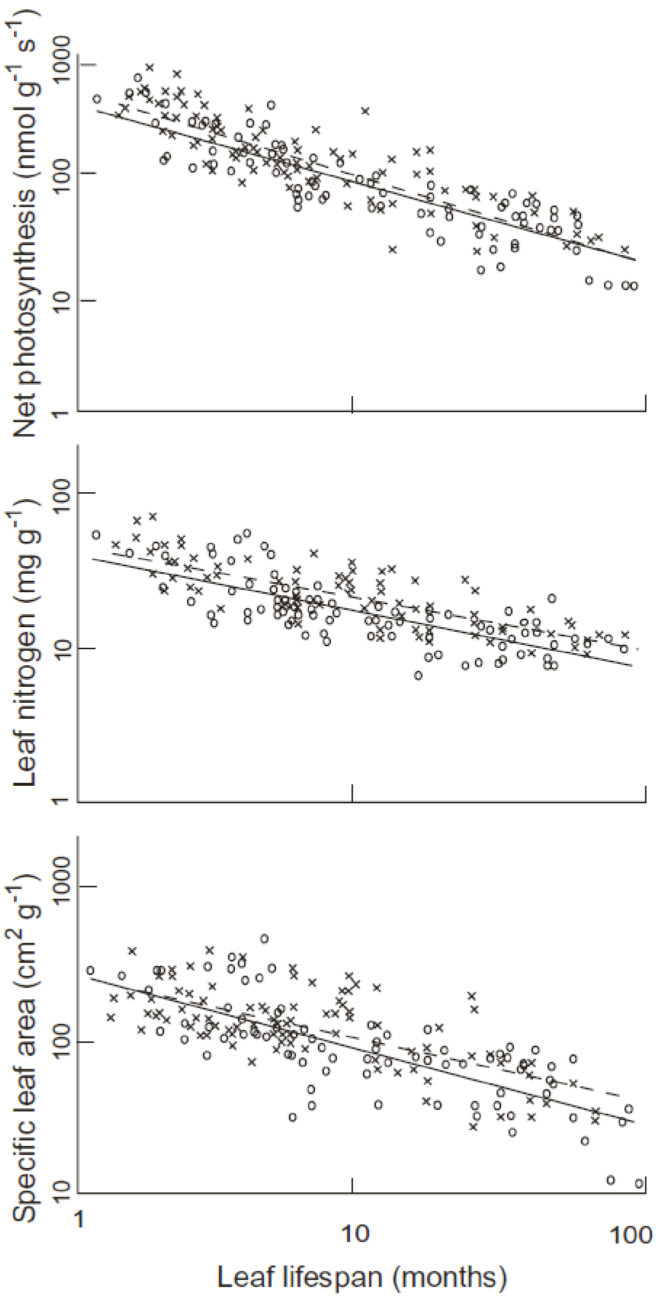


FIGURE 5.12. The effect of leaf life span on photosynthetic capacity (photosynthetic rate measured under favorable conditions), leaf nitrogen concentration, and specific leaf area. Symbols same as in Figure 5.10. (Redrawn with permission from *Proceedings of the National Academy of Sciences U. S. A.*, Vol. 94 © 1997 National Academy of Sciences, USA; Reich et al. 1997.)

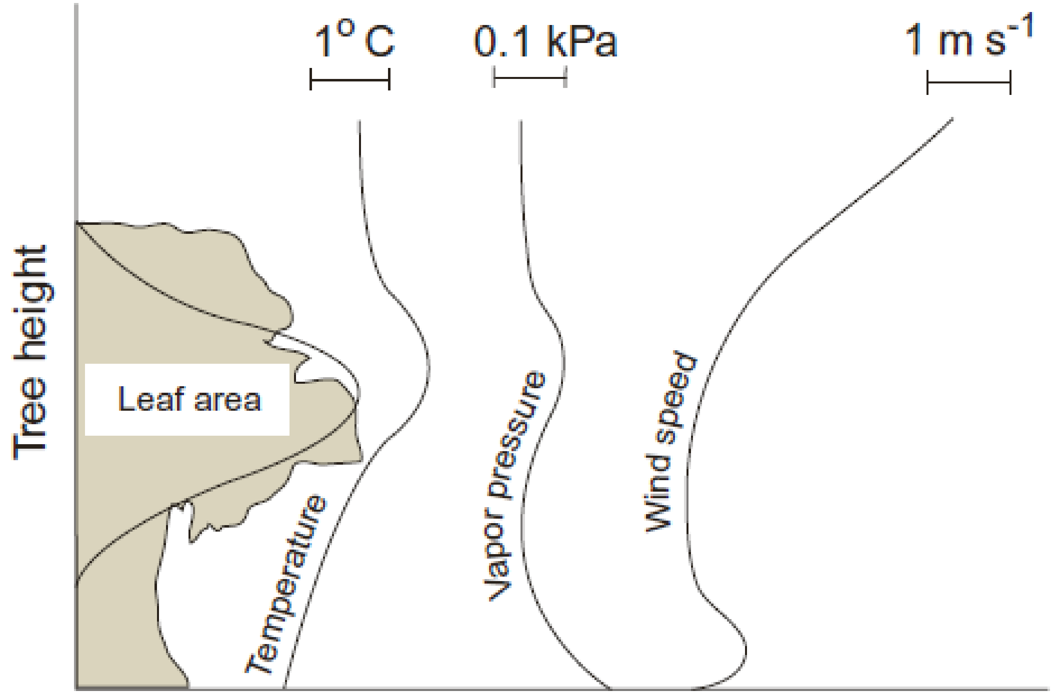


FIGURE 5.16. Typical vertical gradients in temperature, vapor pressure, and wind speed in a forest. Temperature is highest in the midcanopy where most energy is absorbed. The increase in wind speed at the bottom of the canopy occurs in open forests, where there is little understory. (Redrawn with permission from Academic Press; Landsberg and Gower 1997.)

