The University of South Bohemia
Institute of Physical Biology, Nové Hrady

PhD thesis

Non-metabolic use of solar energy in plants

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17.6.2009

Mgr. Alžběta Rejšková

Annotation

Non-metabolic use of solar energy in plants can be seen as plant thermoregulation driven directly by solar irradiance. Adaptations leading to warming up are particularly important in cold habitats. Cooling processes are needed everywhere where there is short-term or long-term excess of solar energy. Plants are of utmost importance for ecosystem and landscape functioning. Vegetation has a potential to regulate the Earth's surface temperature and improve conditions for other living organisms. By regulating energy and water fluxes between land surface and the atmosphere vegetation is closely related to the climate system.

Anotace

Nemetabolické využití sluneční energie lze u rostlin považovat za termoregulační proces poháněný přímo sluneční energií. Adaptace umožňující zvýšení teploty jsou obzvlášť důležité v chladných oblastech. Chladící procesy jsou zapotřebí všude, kde bývá krátkodobě či dlouhodobě nadbytek sluneční energie. Rostliny jsou nanejvýš důležité pro fungování ekosystémů a krajiny. Vegetace má schopnost regulovat teplotu zemského povrchu a zlepšovat podmínky pro ostatní živé organizmy. Tím, že ovlivňuje toky energie a vody mezi zemským povrchem a atmosférou, je úzce svázaná s fungováním klimatického systému.

Acknowledgement

I would like to thank Jan Pokorný for providing me with new ideas, new landscapes, and new perspectives. I would also like to thank Hanka Čížková for her scientific assistance and for giving me home in Třeboň. I am much indebted to Andrea Kučerová who generously read the text and made many helpful suggestions and corrections. I am grateful to Jakub Brom and other colleagues for all their help. Furthermore I would like to thank Jan Květ and his family for the flowers in their garden and their friendship.

I would also like to thank many people in Prague. First of all my mother, father, sister, Vojtěch and friends for being so helpful, patient and supportive. Many thanks to Helena Lipavská and other colleagues from the Department of Plant Physiology, Charles University in Prague for being my scientific guides. Last but not least I want to express my thanks to the reviewers who will read this long text. I am looking forward to their comments.

This work has been supported by the Ministry of Education, Youth and Sports of the Czech Republic, under the Tokenelek project (No. 2B06023, National research programme II, 2B- Health and Quality of Life).

To Jan Pokorný (for a lot of reasons)

Non-metabolic use of solar energy in plants
Author: Alžběta Rejšková

List of abbreviations

A - CO_2 assimilation
β - Bowen ratio, $\beta=C/LE$
ab - abaxial
ad - adaxial
C - sensible heat flux, convective transfer
c_i - Intercelular space CO_2 concentration
CWSI - Crop Water Stress Index
DBH - diameter at breast height
E - transpiration rate
E_C - evaporation from canopy
E_S - evaporation from the soil
E_T - transpiration
ET - evapotranspiration
F - fluorescence
G - ground heat flux
g_a - boundary layer conductance
g_s - stomatal conductance
g_w - leaf conductance for diffusion of water vapour
In - incoming
IPCC - Intergovernmental Panel of Climate Change
IR - infrared radiation (7.5 – 13 μm)
K_L - leaf-specific conductance, i.e. hydraulic conductance normalized by leaf area
K_{leaf} - leaf hydraulic conductance
LAI - leaf area index
LE - latent heat flux
LR - long-wave radiation, > 4 μm
M - respiration reactions
NIR - near infrared region (app. 700 to 1400 nm)
Out - outgoing
PAR - photosynthetically active radiation, (400 –700 nm)
RF - radiative flux, total radiation incident on surface of Earth
R_N - net radiation flux
SPAC - Soil-Plant-Atmosphere Continuum
SR - shortwave radiation (0.1-4 μm)
TOA - top of the atmosphere
UV, UV-B ultraviolet radiation
VPD - water vapour pressure deficit
ψ_{air} - water potential of the air
ψ_{leaf} - water potential of leaf
ψ_{root} water potential of root
ψ_{soil} water potential of the soil
$\Delta\Psi_{plant}$ - water potential gradient from roots to shoots

1. Introduction

Non-metabolic use of solar energy in plants, as presented in the following text, can be seen as plant thermoregulation, i.e. warming and cooling, driven directly by solar irradiance. Plants are often exposed to temperatures unsuitable for or limiting their growth and reproduction. Only few plants have been shown to improve their temperature through energy consuming metabolic processes. Temperature of the majority of plants seems to be wholly dependent on energy exchange with the environment. This relation, however, may be to some extent influenced by different species-specific ways of morphological, anatomical and ecological adaptations. The adaptations leading to warming up are particularly important in the cold high latitudes or high altitudes habitats. Cooling processes are needed everywhere where there is short-term or long-term excess of solar energy, be it in the tropics and hot deserts or in the high mountains during bright summer days. The cooling processes are to a large extent related to transpiration processes and as such tightly interconnected with the water cycle.

The active role of vegetation in the existing climate system is often largely overlooked. The aim of my work is to contribute to 1) quantifying non-metabolic use of solar energy in plants and 2) understanding of the role of vegetation in distribution of solar energy in the landscape.

The presented thesis consists of two parts, the text itself and attachments. The first part is a review of a broad interdisciplinary topic dealing with the non-metabolic use of solar energy in plants and ecosystems and with the role of vegetation in climate systems ranging from local to global scales. The second part, i.e. the attachments, comprises of papers dealing with the results of my research carried out in collaboration with other colleagues. The articles related to the topic of this thesis and written in English are presented in full and referred to in the text where appropriate. Other articles are attached only as abstracts.

The text of the thesis begins with an introduction of basic physical characteristics of solar radiation and water (chapters 2.1 and 2.2) in the context of ecosystems functioning. The overview is based mainly on books (Gates, 1980; Jones, 1992; Geiger, 1993; Olejnik et al., 2002; Geiger, 2003) and contains important information that serves better understanding of plant physiological and ecological features discussed in the following chapters. Although most of the information can be considered as common knowledge, it is included in the text because, according to my experience, it is not always well known to the people with scientific background in biology. Chapter 2.2.1 focuses on water cycling on Earth, with water cycle being divided into global, local and micro water cycles. Important mechanisms of micro-cycling, such as water conservation within vegetation canopy, water interception and fog water input, are suggested and relevant literature is referred to. In chapter 3, energy balance of different plant organs, i.e. of leaves, flowers (inflorescences) and stems, is described. Energy balance of fruits is not included due to the variability of plant fruits and lack of information about this topic in scientific literature. It is shown that all of the studied organs have developed some special adaptations that serve both metabolic and non-metabolic energy use optimization. Special attention is paid to leaf spectral properties and their changes, as they are usually the most influential for leaf as well as whole plants' energy balance. The discussion about energy relations in flowers and inflorescences (chapter 3.2) provides background information for one of the attached articles (Rejšková et al., 2010) on warming up and cooling down as an interesting and in plant physiology scarcely studied phenomenon. The fourth chapter considers the adaptations of plants to solar irradiance at the whole plant and canopy levels. Impacts of different structures and architecture as well as the most important life strategies of plant solar use are discussed here. Transpiration as a process of crucial importance in the plant energy balance is described. Most of the principles and examples are discussed on tree species, as due to their size, they are usually the most influential in ecosystems. In chapter 5, the dynamics of energy fluxes in stands and ecosystems with a particular focus on albedo and evapotranspiration changes are discussed. The sixth chapter draws on the facts discussed in the forgoing chapters and relates plants functioning to the climate functioning thereby contributing to the highly topical debate of climate change from the perspective of vegetation functioning within the complex climate system.

Whereas within the experimental period of my PhD. studies I realized that gaining valuable and reliable data and interpreting them in a correct manner is a laborious process. In writing the thesis I realized that translating the information into meaningful whole is actually the most demanding process of all. To integrate the results of costly research carried out in individual scientific fields into a web, which would help us understand the whole is a challenge facing modern science. While working on my PhD. I realized that to write a good scientific text, be it a short article or a voluminous book, is a very demanding task and I admire everybody capable of doing it in high quality. I have tried my best to collect as much information as possible and incorporate it in a text that would be both informative and readable. I would be greatly honoured if the reader of this thesis would find the presented text has at least partly met my objective.

2. Basic physical characteristics of solar radiation and water in the presented context

2.1 Solar radiation on the Earth

It is the energy of the Sun that enables life on Earth to run contrary to the second law of thermodynamics, to act against the universal tendency of maximizing entropy. Although the solar energy absorbed by the Earth is ultimately returned to the space as heat, it is temporarily used to create potentials instead of minimizing them, and to give rise to the incredible variability of living processes.

For a mean distance of 149.7 x 10^6 km, the intensity of solar radiation incident upon a surface perpendicular to the sun's rays measured in an aircraft above the atmosphere is 1367.7 Wm^{-2} (±2 %). This quantity is called the solar constant. It changes by about ±3.4 % with the changing distance of the Earth from the Sun during the course of the year (Geiger, 2003). The intensity of solar radiation is subjected also to solar activity. Any increase in abundance of sunspots results in an increase of emission of solar radiation. The number of sunspots reaches a maximum approximately every 11 years (Schwabe cycle), however, the amplitude of periodical function is modulated in 70-100 years (Gleissberg cycle). These changes contributed to about 0.1 – 0.6 % fluctuations in irradiance in the past 300 years (Gates, 1993). From a longer perspective the incidence of radiation on the Earth and its distribution has been changed with changing characteristics of the planet motion around the star, namely with the changes of eccentricity, obliquity and precession with possibly dramatic consequences for the climate.

According to the Stefan-Boltzmann law of radiation, all blackbodies radiate so that the flux density of emitted radiation summed over all wavelengths is proportional to the fourth power of the absolute temperature of the surface.

$$E= \varepsilon\sigma(T_s)^4 \qquad \text{eq. 1}$$

where T_s is temperature of the surface in K (K= 273,15 + °C), ε is emissivity, and σ is Stefan-Boltzmann constant ($5.675 * 10^{-8} W\ m^{-2}\ K^{-4}$). A blackbody is a substance which both absorbs and emits all radiation in the continuous spectrum. Its emissivity equals 1. The emissivity of natural materials is lower than 1 and the objects of such qualities are called grey bodies. Some natural materials approach the features of blackbodies in some parts of their spectra. The maximum intensity of radiation of the body may be calculated from Wien's displacement law.

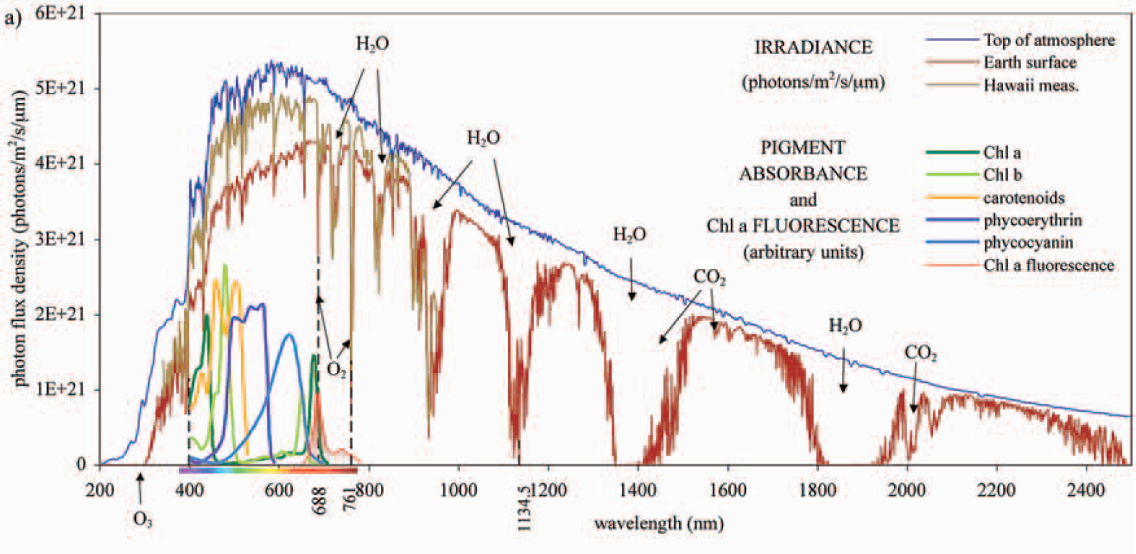
$$\lambda_{max} = 2897/T_s \text{ (in microns)} \qquad \text{eq. 2}$$

where λ_{max} is the maximum intensity of radiation. The higher the temperature of the body, the more is the maximum of its radiation displaced toward shorter waves. The emission spectrum of a blackbody is highly asymmetric. Therefore another useful parameter is the median wavelength λ_m, which divides the emitted energy into two equal portions.

$\lambda_m = 4110/T_s$ eq. 3

According to our common physical assumptions the radiation emitted by the Earth will be in a radiative equilibrium with radiation received from the Sun. Although quantitatively the same, the incoming and outgoing radiation to and from the Earth differs fundamentally in spectral qualities as follows from above. The radiation emitted from the Sun with its surface temperature of approximately 5780 K, has the peak at about 0.5μm, which implies that the most intense solar radiation occurs in blue-green range of visible light (Figure 1). The Earth with its surface temperature of 287 K emits the maximum of energy at about 10 μm, i.e. in the infrared region. A median wavelength of the Sun is thus 0.71 μm and that of the Earth is 14.3 μm. About 99% of solar radiation is in the range from 0.15 to 4.0 μm, whereas radiation emitted by the Earth and its atmosphere lies between 3.0 and 100 μm. Thus the two emission spectra overlap only between 3.0 and 4.0 μm, where there is only about 1% of the total output of the radiation of both bodies. Based on this fact the wavelength 4.0 μm is usually used as the division between shortwave (solar) and longwave (terrestrial) radiation. (Geiger, 2003).

Figure 1. Solar spectral photon flux densities at the top of the Earth's atmosphere and at the Earth's surface, and in vivo estimated absorption spectra of photosynthetic pigments of plants and algae. According to Kiang et al., 2007.



The maximum irradiance (at midday) commonly lies between 800 and 1000 W m^{-2} during the growing season over much of the Earth's surface. This indicates that approximately 25 to 40 % of energy incident on the upper layer of the atmosphere (mean solar constant) is reflected, scattered or absorbed in the atmosphere and does not reach the surface. The absorption of radiation in the atmosphere is markedly wavelength dependent. High proportion of ultraviolet radiation especially of the shortest wavelengths is absorbed in the atmosphere. As there is an atmospheric window in the visible/ photosynthetically active radiation PAR, the atmosphere is mostly transparent for radiation in this region. When we approach shortwave and longwave infrared regions, the atmosphere becomes opaque again, especially in some wavelength regions. This is mostly due to water molecules and other “greenhouse gases” (i.e. gases with high absorption of radiation in the IR part of the spectrum) present in the atmosphere. The absorption of radiation in the atmosphere is a function of two variables: a) path length through the atmosphere which the solar beam has to wing and b) the content of absorbers present in the atmosphere, where by far the most varying and dynamic is water vapour. Light on its way through the atmosphere is not only absorbed but also scattered on molecules and particles. There are two types of scattering: Rayleigh scattering by molecules smaller than the wavelength of light, which is most effective for shorter wavelengths and causes therefore the sky to be blue; and Mie scattering by larger particles such as dust and water droplets which is relatively wavelength independent (Jones, 1992).

Through changing the chemical composition and particles content of the atmosphere, especially of its lowest layer troposphere, the spectrum as well as the amount of radiation coming on the surface can be changed. These changes have become lately a hot topic in connection to global warming. Materials produced by the Intergovernmental Panel of Climate Change (IPCC, 2007) describe these changes using a term radiative forcing. It is a measure of influence a factor has in altering the balance of incoming and outgoing energy in the Earth-atmosphere system. It expresses the change relative to preindustrial conditions in the year 1750. The radiative forcing of greenhouse gases is positive because molecules absorb parts of the spectrum in specific long-wave IR and by reemitting the radiation in all directions part of the energy is returned to the surface instead of leaving the atmosphere. This process has been described as a principle of recent climate warming (IPCC, 2007). The larger particles, on the contrary, cause negative radiative forcing (i.e. cooling effect) because they are shading the surface by dimming the incoming radiation. According to IPCC (2007) the combined average net effect of human activities since 1750 has caused radiative forcing to increase by 0.6-2.4 Wm^{-2}.

About 45 % of the energy brought by the light incident on the surface is brought by radiation from the photosynthetically active radiation (PAR) region (400-700 nm). The ultraviolet (UV) radiation has highest energy content per moles of photon, but due to its small portion it represents only 7 % in the total radiation. The remaining 48 % of energy is brought by the photons in the IR region, mainly in the short IR region as energy content markedly decreases with the longer wavelength of the spectrum (Gates, 1993).

An important component of radiation balance in the ecosystems is - apart from the direct sunlight - also the diffuse radiation, i.e. sum of scattered, reflected or transmitted radiation coming randomly from all directions, i.e. from the sky as well as from the ground. Even when the sky is clear, between 10 and 30 % of total solar irradiance is diffuse radiation. The proportion of diffuse radiation is much lower in drier climates. The diffuse radiation may be used in the ecosystems with higher efficiency as it tends to be enriched in the visible wavelengths. The average proportion of direct plus diffuse radiation in the PAR is thus approximately 50 %.

2.1.1 Energy exchange between the Earth's surface and the atmosphere, energy distribution in ecosystems

Not all the energy incident on the Earth surface serves for direct use in ecosystems. The net flux of all radiation (shortwave and longwave) across unit area of a plane is called net radiation (R_N) (Jones, 1992). It is the sum of all incoming radiation minus all outgoing radiation reflected from the surface. Solar energy is heterogeneously absorbed by the Earth's surface according to the characteristics of the surface cover. Part of the energy is reflected straight away after the incidence. The ratio of reflected to incident radiation is called albedo. It differs substantially according to the absorptive characteristics of the surface. Dark surfaces such as water surfaces, wet soil or vegetation strongly absorb solar irradiance whereas light surfaces such as snow, dry soils or sand are more reflective (Gates, 1993). The values of albedo in natural habitats spans from only a couple of units of percent for some dark and wet surfaces to more than 90 % for clean snow. Also in this case we mustn't forget that reflective features of materials are wavelength dependent (albedo is in more details discussed in chapter 5.1).

Because IR part of the radiation spectra also contributes to radiation balance of the ecosystems, net radiation is influenced by meteorological factors which affect the surface temperature such as wind speed, humidity and leaf resistance (Jones, 1992). As the net input of IR radiation into the system is given by the energy balance between the surface and the environment, it is also dependent on the radiation characteristics of the surroundings, in particular the sky. The sky is commonly colder than the Earth's surface which results in energy loss from the surface. The temperature and simultaneously the emission of radiation from the sky depend tightly on the extent of cloud cover. Based on empirical results Jones (1992) stated that clear sky behaves approximately as a black body with its temperature about 20 °C below the temperature in the meteorological screen. Clouds are more effective emitters and have a mean radiative temperature that averages only about 2 °C below the mean screen temperature. This is however a simplified concept. To date the temperature of the sky may be estimated according to the Stefan-Boltzmann law (eq.1) from energy balance measured by net radiometers. Using this method Novák (2008) showed that the sky temperature as manifested at the Earth surface and consequently the difference between the surface temperature and temperature of the sky may differ substantially throughout the day. This is partly caused by near surface meteorological conditions such as haze or fog. The net IR balance is closely related to the temperature of the surface. Although also this method is probably at least partly inconsistent, for example because we do not know what is the temperature we actually measure and because we assume that the sky is a black body, it enables us to measure net energy balance in its temporal and spatial dynamics.

Net radiation in an ecosystem is divided in varying proportions into four parts. These are latent heat flux, sensible heat flux, ground heat flux and storage of energy. The partition of net radiation into these four processes depends on both physical and biological factors. In general, the structure of heat balance is formed mainly by three factors: a) amount of solar energy reaching the active surface depending on latitude and seasonal/daily course of sunshine, b) physical features of the active surface, mainly richness and structure of the plant cover and c) habitat moisture (Olejnik et al., 2002).

Latent heat flux (LE) represents the energy used for evaporation of water from the surface. The amount of energy released or absorbed by a substance during a change of phase (i.e. solid, liquid, gas) is called latent heat of vaporisation of water. The term latent means hidden because the supplied energy is not expressed by rising temperature, it is used for the phase transition. The transition of liquid to gas phase is an endothermic reaction, i.e. it is accompanied by energy consumption and thus local cooling. On the contrary, condensation is an exothermic process attended by energy release and local warming. The dynamic system of phase transitions of water plays a crucial role in thermoregulation of living systems as will be shown in the following chapters.

Sensible heat flux (C) represents the sum of all heat exchange between the surface and the surroundings by conduction or convection. It is positive when surface is warmer than the surroundings and heat is lost from it and negative in the opposite way. Its proportion in the energy balance of an ecosystem grows extensively when water is not available and latent heat decreases.

The third energy flow in an ecosystem is the ground heat flux (G). It is positive when the ground is warming, i.e. when it takes energy from its surroundings. G is commonly positive during day and negative during night. The heat balance is usually moderately positive during warm periods of year and moderately negative in the cold periods making the net yearly ground heat flux approaching zero. During day of growing period G ranges from 2 % of R_N in the dense canopy to more than 30 % of R_N in sparse canopies with little shading of the soil (Jones, 1992). In addition to shading plants may contribute to the insulation of the soil from the energy coming from the surroundings when a thick layer of dry organic matter covers the surface (especially in spring). The magnitude of G depends also on the physical characteristics of the soil or material covering the surface. The water content in the soil is an important factor, as water is a good heat conductor.

The absorbed energy is partly stored in the processes running on the Earth's surface, in particular those taking place in living systems. The energy stored in vegetation is the last and markedly smallest part of R_N. Principally there are two energy sinks within a plant stand: a) metabolic sink where energy is stored in chemical bonds of bio-molecules and b) physical sink which represents the heating of the plant material itself. The sum of the two fluxes is usually so small that it can be neglected when the energy fluxes are studied in the landscape.

Net photosynthesis of ecosystems is an integral value of photosynthesis of the whole canopy. Leaf area index (LAI, i.e. number of equivalent layers of leaves the vegetation displays relative to a unit ground area) of a canopy reaches usually values between 3 and 9. In a closed canopy ecosystems maximum net photosynthesis rates would be about 1.6-2.2 mg CO_2 $m^{-2}s^{-1}$ (Šetlík et al.) which equals about 1.0-1.4 mg $m^{-2}s^{-1}$ of sucrose ($C_{12}H_{22}0_{11}$), the immediate product of photosynthesis. The energy content of sucrose is 16.7 kJ g^{-1} or 480 kJ mol^{-1}. It follows that when vegetation photosynthesizes at its maximum, 17.0-23.4 J of energy is fixed every second per every square meter of the canopy. In other words maximum actual net energy flux into photosynthesis is commonly 17.0-23.4 Wm^{-2}. This represents only about 1.7-2.3 % of the total summer irradiance of 1000 Wm^{-2} and about 2.4-3.3 % of net radiation, on assumption that this would be approximately 700 Wm^{-2}.

The above ground biomass of clover we harvested in May 2008 contained approximately 2 kg of water on one square meter. If we assume that the surface warmed up 4 °C per hour and knowing that heat capacity of water is 4184 J $kg^{-1}K^{-1}$ (at 20 °C) we can conclude that the heat flux sustaining warming up of the biomass was approximately 10 Wm^{-2}. This value represented again only a minor part, 1 and 1.4 % of total incoming radiation and net radiation respectively. From these examples we see that energy stored in vegetation represents only units of per cents of both total and net radiation.