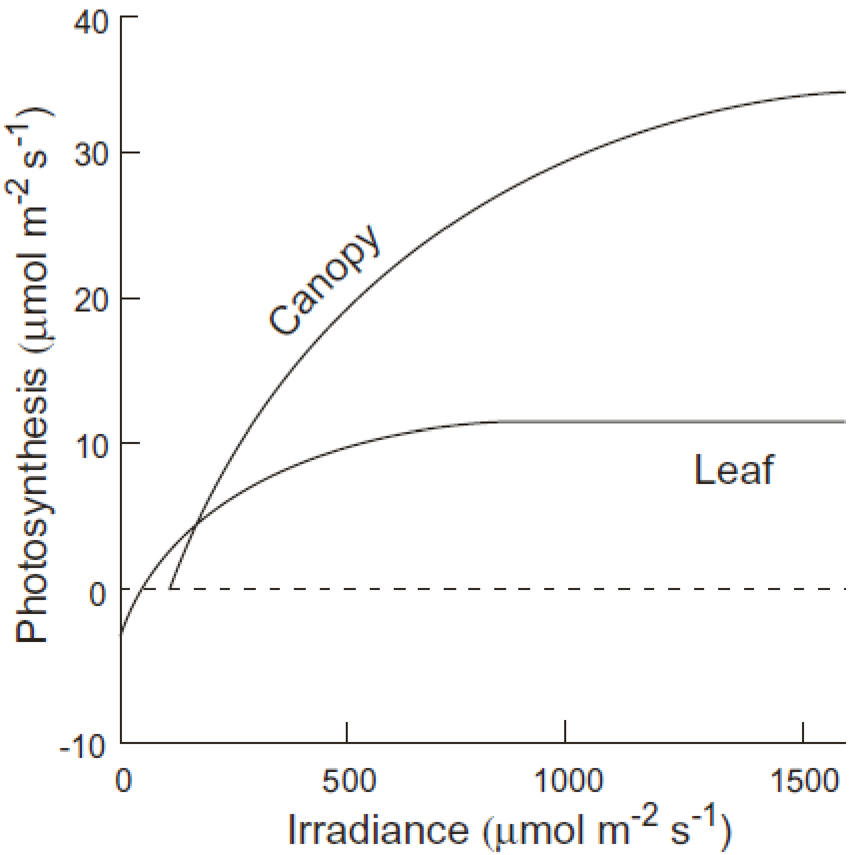


FIGURE 5.17. Light-response curve of a single leaf and a forest canopy. Canopies maintain a constant LUE (linear response of photosynthesis to light) over a broader range of light availability than do individual leaves. (Reprinted with permission from *Advances in Ecological Research*; Ruimy et al. 1996.)