Distribution of energy into flows mentioned above differs markedly according to the surface spectral characteristics and water availability. Soil and air heat fluxes depend mainly on temperature gradients existing in the air and surface strata near the active surface, which in turn is related to the density and structure of the plant cover. An active surface is any surface through which energy and matter are passing and simultaneously changing its characteristics (Olejnik et al., 2002). Especially the two largest flows, i.e. latent heat flux and sensible heat flux, may consume up to 80 % of net radiation, meaning that one or the other is concurrently suppressed to almost zero. The distribution is closely related to water abundance in the ecosystem, which is a precondition for evapotranspiration. This argument may not be relevant in areas where the air relative humidity approaches 100 %. In this situation the non-existent gradient of vapour pressure deficit between surface and air does not enable latent heat flux to be high. However under common situations the areas with sufficient water storage consume a large amount of solar energy in the transpiration process whereas dry areas heat up extensively during high solar input. These differences are very important in the energy relations of landscape and may have a lot of environmental consequences. The heterogeneity of energy fluxes gives rise to weather patterns (Gates, 1993). The energy balance of an ecosystem may be also highly influenced by supplementary energy brought with advection air, particularly dry and warm air. Advection represents the horizontal flow of energy applied to the layer of air close to the surface.

2.2 Water characteristics important in the biosphere and water cycle

Water creates the life-enabling milieu and takes part in all living processes (e.g. Ripl, 2003). The simple but unique structure makes water a substance of many characteristic features, which distinguish it from other elementary substances and assign it a crucial role for the existence of life. Water is the only substance on the Earth that is present in all three states - gaseous, liquid and solid. The electric charge arrangement in tetrahedron around the central oxygen atom and the dipole structure makes water organize itself in a dynamic network of molecules connected by hydrogen bonds. This network structure influences all chemical and physical features of water. It is also the reason why liquid as well as solid phases of water exhibit an extraordinary high number of structural forms (Ludwig and Paschek, 2005).

Water has the highest surface tension of non-metallic liquids. Strong cohesive properties which hold the water column together and strong adhesive properties which stick the water to wettable surfaces make water resistant to tension rupture. These features are a prerequisite for important physiological and physical processes in nature, in particular transpiration pull in plants and water capillarity in soil (ability of soil to hold water). Due to strong cohesive and adhesive forces water effectively counteracts gravity. Strong cohesive properties also make water create droplets.

The best known anomaly of water is its maximum density in its fluid state at the temperature of 277 K (4 °C). Another anomaly of water is that the density of ice is lower than the density of water at the freezing point. These features cause water to freeze from the surface and not from the bottom thus enabling the aquatic life to survive freezing conditions in the layer of the heaviest water close to the bed. As follows from above, the expansion of water (change of volume with temperature) is low and it does not simply increase with rising temperature. It first decreases to roughly 4 °C where water has its maximum density and increases only from this point. Materials, which have negative expansion within limited temperature ranges (or in other words contract with an increase of temperature although only within limited temperature ranges), are very rare.

Water has very high heat capacity, i.e. the heat energy required to increase the temperature of an object by a certain temperature interval. The heat capacity of water at constant pressure changes with temperature having its minimum at 311 K. It is particularly high in the under-cooled temperature region. As water occupies commonly 80 to 90 % of volume of living organisms it largely determines their heat capacity as has been mentioned already. Having high heat capacity means being rather robust against temperature changes because a lot of energy has to be absorbed to get warmer or lost to get cooler (Olejnik et al., 2002). More than 70 % of the Earth's surface is covered by oceans. To warm or cool these large masses of water large fluxes of energy are needed. So, water stabilizes the temperature conditions of the Earth as the large heat capacity of the oceans and seas act as heat buffers.

Concurrently, unusual amount of energy is needed also for the phase transitions of water because a lot of energy is needed for breaking the hydrogen bonds. The amount of energy needed to vaporize water (latent heat of vaporization) is temperature dependent. The higher the temperature the less energy is needed for vaporizing water. The latent heats of water for temperatures common in nature according to Gates (1980) are presented in column E of table 1.

Table 1. Changes in density of dry (B) and water vapour saturated (C) air, in water content in saturated air (D) and in latent heat of water (E) with increasing temperature.

A	B	C	D	E
Temperature (°C)	Density of dry air (kg m^{-3})	Density of saturated air (kg m^{-3})	Water content in saturated air (g)	Latent heat (MJ/kg)
0	1.292	1.289	4.80	2.501
5	1.269	1.265	6.74	2.489
10	1.246	1.240	9.33	2.477
15	1.225	1.217	12.75	2.465
20	1.204	1.194	17.19	2.454
25	1.183	1.169	22.90	2.442
30	1.164	1.145	30.18	2.430
35	1.146	1.121	39.36	2.418
40	1.128	1.096	50.81	2.406
45	1.110	1.068	64.97	2.394

The physical anomalies of water are fundamental for water functioning in nature. Unlike with other liquids the diffusion coefficient of water at constant temperature rises with increasing pressure and only later begins to decrease as is common for other liquids. Also viscosity of water is anomalous. Although it decreases exponentially with temperature, unlike other liquids it first decreases with increasing pressure and only when the pressure exceeds 200 MPa it rises linearly with rising pressure. The compressibility of water causes the sea level to be reduced by about 40 m giving us 5 % more land. All parameters describing the physical and chemical features are reviewed at http://www.lsbu.ac.uk/water/anmlies.html#65

Spectral characteristics are equally essential for the functioning of water in nature. Strong absorption of water in the microwave region is caused by excitation of molecular rotations. In the infrared range water exhibits strong absorptions caused by stimulated vibrations of its molecules. Around the visible region water exhibits a narrow window of transparency. In the UV (10-400 nm) and in x-rays (<10 nm) regions water is again a strong absorber due to successively photoelectric effect, Compton scattering and finally pair production. As plants have high water content, their absorption characteristics are substantially influenced by water (see chapter 3.1.1). Absorption features of water also largely influence light conditions in aquatic systems. As water intensively absorbs red radiation, it is the blue light that penetrates through water most.

Physical and chemical properties of water are crucial also in the atmospheric processes of movement of air masses (parcels), forming clouds and precipitation. The density of air decreases when it is saturated with water vapour (see table 1, column B and C). However, the decrease is only minor if compared with the decrease of air density due to temperature. As the temperature lapse rate (i.e. change of temperature with height) may be high, it is the temperature which under common conditions predominantly influences the movement of air parcels and the change of density due to different water vapour content plays only a small role. On the other hand the temperature of an air parcel is substantially influenced by water, as due to phase changes of water, large amounts of energy may be released or consumed, resulting in cooling or warming of the air. Therefore, water has a substantial impact on convective movements of clouds although not directly through changing density of the air (see chapter 6.1). As the absolute amount of water contained in the saturated air rises markedly with the air temperature, via convective movement much more water is carried to the atmosphere with warm air than with cold air (table 1, column D).

Water is involved in many processes of solar energy dissipation on different levels in both time and space. From the quantity point of view the most important process is the cyclic process of evaporation and precipitation (condensation), which cools hot spots and warms cold spots through energy consumption or release in phase transition. Energy is dissipated also at subcellular level in all chemical dissolution and crystallization processes and within the cells of living organisms also in processes of water disintegration and recombination – carbon fixation and respiration (Ripl, 2003).

2.2.1 Long, short and micro water cycles

The hydrological cycle describes water phase transitions and its movement in the atmosphere, hydrosphere, lithosphere and biosphere. About 96.5 % of the Earth's water resides in the oceans. Only the remaining 3.5 % of water are present on land, most of it within the glaciers and ice caps and deep groundwater. So the surface water, shallow groundwater, soil moisture and water included in the biosphere represents only a small fraction of the total water budget. The amount of water present in the atmosphere is even by two orders lower (Kuchment, 2004). The small absolute amount may appear insignificant in terms of the importance of terrestrial and atmospheric water for climate on the Earth. However, the dynamics and the high turnover of processes in which water is involved, its functioning in the living world and its capability of transferring large amounts of heat make water on land and in the atmosphere a substance of inevitable importance for the whole planetary system.

The hydrological cycle is powered by solar and gravitational forces. Based on the review by Kuchment (2004) about 36 % of solar energy absorbed by the Earth is used globally for evaporation of water. The evaporated water usually remains in the atmosphere for only about 8–10 days before it falls back to the surface as precipitation. About 85 % of water is evaporated from the oceans, only the remaining 15 % from the land. The average annual evaporation from the ocean surface unit area is 1400 mm and for the land approximately three times less. Evaporation from the oceans is highest during the autumn–winter period, when the water surface is warmer than the air. In summer, the water surface becomes colder than the air and evaporation is low and in some areas even condensation occurs. The total annual evaporation from the ocean surface is larger than the precipitation. The surplus of the evaporated water is transported by air currents from the oceans to the continents. About 40 % of the precipitation falling over continents returns to the oceans as river runoff, or as direct groundwater discharge to the oceans. The transport of water between the ocean and the land areas is called the global water cycle. About 60 % of terrestrial precipitation is re-evaporated. Exchange of water between land and the atmosphere constitutes the terrestrial water cycle. According to Kuchment (2004), the water transported from the oceans is on average recycled and precipitated 2.7 times over land before it runs back to the oceans. The mean annual precipitation over the Earth's land is about 800 mm. The least precipitation occurs in Antarctica (about 178 mm), and in Australia (456 mm). The most humid area is South America, where the mean annual precipitation is about 1600 mm. The distance from a moisture source is another important factor in the continental distribution of precipitations (Makarieva and Gorshkov, 2007). Precipitation is impacted by orography which influences ascent of air parcels to colder areas and thus supports precipitation in some places. Preferential precipitation is considered by some authors also in relation to the lower surface temperature or surface moisture (e.g. Ripl, 2003; Bisselink and Dolman, 2009; see chapter 6.1.1).

The terminology for describing different parts of hydrological cycle is not quite consistent in literature. Ripl (2003) uses the term long or open water cycle for the global water cycle. He then calls the terrestrial cycle short cycle to refer to the exchange of water between the atmosphere and land or ocean solely, without connecting these two systems. More commonly used alternative for terrestrial water cycle is the term local hydrological cycle (Kedziora and Olejnik, 2002). In my opinion these two scales are not sufficient to describe the whole system of water cycling on the Earth, in particular on its terrestrial part. This model lacks a more detailed level of water cycle. Following the hierarchical system of description, i.e. going from global to local, Kedziora and Olejnik (2002) introduced an apt term “micro water cycle” that depicts the water which circulates between top soil layers and near surface layers of the atmosphere within plant communities and near them.

Studying the processes involved in water cycling within ecosystems is very difficult. The relationship between the structure of plant cover and the structure of water balance remains one of the insufficiently recognized problems within landscape ecology (Kedziora and Olejnik, 2002). The micro cycling of water is rarely considered, although its impacts on microclimatological conditions cannot be disproved. The trunk area of a dense forest remains cool and moist during day if compared with the warmth of the crown area and out of the forest (von Glasow and Bott, 1999; Makarieva et al., 2006). It is due to the lower insolation, reduced mixing of the air aloft in the stand sheltered against wind and relatively high evaporation from the vegetation surface. On the contrary, during the night the bottom part of the forest remains warmer, because it is the crowns that are exposed to the sky and that are exposed to radiative cooling (von Glasow and Bott, 1999; Makarieva et al., 2006). The denser the vegetation, the smaller the fluctuations of air moisture as well as soil temperatures and air temperatures near the ground (von Glasow and Bott, 1999). As the vegetative covering increases the microclimate becomes milder (Geiger, 2003). Air temperature in natural forest ecosystems with well-developed closed canopies increases during daytime in upward direction, because the crowns are heated by absorption of solar radiation (Makarieva et al., 2006). Air temperature lapse rate (for definition see chapter 6.1) becomes negative (temperature inversion). Therefore water vapour under canopy remains in aerostatic equilibrium, upward fluxes from beneath the canopy are absent and ground surface remains always wet. Partial pressure of water vapour remains practically constant under the canopy and relative humidity which is equal to 100% immediately above the surface of the wet soil decreases with height. Aerostatic equilibrium here prevents abundant losses of soil water to the atmosphere. At night the temperature lapse rate under the canopy is very high because of the rapid cooling of the crowns and water vapour becomes saturated in the whole column. Above the closed canopy, similarly to the situation in open areas, night time temperature inversions are common, which leads to condensation of water (fog). Whereas the water condensed near the ground in open areas is lost from the ecosystem as soon as the sun rises the following day, fog formed above the canopy at least partly gravitates to the ground where it is prevented from leaking to the atmosphere during the day. The described system functions properly only in high forest stands with closed canopies. The authors (Makarieva et al., 2006) argued that recovery of such natural, closed canopy ecosystems in wide areas could intensify the water cycle on land.

According to Ripl (2003) the micro cycling of water, or in the author's own words the short-circuited water cycle between evapotranspiration and precipitation, is the most crucial stabilizing process in landscape and its plentiful presence is a sign of landscape long-term stability. Cooling and warming through evaporation-precipitation processes regulate temperature extremes in the landscape in both time (day-night) and space (hot spots, cold spots) fluctuations. Minimising temperature potentials in landscape supports more balanced microclimatic conditions near surface without excessive convective processes. Micro cycling of water in landscape is closely related to vegetation functioning. First, vegetation itself as well as debris and humus layers of the upper soil zone disposes of large water retention capacity. Second, the evapotranspiration-condensation process is optimized under and within vegetation canopy, especially in the foliage of trees where leaves serve as both evaporating and cooling structures (Ripl et al., 2004). Thus vegetation break down or elimination can be detrimental to functioning of landscape and can lead to desertification (Ripl, 2003) (see also chapter 6).

2.2.1.1 Interception and fog importance for local water cycle

Because of its large and varied surface (rugged canopy structure, large leaf area index) vegetation can efficiently intercept water droplets or highly condensed water vapour straight from the air (Dawson, 1998; Ripl, 2003). This process is most marked in tall vegetation of many coastal and montane areas regardless of climatic zone (Bruijnzeel et al., 2005). Fog inputs via canopy drip in summer was shown to constitute 30% or more of the total water input in redwood *Sequoia sempervirens* (D. Don) forests in coastal California. Water droplets were even directly absorbed by leaves of this species and caused the xylem sap transport to reverse in direction during heavy fog events. (Burgess and Dawson, 2004). Fog interception for a range of evergreen types forests across the humid tropical to subtropical and warm-temperate "maritime" climatic spectrum exhibits a fairly narrow range between 0.95 – 2.45 mm d^{-1}, net fog interception (lowered by the effect of wet-surface evaporation) being 0.65 – 2.15 mm d^{-1}. Holwerda et al. (2006) estimated fog deposition in a 3 m tall Puerto Rican elfin cloud forest to be approximately 783 mm y^{-1}, which corresponded to 18 % of the annual rainfall showing that the fog deposition to the forest may represent a substantial part of annual water budget. Dawson (1998) stated that in California redwood coastal forest fog interception input represented 34 % of the overall annual hydrologic input. Absence of coastal forests reduced fog drip fraction on total hydrological input by 17 %. Bruijnzeel (2005) suggested that cloud forests tend to have enhanced water yields due to added moisture inputs from cloud interception and somewhat lower water use. Diminished dry season stream flows have been reported for various parts of the tropics that experienced a considerable reduction in montane forest cover (Bruijnzeel, 2005). Although it is difficult to directly attribute the hydrological changes to the loss of the fog stripping capacity of the former forest, reduced infiltration and water retention capacities of the soil due to erosion after forest clearance or diminished rainfall related to larger-scale climatic fluctuations, it is highly probable that this change is connected with the changes in vegetation cover. Although this may not hold true everywhere (Cameron et al., 1997) the importance of fog deposition by natural vegetation seems to be of large importance for the catchments in question (Bruijnzeel, 2005).

In the inland non-mountainous areas the most common type of fog is radiation fog (Bruijnzeel et al., 2005). It develops under stable atmospheric conditions when temperature inversion is present near the surface due to long-wave radiative cooling of the atmospheric surface layer, which reduces the air temperature below dew point. Although fog inputs are highly variable in time and space, fog evolves mostly during night or early in the morning in moist areas as a consequence of a combination of sufficient cooling and an adequate supply of atmospheric moisture (Bruijnzeel et al., 2005). In their numerical model, Von Glasow and Bott (1999) described the influence of tall vegetation on fog radiation development in evergreen forest under geographical latitude 50° at the end of October. They depicted evolution of radiation fog as a four-stage process. Fog starts to form in the evening in the most dense vegetation layers where radiative cooling is highest and relative air humidity grows quickly. In the second stage fog disperses throughout vegetation, in the third stage it grows above the vegetation. The last stage is the fog dispersal after sunrise due to enhanced turbulent fluxes as a consequence of air heating. Fog water is deposited in vegetation via sedimentation (i.e. due to gravitational settlement of droplets) and impaction (interception of fog droplets driven horizontally by wind). At low wind speeds typical for radiation fog, sedimentation is the dominant process for fog water interception, at higher wind speeds interception prevails. The authors estimated the hydrological input of sedimentation and impaction to be 1.8 - 4.5 and 0.5 -1.5 g m^{-2} h^{-1}, respectively. Big droplets can be formed on the needles and accumulated at the base of twigs so that fog drip may be present even if the maximum storage capacity of the leaf is not exceeded (von Glasow and Bott, 1999). Vautard et al. (2009) published recently a study in which they show that frequency of low-visibility conditions such as fog, mist and haze has massively (of about 50 %) declined in Europe over the past 30 years in all seasons. The authors assigned this trend to air-quality improvements. In my opinion, a potential decrease of horizontal precipitation due to decreased air humidity as a consequence of landscape progressive drainage should be also considered. Von Glasow and Bott (1999) showed that fog formation is delayed and its height is lowered if moisture flux from vegetation is reduced. Formation of inland fog is dependent on local sources of water vapour that are through transpiration tightly bound to present vegetation and its functioning.

3. Non-metabolic use of solar energy in different plant organs

Every aboveground plant organ is submitted at least to a small amount of solar radiation. Its optimal distribution is crucial for the organ and subsequently the plant functioning. The temperature of an organism is a manifestation of its energy balance. Plants show only limited means of thermoregulation and their temperature is to a large extent subordinated to the actual conditions of their surroundings; however, at least to a certain extent they are capable of actively using solar energy for improving their temperature comfort. Mechanisms of energy use optimization vary, incorporating both physiological and morphological (anatomical) adaptations.

3.1 Leaves

Leaves, as the main photosynthetic organs, represent the largest area of the aboveground part of most plants. In connection with their function leaves often occupy places exposed to direct solar radiation. As already mentioned in chapter 2.1.1, only units of solar energy are used in the processes of photosynthesis. Therefore leaves have to be able to cope with surplus of solar radiation to maintain a balanced energy budget. Most chemical and biological processes in the living world are temperature dependent. The temperature of leaves is therefore a very important parameter in plant physiology.

3.1.1 Optical features and radiation balance of leaves

Energy budget of a leaf is primarily dependent on solar energy input. Leaves are plant organs of photosynthetic processes and this fact is strongly reflected in their absorption spectrum. Uptake of light by leaves is regulated at multiple levels. Intensity of absorbed light is regulated by leaf orientation (vertical to horizontal), leaf macro-structural properties (leaf thickness and size, stomatal density, leaf veination, cell shapes and sizes, air spaces distribution in the tissue etc.) and biochemical composition (Ustin et al., 2001; Kiang et al., 2007). How and why the optical properties of pigments, cell membranes, and cell walls evolved the way they did is still not well understood (Jacquemoud and Ustin, 2001), however, the characteristics observed on a whole range of photosynthetically active organisms suggest that the evolution of plant optical features was not random (Kiang et al., 2007).

3.1.1.1 Absorption spectra of leaves

The absorption spectrum characteristics of vegetation are influenced primarily by biochemical composition of leaf. Correspondingly, the intensity of reflectance at specific spectral bands can give information on leaf chemistry (e.g. Levizou et al., 2005). The most influential substances for leaves absorption are chlorophylls and water, although other chemical components, in particularly other pigments, may also play a substantial role (Gates, 1980). Absorption of photons is caused by changes in spin and angular momentum of electrons, by transitions between orbital states of electrons in particular atoms and by vibrational-rotational modes within polyatomic molecules (Blankenship, 2002). To a large extent absorption spectrum is influenced also by light scattering within the leaf. An extensive bibliography of works on leaf optical properties published before 1996 was compiled by Jacquemoud (1996). The list is available on http://www2.geog.ucl.ac.uk/~mdisney/leaf.html. Most common methods of studying leaf optical properties were summed up by Jacquemoud and Ustin (2001).

Although leaves are very variable in their form and their optical properties are influenced by many factors, changes in leaf absorptance in a major fraction of flora are surprisingly little (Ehleringer and Comstock, 1989). Likewise, leaf optical features are not clearly differentiated according to different environments. Knapp and Carter (1998) found no marked overall differences in leaf optical properties between groups of sun and shade temperate species although the differences between individual species were observable. The authors found average absorptance in the visible spectrum (400 –700 nm) to be 87 % in understory leaves and 83 % in species of opened sites and average reflectance in the near infrared region (750–850 nm) to be 48 % and 51 % in leaves of understory and open space species respectively. Similarly, Lee and Graham (1986) found that groups of tropical sun and shade species had surprisingly similar optical properties.

The spectral composition of light reflected by a leaf does not generally change much with sunlight angle of incidence (Gates, 1980). The overall absorption of the whole spectrum of solar radiation by a broad leaf is 0.48-0.56 for high sun and 0.34 to 0.44 for low sun, with an absorptance of 0.50 being a good estimate except very early or very late in the morning when

0.40 would be a reasonable value (Gates, 1980). Conifers such as pine, cedar, spruce or fir have the absorptance throughout ultraviolet, visible and near infrared region much higher, reaching almost 90 % (Jones, 1992) due mostly to their darker pigmentation (Gates, 1980).

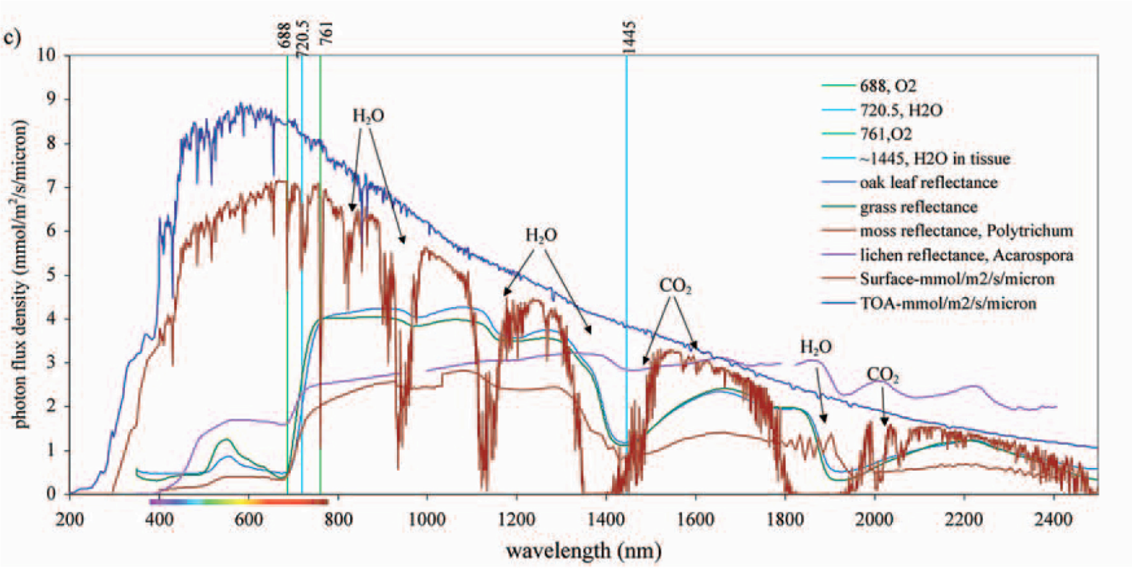
Although only about 45 % of the incident shortwave radiation (0.1- 4.0 μm) is in the PAR, about 80-85 % of all shortwave radiation absorbed by leaves is in this region (Jones, 1992) due to strong absorption of PAR light by photosynthetic pigments, mainly chlorophylls (Jacquemoud and Ustin, 2003). Absorptance in the visible range is particularly high for conifers with some values as high as 0.97 (Gates et al., 1965). Absorption of chlorophylls is highest in the blue and red region (Jones, 1992). Leaves of common plants absorb 80-95 % of blue (400-500 nm), 60-80 % of green (500-600 μm), and 80-90 % of red (600-700 μm) light (Loomis, 1965). The efficiency of light absorption by chlorophyll is dependent not only on its concentration in the plant tissues but also on its distribution and consequently on the ultrastructure of chloroplasts, i.e. on the orientation and number of grana stacks and the distribution and composition of pigment complexes in the light-harvesting antennas (Ustin et al., 2001).