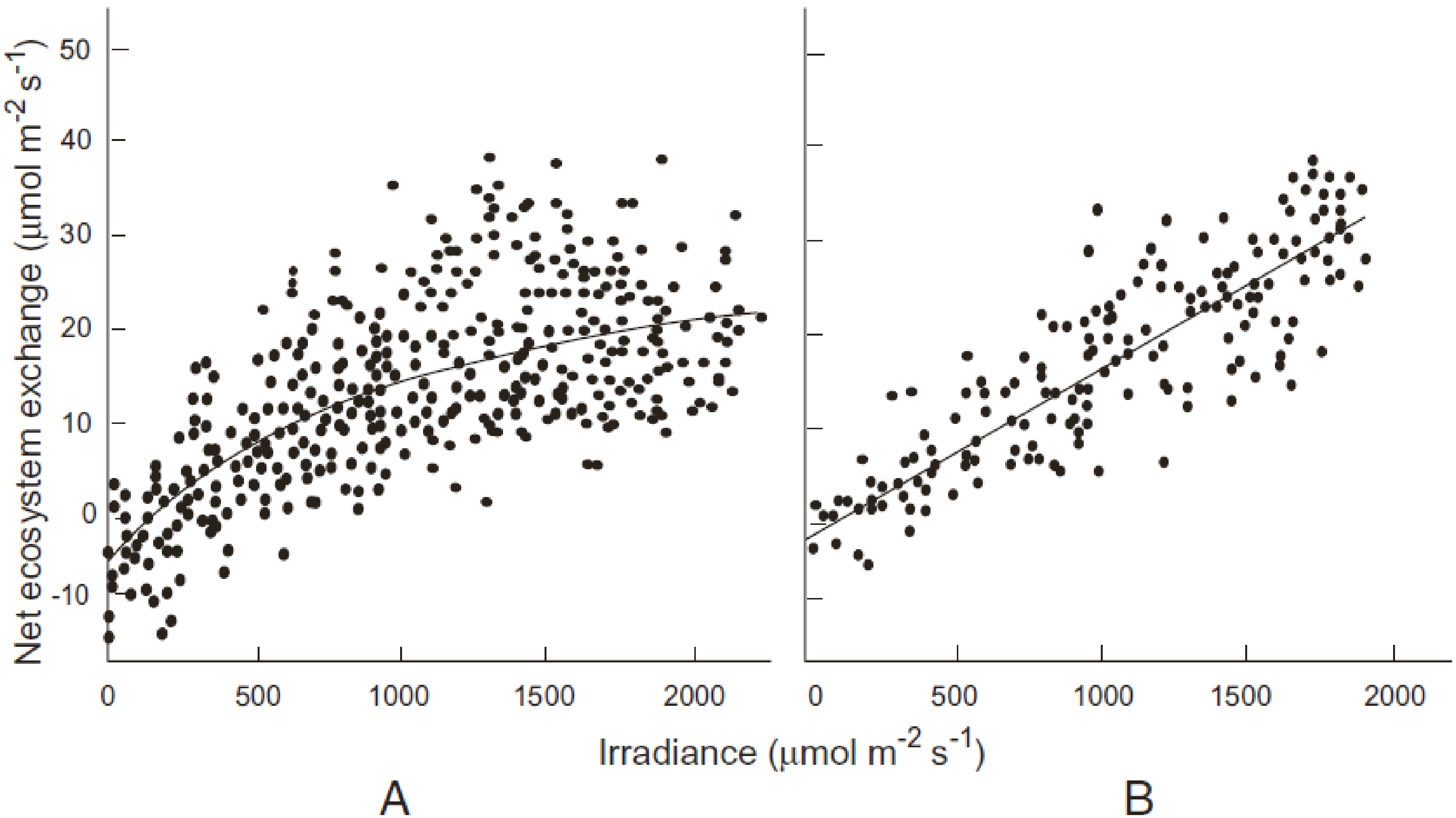


FIGURE 5.18. Effect of vegetation type and irradiance on net ecosystem exchange in forests (**A**) and crops (**B**). Forests maintain a relatively constant LUE up to 30 to 50% of full sun, although there is considerable variability. Crops maintain a constant light LUE over the entire range of naturally occurring irradiance. (Redrawn with permission from *Advances in Ecological Research*; Ruimy et al. 1996.)

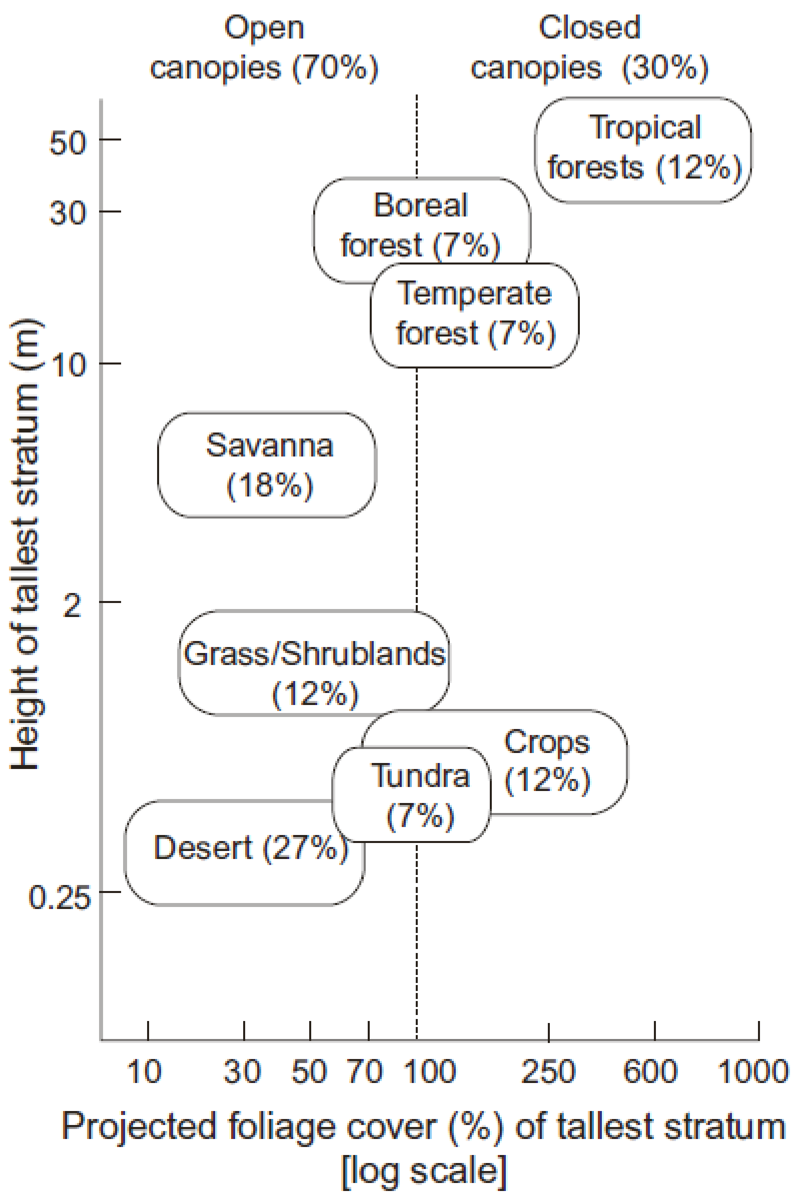


FIGURE 5.20. Projected foliage cover and canopy height of the major biomes. Typical values for that biome and the percentage of the terrestrial surface that it occupies are shown. The vertical line shows 100% canopy cover. (Reprinted with permission from *Climatic Change*, Vol. 18 © 1991 Kluwer Academic Publishers; Graetz 1991.)

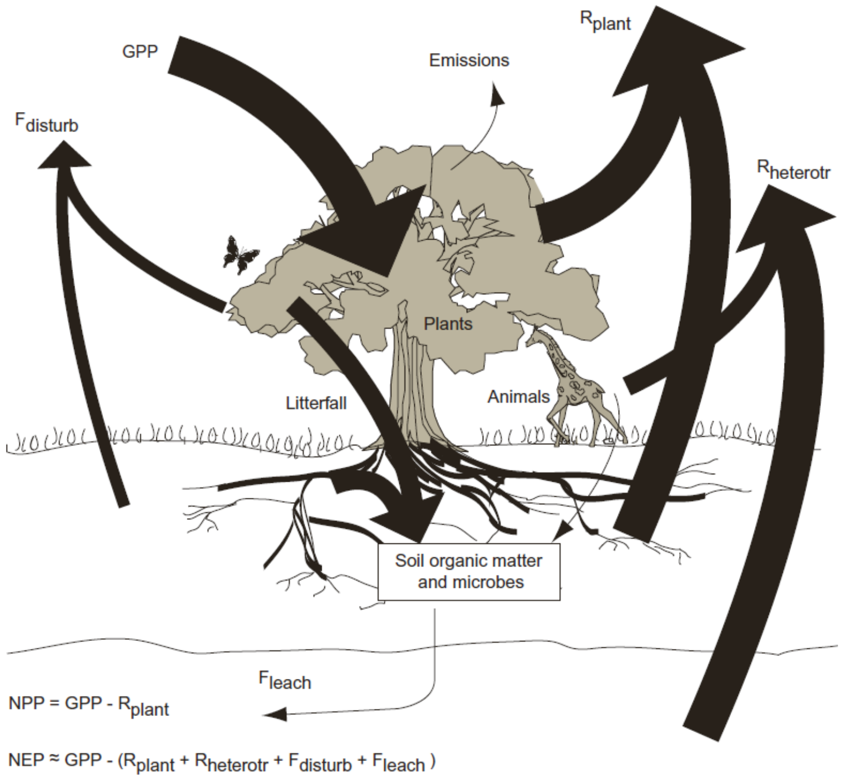


FIGURE 6.1. Overview of the major carbon fluxes of an ecosystem. Carbon enters the ecosystem as gross primary production (GPP), through photosynthesis by plants. Roots and aboveground portions of plants return about half of this carbon to the atmosphere as plant respiration (R_{plant}). Net primary production (NPP) is the difference between carbon gain by GPP and carbon loss through R_{plant}. Most NPP is transferred to soil organic matter as litterfall, root death, root exudation, and root transfers to symbionts; some NPP is eaten by animals and sometimes is lost from the ecosystem through disturbance. Animals also transfer some carbon to soils through excretion and mortality. Most carbon entering the soil is lost through microbial respiration (which, together with animal respiration, is termed heterotrophic respiration; $R_{heterotr}$). Additional carbon is lost from soils through leaching and disturbance. Net ecosystem production (NEP) is the net carbon accumulation by an ecosystem; it equals the carbon inputs from GPP minus the various avenues of carbon loss: respiration, leaching, and disturbance. If an ecosystem were at steady state, in the absence of disturbance, carbon inputs in GPP would approximately balance the carbon outputs in plant respiration (about 50% of GPP), heterotrophic respiration (40 to 50% of GPP), and leaching (0 to 10% of GPP). Most ecosystems, however, generally show either a net gain or net loss of carbon (i.e., positive or negative NEP, respectively), due to an imbalance between GPP and the various avenues of carbon loss.