48 % of incoming solar radiation is within the range of wavelengths longer than PAR. Most energy brought by this radiation is included within the near IR region up to 2500nm. Plant absorption in this region is very low forming near-infrared absorption plateau (700-1100 nm). Reflectance and transmittance are caused here by multiple scattering related to the internal structure, mainly to the fraction of air spaces within tissues (Jacquemoud and Ustin, 2001, 2003). Thus it is the dry matter that predominantly sets spectral characteristics of a leaf in this region. Conifer species have dense mesophyll structure, and, hence, their leaves/ needles tend to be darker also in this wavelength region than those of broadleaf plants (Kiang et al., 2007). Near infrared reflectance generally increases and transmittance decreases with an increase in leaf thickness. This can be explained primarily by the greater number of interfaces between cell walls and intercellular air in thicker leaves (see Knapp and Carter, 1998).

The sharp absorption transition from visible to near infrared wavelengths gives a great advantage for energy balance of a leaf. Radiation in near infrared region (app. 700 to 1400 nm), though not any more useful for photosynthesis, is still very rich on energy (Jones, 1992). Low absorptance in this region thus means an effective protection against leaf overheating. A plant leaf is essentially decoupled from this part of the solar spectrum and therefore remains much cooler than it would if it absorbed all incident solar radiation in a homogenous way (Gates, 1980).

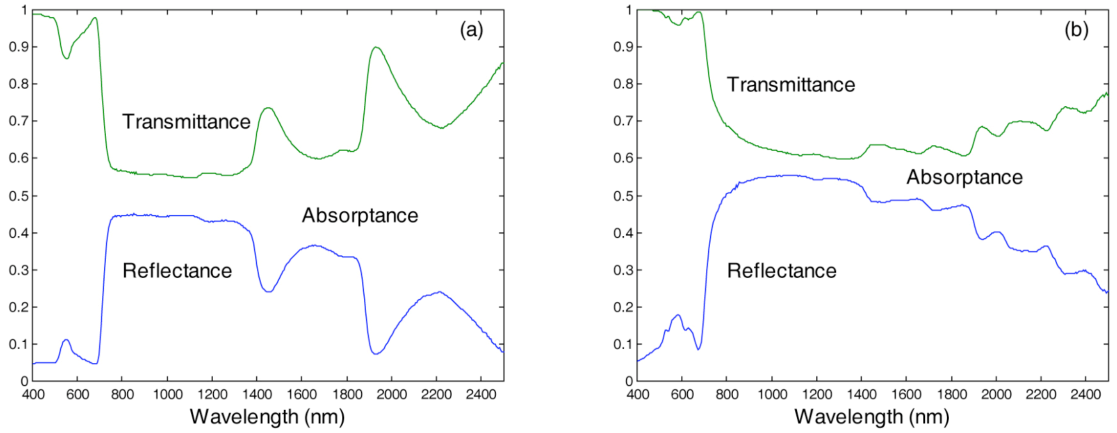
The sudden decrease of absorption between 700 and 730 nm is called red edge (see reflectance spectra in Figure 2). Its precise position is largely dependent on the nature of pigments in the leaf. Curran et al. (1995) showed that in slash pine (*Pinus elliottii* Engelm.) the point of maximum slope in the reflectance spectra of leaves (i.e. the red edge) is related positively to chlorophyll concentration. The higher concentration of chlorophyll moves the red edge to longer wavelengths. Based on a combination of data from recent literature, Carter and Knapp (2001) stated that the blue shift of red edge (shift to the shorter wavelengths) is generally related to a decrease of concentration of chlorophyll during plant stress.

Figure 2. Solar spectral photon flux densities at top of the atmosphere (TOA) and at the Earth's surface, with reflectance spectra of terrestrial plants, moss, and lichen and O_2 and H_2O absorbance lines. According to Kiang et al., 2007.



The middle-infrared (1100-2500 nm) part is again a zone of strong absorption. The absorption of leaves in wavelengths longer than 1400nm is determined predominantly by vibration-rotation absorptive characteristics of water. There are two major and two minor water absorption peaks that affect the reflectance of healthy leaves, centred near 1450 and 1950 nm and 970 and 1200 nm respectively, (Figure 3) (Jacquemoud and Ustin, 2003). Absorptance gradually increases with elongating wavelengths to nearly 100 % absorptance occurring at wavelengths greater than 3000 nm (Loomis, 1965). If a leaf wilts and dries absorption in this region is influenced predominantly by dry matter (dry carbon compounds like cellulose and lignin, nitrogen, sugars, and other biochemical compounds) (Jacquemoud and Ustin, 2001; 2003).

Figure 3. Reflectance and transmittance spectra of fresh (a) and dry (b) poplar leaves. According to Jacquemoud and Ustin (2001).



It follows that water content in leaves is closely related to foliar reflectance (Cecatto et al., 2001). Foley et al. (2006) showed that in the visible spectrum (350-716 nm) the foliar reflectance to water content changes were not immediate. The reflectance did not change until wilting of leaf was observed. However in the near infrared region (717–1265 nm) and shortwave infrared region (1266-2500 nm) the reflectance was affected immediately by small changes in water content. The effect of water may be clearly observed on a comparison of hemispherical reflectance for fresh and dried leaf (Figure 3a,b) (Jacquemoud and Ustin, 2001).

Similarly to and because of liquid water, leaves are good absorbers in the far infrared, i.e. thermal region (Gates, 1993). Apart from water it is also the molecules of leaf cuticle, epidermis or mesophyll that show high absorption at wavelengths greater than 12 μm. The resulting absorption of leaves in the wavelength region greater than 4μm resembles almost the qualities of a black body and reaches mostly values between 0.94 and 0.99 (Idso et al., 1969) or 0.97 to 0.99 according to Gates (1993). So reflectance in IR region is mostly lower than 0.05 (Gates, 1993) although exceptionally leaves of some species, such as *Citrus limonia*, have reflectances higher than 0.1 (Gates and Tantraporn, 1952). The far infrared reflectance spectra of different species have surprisingly variable patterns. These changes, however, are only small on absolute basis (Gates, 1993).

The energy input from the sun to the leaf in far infrared part of spectrum is low. Anyway, this wavelength region plays an important role in leaf energy balance. Most leaves have temperatures about 300 K. According to Wien's law radiation emitted from a blackbody at 300K peaks at 10μm. Therefore it is in the far infrared region where plant leaves emit radiative energy and balance the energy excess collected throughout the whole spectrum and expressed through leaves temperature. Also other objects surrounding leaves, including ground and sky emit in this region due to their temperature. Therefore, although low in solar spectrum, radiative energy exchange in this region is very important for energy balance of leaves.

3.1.1.2 Features of light reflected from a leaf

Light reflected from a leaf has a complex character. There are many optical interfaces in a leaf and each light ray encounters different internal surfaces and is reflected and transmitted in different directions. The character of reflected light is thus variable and depends on many factors. Light is scattered primarily by particles of two types: air cavities and cell organelles, mostly chloroplasts, with diverse refractive indexes (Berdnik and Mukhamedyarov, 2001). Near infrared light reflected from a leaf is more diffuse than visible light because it passes through more interfaces (Gates, 1980). Most canopy reflectance models assume leaves to be Lambertian, i.e. perfect scatterers (Jacquemoud and Ustin, 2001). However, most leaves exhibit a combination of diffuse and specular reflectance (McClendon, 1984). The specular component of reflectance is marked especially by leaves with sheen (Gates, 1993). The angular distribution of the diffuse component resulting from multiple scattering of light within the leaf is quite isotropic while its spectral variation depends on leaf biochemistry (Bousquet et al., 2005). The specular component results from scattering at the leaf surface. Consequently it depends on surface biophysical properties and reflects roughness of the epidermis/cuticle layer. Its spectral variation depends only little on leaf biochemistry. Unlike mesophyll diffuse scattering, surface scattering is characterised by polarisation of the incident light (Bousquet et al., 2005). Brakke (1994) showed that specular reflectance was similar in the visible and near-infrared regions in *Acer rubrum* and *Quercus alba*. The diffuse reflectance was lower in the visible range due to absorption by plant pigments. Scattering from the abaxial surface was less specular than that from the adaxial surface because of surface roughness. Diffuse reflectance of visible radiation from the abaxial surface was increased by scattering from the spongy mesophyll.

3.1.1.3 Special spectral characteristics of some leaves

Absorption spectra may be substantially influenced by trichomes or epicuticular waxes. It is not possible to generalize impacts of these extraepidermal features on absorption spectrum as they vary considerably in different species and may behave differently with changing wavelengths. Spectral functions of trichomes are suggested to be for example: reflection of radiation as protection, reflection of radiation on mesophyll to improve light conditions, reradiation or leaf shading (Gates, 1980; Wagner et al., 2004). Hairs may also change the ratio of diffuse to specular radiation (McClendon, 1984). Changes in trichome density can distort reflectance spectra and considerably affect reflectance indices used for nondestructive analysis of leaf chemistry and physiology without relation to changes in pigment contents (Levizou et al., 2005).

Trichomes density is often positively correlated to prevailing air temperatures and negatively correlated to leaf water potential (Levizou et al., 2005). Ehleringer (1984) monitored an increase in leaf pubescence along a gradient of decreasing precipitation among many different genera and families correlated with absorptance decrease in 400-800 nm range. Ehleringer and Björkman (1978) showed that pubescence of leaves of *Encelia farinosa* can reduce absorptance of visible ranges from 85 to 30 %. Lower absorptance reduced heat load and water consumption. Pubescence of this drought-deciduous desert shrub *Encelia farinosa* appeared to be reflective only after the hairs dried out. Absorption was influenced over a larger part of solar spectrum (400–3000 nm), however the reflectance was more enhanced in near infrared radiation (700–3000 nm) over photosynthetically useful solar radiation (400–700 nm) (Ehleringer and Björkman, 1978). Liakopoulos et al. (2006) showed trichomes to function as protection against excessive light to the developing photosystems of young leaves of *Vitis vinifera*. Kenzo et al. (2008) showed that hairs improved water use efficiency and energy budget of tropical *Mallotus macrostachyus*. Positive correlation between trichome presence and light intensity and exposure to UV-light has been shown (see Levizou et al., 2005). However, the relation between trichomes presence and density, temperature (light) increase and water decrease is not so unambiguous. Many plants of high mountains, which grow under the conditions of sufficient water supply, low temperatures and high irradiances have dense trichomes. Gauslaa (1984) measured in alpine plants only little effect of pubescence upon total reflectance. Tsukaya et al. (2002) suggested thermal insulation capacities of dense layers of woolly trichomes in Himalayan *Saussurea medusa*, however, Yang et al. (2008) found only little effect of pubescence on thermal conditions of this species. Although highly pubescent, the major warming effect of downy inflorescences of *Saussurea medusa* Maxim. appeared to result from the compact structure and dark colour of inflorescences. Therefore, in these biotopes, trichomes might preferably serve other functions such as preventing leaf surfaces from overwetting (Körner, 2003a). Also Wuenscher (1970) failed to confirm any effect of thick hair layer on the radiation absorption in leaves of

Verbascum thapsus. Rather the hairs served to increase water vapour resistance and decrease transpiration as this species grows on dry sites.

Certain types of hairs have protective functions against deleterious UV-B radiation (Karabourniotis et al., 1998). Vigneron et al. (2005) showed that the whole aerial part of *Leontopodium nivale* is covered with filamentary hairs which absorb and selectively dissipate ultraviolet radiation. Similarly, bracts of Himalayan giant glasshouse plant *Rheum nobile* Hook. f. & Thomson protect the reproductive organs by absorbing UV radiation while transmitting PAR and IR radiation (Omori et al., 2000). Karabourniotis et al. (1992) showed that pubescence layers of *Olea europaea* L. and *Olea chrysophylla* L. were almost transparent in the visible, but absorbed considerably in the UV-B region, with maximum at 310 nm. The authors reported that UV-screening pigments were contained within hair cells of some plants. The diffuse polyphenol deposition in the cell walls makes the trichome layer a very effective filter against UV-B radiation (Karabourniotis et al., 1998).

3.1.1.4 Absorption spectrum changes of leaves during development and stress

As already mentioned, changes in biochemical composition and structure result in variations of leaf spectral properties. The changes may be induced by various environmental factors, by abiotic and biotic stresses, however they can also be connected solely to leaf developmental changes (Jacquemoud and Ustin, 2003).

Spectral properties of leaves change during leaf maturation and senescence. Maturation is often connected with development of intercellular air spaces in mesophyll (e.g. Gausman et al., 1970), which consequently leads to light reflectance increase and light transmittance decrease. Maturation of leaves may also result in change of density or overall presence of trichomes (Wagner et al., 2004). In the case of deciduous trees leaf developmental changes have seasonal character. During the growing season, especially at its beginning and at its end the spectral characteristics change with changing concentration of pigments as well as with structures due to developmental changes (Gates, 1980). Seasonal changes in leaf absorptance may be also regulated at the entire plant level. Ehleringer and Björkman (1978) showed that throughout a growing season *Encelia farinosa* produced leaves with different pubescence density and thickness according to changing temperatures and water availability.

Leaf optical properties may be adapted or acclimated to changing irradiance or thermal conditions. The absorptivity of leaves at all wavelengths decreased whereas the reflectivity and transmissivity increased when an alpine perennial herb, *Selinum vaginatum* was grown in a habitat with high thermal load (Purohit et al., 1988). Presence of pubescence on leaves of

Encelia farinosa also varied among different populations growing in places with different water supply (Sandquist and Ehleringer, 1998).

Absorption and reflection spectra of leaves may be substantially changed during stress. Plant abiotic and biotic stresses commonly induce degradation of leaf chlorophyll, which results in reflectance and transmittance increase over the whole visible spectrum (Jacquemoud and Ustin, 2001). The changes tend to be more marked at visible wavelengths (400–720 nm) than in the remainder of the incident solar spectrum (730–2500 nm). A particularly generic response is the increase of reflectance in the far-red 690–720 nm and as already mentioned changes in red edge position (Carter and Knapp, 2001). Spectral changes during stress are often connected to changing relative water content (Pu et al., 2003). Penuelas and Inoue (1999) showed that reflectance of leaves of wheat (*Triticum aestivum* L.) and peanut (*Arachis hypogea* L.) increased at all wavelengths (500 to 2500 nm) with decreasing leaf water content from fully turgid to dry state. The characteristic spectral features of water have been used in a number of hyperspectral remote sensing methods for assessing plant water status related to abiotic conditions or plant stress (see Pu et al., 2003). Remote sensing of vegetation water content can be used also for example for predicting fire risk as a consequence of extremely low water content in biomass (Jacquemoud and Ustin, 2003).

Stress also often induces synthesis of a whole range of protective pigments, such as certain anthocyanins or carotenoids that absorb solar radiation within specific wavebands (see Merzlyak et al., 2005 for literature review) and limit light entering the mesophyll (Liakopoulos et al., 2006) or reacting with photosynthetic apparatus. The red pigmentation is often even visible, e.g. in leaves of *Aloe arborescens* Mill. subjected to high sunlight. Stress conditions may cause also ultrastructural changes such as deep rearrangement of chloroplasts (Merzlyak et al., 2005). An overview of other studies dealing with changing absorption spectra, in particularly in visible and near IR wavelength band, as a consequence of plant stress is presented in the discussion of the study by Carter and Knapp (2001).

3.1.2 Leaf energy budget

Except for massive leaves, heat storage of a leaf is in general small (Jones, 1992). Apart from special cases such as heat evolution due to alternative respiration in cucumber leaves (Ordentlich et al., 1991), metabolism has no measurable effect on leaf temperature. Also a leaf, usually attached to a plant by a narrow petiole has no significant amount of energy conducted from the plant (Gates, 1980). Therefore from the energy budget point of view a leaf may be studied as an isolated entity influenced entirely by its surroundings.

Similarly to the energy balance of the whole ecosystem (chapter 2.1.1) a leaf exchanges its energy with its surroundings through several energy fluxes. The incoming energy flows, i.e. the sources of energy, are: shortwave radiation (SR_{in}) and long-wave (LR_{in}) radiation coming from the Sun and reflected or emitted by the sky and the surroundings, both in direct as well as diffused form. The outgoing flows of energy are long-wave radiation (LR_{out}) dependent on the leaf's temperature, shortwave radiation reflected (r) or transmitted (t), latent heat flux (LE) connected with vaporization of water and convective transfer (C) which might be positive or negative depending on temperature differences between the leaf and the surrounding air. A minor part of energy budget of a leaf is represented also by energy consumed in processes of CO_2 assimilation (A) and energy released in the respiration reactions (M) and through fluorescence (F), which is a side-effect of electron excitation in photosynthesis. A leaf is a bilateral object and the energy exchange with the environment needs to be evaluated for both, upper and lower side of it. The energy balance of a leaf may be described as follows (adapted according to Lambers et al., 1998):

$$[SR_{in}-(r+t)SR_{in}] + [LR_{in} - LR_{out}] + C + LE + M + A + F = 0 \qquad \text{eq. 4}$$

3.1.2.1 Efficiency of solar energy use in photosynthesis

M, A and F can be neglected as their contribution to leaf energy balance is only of minor importance. As was already discussed in chapter 2.1.1, the energy flux into photosynthesis is only small. The energy content in $\{CH_2O\}$ is about 470 kJ mol^{-1}. A theoretical minimum quantum requirement for fixation of CO_2 is 8 absorbed quanta per one CO_2 fixed (Šetlík et al.). The energy of photons from the blue part of PAR (460 nm) contains about 260 kJ mol^{-1}, the energy of photons from the red part of PAR (680 nm) contains about 176 kJ mol^{-1}. An easy calculation shows that the maximum efficiency of CO_2 fixation (8 quanta per one CO_2) equals 22.6 % and 33.4 % for blue and red light respectively (table 2). The quantum requirement measured in laboratory corresponds to about 12 absorbed quanta per one CO_2 fixed (Šetlík et al.). Under natural conditions the quantum requirements are usually higher because photosynthesis is often saturated by incoming radiation and thus a certain part of energy is lost. Jones (1992) assigned mean quantum requirements of about 19 for C4 leaves and of about 15 to 22 (depending on temperature) for C3 leaves. The efficiencies of primary photosynthetic processes for red and blue light are summed up in table 2.

Table 2: Efficiency of light of different wavelengths in photosynthetic processes of fixation CO_2 into $\{CH_2O\}$. Theoretical minimum quantum requirement and mean quantum

requirements for. C3 and C4 plants (Jones, 1992) are presented. Rs = solar energy over the whole spectrum, its estimation is described in the text.

Light, wavelength	Efficiency of CO_2 fixation (in %)			
	Theoretical minimum value	C4 plants	C3 plants	C3 plants
	8 quanta/CO_2	15 quanta/CO_2	19 quanta/CO_2	22 quanta/CO_2
Blue (460nm)	22.6	12.1	9.5	8.2
Green (520nm)	25.5	13.6	10.8	9.3
Red (680 nm)	33.4	17.8	14.1	12.1
Rs	11.5	6.1	6.8	4.2

Drawing on the fact that the energy content of the green light is approximately equal to the mean of energy content of all radiation in PAR and that PAR represents about 45 % of the whole spectrum of solar radiation and using this value in our computations, we can see that approximate efficiencies decrease to rather low values around 5 % (last row in table 2). Moreover, the values presented in table 2 represent approximate efficiencies of primary photosynthetic processes only, or in other words of the gross photosynthesis rate. To calculate the efficiency of net photosynthesis rates, we have to substract the losses connected to concurrently running respiration processes. Light respiration is species specific and it changes with leaf development as well as with environmental factors. It is directly influenced by temperature. For example Baker et al. (1972) showed that light respiration of cotton leaves varied with temperature (25 to 42 °C) from 8 to 15 % of gross photosynthesis at the light intensity of 700 Wm^{-2}. If we consider common light respiration at 10 % (Šetlík et al.), we see that only about 4.5 % of total radiation is used by a leaf in net photosynthesis. However, we mustn’t forget that this applies to an isolated leaf only and that if we considered a whole plant over a longer time period the net photosynthesis rate would be lowered by seasonality, night respiration losses, biosynthesis and growth processes, inconvenient environmental conditions etc.

3.1.2.2 Main energy fluxes

Most energy absorbed by a leaf is divided into three energy flows: re-radiation in the long-wave part of the spectrum, convective heat exchange with the air and energy consumed in the phase exchange of water evaporation process (transpiration). The most significant factor in energy loss of individual leaves is the radiant energy loss. According to Gates (1980) re-radiation is responsible for the major part of energy loss from all leaves and the roles of convection and transpiration are always considerably smaller than the role of re-radiation. Drawing on the already discussed estimation that a leaf absorbs about 50 % of the total incoming radiation, on a clear day with maximal solar radiation input of 1000 W m^{-2} a leaf absorbs about 500 W m^{-2}. We assume that a leaf in the IR part of the spectrum resembles almost a blackbody and set its emissivity equal to 1. If the only way the leaf could cool down would be through re-radiation (in a vacuum), i.e. the leaf would have to re-radiate 500 Wm^{-2}, the temperature of the leaf would, according to the Stefan-Boltzmann law, equilibrate at 33.5 °C. With increasing energy input the temperature of a leaf cooled down solely by re-radiation would quickly rise to lethal values. If a leaf with solar energy load of 500 Wm^{-2} were to remain at 25 °C, with re-radiation flux of almost 450 Wm^{-2}, it would have to dissipate approximately 50 W m^{-2} by either convection or transpiration. If those 50 Wm^{-2} were to be dissipated solely by transpiration, the leaf would have to transpire 0.02 g H_2O m^{-2} s^{-1}, which corresponds to 1.1 mmol H_2O m^{-2} s^{-1}. This is a reasonable and for natural conditions a rather low transpiration flux, which results in evaporation of 72 g H_2O m^{-2} h^{-1}. More information about evaporation cooling is in chapter 4.3.

Apart from re-radiation and latent heat flux, leaves under natural conditions are influenced by convection, which can represent both source and sink of energy for a leaf. Generally, small leaves are strongly influenced by or coupled to the temperature of the surrounding air and have a large convection coefficient whereas large leaves due to a thick boundary layer are to a certain level decoupled from the ambient air. Their convection coefficient is low (Gates, 1980). The convection coefficient is a complex function of wind speed and characteristics of the surface over which the flow occurs (Gates, 1980). In case of leaves, it depends on size, thickness, and shape as well as surface roughness but also on location in the canopy etc. The boundary layer is a zone adjacent to a leaf, where mean velocity of air movement is significantly reduced. The depth of the boundary layer tends to be about two orders of magnitude less than the size of the leaf. Its accurate width is difficult to estimate (Jones, 1992). Convection contributes largely to the energy balance of a leaf, especially when the net radiation load to a leaf is very high (clear day) or negative (clear night) and leaf temperature tends to deviate to a large extent from the temperature of the air. The role of convection increases also with wind velocity.