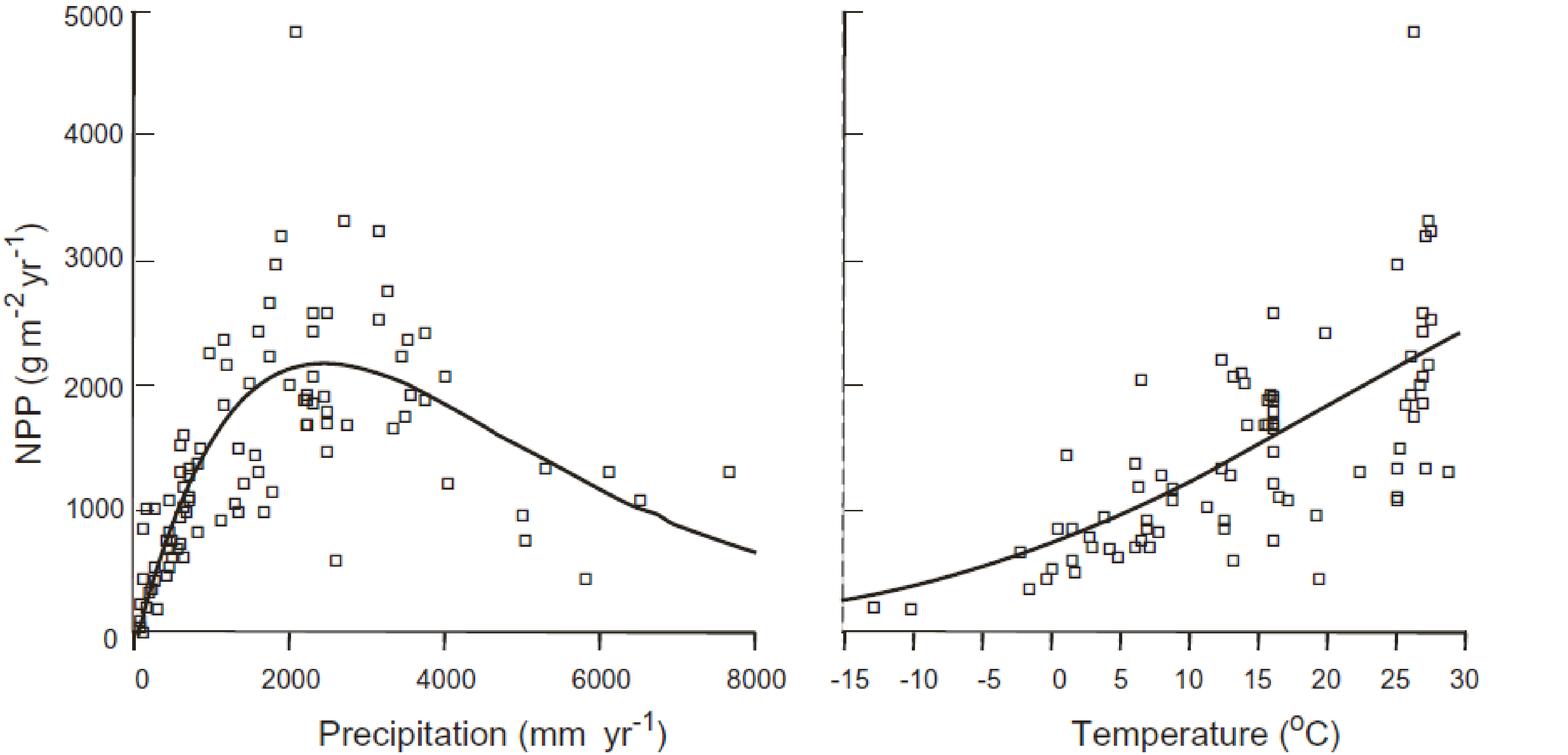


FIGURE 6.3. Correlation of NPP (in units of biomass) with temperature and precipitation. NPP is greatest in warm moist environments such as tropical forests and lowest cold or dry ecosystems such as tundra and deserts. In tropical forests, NPP declines at extremely high precipitation (>3 m yr^{-1}), due to indirect effects of excess moisture, such as low soil oxygen and loss of nutrients through leaching. (Figure modified from Schuur Unpublished; data from Lieth 1975, Clark et al. 2001b, and Schuur et al. 2001.)

Table 6.3. Net primary production of the major biome types based on biomass harvests[a].

Biome	Aboveground NPP ($g\,m^{-2}\,yr^{-1}$)	Belowground NPP ($g\,m^{-2}\,yr^{-1}$)	Belowground NPP (% of total)	Total NPP ($g\,m^{-2}\,yr^{-1}$)
Tropical forests	1400	1100	0.44	2500
Temperate forests	950	600	0.39	1550
Boreal forests	230	150	0.39	380
Mediterranean shrublands	500	500	0.50	1000
Tropical savannas and grasslands	540	540	0.50	1080
Temperate grasslands	250	500	0.67	750
Deserts	150	100	0.40	250
Arctic tundra	80	100	0.57	180
Crops	530	80	0.13	610

[a] NPP is expressed in units of dry mass. NPP estimated from harvests excludes NPP that is not available to harvest as a result of consumption by herbivores, root exudation, transfer to mycorrhizae, and volatile emissions.
Data from Saugier et al. (2001).