It is obvious that although the energy budget of a leaf depends primarily on the amount of incoming solar energy, the temperature of a leaf is a result of a complex interaction of a particular leaf with its environment. The surrounding environment of a leaf under natural conditions is not homogenous and net radiative flux from or to the leaf is a result of radiative exchange with all surrounding objects and environments, beginning with neighbouring leaves and soil and ending with radiation from clouds and sky. In order to estimate the net radiative balance of a leaf we have to take into account that radiative exchange differs for the adaxial (ad) and abaxial (ab) side of a horizontally positioned leaf and that this is reflected in the net radiative flux (RF) of the whole leaf.

$$\text{Net RF} = (\text{RFab}_{\text{In}} + \text{RFad}_{\text{In}}) - (\text{RFab}_{\text{Out}} + \text{RFad}_{\text{Out}}) \qquad \text{eq. 5}$$

Mellor et al. (1964) computed fluxes of energy for a leaf of *Xanthium pennsylvanicum* (Wallr.) under controlled laboratory conditions (in Gates, 1980). The authors assumed leaf absorptivity of 0.46 for the incoming shortwave radiation. The ceiling emitted long wave radiation at surface temperature 25 °C, at floor temperature 22 °C. The thermal emissivity 0.95 was used for the leaf. The flux of longwave radiation was different for the abaxial and adaxial side. The results are presented in table 3.

Table 3. Energy balance of a leaf of *Xanthium pennsylvanicum* under controlled laboratory conditions (Mellor et al., 1964). Energy fluxes are given in W m^{-2} and in % of total

Energy absorbed	W m^{-2}	% of total
Shortwave from light source	600	41
Longwave from ceiling and floor	837	57
Reflected shortwave	28	2
Total	1465	100
Energy lost		
Transpiration	467	32
Thermal radiation emitted	921	63
Convection	77	5
Total	1465	100

Re-radiation in this case dissipated about 63 % of energy, transpiration 32 % (eqv. 0.19 g H_2O m^{-2} s^{-1}) and convection, which was actually computed by the authors only to balance the heat budget, represented only 5 % of the total incoming energy.

It is obvious that longwave radiation is difficult to measure accurately (Jones, 2003). In practice the radiative flux to and from the canopy may be estimated using net-radiometer, which monitors both radiation incoming from above and reflected from the ground throughout the whole radiation spectrum including IR wavelengths. In combination with measuring air humidity and temperature we are able to estimate energy fluxes of the ecosystem. In table 4 actual energy fluxes in the herbaceous wetland on Mokré Louky near Třeboň at midday July 27th 2005 are presented as an example.

Table 4 Actual energy fluxes in the herbaceous wetland on Mokré Louky near Třeboň at midday July 27th 2005. For more details see also Rejšková et al., subm. (in attachment)

Energy absorbed	W m^{-2}	% of total	% of total (leaf)
Shortwave incoming radiation from the sun	846	70	70
Incoming longwave radiation (sun+sky)	368	30	30
Total	1214	100	100
Energy lost			
Shortwave radiation reflected	155	13	35
Infrared radiation emitted from the surface	471	39	39
Latent heat flux (evapotranspiration) / LE	343	28	LE+C=26
Sensible heat (≈convection) / C	209	17	LE+C=26
Ground heat flux	36	3	0
Total	1214	100	100

If we measured a leaf and not the whole stand the ground heat flux would be eliminated. The reflected part of shortwave radiation would be higher and consequently net radiation upon a horizontally oriented leaf plain (net radiation input on a leaf) would decrease. Gauslaa (1984) measured leaves of *Salix glauca* L. to reflect about 35 % of radiation between 400 and 1400nm but according to Gates (1980) the reflection could be even higher reaching 50 %. If temperature of the leaf as well as of the soil under it approached 30 °C, the emitted radiation from the leaf would remain the same. As is indicated in table 4, only 26 % of incoming energy would than remain for both latent heat and sensible heat fluxes. If the transpiration should remain the same for the leaf as for the stand, i.e. 0.14 g H_2O m^{-2} s^{-1} or 7.8 mmol H_2O m^{-2} s^{-1}, which is a high but for a wetland species possible value, sensible heat would be negative and the leaf would slowly start to cool down. This would lead to a new balance with slightly lower longwave emittance and correspondingly changed other values.

As can be seen from this example, energy budget of a leaf under natural conditions is a very dynamic process. Consequently also the temperature of a leaf may change dramatically in a very short time, especially with abrupt changes of incoming shortwave radiation during a partly clouded day (Gauslaa, 1984) or with changing wind speed. Leaves and the whole canopies may be adapted or to a certain level acclimated by their size and shape and surface features to couple or decouple more from convection and radiation according to the environment they are growing in. However, this is always a long-term and usually only to a small extent reversible process. At a certain moment absorption, reflection and transmission of both shortwave and longwave radiation is a passive process in the majority of leaves which is determined solely by the existing meteorological and environmental conditions. The only active process by which a leaf can momentarily influence its energy balance is redistribution of incoming energy into latent heat flux or sensible heat flux through supporting or limiting transpiration process. The only dynamic and active way of non-metabolic use of solar energy is the transpiration process.

3.1.2.3 Leaf temperature under natural conditions

As follows from above leaf temperatures in nature may be distinctively variable within a very small area according to the actual exposure to radiation, water relations as well as air temperature and air movements. Temperatures of leaves within a canopy and even within a plant may thus, under suitable circumstances, differ by several degrees. For example shaded leaves of herbs growing in grassland, which may stay wet during substantial part of a day, have temperatures much lower than sunlit leaves extruding from the canopy (personal observations as measured by IR camera). These differences are even more marked within high stands such as forests. Different plants standing side by side respond differently to environmental factors and differ in their transpiration rates. In table 5 differences in temperatures of sun and shade leaves of some tree species are demonstrated (adapted from Feller, 2006). Although the author did not present the incoming radiation data and more details on time of the measurement and placement of measured leaves within the tree crown, we get a basic idea that temperature of shaded and insolated leaves of individual plants under natural conditions differ substantially. Insolated leaves reached temperature up to more than 10°C higher than shaded leaves (table 5, column E). Insolated leaves were generally also substantially warmer than the air. The only exception was *Salix alba* L. which might have been caused either by high transpiration of this wet habitat species or high reflectance of its leaves which have whitish and wax like appearance (table 5, column F). On the contrary, shaded leaves were mostly cooler than the ambient air (table 5, column G). Feller (2006) also showed that both insolated and shaded leaves of *Quercus robur* L. cooled down by several degrees of Celsius when exposed to slight wind.

Table 5. Temperatures of sun (column C) and shade (column D) exposed leaves (means of 6 to 10 measurements) of some woody species measured by infrared thermometer on hot days. Air temperatures were measured with a classical thermometer in the shadow (to resemble conditions in a meteorological screen) near the leaf to be analysed (adapted from Feller, 2006). Column E shows mean difference in temperature between insolated and shaded leaves. Column F shows mean difference in temperature between insolated leaves and air temperature. Column G shows mean difference in temperature between shaded leaves and air temperature. n.a. not available

A	B	C	D	E	F	G
Temperature (°C)	Air	Leaf $_{sun}$	Leaf $_{shade}$	L_{sun}-L_{shade}	L_{sun}-T_{air}	L_{shade}-T_{air}
Fagus sylvatica	25.5	29	24.7	4.3	3.5	-0.8
Fagus sylvatica	29.5	32.1	25	7.1	2.6	-4.5
Corylus avellana	25.5	37.5	26.6	10.9	12	1.1
Corylus avellana	29.5	40	28.7	11.3	10.5	-0.8
Corylus avellana	28	41.3	23.2	18.1	13.3	-4.8
Corylus avellana	n.a.	35.9	27.2	8.7	n.a.	n.a.
Fraxinus excelsior	31.5	24.7	28	6.7	3.2	-3.5
Fraxinus excelsior	38	41	32.9	8.1	3	-5.1
Cornus sanguinea	31.5	25.2	29.2	6	3.7	-2.3
Cornus sanguinea	38	41.2	34.2	7.3	3.5	-3.8
Salix alba	31.5	32.5	28.4	4.1	1	-3.1
Salix alba	38	36	31.7	4.3	-2	-6.3
Acer pseudoplatanus	40.5	41.2	36.7	4.5	0.7	-3.8
Acer pseudoplatanus	n.a.	42.6	32.7	9.9	n.a.	n.a.
Acer pseudoplatanus	24	35.6	25.6	10	11.6	1.6

A historical review of early temperature measurements of leaves was presented by Jackson (1982). The influence of transpiration on leaf temperature began to be discussed and the capacity of transpiration to reduce temperature of a leaf below temperature of the air was measured as early as in the 1920s. In the 1930s the importance of radiative cooling and leaf orientation was added to the discussion. Then throughout the following decades the discussion about the importance of transpiration, convection and re-radiation for leaves under natural conditions followed with support for different theories according to species and conditions used. During the 1960s and the 1980s the importance of water supply for temperatures of crop leaves to be below or above air temperature was gradually acknowledged. Once measurements were conducted in semiarid conditions leaves were proven to be cooler than air when supplied with water, especially when leaves were studied within canopies and not separately. Idso and Baker (1967) stated that for a single leaf, re-radiation was the major mode of heat transfer, whereas for canopy as a whole transpiration was the dominant mechanism.

Leaves usually tend to have temperatures close to the air temperature. The real situation may divert from this assumption substantially under some circumstances in bright sunshine, when leaf temperature of some species may exceed by 10 °C to 20 °C the temperature of ambient air (Gates, 1980; Gauslaa, 1984). Special morphological adaptations of some plants to high temperatures are further discussed in chapter 4.1. Some leaves can overcompensate the large amounts of incoming radiation by evaporative cooling so that they are always cooler than the air (Gates, 1980). The importance of transpiration can be clearly demonstrated when a leaf is detached from a plant, thus isolated from the transpiration flux (e.g. Pokorný et al., 2007). The influence of the transpiration flux on leaf temperature may also change with changing temperature of the air. Gates (1980) measured temperature of leaves of *Mimulus lewisii* Pursh on different sites with air temperatures from 17 to 37 °C. Leaf temperatures of plants growing always on wet spots ranged from 23 to 35 °C. In a following chamber experiments the leaves of *Mimulus lewisii* showed to be warmer than the air below air temperatures of about 30 °C and cooler than the air above 35 °C of the ambient air. This example indicates that plants with sufficient amount of water are capable of accommodating their temperature by transpiration to maintain their leaves within suitable temperature conditions and thus undergo thermal regulation. To what extent this is indeed regulated by the plants themselves and to what extent by the existing environmental conditions (decreasing water vapour pressure deficit, increasing irradiation etc.) is a complicated and still not sufficiently understood question which will be discussed in more detail in chapter 4.3. In this context it is interesting to mention a comparison of maximum temperatures in leaves made by Gauslaa (1984). The author showed that maximum leaf temperatures under high irradiances of multiple species from different parts of the world differed only little although the ambient temperature they were exposed to differed substantially (table 5). This indicates that a leaf has to be adapted anatomically or physiologically to maintain internal temperatures within a certain limit if a plant is to survive under the conditions of its natural environment.

Table 5. Maximum leaf temperatures of a group of native species in different parts of the world with substantially different environmental conditions. Mean leaf temperatures, corresponding air temperatures and their difference are given.

Area	T_{Leaf} (°C)	T_{Air} (°C)	$T_{Leaf} - T_{Air}$ (°C)
Norway, 900-1400 m a.s.l.	36.8	19.3	17.4
Alps, 2000 – 4350 m a.s.l.	43.5	19.2	24.3
Spain, Costa Brava	40.4	31.7	10.6
Mauretania	44.4	43.7	0.7

Leaf temperature may also decrease below air temperatures when net radiation flux is negative. Leuning (1989) showed that during a clear night both larger leaves of *Eucalyptus pauciflora* Sieb. ex Spreng (mean width 48 mm) and smaller leaves of *Eucalyptus viminalis* Lab. were, due to re-radiation, within 2 to 4 °C colder than the ambient air near zero temperature. Due to convection the larger leaves were colder than the smaller ones and both leaf and air temperatures lowered while nearing the ground. Due to temperature release in the condensation process leaves covered with frost or dew were several degrees warmer than dry leaves.

Although temperature measurements have been conducted for a long time, there are not many studies describing detailed temperature dynamics within canopies. It is also often questionable how to measure temperatures of air and leaves to be comparable. First, the temperature of leaves has to be measured without harming the leaf or changing its energy budget (using of very thin thermocouple is required). The second question is how to measure temperature of the air so that it corresponds correctly with conditions the leaves are exposed to. Most authors who used direct measurements measured air temperature in the shade near the measured leaf no matter if the leaf itself was in shade or in sun. This may be misleading as temperatures of the air may differ in sun and shade and leaves are not exposed to temperatures in the meteorological screen. On the other hand exposing a thermometer to the sun brings an error connected to the warming up of the thermometer itself due to incoming radiation. Problems of direct temperature measurements can be partially avoided by using remote sensing techniques such as IR point thermometers or IR cameras. Usefulness of IR cameras in studying plant temperatures was shown for example by Lamprecht et al. (2007). However, if we want to compare temperature of the studied material with ambient air, which is often the case in ecological studies, we have to combine remote sensing with direct measurements of air temperature, which may introduce other inaccuracies into our research. Moreover remote sensing has also some disadvantages. Apart from the fact that setting emissivity to different surfaces in the field conditions may be erroneous, IR camera measures only the "visible surfaces" and therefore cannot monitor the temperatures deeper in the canopy that may differ substantially. Also the background temperature can lead to inaccurate temperature results although the currently used IR software successively minimises this risk (Jones, 2003). In any case, the IR camera enables us to study accurately and rather easily the dynamics of temperatures in time and space on the whole scale ranging from individual leaves to whole canopies.

We may conclude that the proportion of the main energy fluxes influencing leaf energy balance (and temperature), i.e. incoming and outgoing shortwave and longwave radiation, latent heat flux and convective heat transfer, differs substantially according to meteorological conditions, time of the day, time of the year and according to the internal characteristics of the leaves, i.e. optical characteristics, water content, water supply etc. In any case, leaves if supplied with water are generally capable of using large amounts of incoming solar energy to cool themselves and this process is controllable. The importance of this process for plant stands and environment will be discussed later (chapter 4.3).

3.2 Flowers

Flowers (in this text also inflorescences, unless specifically defined) serve plants for reproduction. It seems that optical features of many (in particular visually marked) flowers are primarily adapted to attract pollinators. However, flowers must ensure not only successful pollination but also suitable conditions for the whole reproduction process, i.e. development of reproductive organs, pollination and fertilization as well as development of seeds. Reproductive processes tend to be more temperature sensitive than vegetative processes (Patiño and Grace, 2002). Therefore we may assume many flowers to be adapted to improve their temperature conditions in a way that stems from the prevailing ambient conditions of their environment. Moreover, flowers structure has to be adapted to protect the reproductive organs and seeds from adverse effects of the environment (e.g. Sklenář, 1999). Some flowers with green parts have been shown to serve also photosynthetic purposes (Ehleringer and Forseth, 1980).

Surprisingly, energy balance in flowers and inflorescences has been studied only little in comparison with leaves, although it represents a highly important part of plant development. With the exception of some unique flowers from the thermogenic group which are able to warm themselves up thanks to special ways of metabolism (Seymour and Schultze-Motel, 1997; Seymour and Schultze-Motel, 1998; Lamprecht et al., 2002a; Lamprecht et al., 2002b), little is known about specificities of temperature conditions in flowers. All thermogenic plants described so far are members of a few ancient families (e.g. *Araceae, Nelumbonaceae*), mainly from the tropics, which belong to the same clade in only two classes of early angiosperms (Dieringer et al., 1999). The rest of the plant kingdom does not appear to be able to thermoregulate flowers metabolically and are thus reliant on external energy, i.e. direct energy from the sun or indirect from the environment.

3.2.1 Energy budget of flowers

The structure of flowers is generally more complicated than the structure of leaves. This fact makes it very difficult to measure or model the overall flower energy budget or assess flower temperature dynamics. By structure I mean the entire architecture of the flower as well as arrangement, structure and surface characteristics of its parts. Flowers have evolved in most peculiar shapes and we may well assume that their use of solar energy varies to a large extent. Due to their size, temperature of small flowers tends to be strongly coupled with air temperature in a way similar to small leaves. Small masses and generally low heat capacity make flowers quickly respond to changes of environmental conditions (Gates, 1980). However, flowers may also be large with much higher masses especially in central parts where reproductive organs are accumulated. This as well as a special morphology could in some cases cause certain decoupling from the ambient temperature.

Also light absorption of flowers differs in comparison with leaves. The colour of flowers is influenced by pigment composition and surface micro-structure of its parts. Through their specific absorptivity pigments, mainly different types of carotenoids, anthocyanins and flavonoids, distributed in epidermis and mesophyll cells, can change the light spectrum reflected from the flower, i.e. the colour. The colour as well as its brightness and texture (velvet etc.) is, however, influenced also by epidermis structure. Kay et al. (1981) having studied 201 different species, described six types of petal epidermis anatomy, including papillate cells epidermis with a light trapping mechanism. The authors showed that the absorbed light was reflected from aerenchymous unpigmented reflective mesophyll or from a reflective layer of starch grains in the upper mesophyll and returned to the exterior by combination of external and internal reflection and refraction.

The absorption spectrum of flowers may be influenced also by structures protruding from the surface (trichomes) or chemical compounds excreted to the exterior (waxes etc.) that provide flowers with silver tinge or even shift the colour. Whereas leaves are generally effective absorbers in the PAR region, absorption of PAR differs in flowers in a species-specific manner according to their colours and results in different radiation input to these plant parts. For example, Patiño and Grace (2002) measured very low absorptance in visible range of white corollas of *Ipomea aquatica* and *Merremia borneensis* and only slightly higher absorptance in purple corollas of *Ipomea pes-caprae*. As white surfaces reflect most of the incident irradiance it can be assumed that net radiation of white flowers is the lowest. Dark surfaces generally warm up more quickly than light surfaces when irradiated because they absorb more intensively in the PAR region. Using an IR camera, we found that surface temperatures of dark purple *Chrysanthemum* were on average by 1.3 °C warmer than the cream white flowers (data not shown). Jewell et al. (1994) asserted that in bright sunshine, the apex of flower keels of *Lotus corniculatus* L. was on average by 5.7 °C warmer in dark-keeled than in light-keeled individuals. Molgaard, (1989) measured higher temperatures in yellow *Papaver radicatum* than in white ones. However, the effect of colour on flower temperature and its energy balance cannot be expressed in a straightforward manner. McKee and Richards (1998) observed three colour variants of *Crocus chrysanthus* and one of *Crocus tommasinianus* and found that white and purple flowers showed the greatest flower warming and yellow flowers the lowest. Moreover, many authors provided evidence of substantial temperature elevation in light coloured flowers from arctic and alpine environments, a topic discussed later (chapter 3.2.2).

Epidermal cell shape and pigmentation influence also tissue optical properties in ultraviolet spectral regions. Patiño and Grace (2002) demonstrated strong radiation absorption for all three convolvulaceous species (*Ipomea aquatica*, *Merremia borneensis*, *Ipomea pes-caprae*) in the UV range. Absorption of UV radiation may also differ within a leaf and create ultraviolet patterns leading to spectral polymorphisms of some plants (e.g. Utech and Kawano, 1975). To my knowledge, the spectral properties of flowers in IR region have not been separately studied. But there is no reason to suppose that they would be much different from those of leaves. Spectral properties of flowers are in these spectral ranges also mostly influenced by water content in tissues and their emissivity within IR (7.5 μm to 13 μm) is therefore high. Drawing on data available in literature (Gates, 1964; Idso et al., 1969; Jackson, 1982; Ogawa et al., 2002; Qin et al., 2005), we used flower emissivity of 0.97 in our measurements, a value commonly used for vegetation in general. Light in the NIR region is largely reflected or transmitted in flowers similarly as in leaves. The reflectance edge of petals shifts to shorter wavelengths than in leaves, which is determined by abundance of different pigments. Whereas it is at around 700 nm for the green leaf, it is at 600 nm for the red petal of rose and at 400 nm for the white petal of *Magnolia* (Gates, 1980).

3.2.2 Use of solar energy for warming up in flowers

Walking along wakening gardens in the spring we find it hard to understand how fragile vernal flowers can survive freezing temperatures that still occur at that time of the year. Flowers growing under harsh conditions often close to prevent the reproductive organs from snow, rain, frost or radiative losses (van Doorn and Meeteren, 2003; Von Hase et al., 2006). The determining factors for opening/ closing of flowers and sensitivity to them are species specific. For some species it is temperature (Von Hase et al., 2006), for others humidity or light conditions or a combination of more factors (van Doorn and Meeteren, 2003). We observed opening/ closing behaviour of *Anemone nemorosa* L., which reacted to both temperature and light conditions (data not shown). *Bellis perennis* L., another species we used in our study, responded mainly to light (van Doorn and Meeteren, 2003). The threshold limiting flowers closure/opening is environment dependent, i.e. for example different temperatures make flowers open in alpine and desert environments (Körner, 2003a; Von Hase et al., 2006). Some flowers after opening track the sun to a various extent. Heliotropism is the most obvious way of collecting solar energy. The flowers of heliotropic species have often bowl or satellite disk shape and light shiny petals. As mentioned before many of these flowers have been reported to enhance temperatures compared to the temperature of the ambient air (Kevan, 1975; Ehleringer and Forseth, 1980; Knutson, 1981; Kjellberg et al., 1982; Stanton and Galen, 1989; Totland, 1996; McKee and Richards, 1998; Kudo, 1995; Luzar and Gottsberger, 2001). The authors suggested these flowers act as parabolic mirrors reflecting sun rays from inner sides of petals focusing it to the centre on sporophylls. Studies of flower survival under low temperatures have been conducted mostly in alpine and arctic regions. We studied temperature dynamics in three vernal light-coloured species of temperate zone (Rejšková et al., 2010; see attachment). *Anemone nemorosa* is a white petalled species showing heliotropic movements. Although we measured enhanced temperatures in floral centres and although the centres were warmer than the petals, our results did not prove sun rays concentrating abilities of this temperate species.

Kevan (1989) divided arctic flowers into six groups according to the manner of attaining elevated temperatures. In the first category he included disc flowers, which according to the author enhance their temperatures in relation to the cosine of the angle of insolation. We supported this statement by measuring enhanced temperatures in directly insolated inflorescences of *Bellis perennis* (Rejšková et al., 2010; see attachment), although the influence of solar rays angle of incidence was not tested. When inflorescences were exposed to direct irradiance a certain surplus of energy was recorded although the final temperature of the discs was related mainly to the temperature of the environment. The second category comprises of the already mentioned bowl-shaped light coloured heliotropic flowers concentrating sun rays in their centres. The third category Kevan (1989) includes bowl-shaped or inverted bells like flowers that are not heliotropic but still reach higher temperatures in their centres due to the combined effect of the shape of corolla, its reflective properties and the mass of stamens and pistils in the flower centres. The fourth group is made up of flowers resembling hanging bells. Kevan (1989) assigned them the capability to trap rising warm air from the ground. The fifth group encompasses flowers that function as “micro-greenhouses”. Presumably the relatively massive pistils of these flowers absorb short-wave radiation and re-radiate it at longer wavelengths, which are trapped within the flowers by reflective inner surfaces of petals. The last group consists of “hairy heat traps” with a mechanism similar to micro-greenhouse flowers. Flowers in this group are insulated by dense hairs which probably also trap long-wave radiation.

We may simplify Kevan’s system and define three ways of use of solar energy for warming up of flowers. The first way is to concentrate direct radiation in the very place of the reproduction process. Radiation can come straight from the sun or it can be reflected from the snow. It can also fall straight to the centres or be directed there via highly reflective petal inner surfaces if the overall shape of the flower is suitable. The second way is connected with all hairy or fussily organised structures that absorb incident light and retain the gained warmth either through trapping long-wave radiation or through insulating features or both. A nice example of this ecological behaviour are hairy catkins of *Salix* species that have been shown to have markedly enhanced temperatures during still very cold ambient temperatures. A similar effect is, however, responsible for warming up of all fussily organised central parts of flowers. We suggested this mechanism for *Anemone nemorosa* and *Bellis perennis* (Rejšková et al., 2010; see attachment). The presented mechanism may as well apply to all compact flowers' stages when they are covered with hairs. Based on our measurements we suggested this mechanism also for hairy buds of *Pulsatilla patens*, which tended to warm up when lit by the sun (data not shown). The third way is what Kevan described as the "micro-greenhouse effect". It is based on different optical properties of corollas in different parts of the light spectrum. Whereas the corolla is translucent for shortwave radiation, i.e. the energy-rich photons enter to the flower interior, it is reflective for longer wavelength light, i.e. this light is trapped inside the flower and warms the internal part. This method can be successfully used also by the flowers that are bent to the ground out of protective reasons but also by plants temporarily closed because of inconvenient weather. However, our results did not confirm this mechanism for white bent flowers of *Galanthus nivalis* L. (Rejšková et al., 2010; see attachment). To prove directly the suggested processes would demand many fine optical and spectroscopic methods that have so far not been largely included in the studies of temperature dynamics in flowers. In our research we as other authors, used only indirect methods of measuring temperature. However, the use of an infrared camera in our trials made it possible to measure well the temperature distribution in individual floral parts and study the temperature dynamics of the flowers in detail (for further details, results and discussion see the attachment).

It may be concluded that we are far from understanding flower survival under low temperatures. It is clear that plants use direct solar radiation to warm themselves up in a strongly species specific manner. Different species probably also use different parts of the spectrum. Although white petals of *Anemone nemorosa* have been documented to be of high reflectance (Kay et al., 1981) we showed that they responded to changed irradiance by changing temperature. As they absorbed very little in the visible light due to their white colour, this must have been caused either by UV-light or near IR light coming from the sun. Kay et al. (1981) indeed reported *Anemone nemorosa* to contain UV – absorbing compounds in epidermis of their petals. We showed that similarly to leaves (Gates, 1980) the flowers and inflorescences of *Anemone nemorosa* and *Bellis perennis* reacted almost instantaneously to changed irradiance by changing their temperature. Although flowers seem not to be only passive in using incoming solar radiation and many species have adapted different ways of improving energetic situation during the reproductive process, it is highly likely that, similarly to leaves, flowers are tightly coupled to incident solar energy. When there is only scarce irradiance, flowers are cold or their tissues are even freezing. Therefore they have to be adapted to survive frost.

3.2.3 Use of solar energy for cooling down in flowers

Most flowers are designed to attract pollinators. As such they are often put forth to be as visible as possible and are therefore exposed directly to the sun and high input of energy. Whereas warming up strategies of plants growing in cold climates have already been partly studied, the adaptation of flowers to overheating has been largely marginalized. Nevertheless danger of damage from excess light and overheating could be present not only in hot climates, but also in arctic or alpine climates where solar input may be temporarily very high. Excess temperatures in flowers have been studied only little. The first study of this sort was conducted by Patiño and Grace (2002) on three tropical *Convolvulaceae* spesies of different colours. Galen (2006) was the first to study risks of overheating in heliotropic alpine snow buttercup (*Ranunculus adoneus* A. Gray).

There are three possible ways for flowers to cool down. First, the overall architecture of the flower and the optical properties of all its parts may be adapted to divert sun light from the inner parts important for reproduction. Second, flowers could cool themselves by transpiration. And third, similarly to leaves, flowers of hot and dry climates can minimize their size that helps them use convective processes and couple their temperature with the temperature of the air.

Intensive reflectivity of corollas of some species (Kay et al., 1981) in addition to its attracting function may be seen also as an adaptive feature improving energy budget of the flowers. Patiño and Grace (2002) showed that heliotropic trumpet shape flowers of *Ipomoea pes-caprae* ssp. *brasilensis*, *Ipomoea aquatica* and *Merremia borneensis* with highly reflective corollas served as radiation shield or parasol to maintain gynoecium at its functional temperature. This effect was combined with evaporative cooling. Despite being almost astomatous, corollas had high conductance to water vapour and dissipated between 20 and 80 % of the absorbed energy via evaporation. The corollas of these species open in the morning, wilt around noon and fall early in the afternoon. Then the sepals with 68–182 stomata mm^{-2} on the abaxial surface, i.e. density comparable with those on leaves, close and cool the gynoecium to optimal temperature. Sepals often have stomata densities similar to those of foliage leaves whereas petals usually have fewer stomata, non-functional stomata or no stomata at all (Blanke and Lovatt, 1993). If stomata are present on the corollas they are often unevenly distributed in the bottom, middle and upper parts of the petals, such as in tulip (Azad et al., 2007) or in tropical *Convolvulaceae* (Patiño and Grace, 2002). Transpiration of some flowers is sometimes surprisingly high (e.g. Blanke and Lovatt, 1993). Stomata in flowers may also be modified and serve other purposes, such as those in nectarines of

Myosotis sylvatica Hoffm., which are constantly opened and serve for nectar secretion (Weryzsko-Chmielewska, 2003).

Solar tracking flowers lack the ability to orient themselves away from the sun's rays to maintain optimal temperature under high temperature. Galen (2006) showed that excess heat generated by heliotropism in *Ranunculus adoneus* was balanced by increased transpiration. Flowers facing the sun exhibited higher transpiration (1.06±0.10 mol H_2O m^{-2} s^{-1}) than flowers oriented away from the sun (0.84±0.10 mol H_2O m^{-2} s^{-1}). Transpiration protected reproductive organs from thermal damage at the expense of water. It seems therefore probable that even in cool alpine habitats, plants with solar-tracking flowers are able to tolerate hotter conditions only if soil moisture is plentiful but not under drought (Galen, 2006). This may be another limiting factor for early spring flowers from temperate zones. Warmer and dryer springs could thus cause change in their distribution.

3.3 Stems

Stems are generally the most voluminous organs from the aboveground part of plants. It is primarily the volume, which distinguishes them in terms of energy budget from leaves and reproductive organs. The larger the stem, the more it is decoupled from momentary temperature changes of the external environment (Gates, 1993). Heat flow to and from the large stems is substantially time delayed which may result even in reversed temperature maxima and minima, such as in cacti Gates (1980). Because the direct impact of transpiration in cacti stems is minimized (evaporation is generally low), stem temperatures are largely decoupled also from the latent heat flux. In contrast, internal stem temperature of intensively transpiring trees is likely to be influenced by large amounts of water flowing through the xylem tissues (water use of trees is discussed in chapter 5.2.2) because moving water carries large amounts of energy (heat capacity of water is 4184 J $kg^{-1}K^{-1}$ at 20 °C). When transpiration is low and trunks are hidden under the canopy, thermal conduction, though relatively small, is the principal mode of heat transfer in trunks. Thermal conductivity coefficient depends on moisture content (Turel et al., 1967).

Due to the slowed down energy exchange between stem interior and the environment temperatures of trunks tend to be heterogenous. As early as at the end of the 19th century some authors measured that temperatures within unevenly insolated tree trunks reached as much as 25 °C differences between the northern and southern side of the trunk (e.g. Harvey, 1923). Also spatial distribution of water in the tree trunk is not homogenous. Water distribution as well as its motion varies in sapwood and heartwood of the stem as well as in the early wood and latewood of an annual ring (From et al., 2001). Flow velocities can be very high in some species. For example in oak, peak transpiration flow velocities reached about 45 m h^{-1} in the youngest growth ring (Čermák et al., 1992). The radial profile of flow velocities is strongly species-specific being symmetrical in some species (e.g. spruce) and assymetrical in others (e.g. oak).

Trees contain large volumes of water. A 57 m tall and over 450 years old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) contained 1426 l of free water. Most of this water was in the stem sapwood below the height of 46 m, i.e. in the lower crown and bare stem (Čermák et al., 2007). The portion of water stored in xylem used for daily transpiration differs markedly from units to tens of percent of total stored water in different species and indviduals (for results review see Čermák et al., 2007). For example, measurements of Schulze et al. (1985) showed, that 14 and 24 % of the daily transpiration was formed by the stored water in *Larix deciduas* and *Picea abies* respectively. Transpiration flow in stems is directly connected to transpiration rates of leaves. Consequently it is subordinated to diurnal as well as seasonal changes. It is also substantially influenced by actual environmental conditions.

Stockfors (2000) measured temperature variation in the stem of a 30-year-old Norway spruce (*Picea abies* (L.) Karst.) during 40 summer days. Although mean temperature variation within the stem was only 3.7 °C, for 8 % of the time it was more than 10 °C, with maximum temperature difference 21.5 °C. Stem temperatures are usually higher in the upper parts of the canopy, where stems are more exposed to sunlight and temperature amplitudes are thus larger. Stem tissues also warm faster at the top of the tree than at the base of the stem because of the different diameter of the organs (Ceschia et al., 2002). The temperature gradients throughout trunks resulted in strong spatial and temporal variations in respiration (Stockfors, 2000; Ceschia et al., 2002).

Temperature variability in different parts of trunks is most marked in deciduous trees during freezing sunny days (Harvey, 1923; Bolstad et al., 2004). Whereas during the growing season trunks of deciduous trees are protected by the canopy against radiation fluxes (Turel et al., 1967), during leaf-off periods south-side stem temperatures are higher and more variable than north-side temperatures in Northern hardwood stands (Bolstad et al., 2004). Southern exposure of trunks to high loads of direct solar light in winter is particularly dangerous. Thawing and abrupt refreezing combined with low sap flow lead to sun sculd, i.e. injury to cambium tissues on the insolated side of the trunk (Harvey, 1923; Karels and Boonstra, 2003). Karels and Boonstra (2003) studied the influence of bark colour on thermal dynamics of cambium of deciduous trees. They compared brown painted bark of birch with white coloured birch and found that brown coloured bark was associated with increased cambium temperatures and greater cooling rates after shading, which led to more abrupt refreezing connected to higher incidence of cambium wounding. Deciduous tree species throughout North America have lighter-coloured and more reflective bark than species restricted to more southern forests. This indicates that sunscald injury may be an important selective mechanism in northern boreal forests. Differences between temperatures of white barked birches and other dark barked species exposed to direct sunlight are observable also in the temperate zone and detectable with IR camera (personal observations). These relations have been known for a long time in orchard management. In early spring trunks of fruit trees are painted white to avoid overheating. This process is dangerous because in the evening the abrupt cooling may cause frost cracking, which occurs when the outer layer of a tree is colder and contracts faster than the core (Kubler, 1983). Reducing cambium heating in spring has also been used to postpone early sprouting of peach and apple trees to protect blossoms agains spring frosts.

A question may arise whether the prevailing brown colour of bark has any ecological advantages in terms of heat budget or prevention against damage connected with surplus or lack of heat. In other words, why is bark not light and reflective more often also in other parts of the world at least in deciduous trees which are seasonally exposed to high amounts of sun irradiance? The colour and morphology of trunks is subordinated to multiple selective mechanisms which are probably decisive to different extents in different environments. Those may, among others, be mechanical and chemical defense mechanisms against insects (Franceschi et al., 2005) and other herbivors or bark morphology features influencing interception and pattern of precipitation dripping and run off. However, Nicolai (1986) studied thermal properties of bark of 24 Central European tree species and came to some interesting conclusions. As already discussed, tree species with white bark avoid overheating of their surface by reflecting radiation. Species with fissured and scaly barks have been found to shade inner parts of their bark, which provided high insulation of the trunk. In contrast, smooth and thin barks show no adaptation to avoid overheating. The author concluded that the species with the latter type of bark, such as *Fagus sylvatica* L., tend to form closed stands and are not able to occur in open stands. This is, however, not quite true, as beaches appear often as solitaires in mountaneous regions. Nicolai (1989) showed the importance of bark properties for thermal properties of trunks also in 26 species of two different African ecosystems: a subtropical moist forest and savanna. The author classified trees from the subtropical moist forest into three functional groups a) species with thin and smooth bark with low values of insulation upon the bark, b) species with a more structured bark type and medium insulation values and c) species with deep-fissured or scaly bark types and high insulation values. Only the trees in the c) category were able to survive openings in subtropical forests and stand alone on edges of forest gaps. Trees in savanna either shaded their trunks by leaves or they exhibited one of two defense mechanisms against trunk overheating, i.e. bark with good insulation capacity or bark with high reflectivity (white bark).

Voluminous stems are common also in cacti and succulents in general. It is true also for large succulents such as cacti and euphorbia that their internal temperature departs to a certain level from the ambient temperature (Gates, 1993). Succulents have impervirous waxy cuticles and often CAM metabolism and therefore their transpiration rate and consequently transpiration cooling is very low (adaptation to low water supply). Their only defence against excessive heat is minimizing the absorbed radiation. Succulents are often of vertical form, which reduces irradiance during midday. The midday sun load reduction is supported often also by presence of a dense crown of thorns which reflects sunlight (Gates, 1980). The stem morphology of cacti, its height and branching architecture is influenced by many factors (temperatures, water supply), which they have to adjust to along a climatic gradient (Cornejo and Simpson, 1997). During the parts of the day when the irradiance is high and the sun is at its zenith, the top surface of an erected cactus is commonly warmer than the air temperature. The internal stem temperature, however, remains lower than the air. During night temperature inside the stem tends to be higher than the air temperature due to heat storage capacity of the cacti body. The temperature inside the columnar stem of saguaro (*Carnegiea gigantea* (Engelm.) Britton & Rose) is shifted relative to the air temperature so that internal temperatures are coolest in the afternoon and hottest after midnight. Surface temperatures of succulents also vary enormously from the sunlit to the shaded side (Gates, 1980).

As has been said energy budget of stems can be basically regulated only through two processes: 1) radiation can be limited at its entrance to the internal space by adapting bark or cuticular features in trees and succulents respectively, or 2) the architecture and volume of stems can be adapted to optimize temperature exchange. It seems that due to their nature, stems are generally pushed to restrict rather than intensify their solar energy use.

4. Non-metabolic use of solar energy at plant level; thermoregulation of plants

Plants as sessile organisms have limited possibilities to regulate their temperature. There are basically only two ways they can do it. From a longer perspective, they can adapt or acclimate their structure and architecture of organs in a manner optimised to the prevailing conditions.

Momentary reactions to fluctuating conditions can be achieved through regulation of physiological processes, which influence temperature, i.e. primarily transpiration.

Environment can be interpreted as a filter removing species that lack traits for persisting under particular set of conditions (Keddy, 1992). This filtering effect is most obvious in environments of extreme conditions where only the fully adapted forms are able to survive. In habitats with suitable conditions for plant growth, survival of plants is often limited rather by competition than directly by environmental constraints. A group of species that use the same resources and respond to the environment in a similar way is defined as a plant functional type (Pausas and Austin, 2001). Environmental limits of some habitats can be highly variable and impose burdens on plants of contrasting and even contradicting manner (drought vs. overflowing, heat vs. frost etc. such as in the Arctic areas, e.g. Crawford, 1999). Plants have a high potential to acclimate to interacting environmental limitations (Niinemets and Valladares, 2004). Species richness tends to increase with temperature and water availability and increased environmental heterogeneity. However, due to simultaneous operations of environmental parameters, relations influencing richness of plant species are hard to identify (Pausas and Austin, 2001).

Mechanisms of optimization of plants thermal conditions via non-metabolic use of solar energy are important throughout all habitats, some of them, however, are best observable under conditions of extreme temperature or irradiance when energy fluxes are large.

4.1 Structural and behavioural adaptations of plants for warming up and cooling down

Having already discussed energy budgets of different plant organs (chapter 3) we can proceed to study energy budgets of whole plants. Scaling from an organ (a leaf) to the whole plant level is a problematic task. Measurements of gaseous fluxes in individual leaves expressed on a unit leaf area basis are often tacitly assumed to represent standard properties for the whole plant or even species (Meinzer, 2003). However, this assumption may lead to large errors as quantities as well as qualities of physiological processes may differ in different leaves of the same plant according to the leaf age, position on the plant, actual and mean long-term solar irradiance etc. Leaves may even have different shapes within one crown. For example Hanson (1917) showed that peripheral leaves of *Fraxinus pennsylvanica* Marsh. were usually more deeply lobed, more prominently toothed, and smaller than the leaves from the centre of the same tree. The verity of results may be also negatively influenced by measurement itself as the conditions within a measuring chamber inevitably differ from the conditions outside to which leaves are exposed. We have experienced the latter problem while measuring transpiration rates in leaves of the wetland species *Phalaris arundinacea* (Rejšková et al., subm.; see attachment). However, the desirable scale for characterizing ecophysiological behaviour and responses of plants is often the individual because only integration of all processes in the whole organism shows its survival, growth and reproductive capacities (Meinzer, 2003). Also energy relations need to be studied on a whole plant or whole canopy level to be connectable with development, growth and reproduction of the plant. Relations and consequences of canopy energy and water fluxes will be discussed in chapter 5 and 6. In this chapter I would like to focus on individual plants, their architecture and their structural behaviour related to light, temperature and drought conditions, three environmental aspects closely interconnected in influencing plant energy budget.

4.1.1 Phototropism and heliotropism

Phototropism in general is the plant's response to light. Plants seek a favourable position to the light source for their leaves. The positioning of leaves is derived from light conditions of particular habitat and from light demands of individual leaves. The positioning may have different patterns. From the energy point of view it may be advantageous for leaves to orient themselves in different directions, for example towards the zenith or to the south under certain conditions, or by contrast to catch morning or evening sun. Under many circumstances, however, it is the random distribution of leaves around the stem under suitable inclination, which represents the best solution. Under different circumstances, the overall gain may be highest when keeping the position rigid during the whole day, season or life as well as when dynamic adjusting of leaves to the changing solar irradiance is processed (Lamprecht et al., 2007).

The amount of solar irradiance incident on a leaf blade is affected by both the angle and the azimuth of the leaf. In general, increasing the angle results in a decrease of the amount of irradiance incident on the leaf especially when the sun is at high angles during midday in summer (Ehleringer and Werk, 1986; Falster and Westoby, 2003). On the contrary, when the sun is at low angles on the sky (morning, afternoon, winter), steeper angles increase light capture by leaves, which may represent an energetic advantage (Falster and Westoby, 2003). When exploring whole plant or whole canopy energy budget it is therefore important to take into account both spatial and temporal changes of insolation of all leaves. Falster and Westoby (2003) showed that whole-day overall light interception of perennial Australian forest species was lowered in species with steeper-positioned leaves at the expense of potential carbon gain. On the other hand leaves with shallower angles had to face increased leaf temperature, higher risk of overheating, and higher risk of photoinhibition, especially when transpirational cooling was limited by water deficits. Ehleringer (1988) and Smith et al. (1998) showed by investigating leaf angles patterns of many species across precipitation gradients that leaves became progressively steeper in both herbs and shrubs with increasing aridity. Steeper leaf angles may be benefitial in high light environments, such as at the top of canopies or in more open habitats (Falster and Westoby, 2003). In light limited environments such as within understorey sites shallow leaf angles are advantageous (King, 1997). Despite the presented tendencies, a wide range of leaf angles is distributed throughout all light environments in vegetation (Falster and Westoby, 2003).

Light interception is to a large extent influenced also by self-shading. Self-shading varies substantially between species and habitats. Falster and Westoby (2003) showed that within 38 species of Australian forest self-shading ranged from 13 % to as much as 60 % of the projected leaf area. Many species growing under canopy, such as *Chrysosplenium oppositifolium* L., tend to minimize self-shading. In low light, high self-shading is a distinct disadvantage (Givnish, 1988). On the contrary, due to light absorption reduction suitable leaf angles and higher levels of self-shading provide structural photoprotection for plants in high light environments, minimizing potential damage from photoinhbition (e.g. Nilsen, 1990; Oliveira and Penuelas, 2002; Falster and Westoby, 2003; Pearcy et al., 2005). Surprisingly, Falster and Westoby (2003) found that self-shading of smaller-leafed species was higher than that of species with larger leaves, despite smaller LAI and less leaf area per meter stem. This was due to crowding of leaves close to each other and to proximity of leaves to the stem. It is thus obvious that self-shading depends rather on crown architecture than on leaf size and LAI.

Dynamics of acclimation of leaves to their light environment was nicely shown by Muraoka et al. (1998) on leaves of a perennial herb *Arisaema heterophyllum* Blume. The orientation of single palmately compound leaves of this species are determined by inclination of leaflet mid-vein and folding of leaflet blade. Leaf positioning differed markedly at the forest (understorey) and deforested (open) site. In the forest the plant behaved in a manner maximizing diffuse light capture. The leaves were flatter and had smaller angles of inclination. Mean light capture efficiency (the ratio of actual diffuse light captured by a leaf to maximum receivable light) reached 98 %. In contrast, at the deforested site leaflet folding occurred, which varied diurnally reaching the maximum around noon. Similarly, at a temporarily sun exposed forest site a leguminous species *Amphicarpa bracteata* L. responded within minutes to penetration of the direct solar beam by reorienting its leaves to steep angles. In contrast, plants of this species in locations under closed canopy showed little diurnal leaf movement (Prichard and Forseth, 1988).

Heliotropism is a special form of phototropism. It is the most obvious manifestation of plant solar energy use for both metabolic and non-metabolic functions. It represents the active diurnal motion of plant organs (leaves or flowers) in response to the direct sun light incidence. It is also called sun tracking. Some plants track the sun the day round, some follow it only for a certain part of the day. The most common example of all sun-trackers is probably the sunflower (*Helianthus annuus* L.). Its young inflorescences turn with the sun to collect as much heat as possible. On the contrary, the old flowers keep the East-north to East orientation to protect the germinating pollen and the seeds against overheating (see Lamprecht et al., 2007). Heliotropism of flowers is believed to be most important for species blooming under cold conditions (e.g. Ehleringer and Forseth, 1980). Its role in alpine, arctic and vernal species with relatively large flowers and its impact on intrafloral temperatures is discussed in chapter 3.2.2 and in Rejšková et al. (2010, see attachment). When a plant has many flowers it is more advantageous from an energetic point of view to distribute them around the periphery rather than to concentrate them on the sunny side only (Lamprecht et al., 2007).