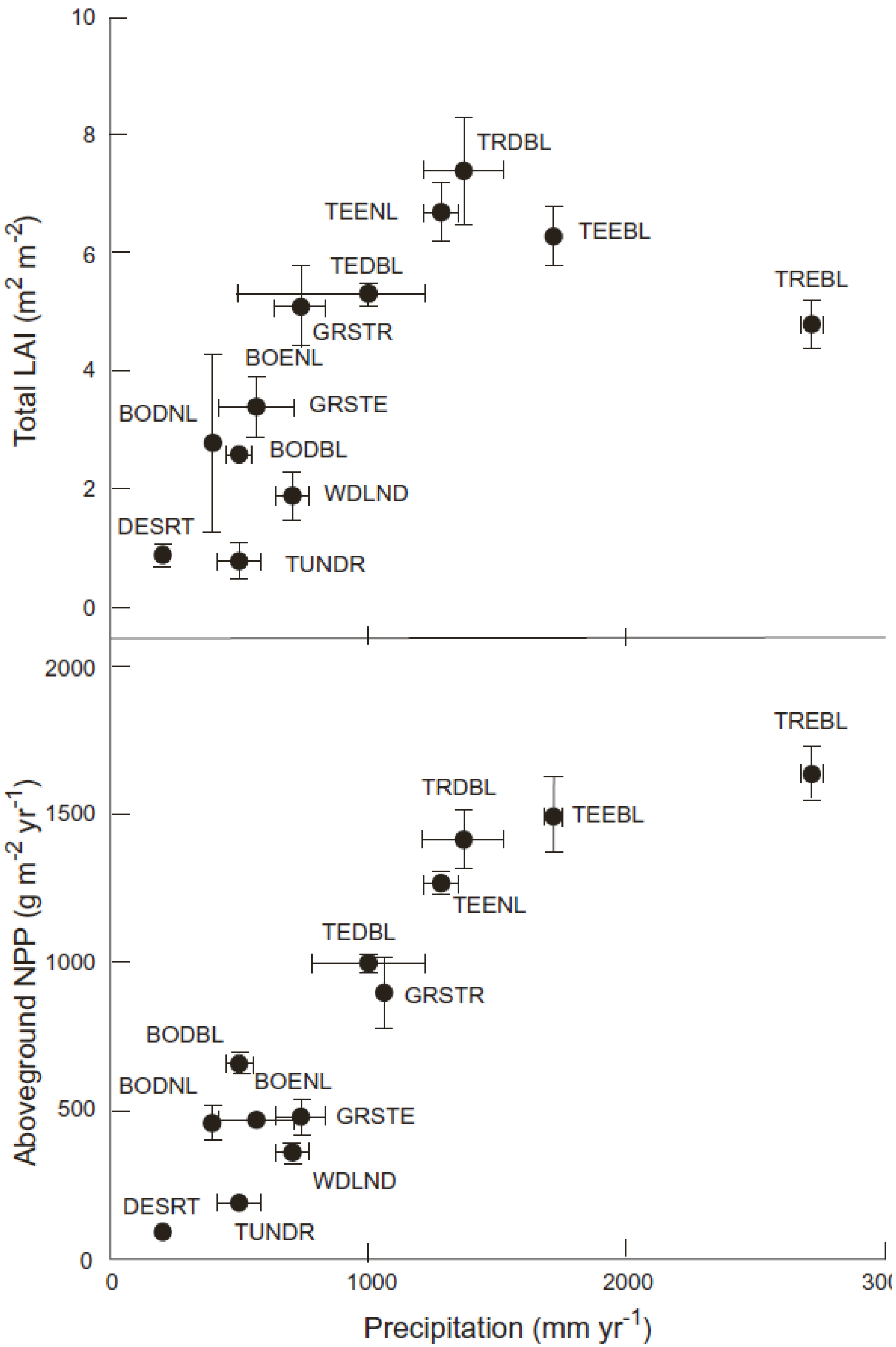


FIGURE 6.4. LAI and aboveground net primary production of major biome types as a function of precipitation. DESRT, desert; TUNDR, tundra; BOENL, boreal evergreen needle-leafed; WDLND, woodland; BODBL, boreal deciduous broad-leaved; BODNL, boreal deciduous needleleaved; GRSTE, temperate grassland; TEDBL, temperate deciduous broadleaved; TEENL, temperate evergreen needle-leafed; TRDBL, tropical deciduous broad-leafed; TREBL, tropical evergreen broadleaved; GRSTR, tropical grassland; and TEEBL, temperate evergreen broad-leafed. (Redrawn with permission from Blackwell Scientific; Gower 2002.)

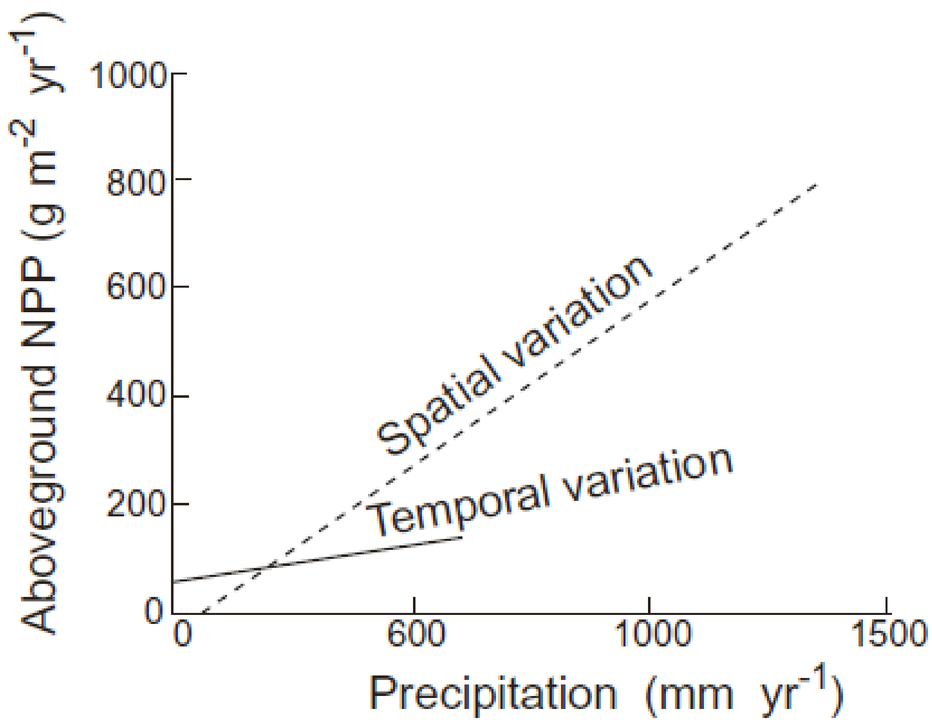


FIGURE 6.5. Correlation of grassland NPP with precipitation across grassland sites (spatial variation) and through time for a single site (temporal variation). A single site responds less to interannual variation in precipitation than would be expected from the relationship between average precipitation and average NPP across all sites, because a single site lacks the species and productive potential capable of exploiting high moisture availability. (Redrawn with permission from *Ecological Applications*; Lauenroth and Sala 1992.)

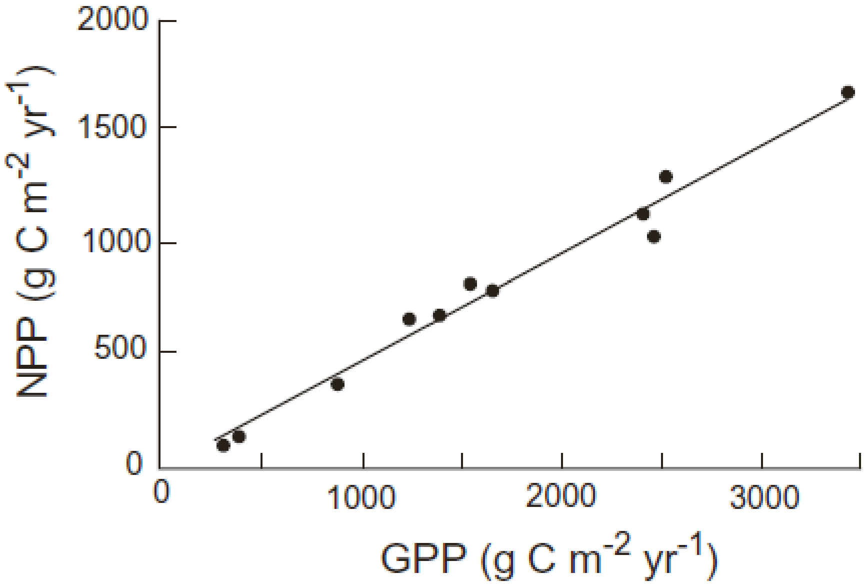


FIGURE 6.6. Relationship between GPP and NPP in 11 forests of the United States, Australia, and New Zealand (Williams et al. 1997). These forests were selected from a wide range of moisture and temperature conditions. GPP and NPP were estimated using a model of ecosystem carbon balance. The simulations suggest that all these forests show a similar partitioning of GPP between plant respiration (53%) and NPP (47%), despite large variations in climate. (Redrawn with permission from Academic Press; Waring and Running 1998.)

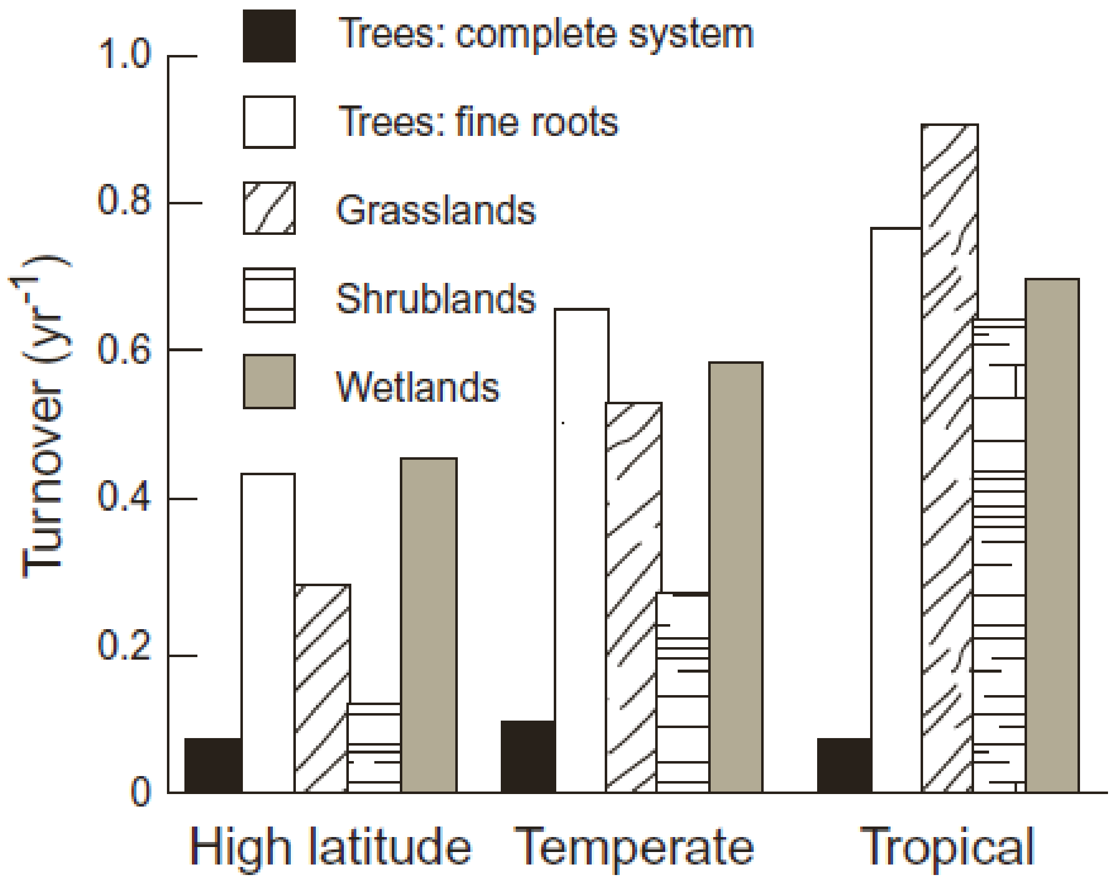


FIGURE 6.7. Synthesis of information on root turnover in major ecosystem types along a latitudinal gradient. (Redrawn with permission from *New Phytologist*; Gill and Jackson 2000.)