In terms of whole plant energy balance heliotropism of leaves is the most important. It is widespread in many families of both C3 and C4 plants, especially in desert plants. In annual flora investigated by Ehleringer and Forseth (1980) solar tracking increased as the length of the growing season shortened. A whole scale of heliotropic movements is placed between two extremes: diaheliotropism, i.e. orienting of leaves perpendicularly to the incident radiation and paraheliotropism, i.e. the leaf orientation is parallel to the incident radiation. Leaves that are perpendicular to the sunrays enhance the photosynthetic rate, whereas leaves parallel to the sun rays reduce their temperature and transpiration rates (Ehleringer and Forseth, 1980). Leaves of *Lavatera cretica* L. can be used to illustrate diaheliotropic movements. Their laminas track the solar position throughout the day not diverging from the solar azimuth by more than 12° from sunrise to sunset and tracking also solar elevation. On an overcast day the leaves reorient themselves to a horizontal position (Schwartz and Koller, 1986). *Pterodon pubescens*, a Brazilian woody legume, represents a species with paraheliotropic leaflet movements. Caldas et al. (1997) showed that due to the reorientation to the sun, the leaf area of *Pterodon pubescens* exposed to vertical radiation was reduced by as much as 40 % at midday. The plant, however, maintained an elevated rate of photochemical reactions indicating that paraheliotropic movements served to optimize photosynthesis. In many plants, such as in a number of legumes, paraheliotropic movements are daily and seasonally directly associated with actual light intensity, temperature and drought. Through reorienting their leaves these plants react to the actual conditions in order to control excess water loss, leaf above optimum temperatures and photoinhibition (see Ehleringer and Forseth, 1980; Yu and Berg, 1994).

There are some popular examples of leaves heliotropism. One of them is the North American *Silphium laciniatum* L., which was named Compass plant because its leaves commonly point to North-South directions. Leaves of *Silphium laciniatum* are nearly vertical, i.e. the adaxial and abaxial surfaces face East or West (Zhang et al., 1991). Newly emerged leaves have random orientation, but within 2-3 weeks compass orientation is achieved by twisting of the leaf petiole (Zhang et al., 1991). Jurik et al. (1990) showed that the natural orientation of Compass plant leaves with highest light interception early and late in the day resulted in equivalent or higher carbon gain and in increased WUE if compared to leaves with other orientations. Similarly, cauline leaves of a European species *Lactuca serriola* L. exposed to the sun oriented themselves in North-South position whereas if grown in shade the leaves oriented themselves randomly (Werk and Ehleringer, 1984).

Some plants exhibit only partial heliotropism. Whereas some leaves of *Phaseolus vulgaris* tracked the sun a significant proportion of leaves pointed to other directions, with as much as 20% of leaves oriented towards the North (Barradas et al., 1999). Pastenes et al. (2005) showed that as water demand increased, paraheliotropic movements were intensified in *Phaseolus vulgaris* L. to avoid photoinhibition resulting from direct exposure to the sun.

Some plants also have an ability to produce reversible nyctinactic movements in order to prevent stress of low temperatures. A large caulescent rosette species of the paramo zone of the Venezuelan Andes, *Espeletia schultzii* Wedd. (*Compositae*) closes at night the rosette leaves around the apical bud. These nyctinastic movements protect the bud from freezing temperatures and prevent rapid heating of young leaves just after sunrise (Smith, 1974). The insulating effect of nyctinastical movements was confirmed also in four “giant rosette” species, *Senecio keniodendron*, *Senecio brassica*, *Lobelia keniensis* and *Lobelia telekii*, which inhabit the alpine areas of the tropical Mountain Kenya. Upon onset of the nocturnal frost the adult leaves nyctinastically bent inwards and formed a “night-bud” around the central leaf bud. Thus freezing was avoided by a delay of cooling which was sufficient until re-warming by the next day's sunshine (Beck et al., 1982). Interesting structural adaptation has been described also for an Andean caulescent giant rosette plant *Espeletia timotensis* Cuatr. This species keeps an insulating layer of marcescent leaves which defend it against hard conditions. Experimental removal of dead leaves had lethal effects on the plant (Goldstein and Meinzer, 1983).

4.1.2 Plants overall shape and architecture in different light and temperature environments

Forms and structures were the first qualities studied by researchers within the plant kingdom. Therefore it is startling that we still lack proper understanding and physiological explanations of form and dimension regularities in relation to the environmental co-occurring aspects (e.g. Bragg and Westoby, 2002; Westoby et al., 2002). Plants between and within sites vary enormously in their dimensions, shape, structure and overall architecture, reflecting both the genetically determined developmental programs, as well as effects of the environments (e.g. Housman et al., 2002). Only when variations in twig cross-sectional area, individual leaf size and total leaf area supported by one twig are considered, the differences of these parameters differ in orders of magnitude across the environments and species (Westoby and Wright, 2003). The wide range of traits among species growing interspersed within a single vegetation type is striking (Westoby et al., 2002).

4.1.2.1 General trends throughout environmental gradients related to plant heat balance

Although costs and benefits of structural differences are insufficiently understood, some general tendencies along the environmental gradients can be identified. The tendency of plants towards steeper angles of leaves with increasing aridity (Ehleringer, 1988; Smith et al., 1998) has already been mentioned. Ehleringer and Werk (1986) found also a consistent trend of decreasing leaf absorptance with decreasing precipitation. With decreasing rainfall plant water acquisition costs increase. As a consequence, a combination of high irradiance and drought favour smaller leaves (Westoby et al., 2002). Also leaf mass per area is well known to be higher at low rainfall, owing to thicker leaves, denser tissue, or both (for citations see Westoby et al., 2002). Long-living leaves are usually more robust, i.e. thicker with denser tissue, which is a reason why leaf life span is correlated with leaf mass per area. This seems, however, not to be true in dense-shade environments where leaves often have long life span although their leaf mass per area is low (see Westoby et al., 2002). Although related also to other factors, strong light environments favour also closely ramified branching (Westoby et al., 2002). At sites with low rainfall, a twig at a given cross-section supports a smaller leaf area than is usual for the same species at sites with ample precipitation (Westoby and Wright, 2003). These trends in plant structure correspond to the results of Housman et al. (2002) who observed that the shrub species *Encelia farinosa* (*Asteraceae*) exhibits geographic variation in aboveground architecture and leaf traits in parallel with environmental variations in temperature and moisture. Plants in desert populations produced smaller, more pubescent leaves and were more compact and branched than plants in more mesic coastal environments. Small size and pubescence reduced leaf temperatures and thus increased water-use efficiency but at the cost of lower photosynthetic rate, which resulted in slower growth.

Corner (1949) described two overall rules for architecture of plants with cross-species acceptance: 1) the thicker the plant axis (stem), the larger the individual appendages, i.e. leaves, inflorescences, fruits and 2) the more closely spaced branching, the thinner the ultimate axes and the smaller the appendages. Indeed, it has been documented that species with thicker twigs tend to have larger leaves and branch less often than species with thin twigs. Also the total leaf area is strongly correlated with twig cross-section area (Westoby and Wright, 2003). Similar relations were confirmed also for inflorescences (Midgley and Bond, 1989). Total leaf area should be coordinated with stem diameter for both mechanical and hydraulic reasons (see Westoby et al., 2002). In dry hot climates, hydraulics plays a particularly important role in the evolution of shoot morphology. High leaf temperatures and low relative humidity increase vapour pressure deficits (VPD) and consequently potential transpiration rates. Testing congeneric shrub species from contrasting habitats, Preston and Ackerly (2003) showed that the size of leaf area for a given conducting stem area declines along environmental gradients with increasing evaporative demand or drought stress. Changes in absolute total leaf area occurred primarily through changes in individual leaf size.

All structural tendencies throughout environmental gradients are often fuzzed by other factors entering the field. For example when studying plant structure throughout precipitation, light and temperature gradients, the tendencies are marked with nutrient availability. Plant appearance is also largely impacted by exposure to mechanical constraints, such as wind. Niklas (1996) showed that *Acer saccharum* L. trees chronically exposed to wind had reduced overall leaf size as well as leaf distribution. The petioles evolved shorter and narrower with a smaller volume fraction of lignified tissues. As a consequence the leaves were able to twist and bend more easily due to smaller petiolar rigidity and stiffness and mature leaves thus imposed less drag on their subtending stems. Wind exposure may largely differ also within one site, with wind rates increasing in the upper part of the crown or canopy (Niinemets and Valladeres, 2004).

4.1.2.2 Evergreen vs. deciduous patterns and leaf area reduction in different environments and under stress

Probably the most obvious behaviour pattern of plants is the life strategy of being evergreen or deciduous. Deciduous plants, due to their ability to regulate exposure to harsh conditions, are in general more prevalent in areas of high seasonality. The limiting periods are usually either hot and dry summers or winters freezing or cold enough to be classified in effect as dry. The greater the length and intensity of the dry season, the greater the tendency to deciduous plants to dominate. There are, however, some exceptions. For example, shrubs in dry savannas that tap water stored in deep soil profiles are evergreen because they experience in reality low seasonality in moisture and subsequently leaf temperature. Evergreen leaves, on the other hand, are favored by infertile soils. This is true also under highly seasonal climatic conditions where evergreen conifers replace deciduous trees on poorer soils. Their longer photosynthetic season, lower amortized costs of leaf construction and replacing of leaf nutrients, as well as tougher laminae that can better endure frost, drought, and/or herbivore attack offer advantages in their favour. Distribution in particular cases is, however, influenced also by herbivory pressure, rooting costs, leaf shedding or fires. Information on evergreen vs. deciduous patterns described here is based on a nice review by Givnish (2002).

Deciduousness may also appear as a direct reaction to actual conditions. Reducing leaf number via abscission can be induced by many environmental factors including temperature, light, water, soil conditions but also parasitic organisms. For many broad-leaved and evergreen species of the tropics and temperate zones the onset of drought is a signal for abscission (Addicott, 1968). Drought-induced leaf senescence minimizes transpiration fluxes and help to maintain favourable water balance of the whole plant under temporarily inconvenient conditions while contributing to nutrient remobilisation for youngest leaves, fruits or flowers (e.g. Munné-Bosch and Alegre, 2004). Reduction of leaf area may be also a result of reversible reduction via curling, folding or changing of leaf angles and position as mentioned earlier. Some species, such as *Cistus* spp., combine both strategies for avoiding adversed effects of high irradiance and water stress by being semi-deciduous and by regulating light interception via leaves positioning (Werner et al., 1999).

Thermotropic movements of leaves leading to minimized leaf area are observed in some plants also in reaction to cold stress as a way of protecting leaves from photoinhibition and membrane damage resulting from high irradiance and freezing temperatures (Nilsen, 1992). Leaves of *Rhododendron* L. curl and change from vertical to pendent position under freezing conditions. Leaf angle is controlled by hydration of the petiole, as affected by soil water content, atmospheric vapour pressure, and air temperature. In contrast, leaf curling is a specific response to leaf temperature (Nilsen, 1990). Leaves that are horizontal and flat have a greater exposure to the sky and through changing their position they regulate re-radiation.

Physiological importance of leaf curling is not quite clear but may serve to slow the rate of thawing following freezing and vice versa (Nilsen, 1992).

4.1.2.3 Crown shape and whole plant architecture

The functional role of crown architecture is to maximize light capture and photosynthesis in shaded understories and minimize exposure to excess radiation loads in open high light environments. Multiple functions and constraints influence crown design, leading to high plasticity in response to environmental conditions. Temperatures of leaves within canopy strongly depend on canopy architecture (leaf area density, branching habits) (Leunzinger and Körner, 2007). Designing a plant crown is a trade-off between potentially most effective light-capture (and optimization of other conditions for leaves) and lowest additional costs required for biomechanical support of higher growth (Pearcy et al., 2005). Although variation in light within plant canopies constitutes the most dramatic environmental gradient which plants commonly experience, wind speeds, temperature and water availability co-vary with light. These interactions become especially amplified during soil water stress, which leads to limited foliar cooling via transpiration and thus to extreme leaf temperatures (Niinemets and Valladeres, 2004).

Light penetration into vegetation stands differs enormously according to crown and canopy architecture. Differences in incident irradiance between upper and lower canopy leaves are 20- to 50-fold for temperate forest ecosystems and as much as 50- to 200-fold for tropical rain forests (for citations see Niinements and Valladeres, 2004). A nice example of the role of crown architecture in solar energy use is the conical-shaped crown of conifers. Their shape and branch layering increase sun interception from low sun angles for both solitaire trees as well as canopy treetops. This is especially beneficial in high latitudes. In addition, conical crowns create larger gaps at the top of the canopy and thus enable greater sunlight penetration and less shading of lower branches by the upper branch layer (Smith and Brewer, 1994). The canopy may be also seen as a blanket for subcanopy plants. The above layers of leaves provide a strong temperature ameliorating effect to leaves of the understorey layer (Nilsen, 1990). Holmgren (2000) discussed also the ameliorating effect of canopy to growth and survival of small plants. A wide range of plant communities has been shown to improve water relations of the individuals growing in their shade.

The shape of individual plants growing under canopy is influenced by structural traits of the canopy itself, although also here the tendencies derived from the habitat features mentioned earlier can be identified. When studying plant structure we mustn't forget root architecture. Features such as rooting depth, root distribution and lateral root spreads are important for plant functioning but so are plants below-ground/above-ground allometries. In terms of plant energy budget, roots are essential for providing sufficient water supply and their importance thus grows with decreasing water content in the soil. Schenk and Jackson (2002a) showed that although deeply rooted shrubs and trees were found in all climates, maximum rooting depths of all growth forms in general tended to be shallowest in arid regions and deepest in subhumid regions. This result somewhat contradicts the commonly held view that plants tend to be most deeply rooted in the driest environments. However, if we consider that in subhumid climates there is a seasonal surplus of water that can accumulate at depth and a seasonal evaporative demand for that water during the dry season, the fact that roots are directed to the deepest soil layers in these habitats is not surprising anymore. Also, it has to be taken into account that these results considered maximum rooting depth. When depths at which plants have 50% or 95% of their root biomass (the depths above which 50 % or 95 % of all roots were located) were compared these were significantly deeper in drier than in humid environments (Schenk and Jackson 2002b). Also rooting depths relative to above-ground size increased with aridity (Schenk and Jackson 2002a).

Lately spatial organization of individual plants has become a subject of interest in modelling fields, mostly for practical applications. In contrast to crop models, which describe plants in global terms such as biomass, yield, and number of flowers and fruits, architectural plant models attempt to capture spatial arrangement of plant components and their development over time, with interactions between a plant and its environment being one of the most important issues (e.g. Prusinkiewicz, 1998). Chelle (2005) presented a new attitude to plant modelling which tries to cover the spatially and temporally heterogeneous phylloclimate, i.e. physical environment experienced by each aerial organ in the studied plant canopy.

4.1.2.4 Plants growing near the soil surface

Plants growing near the soil surface represent a very interesting functional group from the energy balance point of view. As they are hidden within the soil surface boundary layer, they are to a large extent decoupled from the convection of the ambient air. It is thus reasonable to compare temperature of these species not only to air temperatures but also to the temperatures of the surface, which may be in this case determining.

Cushion plants are one of the most common growth forms in the Alpine habitats. Their low stature, dense canopy, and compact form allow them to largely decouple their microclimate from their surroundings (Cavieres et al., 2007). The crowded leaves of cushion plants more or less share a common boundary layer. Thanks to their structure cushion plants maximize the absorptance of light (they absorb about 80 % of solar irradiance) while minimizing heat losses (Gauslaa, 1984). According to the commonly held assumption, cushion plants tend to be warmer than the air during daytime when irradiance is high and colder than the air during night time due to re-radiation (Gates, 1980). Measuring conducted in natural environments showed that this correlation must not be always true. Arroyo et al. (2003) compared temperature of *Azorella monantha* Clos. cushions and the surrounding bare ground during midday on summer days in the Chilean Patagonian Alps. The authors showed that while the temperature of bare soil decreased with elevation, temperature on the cushion surface remained constant, 6–7 °C higher than the actual air temperature. Cavieres et al. (2007) showed that *Laretia acaulis* and *Azorella monantha* cushion species in the Ands of Central Chile maintained lower substrate temperatures than their surroundings during the day over most of the growing season and similar temperatures during the night. Soil temperature on bare ground during the day exceeded 30 °C, while temperature within cushions remained below 20 °C (Cavieres et al., 2007). So, whereas in the colder and windier Patagonian Alps cushions of *Azorella monantha* were warmer than the air, in the warmer mountains of Central Chile they were colder than the hot air. Therefore cushions in both habitats in effect generated thermally more stable sites microhabitats with less prevalence of extreme temperatures than bare ground (Cavieres et al., 2007).

Cushion plants also lowered freezing within their micro habitat and improved moisture conditions. Cavieres et al. (2007) showed that the proportion of freezing temperatures changed from 0 % at 2800 m to 1 % at 3600 m within the cushion, whereas in bare ground, the proportion of days with freezing temperatures increased with elevation from 0 % at 2800 m to 32 % at 3600 m. Soil beneath the cushions of *Laretia acaulis* (Cav.) Gill. & Hook maintained higher humidity than the surrounding soil, which was explained by high evaporation rates in bare ground and low transpiration rates of cushion plants. The difference in moisture content under *L. acaulis* cushion plants and on bare ground at 2800 m even increased in the course of the growing season (Cavieres et al., 2006). By combining more benign microhabitats and trapping seeds, cushion plants, especially at high elevations, function as nurse plants, i.e. those that facilitate the establishment of other plant species beneath their canopy (Arroyo et al., 2003; Sklenář, 2009). While amelioration of freezing temperatures can be more important at higher than at lower elevations, drought amelioration seems to be more important at lower elevations, in particular in arid mountains (Cavieres et al., 2006).

An interesting thermoregulative behaviour was shown by Matsumoto et al. (2000) in *Aster kantoensis*. During sunny days this rosette shaped species avoided leaf overheating through lifting its caulescent rosette leaves up from the heated soil. As a consequence of this behaviour and in combination with a rather high transpiration rate (as high as 10 mmol H_2O $m^{-2}s^{-1}$ as long as the soil water supply was not severely limited) leaf temperature was much lower (35-39 °C) than soil surface temperature (max. 60 °C).

4.2 Transpiration as a cooling process

The importance of transpiration process for solar energy use in plants has been discussed in the previous chapters. In this chapter I would like to look at this topic under more scrutiny. Most plant tissues contain large amounts of water. Biomass of non-woody tissues typically comprises 80-95 % of water. However, only less than 1 % of the water absorbed by plants is actually retained in biomass (Lambers et al., 1998). Vast majority of water taken up by roots is merely transported through plants in Soil-Plant-Atmosphere Continuum (SPAC) and transpired into the air without interfering with the plant's metabolism.

Transpiration is usually perceived as something rather negative, a perception rooted especially in agricultural practice, where high transpiration represents a threat of water reserves depletion. This opinion was expressed for example by Zoebl (2006) who wrote: „Though small or larger fractions of absorbed water have beneficial functions for the plant's metabolism, for maintaining the turgor of leaf tissues and canopies, for cooling leaf surfaces and as a medium to transport nutrients, most experts agree that the bulk of the transpiration is apparently a necessary evil". This attitude is reflected also in the plant physiological term "transpiration loss" used commonly to describe the amount of water transported through a plant or a stand.

The sessile plants in their search for balance in life conditioning processes have to suppress or support some processes at the expense of others. Every situation calls for different regulative solutions and different plants choose different strategies of survival. Stomatal opening and closing is influenced by photosynthesis and transpiration. As these two processes require often antagonistic reactions, plants have to make a trade off – either open the stomata for optimal photosynthesis or close them to save water (Roelfsema and Hedrich, 2005). The cooling process of transpiration is often considered merely as a side effect rather than a mechanism to control leaf temperature (Lambers et al., 1998). I would like to demonstrate that at least in some cases and for some plants and ecosystems transpiration cooling is a process of large importance, which is hard to explain only as a result of evolutionary imperfection.

4.2.1 Water movement through plants and its regulation

Transpiration is generally influenced by three factors: 1) gradient of water potentials between the soil and the atmosphere which is the driving force for water movement, 2) resistance of all plant tissues to water movement conditioned by plant hydraulics and 3) water availability in the soil. To a certain level plants may influence all of these conditions. They may adjust water potential (ψ from roots to leaves by changing hydraulic conductivity (Maseda and Fernandez, 2006; Sack and Holbrook, 2006) or by osmotic adjustment (e.g. Jones and Turner, 1978; Morgan, 1984). They may regulate water on its exit from the leaves through regulating stomatal conductance (Buckley, 2005). And to a certain level they may also regulate water reserves in the soil for example by hydraulic redistribution (e.g. Burgess, 1998; see later). Maximization of water flux in a given environment requires harmonization of at least three parameters: stomatal sensitivity, xylem vulnerability to embolism, and root-to-leaf area ratio (Maseda and Fernandez, 2006). Different plants in different environments choose different strategies in order to achieve balance. The different strategies in plant water use have consequently also different impacts on the environment.

Leaf conductance for diffusion of water vapour (g_w) is determined by the stomatal conductance (g_s), the boundary layer conductance (g_a) and the vapour pressure gradient between leaf and air ($\psi_{leaf} - \psi_{air}$), which is determined by temperature and absolute humidity of the leaf and air respectively (Lambers et al., 1998). Boundary layer conductance (discussed also in chapter 3.1.2.2) may be influenced by the plant only in a long-term manner, by structural adjustment of the leaves or the whole plant. The dynamic and almost instantaneous changes are directly connected with opening/ closing of stomatal apertures through changing turgor pressure in the guard cells (e.g. Buckley, 2005).

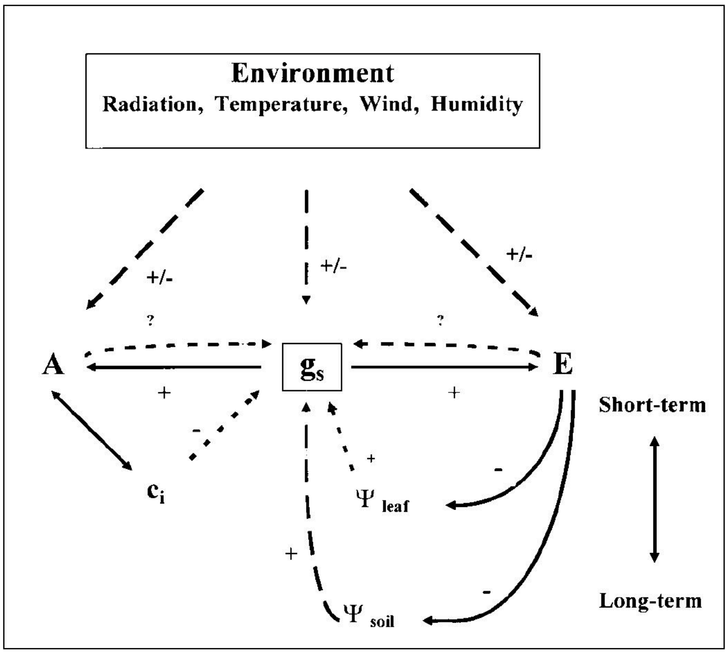
4.2.1.1 Stomatal conductance

The free exchange of gas between leaves and their surroundings is prevented by a cuticle, a cutin-wax layer, with very limited gas permeability. Only about 5 % of water escapes from a leaf through the cuticle (Taiz and Zeiger, 2003). Most gas exchange is thus conducted through stomata. There is an enormous diversity between size, density, distribution and physiological behaviour of stomata among various plants. Amphistomatous leaves have stomata on both sides, hypostomatous on the lower side only. The number of stomates varies substantially and may be very high, up to tens of thousands per square centimetre (Gates, 1980). There are various adaptations of stomata to environmental conditions. Some semi-arid and arid species for example have stomata sunken in the epidermis or located inside deep crypts (e.g. Rotondi et al., 2003) to prevent high transpiration.

Stomatal movements are governed by both endogenous and environmental signals (Roelfsema and Hedrich, 2005). It has been proven that guard cells respond to both light and intercellular CO_2 concentration and hydraulic perturbations, however, although many detailed molecular processes involved in stomatal movement have been identified, mechanisms and interactions of this complicated regulatory system are still not sufficiently understood (for reviews see Buckley, 2005; Messinger et al., 2006; Lawson, 2008). Until today no commonly accepted mechanistic model of stomatal behaviour has been designed and no answer to the intriguing question of how stomata can optimize gas exchange for the entire plant when they have only limited, local information has been provided (Mott and Peak, 2007). So far, most aspects of short-term stomatal behaviour in response to changing leaf water balance are most easily explained by, the hypothesis of "hydro-active local feedback": a metabolically mediated response of guard cells to water status in their immediate vicinity (see Jones, 1998). Some of the interactions involved in stomatal conductance are described in figure 4. It has been shown repeatedly that stomata react in a two-phase manner when the humidity of the surroundings is reduced. Typically, g_s increases for 5–15 min and then declines for another 20–75 min, ultimately approaching a steady state g_s that is lower than the initial value (for citations see Buckley, 2005). Physiological explanation of this process as well as of many other processes, such as stomatal patchiness, are still not clear. However, it seems that plants optimize gas exchange in a more sophisticated and adaptive manner than if performed by individual stomata independently (Mott and Peak, 2007). It is clear that no complete understanding of leaf-level stomatal conductance can be achieved without considering the stomata on a plant as an integrated whole. We know also very little about the internal conductance of CO_2 between the substomatal cavity and the site of carbon fixation and its responses to environmental conditions (Warren and Adams, 2006). Changes in stomatal conductance can be also mycorrhiza induced (Augé et al., 2008). The situation is also complicated because plants have to behave in a way compliant with the whole plant integrity.

Figure 4. Some of the interactions involved in control of stomatal conductance (g_s). g_s affects both assimilation rate (A) and transpiration rate (E). Simultaneously, g_s is influenced by a range of direct or indirect feedback effects. Environmental factors affect any of these

variables. According to Jones (1998).



It is a general assumption amongst plant physiologists and ecologists that stomata evolved to provide CO_2 uptake for photosynthesis while controlling water loss from plants, i.e. they operate in such a way as to minimize water loss relative to the amount of CO_2 uptake (e.g. Jones, 1998). Recent efforts in genetic engineering are thus directed to produce plants with increased water use efficiency by altering stomatal physiology and functions as well as anatomical features, such as stomatal density and size and features of leaf cuticular wax (see Lawson, 2008). However, reducing water use is not a guarantee of plant survival under drought conditions as photosynthesis may be reduced directly by high leaf temperature (Haldimann et al., 2008). This may be illustrated by the fact that although plants with C4 photosynthesis have typically higher water use efficiency than C3 plants, this photosynthetic advantage of C4 over the C3 plants may be lost under drought conditions due to higher metabolic limitations (lower electron transport rates and decreased photochemical efficiency) which become more important than stomatal conductance itself (Ripley et al., 2007). If and to what extent and under what circumstances energy balance, i.e. thermoregulation, may be the overriding reason for regulating stomatal conductance is very difficult to judge. However, there is evidence (stomates of *Phaseolus vulgaris* L. opened in darkness with increasing temperature) that at least in some cases temperature was the signal for stomatal opening, regardless of the concentration of internal CO_2 (Feller, 2006). An interesting phenomenon in this context is the nighttime stomatal conductance (Caird et al., 2007; Kavangh et al., 2007). It has been reported that although plants are able to close stomata tightly under stress, their stomata remain rather opened during night. The night stomatal conductance has been recorded at up to 90 % of daytime conductance leading under relatively low night VPD to transpiration typically 5 % to 15 % of daytime rates, although it can reach as much as 30 % (Caird et al., 2007).

Most trees attempt to maintain homeostasis of leaf water status by regulating leaf water potential to prevent runaway cavitation (air embolism in xylem vessels which leads to breakage of the capillary water column) (Ewers et al., 2005). Maintenance of a maximally efficient conducting system requires the stomata to close as evaporative demand increases in order to prevent shoot water potentials falling below the threshold value at which cavitations occur (Tyree and Sperry, 1988; Jones and Sutherland, 1991). Lowering of gas exchange in leaves may be detrimental as it limits both photosynthesis (Flexas et al., 2006) as well as cooling capacity of the leaf. Some plants tend to reduce the leaf area (see chapter 4.1.2.2) or even sacrifice some branches in order to maintain better water status of the rest of the plant (Tyree and Sperry, 1988; Rood et al., 2000). Mechanisms such as maintaining optimal leaf temperature or avoiding cavitation must not be neglected when reflecting on optimal transpiration rate.

Different species try to achieve a balance between water uptake and expenditure and CO_2 uptake in a different manner according to their physiological predestinations and environmental conditions of their habitats. Increasing VPD above certain critical level generally results in exponential decrease of stomatal conductance. The set-off and magnitude of this decrease, i.e. stomatal sensitivity, vary both within and between species. According to their ability to control transpiration flux, plants have been divided into two broad categories based on the extent to which tissue hydration is kept stable under fluctuating environmental conditions (Tardieu and Simonneau, 1998). The first category includes isohydric plants, the second anisohydric plants. Isohydric plants regulate transpiration rate more effectively through strong stomatal control and maintain a nearly constant leaf water potential during the day at a value which does not depend on soil water status until plants are close to death. On the contrary, the stomata of anisohydric plants exhibit less sensitivity to evaporative demand and soil moisture. Leaf water potential of the plants from the latter category fluctuates markedly with VPD. Recently a third mode of hydraulic regulation behaviour has been described for *Eucalyptus gomphocephala* and called isohydrodynamic (Franks et al., 2007). The water potential in leaves (Ψ_{leaf}) of plants representing the third category is closely related to fluctuations in water potential of the soil which may lead to Ψ_{leaf} decrease into the range likely to induce xylem embolism. This distinguishes them from isohydric species. At the same time, however, their behaviour differs from that of anisohydric plants. Whereas unisohydric plants simply do not bother with much regulation of water use, isohydrodynamic species possess an unusual hydrodynamic regulation mechanism that ensures a relatively constant midday water potential gradient from roots to shoots ($\Delta\Psi_{plant}$) throughout the seasonal variations in soil moisture, Ψ_{leaf} and evaporative demand. The way of maintaining hydrodynamic relations of isohydrodynamic species is not yet known. However, it may be speculated that such behaviour is a result of the whole-plant hydraulic conductance being positively dependent on the transpiration rate over a broad range of water potentials. Anyway, it seems that in terms of hydraulic regulation in isohydrodynamic plants the water potential gradient is a more decisive parameter than the absolute water potential (Franks et al., 2007). The mechanism of this regulation remains unexplained.

Although it seems apparent that isohydry is an advantage in an environment with widely fluctuating evaporative demand or soil moisture, as well as for taller, woody plants in which the cost of recovery from loss of hydraulic conductivity may be too high, as yet, there is no clear picture of the environmental or evolutionary significance for isohydry or anisohydry, and no clear mechanism explaining these strategies either (Franks et al., 2007). The maximal stomatal conductance is limited by leaf anatomy, especially size, structure and distribution of stomata (Larcher, 1995). Körner (1995) presented an overview of maximum leaf conductances in different types of vegetation based on a whole range of studies. The mean maximum values were measured to be 190±71 mmol $m^{-2}s^{-1}$ for broad-leaved deciduous temperate forests and 234±99 mmol $m^{-2}s^{-1}$ for coniferous (mainly boreal) forests. Leuzinger and Körner (2007), however, presented higher maximum g_s variability for broad-leaved deciduous trees ranging from 70 to 340 mmol $m^{-2}s^{-1}$. Also the mean maximum g_s for conifers was shown to reach a wider range from 5.5 to 360 mmol $m^{-2}s^{-1}$ (Schulze et al., 1994; Teskey et al., 1994). According to Körner (1995) the mean maximal values for most of the other natural vegetation types are between 200 and 300 mmol $m^{-2}s^{-1}$ throughout different habitats, excluding desert succulent vegetation. In comparison, anthropogenic vegetation tends to have higher maximum stomatal conductance (cereals ca. 450 mmol $m^{-2}s^{-1}$, broadleaved herbaceous crops ca. 500 mmol $m^{-2}s^{-1}$). Maximal conductance sets limits to transpiration. However, from the point of view of plants control of water vapour, the dynamics of stomata opening/closing is more important than the maximum stomatal conductance values.

4.2.1.2 Hydraulic conductance of plants

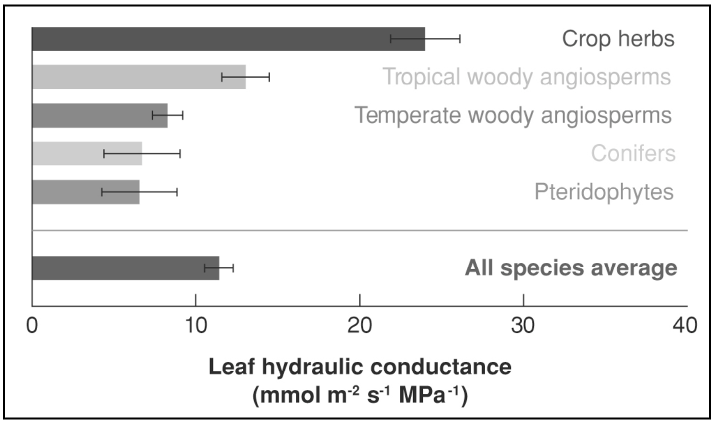
Water movement through plants is largely influenced by the whole-plant hydraulic resistance. Leaf-level water status homeostasis is to a large extent developed during ontogeny through morphological and anatomical adjustments of the whole-plant physical resistance to liquid water (Maseda and Fernandez, 2006). Although stems are most often mentioned in this context, they actually represent a minor part of plant hydraulic resistance. About half of the total hydraulic resistance of trees is located in roots (Meinzer, 2002) and at least 30 % of total resistance in the liquid phase is located in leaves (Sack et al., 2003; Sack and Holbrook, 2006). In response to water deficits, plants at different levels (tissue, organ, individual) seem to increase hydraulic resistance in the short term and reduce it in the long term (Maseda and Fernandez, 2006).

Interspecific variation in hydraulic conductances in connection with leaf CO_2 and H_2O fluxes must be studied at the level of the whole plant (e.g. McElrone et al., 2004; Maherali et al., 2006). Hydraulic conductance varies substantially at all levels throughout the plant kingdom. For a review of some whole-tree hydraulic conductances see Mencuccini (2002). Values of leaf-specific conductance (K_L, i.e. tree hydraulic conductance, normalized by leaf area), calculated as the hydraulic conductance of any plant segment per unit of leaf area that it feeds (i.e. downstream), encompass at least three to six orders of magnitude across species due to differences in sapwood cross-sectional area and individual vessel diameter (Maseda and Fernandez, 2006). According to the hydraulic limitation hypothesis (Ryan and Yoder, 1997) the leaf-specific hydraulic conductance decreases as trees grow in height. This limits their further growth, as taller trees have to close their stomata earlier in the day or earlier during drought, thereby slowing down photosynthesis. Implicitly, larger trees have lower stomatal and canopy conductances than smaller ones in the same environment (for debate of this topic see Mencuccini and Magnani, 2000; Bond and Ryan, 2000; Ryan et al., 2006). Although some results (e.g. Philips et al., 2001) showed that the hydraulic limitation hypothesis is not valid for all species, it appears that in many tree species photosynthesis, g_s and tree water use indeed decrease with age and height (Ryan et al., 2006).

Leaf-specific conductance changes according to environmental conditions, and plasticity occurs also across populations with respect to vulnerability to embolism (Aranda et al., 2005). However, these changes are species-specific which makes it difficult to establish general rules in this field. This is connected also to the unclear distribution of isohydry and anisohydry types among the species. Mencuccini and Grace (1994) showed that Scots pine (*Pinus sylvestris* L.) at drier sites produced less leaf area per unit of conducting sapwood area and had less leaf area per unit branch cross-sectional area in order to maintain water potential gradient in the stems similar to the trees growing on wetter sites. In addition, Poyatos et al. (2007) showed that relative sensitivity of stomatal conductance to both relative or absolute VPD did not increase with evaporative demand across Scots pine populations. Consequently, leaf area-related transpiration rates at a given VPD increased in drier and warmer climates. Gazal et al. (2006) provided a nice example of leaf:sapwood area ratio increase with better and more balanced water supply in *Populus fremontii* trees growing in a semiarid riparian woodland. Also xeric populations of *Pinus ponderosa* had lower leaf:sapwood area ratio and higher whole-tree leaf specific hydraulic conductance than mesic populations (Maherali et al., 2002). On the contrary, in both *Fagus sylvatica* and *Quercus petraea* leaf-specific conductances decreased progressively as water stress increased, followed by an increase in stomatal control of daily water losses. The decrease was stronger in *Fagus sylvatica* and led to a higher decline in its water use at the tree level compared to *Quercus petraea* (Aranda et al., 2005).

Variability of leaf hydraulic conductances (K_{leaf}) of contrasting life forms are presented in figure 5. Substantial hydraulic resistance occurs both in the leaf xylem as well as in the flow paths across the mesophyll to evaporation sites. It is represented both by symplastic and apoplastic resistances (Sack et al., 2003; Sack and Holbrook, 2006). Under a certain limit K_{leaf} generally increases with incident light as well as with rising temperature. By contrast, K_{leaf} declines as leaves dehydrate under high midday temperatures and VPD. K_{leaf} follows an endogenous circadian rhythm and is also dynamic over the lifetime of the leaf. It increases in developing leaves as the vasculature matures. Weeks or months after it reaches its maximum, it begins to decline, with reductions of up to 80–90 % at abscission (for citations see Sack and Holbrook, 2006).

Figure 5. Leaf hydraulic conductance averaged for contrasting life forms (for hydrated whole leaves, including petiole, and when possible for fully illuminated sun leaves). According to Sack and Holbrook (2006).



Long-distance water transport in stems and roots is fundamentally influenced by xylem structure, which varies substantially among different species. Conduit diameters span two orders of magnitude from below 5 µm in conifer needles to over 500 µm in tropical lianas.

They cover an even greater range in length from a few millimetres in tracheids to over 10 m in vines and ring porous trees. Individual conduits are interconnected to form a complex continuum from the smallest roots to the ultimate veinlets of the leaves (Hacke and Sperry, 2001).

Having reviewed a lot of literature data, Maherali et al. (2004) showed that water transport capacity (K_s, as determined by the specific conductivity of xylem) was 270 % higher in angiosperms than in conifers. Root K_s was always higher than stem K_s in all species (Maherali et al., 2006). K_s increased with decreasing rainfall in deciduous angiosperms, whereas there was no correlation between K_s and water availability for evergreen angiosperms and conifers. The authors suggested two possible interpretations of this rule. According to the first one, high K_s could be adaptive in arid environments with high evaporative demand where this adaptation would facilitate increased transpiration without increasing the water potential gradient, while supporting cavitation avoidance. According to the second interpretation, high K_s of species in dry climates maximizes water transport in order to compensate for the long dormant period and to back high carbon fixation during the short life span of deciduous leaves in periods when water is available (Maherali et al., 2004). A third interpretation, rather supplementary than self-explanatory, could be that trees in semi-arid areas are adapted to large transpiration fluxes in order to be able to cool themselves intensively during hot periods with sufficient water supply.

4.2.1.3 Impact of cavitation on hydraulic conductance

Hydraulic conductance may be largely limited by cavitation. Large vessels are more susceptible to cavitation. Therefore conifers and angiosperms that rely on small conduits are more resistant to cavitation than ring-porous trees with large conduits such as *Quercus*, *Ulmus* or *Robinia*. Maherali et al. (2004) having compiled a database of 167 species, concluded that resistance to stem cavitation was higher for conifers than for angiosperms although the values largely overlapped. The adaptive significance of increased resistance to cavitation as a mechanism of drought tolerance seems to be of primary importance in evergreen angiosperms and conifers largely because they need to preserve a water-conducting pathway for leaves year round. Deciduous species may avoid periods of severe water limitation by shedding leaves. Across all species, cavitation resistance increases with decreasing mean annual precipitation. Species with high g_s, and therefore high stomatal sensitivity to water deficits, have xylem more vulnerable to cavitation (Maherali et al., 2004; Maherali et al., 2006). This corresponds with the concept of Oren et al. (1999) that if stomata act to maintain constant leaf water potential through hydraulic regulation, stomatal sensitivity to VPD must be positively correlated with the magnitude of maximum g_s. In other words individuals, species and stands with high stomatal conductance at low VPD show a greater sensitivity to VPD (Oren et al., 1999).

Plants may be divided into two groups: cavitation avoiders, i.e. species with tight regulation of stomatal opening, and cavitation resisters with relatively weak stomatal regulation in order to minimize the gradient of water potential through the xylem. (Sparks and Black, 1999; Martínez-Vilalta, et al., 2004; Maherali et al., 2006). Cavitation resistance varies between different parts of a plant (see Hacke and Sperry, 2001). Root xylem properties generally differ from stem properties and may be more closely linked to the control of the whole plant water transport. Roots typically have wider xylem conduits, and consequently higher segment hydraulic conductivity per unit cross-sectional area than stems. Generally, roots are more vulnerable to xylem cavitation than stems, suggesting that they may be the weakest link along the soil-to-leaf water transport pathway (McElrone et al., 2004).

It has been shown that cavitations may be refilled, even when water in neighbouring conduits is under tension (e.g. Tyree et al., 1999, for other citations see Holbrook et al., 2001). Under certain situations, cavitation seems to occur deliberately in order to improve the whole-plant water balance (e.g. Nardini et al., 2001). Rood et al. (2000) showed that in *Populus deltoides* Bartram ex Marsh. (prairie cottonwood) and *P. fremontii* S. Watson (Fremont cottonwood) drought-induced cavitation underlies branch die-back that reduces transpirational demand enabling the remaining shoot to maintain a favourable water balance. Cavitation may also serve to hydraulically isolate the plant from the drying soil (Hacke and Sperry, 2001).

4.2.1.4 Hydraulic redistribution of water in the soil

The short-term reduction in root hydrological conductance of water has been suggested to function as a soil water saving mechanism and a means of reducing the amount of water lost from the roots to the soil if ψ_{soil} falls below ψ_{root} (Maseda and Fernandez, 2006). However, changing the hydraulic conductance of different roots may also lead to redistribution of water between different soil layers. Hacke et al. (2000) found that taproots of the deep-rooted shrub *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird were considerably more resistant to cavitation than small roots. This allowed water transport from deeper soil layers where water status was more favourable, even when the more susceptible small roots in shallow and dry soil layers became heavily embolized. Soil water redistribution through roots has been confirmed for many species from grasses to trees in various habitats from desert to rainforest climates (Caldwell et al., 1998; Schulze et al., 1998; Burgess et al., 2000; Burgess et al., 2001; Hultine et al., 2003; Oliviera et al., 2005). Domec et al. (2004) found compelling evidence that partial overnight replenishment of soil water by hydraulic redistribution in ponderosa pine and Douglas-fir stands diminished the loss of shallow root function during seasonal drought periods. Burgess and Bleby (2006) even suggested that equalizing of soil moisture is a major activity of roots and that hydraulic conductance may be a more flexible feature in plant water status than originally thought. Vertical and horizontal redistribution of water in roots of *Picea abies* adjusted to the existing water supply pattern and dynamic positive and reverse transport of water in roots of *Quercus suber* were recently demonstrated by Nadezhdina et al. (2005, 2008).

4.3 Transpiration and plant temperature

As follows from the foregoing chapters, transpiration rates vary substantially in time and space. They differ between and among different habitats, species and individuals according to their specific features and a range of environmental factors. Incoming radiation, temperature, advection through air movement (wind), water vapour pressure deficit of the air, and water availability in the soil are the essential environmental factors influencing actual transpiration. Also soil temperature is important for water uptake as low soil temperatures increase the water flow resistance in the SPAC, in particular by decreasing root permeability and stomatal conductance (e.g. Mellander et al., 2004; Sevanto et al., 2006).

Plants, as has been already discussed, influence the transpiration rate by regulating whole-plant hydraulic conductance and actual stomatal conductance. When long-term transpiration rate (commonly yearly transpiration) is studied, parameters such as growing season span, temperature, radiation and water supply patterns have to be taken into account. Distribution of precipitation, and consequently also transpiration rates year round play a crucial role in ecosystem functioning, as plants do not live in the world of average numbers but under actual conditions. Calder (1998) proposed a concept stating that the principal factors controlling evaporation rate vary markedly among different habitats. For example in the uplands of the United Kingdom the humid climate is characterized by high wind speed. Consequently, according to Calder (1998) the transpiration here is prevailingly driven by large-scale advection of energy, which may be under local conditions perceived as the principal limit to evapotranspiration, especially for forests with their high aerodynamic roughness. On the contrary, evapotranspiration in the studied semi-arid parts was limited mainly by soil water availability and plant physiological controls Calder (1998). However, under many circumstances this concept leads to oversimplification as the evapotranspiration rate is at many sites influenced by a combined effect of more factors. Additionally, different factors may be of different importance at different time of the day or year (e.g. Green, 1993).

Selected maximal transpiration rates of leaves of morphologically and ecologically different plant types under the evaporative conditions prevailing in their habitats are presented in table 6 according to Larcher (2003). As transpiration is determined both by leaf structure and actual climatic conditions around the leaf, when comparing these data it has to be taken into account that they only partly predicate the features of the leaves.

Table 6. Maximal total transpiration from the leaves of morphologically and ecologically different types under the evaporative conditions prevailing in their habitat. Drawn from the data of original papers of many authors according to Larcher (2003).

Plant type	Climate	Transpiration with open stomata (mmol $H_20m^{-2}s^{-1}$)
Rainforest trees	Humid tropics	up to 1.8
Dry woodland	Semiarid tropics	0.8 - 2.0
Mediterranean sclerophylls	Semiarid	1.5 - 3.7
Light adapted deciduous forest tree species	Temperate	0.6 - 4.0
Shade adapted deciduous forest tree species	Temperate	0.8 - 2.2
Evergreen conifers		1.4 - 1.7
Herbaceous dicotyledons	Mountains	1.5 - 6.0
Grass species	Meadows	3 - 4.5
Grass species	Reeds	5 - 10
Grass species	Xerothermic sites	2.0 - 9.0
Grass species	Tundra	0.2 - 0.35
Desert plants		2.8 - 10
Cacti		0.6 - 1.8

Probably the most unexpected value from this data set is the rather low value for rainforest tropical trees as daily water use of some tropical species may be very high (see chapter 5.2.2). High humidity of the air in a tropical forest lowers VPD, thereby suppressing transpiration flux. However, some tropical forests are also seasonally dry, during which period their maximal transpiration rate is most probably higher than that proposed by Larcher (2003). As the author did not provide reference to the original citations we may only guess under which conditions and on which leaves (which species and which position in the canopy) the transpiration was measured and whether the mean values are relevant. Anyhow, all of the values have to be taken only as approximations and can be used for estimates of transpiration rates of the whole stand only with highest reservation. When considering the cooling effect of transpiration of the whole stand, knowing the transpiration rate of one leaf is not of much use unless we have a rather low homogenous stand where most of the leaves are in comparable stage and under similar conditions (e.g. Moro et al., 2004). If we want to measure the transpiration rate of large individuals (trees) or whole stands, we have to use methods, which include the variability of transpiration rates of all leaves present on the individual, such as the sap flow method (Čermák et al., 2004). Scaling up the transpiration rate from a series of individuals to stands should be done with respect to existing natural variation under given environmental conditions (Čermák et al., 2004).