TABLE 6.4. Biomass distribution of the major terrestrial biomes[a].

Biome	Shoot ($g\,m^{-2}$)	Root ($g\,m^{-2}$)	Root (% of total)	Total ($g\,m^{-2}$)
Tropical forests	30,400	8,400	0.22	38,800
Temperate forests	21,000	5,700	0.21	26,700
Boreal forests	6,100	2,200	0.27	8,300
Mediterranean shrublands	6,000	6,000	0.5	12,000
Tropical savannas and grasslands	4,000	1,700	0.3	5,700
Temperate grasslands	250	500	0.67	750
Deserts	350	350	0.5	700
Arctic tundra	250	400	0.62	650
Crops	530	80	0.13	610

[a] Biomass is expressed in units of dry mass.
Data from Saugier et al. (2001).

Biome	Area (10^6 km^2)	Total C pool (Pg C)	Total NPP (Pg C yr^{-1})
Tropical forests	17.5	340	21.9
Temperate forests	10.4	139	8.1
Boreal forests	13.7	57	2.6
Mediterranean shrublands	2.8	17	1.4
Tropical savannas and grasslands	27.6	79	14.9
Temperate grasslands	15.0	6	5.6
Deserts	27.7	10	3.5
Arctic tundra	5.6	2	0.5
Crops	13.5	4	4.1
Ice	15.5		
Total	149.3	652	62.6

[a] Biomass is expressed in units of carbon, assuming that plant biomass is 50% carbon.

Data from Saugier et al. (2001).

TABLE 6.6. Productivity per day and per unit leaf area[a].

Biome	Season length[b] (days)	Daily NPP per ground area ($g\,m^{-2}\,d^{-1}$)	Total LAI[c] ($m^2\,m^{-2}$)	Daily NPP per leaf area ($g\,m^{-2}\,d^{-1}$)
Tropical forests	365	6.8	6.0	1.14
Temperate forests	250	6.2	6.0	1.03
Boreal forests	150	2.5	3.5	0.72
Mediterranean shrublands	200	5.0	2.0	2.50
Tropical savannas and grasslands	200	5.4	5.0	1.08
Temperate grasslands	150	5.0	3.5	1.43
Deserts	100	2.5	1.0	2.50
Arctic tundra	100	1.8	1.0	1.80
Crops	200	3.1	4.0	0.76

[a] Calculated from Table 6.3. NPP is expressed in units of dry mass.
[b] Estimated.
[c] Data from Gower (2002).

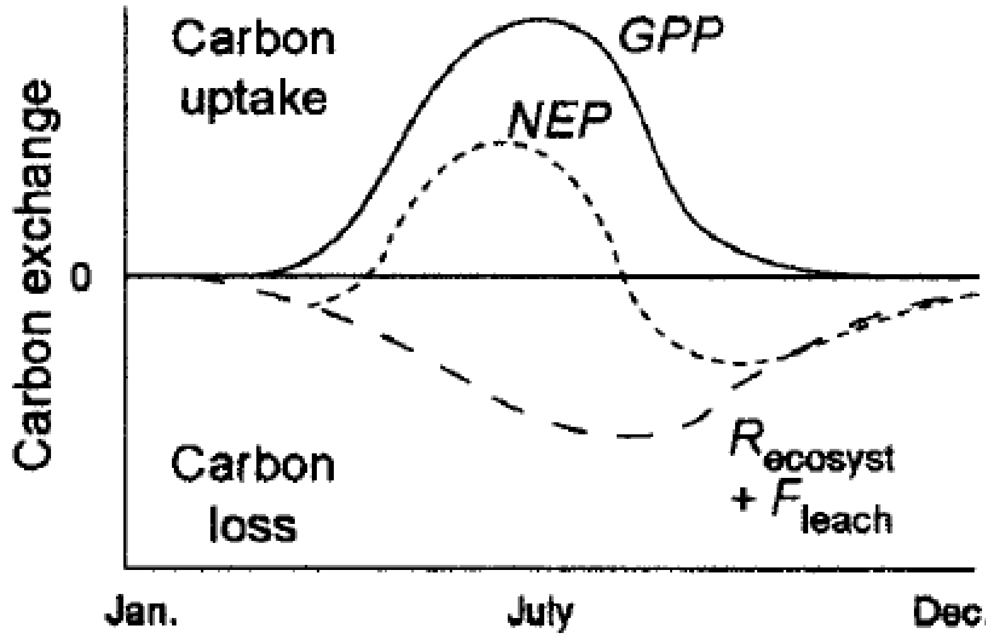


FIGURE 6.9. Representative seasonal pattern of gross primary production, ecosystem respiration, and net ecosystem production of an ecosystem. NEP is the difference between two large fluxes (carbon inputs in GPP and carbon losses, of which $R_{ecosyst}$ and F_{leach} are generally greatest). Annual CO_2 flux in this graph is at steady state because the NEP summed over the annual cycle is close to zero. Here, carbon losses due to disturbance are assumed to be zero.

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