The release of heat from leaves through transpiration is pronounced due to high latent heat of water vaporization (2450 J g^{-1} at 20 °C). If leaves are exposed to water stress, stomata are forced to close and the reduced transpiration rate is expressed by increasing temperatures of the leaves. Gardner et al. (1981) showed that the average midday difference in canopy temperature between drought stressed and non-stressed areas of corn was as large as 7.0°C. In this study the leaves of well-watered plants were 1-2 °C cooler than the air temperature whereas the stressed plants were a couple of degrees warmer than the air. The areas also differed in the standard deviations of midday temperatures. The authors concluded that for the studied biotope a standard deviation of temperature in a plot exceeding 0.3 °C signals that some plants are experiencing water stress. However, Grant et al. (2007) did not find variation of temperatures within canopies of *Vitis vinifera* L. as a reliable indicator of stress and suggested the average temperatures over several leaves per canopy to be more reliable, as the impact of variation in leaf angles is thereby reduced. Anyway, homogenous canopies with good water status tend to have relatively balanced temperatures whereas temperatures of water stressed crops vary considerably according to existing water status of every plant (see Jackson, 1982). The leaf or canopy temperature is directly related to the rate of evapotranspiration from the canopy surface (Leinonen and Jones, 2004). Thermal image processing was used also for measuring temperature differences within one leaf (e.g. Hashimoto et al., 1984). Temperatures of leaves of *Helianthus annuus* L. exposed to water stress were 3-5 °C higher than the non-stressed leaves. The study showed differences in the temperature and water status of different parts of the leaf and concluded that temperature can serve as an indicator of transpiration. Surface temperature as a variable of leaf water budget has been used in thermal sensing methods for estimating g_s as an indicator of drought 'stress' for irrigation scheduling (Jackson, 1982; Alves and Pereira, 2000; Jones, 2004a,b; Leinonen et al., 2006). Thermal imaging combined with fluorescence imaging can potentially be used also to derive leaf water use efficiency as well as different pre-symptomatic responses of plants (Chaerle et al., 2007).

The distribution of temperatures within forests or other heterogeneous ecosystems varies to a more considerable degree than within homogenous croplands. Leuzinger and Körner (2007) measured temperatures by remote sensing IR methods in a 35 m tall mixed forest in NW Switzerland. At the air temperature of 25 °C and ample water supply, conifers (*Picea abies, Pinus sylverstris* and *Larix decidua*) and deciduous broad-leaved trees with exceptionally high transpiration (*Quercus petraea*) or very open, low density canopies (*Prunus avium*) exhibited mean canopy leaf temperatures close to air temperature (0.3 - 2.7 °C above ambient) and the maximum amplitude within a given crown reached 6 - 9 °C. *Larix* had by far the lowest canopy temperature, approximately equal to the ambient air temperature. In contrast, broad-leaved deciduous species with dense canopies (*Fagus sylvatica*, *Carpinus betulus* and *Tilia platyphyllos*) were 4.5 - 5 °C warmer than air temperature and reached temperature amplitudes of 10 - 12 °C within canopy. The results of individual species are summed in table 7.

Table 7. Mean canopy temperature with number of replicates (n), leaf to air temperature differences, temperature rande, minimum and maximum, leaf width and the standard errors (where applicable) and maximum conductnces of three coniferous and five broad-leaved forest trees. According to Leuzinger and Korner (2007).

Species	n	T_{mean} (°C)	$\Delta T_{L\text{-}A}$ (°C)	T_{range} (°C)	T_{min} (°C)	T_{max} (°C)	Leaf width (mm)	Gs (mmol m^{-2} s^{-1})
Larix	1	25.3	0.3	6.0	23.4	29.5	0.4±0.04	250
Prunus	2	26.7±0.2	1.7	7.3±0.55	24.0±0.25	31.4±0.30	41.2±1.2	237
Pinus	2	27±0.17	2.0	6.3±0.85	23.9±0.70	30.4±0.15	1.3±0.06	120
Quercus	12	27.4±0.22	2.4	8.9±0.37	23.3±0.11	32.2±0.36	49.1±1.2	343
Picea	2	27.8±0.07	2.8	8.9±0.05	24.9±0.10	33.8±0.15	1.2±0.05	125
Carpinus	5	29.5±0.21	4.5	10.3±0.24	25.1±0.19	35.6±0.17	36.8±0.8	240
Fagus	9	29.6±0.34	4.6	10.0±0.37	24.9±0.11	34.9±0.37	45.2±1.0	272
Tilia	2	29.8±0.88	4.8	11.8±0.30	25.1±0.25	37.0±0.55	72.3±2.0	207

Lower boundary layer resistance made coniferous species more coupled to atmosphere than the broad-leaved species. The results illustrate the importance of species composition for local climate (Leuzinger and Körner, 2007). Central European forests were shown to have higher capacity to cool down during the long-lasting hot and dry weather recorded in the summer of

2003, probably due to access to deeper reservoirs of water (Zaitchik et al., 2006). For further information on transpiration rates see chapter 5.2.

Relation between plant temperature and transpiration has served as the theoretical base for Crop Water Stress Index (CWSI) (Jackson et al., 1981; 1988; Idso, 1999). The CWSI is calculated by determining the relative distance between the lower baseline representing non-stress conditions and the upper baseline representing no transpiration on a plot of air temperature minus canopy temperature vs. vapour pressure deficit. When the plant is transpiring fully the CWSI is 0, when the plant is no longer transpiring the CWSI becomes 1. CWSI may be used for estimation of the latent heat flux (Jackson et al., 1981; Brom et al., accepted, see attachement). The fact that moisture deficiencies and consequent vegetation stress lead to elevated canopy temperatures and that depletion of water from the soil surface layer causes the soil to heat up rapidly has been lately used in many remote sensing and modelling methods for estimating regional evapotranspiration (e.g Lillesand et al., 2004; Anderson et al., 2007).

5. Non-metabolic use of solar energy in plants at stand and ecosystem level

Vegetation determines solar energy distribution on the Earth's surface in four main areas: 1) surface reflectivity, 2) surface potential to transform incoming energy into latent heat flux, 3) surface interaction with the atmosphere and 4) the ground heat flux. Surface reflectivity (albedo) (1) determines the net energy income to the terrestrial ecosystems and thus represents a crucial component of Earth energy budget. The reasons for and consequences of changing surface albedo connected to vegetation are discussed in chapter 5.1. Surface potential for evapotranspiration (2) is largely determined by plant features discussed in chapter 3.1 and 4.2. Transpiration and evapotranspiration rates of different ecosystems and their importance for landscape functioning are discussed in chapter (5.2). Surface-atmosphere interactions (3) are influenced by a whole range of factors such as orography, global as well as local flows of air masses, water bodies presence etc. Vegetation impacts on convective movements and other relations describing the role of vegetation in the climate system are discussed in chapter 6. From the structural point of view, vegetation influences air movements by its roughness length. This variable is not discussed in detail within this text. It is mentioned in the text only where needed. In general, roughness length influences friction on the interface between the air and vegetation. As objects extend higher above the surface, the roughness length increases. Tall vegetation (in particularly forests) weakens near-surface wind speed and enhances low-level turbulence. This may result in acceleration of initiation of convective flows on a small scale (McPhearson, 2007). Impacts of biomass on ground heat flux (4) are briefly discussed in chapter 2.1.1. This chapter focuses on areas (1) and (2) as changes in albedo and the evapotranspiration rate as a consequence of land use changes may greatly impact energy balance of the surface. Moreover, the issues have been in the centre of scientific debate on climate change.

5.1 Optical characteristics of vegetation surfaces, albedo

Albedo - which etymologically means whiteness (Gates, 1993) – is a direct manifestation of optical characteristics of the surface. It expresses the ratio (percentage) of reflected radiation to incident radiation. For vegetation albedo is always manifestation of surface structure preconditioned by leaf morphology or stand arrangement. The optical characteristics of ecosystems are influenced also by abiotic factors such as different types of soils. However, I will focus here only on the vegetation component. Leaf reflectance often represents the basic impact factor for optical characteristics of vegetation surfaces. Therefore qualities such as glossiness or hairiness and chlorophyll content of leaves are also essential for vegetation reflectance (Yin, 1998). Plants have characteristic reflection spectra (see chapter 3.1). They reflect generally very little in the visual spectrum and a lot in the near IR spectrum (e.g. Liang et al., 2002). This general rule is valid for all hierarchical levels from individual leaves to the vegetation cover, although canopy albedo is influenced also by leaf area index (leaf density), leaf angle distribution, crown shape and shading, relative stem (tree bark) cover and background signals of the soil (e.g. Castro-Esau et al., 2006). Albedo of green vegetation is usually lower than 0.25. Approximate albedo values of some vegetation covers are presented in Table 8. However, it should be mentioned that depending on the actual conditions the spatial differences in albedo within the same given land cover type could be higher than the differences observed among biomes (Davidson and Wang 2004, 2005; Wang and Davidson, 2007).

Table 8. Approximate values of some vegetation surface cover types compiled from works by Stoutjesdijk and Barkman (1992), DeFries and Townsend (1994), Sellers et al. (1996) and Marková et al. (2006). Elevation of the Sun > 40°.

Type of vegetation	Albedo (%)
Grassland	17-23
Cropland (vegetated)	10-26
Tropical forest	13
Temperate or boreal forest (coniferous forests tend to have lower values)	5-18
Ripe cereals or stubble	25-34
Dark or scarce biomass on dark peaty soil	9
Deserts	20-38
Tundra	20

For example in dry habitats vegetation growth and consequently also albedo are strongly controlled by water conditions (Wang et al., 2005). As plant surface spectral characteristics are influenced also by leaf life span, relative leaf age or vegetation height, surface albedo is preconditioned by phenology and physiological stage and overall ecosystem dynamics (Yin, 1998; Wang and Davidson, 2007). On Canadian prairies covered with diverse types of grasses, sedges, rushes, forbs and woody plants, albedo decreased in April to June to values of about 0.07-0.1 and 0.21-0.26 in VIS and NIR range respectively, then increased again in August (Wang and Davidson, 2007). Albedo may be also influenced by wind, humidity of the air and other conditions of the environment (Richardson et al., 2001). Leaning of grass and crops in the wind was shown to cause albedo discrepancy of 0.01 to 0.05 (Song, 1998). The asymmetry of albedo in early morning and late afternoon over grassland and agriculture regions may be caused by dew formation in the morning hours (Minnis et al., 1997).

Albedo is also influenced by light conditions, especially by the angle of light incidence (Richardson et al., 2001). Solar zenith angle varies the reflectance of the surface both throughout the day and throughout the year. The most pronounced effect of solar angle on albedo is observed in the case of water, which is an excellent absorber at high sun elevation (albedo at 50° elevation is 0.025) but at low sun elevations it almost resembles a mirror (albedo at 6° elevation is 0.48 to 0.70) (Kabat et al., 2004). Albedo differs also due to cloudiness and changing ratio of direct and diffuse radiation (Betts and Ball, 1997; Iziomon and Mayer, 2002; Wang et al., 2005).

The only way of mapping albedo globally is by remote sensing. accurate determination of land surface broadband albedo from top-of atmosphere (TOA) observations requires a real knowledge of atmospheric conditions and surface characteristics which can be monitored effectively and with relatively fine spatial resolution only by narrowband multispectral sensors. The derivation of surface broadband albedos from narrowband observations is not an easy process and requires several levels of processing, including (1) atmospheric correction that converts TOA radiance to surface directional reflectance, (2) surface angular modelling that converts surface directional reflectance to spectral albedo, and (3) narrowband to broadband albedo conversions (e.g. Liang et al 2002). Because of all these complex relations albedo remains a largely uncertain parameter in modelling.

5.1.1 Albedo and land use changes

To present an example of albedo shift due to land use changes let us assume an extreme situation when a coniferous forest with albedo 0.1 (Marková et al., 2006) is converted to a concrete parking place with albedo of about 0.45. As a consequence of this change the net radiation changes by 35 %. If on a clear day the incident radiation were 800 Wm^{-2} this change would represent a decrease of R_n of about 280 Wm^{-2}. In natural and agricultural systems green vegetation surface cover commonly takes turns with dry vegetation or bare soil during the vegetation season. Although the soil albedo changes with the surface soil water content (albedo commonly increases with decreasing soil water content), vegetation as well as grass litter and dead biomass have usually higher reflectance in both VIS and NIR bands than dark soil (Wang et al., 2005). Changes in agricultural practices can thus lead to changes in energy input especially in some cropland ecosystems. This can be true for example in savannas and grasslands (Bird et al., 2008), which can have higher albedo in periods when they are dry. If forests or other vegetation green throughout the periods of drought were to replace these ecosystems, R_n would increase in this particular area during the hottest period of the year. Also spring biomass burning temporarily changes (commonly decreases) albedo, whereas grazing increases it (Wang and Davidson, 2007). Albedo changes are discussed also in connection with historical changes in land use. When forests are replaced by croplands or pastures surface albedo increases (Matthews et al., 2003 and 2004), especially in higher latitudes due to snow-masking effect of vegetation (see later). Some authors (Brovkin et al., 1999; Bertrand et al., 2002; Bauer et al., 2003; Matthews et al., 2003) have even assigned a global cooling effect of -0.06 to -0.35 °C to the surface cover changes connected with historical changes in agriculture practices. For citations and more discussion about regional albedo changes see introduction to the article by Matthews et al., 2004. These considerations have led some authors to the conclusion that potential deforestation at high latitudes (Claussen et sl., 2001; Matthews et al., 2004) or even on global scale (Bala et al., 2007) would result in net cooling, even though the process would contribute to rising CO_2 concentrations in the atmosphere.

As already mentioned the most often discussed variability in albedo is connected to periods with snow presence. As mentioned in chapter 2.1.1, snow may reflect as much as 90 % of incoming radiation. The albedo in winter may be therefore extremely variable as a consequence of presence or absence of snow (e.g. Wang and Davidson, 2007). This fact is most marked in boreal forests, i.e. the Northern forests of Eurasia and America, which are areas of sharply contrasting albedo (Groisman et al., 1994). These habitats are dominated by spruce, tamarack, fir, pine, aspen, birch and poplar. Betts and Ball (1997) described the albedo cycle of different vegetation covers of this boreal region. In summer, the representative daily average values of albedo were 0.2 over grass, 0.15 for aspen, and 0.083 for the conifer sites. In winter the corresponding mean albedo for grass, aspen, and conifer sites were 0.75, 0.21, and 0.13 (0.15 for jack pine sites, only 0.11 for predominantly spruce sites). Whereas grass sites were during winter covered with snow and took over its high reflectance, snow fell through the crowns of trees in the forests and the canopy suppressed its reflectivity. This effect was most obvious at conifer sites, as conifer species have more dense canopies than bare broadleaved trees and are predominantly not deciduous. In general ecosystems with some winter canopy have lower albedos than ecosystems with little or no winter canopy (Moody et al., 2007). Givnish (2002) hypothesized that due to increased nitrogen depositions deciduous larch trees might expand in boreal forests in the future, which would potentially lead to an increase of winter albedo in the areas in question. Groisman et al. (1994) described the importance of albedo for the spring snow cover feedback mechanism in northern boreal ecosystems. The recently observed temperature increase in these areas (IPCC, 2007) decreases spring snow cover. The revealed darker surface shows higher absorption of radiation and implicitly its surface temperature rises. This leads to a positive feedback reaction of increased snow melting.

Randerson et al. (2006) studied albedo changes with varying composition and structure of vegetation cover in connection to large boreal forest fires. After a temporary decrease of albedo during the first year after the fire due to a short time effect of deposited carbon, the albedo of the studied site began to rise as grass and shrub cover increased. When considering the impact of boreal fires on climate change, the authors concluded that the multidecadal increase in surface albedo outweighed the negative impact of fire-emitted greenhouse gases. Rautiainen et al. (2004) studied the influence of stand age and crown volume and shape of Scots pine and Norway spruce stands in central Finland. The simulated stand reflectance decreased until the forest was approximately 50 years old and then remained relatively constant. The authors showed that the smaller the crown volume of the trees in mature forest the lower the reflectance of the stand. In conifer stands of high closure, conical crowns had lower reflectance than ellipsoidal crowns. In stands with looser canopy the effect of crown shape on the reflectance was cloaked in the effect of ground reflectance.

Many articles have been published in order to specify variability and dynamics of surface albedo of different ecosystems and under different conditions (e.g. http://www-modis.bu.edu/brdf/userguide/publications.html). As follows from the presented literature review high albedo is considered a positive feature in ecosystems in the ever-growing debate about global warming. However, one thing is being overlooked in this approach. Lower albedo represents higher net energy input at the Earth surface. This, however, does not implicitly mean increase in surface temperature. The surface temperature is a result of R_n dissipation. Also the larger energy input is divided into latent heat, sensible heat and ground heat fluxes and the temperature itself is the result of this distribution. Therefore we have to judge effect of albedo on energy balance according to the ecosystem in question. The low reflectance of vegetation can be as well regarded as a manifestation of high capacity of vegetation to process incoming solar energy more efficiently. If there is enough water in the ecosystem, lower albedo results in higher latent heat flux and consequently in a surface temperature decrease (e.g. Foley et al., 2003). So the real amount of available energy is actually not the most important thing. In the first place we have to be aware of what happens with the absorbed energy.

5.2 Evapotranspiration and latent heat flux in ecosystems

Every single plant and every single habitat may differ in the amount of actual and long-term transpiration rate. On a large scale the differences of individuals diminish and transpiration rate of different ecosystems becomes the important variable. However, even if the species composition were exactly the same it is advised not to automatically predict the same transpiration rate for the habitat as soil and climate conditions may cause large differences (e.g. Ohta et al., 2008, see also discussion in the article Rejšková et al., subm. in the attachment). The surface temperature is most effectively regulated by vegetation with high biomass and sufficient supply of water.

5.2.1 Transpiration and evapotranspiration of different vegetation types

Evapotranspiration (ET) is the sum of transpiration (E_T), soil evaporation (E_S) and canopy evaporation (E_C). Using a biophysical process-based model Choudhury and DiGirolamo (1998) and Choudhury et al. (1998) estimated that E_T accounts globally for about 52 %, E_S for 28 % and E_C for 20 % of total ET. The estimates of Diermeyer et al. (2005) were about 48 % for E_T, 36 % for E_S and 16 % for E_C. Finally, the model based estimate of Lawrence et al. (2007) was 41 % for E_T, 42 % for E_S and 17 % for E_C. According to the global models transpiration is the dominant component of ET across a variety of ecohydrological systems although for understandable reasons not in ecosystems with dry, sparse or no vegetation. Estimates of annual mean, low and high evapotranspiration rates (mm/year) of main vegetation types, based on generalized field data, are presented in table 9 based on Rockström et al. (1999).

Table 9. Estimates of annual evapotranspiration (mm/year) of main vegetation sub-groups, based on generalized field data. Production data of crops are from the FAO (Faostat, 1997). Water use efficiency (WUE) was calculated based on total dry matter yield. The water vapour flow variations due to climatic fluctuations, different biotic and abiotic conditions, and different land management were taken into account and are included in high and low estimates for each subgroup, based on the lowest and the highest ET or WUE accessible field data. According to Rockström et al., 1999. To see the data and references for calculation and classification of subgroups see original article. k = number of references.
* The WUE was calculated related to the total dry matter yield

Biome	**Vegetation subgroups**	**Climatic zone**	**Land surface a**	**k**	**Actual evapotranspiration (mm/yr)**		
			in 1000 km^2		Mean	Low	High
Forest, woodlands	Taiga	boreal	11,560	3	401	380	420
	predominantly coniferous	temperate	3500	4	487	395	580

	predominantly deciduous	temperate	8500	4	729	588	964
	woodland/ woody savannah	temperate	5200	3	416	300	530
	forest dry/deciduous/ seasonal	tropical/ subtropical	7400	2	792	783	800
	forest, wet	tropical/ subtropical	5300	3	1245	880	1493
	savannah/ woodland, dry	tropical/ subtropical	12,700	2	882	870	894
	savannah/ woodland, wet	tropical/ subtropical	1300	3	1267	1100	1500
Wetland	bog	boreal	651	3	221	200	260
	bog	temperate	488	4	674	456	1020
	swamp	temperate	41	3	843	670	720
	swamp	subtropical	16	5	1127	930	1277
	swamp	tropical	508	1	1656	1408	1904
Grasslands	cool grassland	mostly temperate	6940	16	410	130	633
	mountainous grassland	temperate	650	4	655	430	951
	warm and hot grassland	mostly tropical	17,300	7	599	403	862
	mountainous grassland	tropical	650	1	600	402	798
	dry shrubland	tropical	4000	2	270	225	315
			Production (10^6kg/yr)		**Water Use Efficiency (l/kg)**		
Croplands	cereals, grain	temperate	790,476	15	1309	539	2643
	cereals, grain	tropical	625,409	10	1438	591	4369
	cereals, DM *	temperate	4011	19	438	240	646

	cereals, DM *	tropical	664,404	3	331	271	372
	cotton lint		18,509	3	5454	4227	6313
	forage		725,032	19	934	172	2810
	oil-bearing crops	temperate	35,454	3	1892	1530	2117
	oil-bearing crops	tropical	55,225	2	3083	2667	3500
	pulses, dry seed	temperate	43,493	3	3355	1731	5833
	pulses, dry seed	tropical	166,338	5	1866	1250	3003
	pulses, green seed	temperate	9326	2	1149	583	1714
	rice		540,838	4	1099	839	1404
	roots and tubers	temperate	558,137	7	286	139	402
	roots and tubers	tropical	330,786	1	616	369	1299
	roots, tubers for fodder	temperate	11,105	8	326	157	616
	sugar cane		1,120,898	3	123	100	163

High values of evapotranspiration in natural vegetation types are preconditioned by large energy inputs and sufficient water supply. The estimates presented in table 9 show that the tropical and subtropical forests, savannas and woodlands together with subtropical, tropical and temperate swamps use the largest volumes of water on yearly basis. In the temperate regions, swamps and deciduous forests are the most active water users. The second part of the data set presents water use efficiency of some crops based on the total dry matter yield. These data cannot be directly compared to the evapotranspiration data but they stress the differences in water use efficiency of different crops and thus differences in water demand connected to different agricultural practices. It is useful to notice that of the presented crops cotton has far the highest WUE with large consequences for areas of its cultivation.

So far, all the presented evapotranspiration rates (as well as its components) have been a result of large scale modelling. The modelling field has been growing enourmously in the last decades along with the intensifying debate about climate change. If we want to assess the energy balance of landscape, we need to scale down to shorter than yearly (e.g. Lawrence et al., 2007) or monthly (e.g. Fisher et al., 2008) time periods and smaller than global areas, as actual values are more important from this point of view. The most important in the context of landscape energy budget are values for periods with high energy input. For the purpose of studying temporal and spatial ecosystem-scale energy, water and CO_2 fluxes between the biosphere and atmosphere a global network of micrometeorological flux measurement sites FLUXNET has been established. The ecosystems studied within this research network include conifer and broadleaved (deciduous and evergreen) forests, tropical and boreal forests, crops, grasslands, chaparral, wetlands, and tundra with latitudinal distribution ranging from 70°N to 30°S (Baldoccchi et al., 2001). Some modelling experiments have used results of FLUXNET sites for data validation (Fisher et al., 2008). The scope of this text as well as my knowledge of modelling are only limited and therefore I will not present a more extensive review of modelling experiments. However, it may be stated that although much progress has been made recently in vegetation models of surface evapotranspiration (Niyogi et al., 2009) and various algorithms based on remote sensing methods have been used also for estimating regional evapotranspiration in shorter time periods (Courault et al., 2005; Gowda et al., 2008), the models are still not detailed enough to generate sufficient insights in the evapotranspiration dynamics.

As follows from discussions in previous chapters, actual energy distribution is most important for ecosystem functioning. This holds true also for evapotranspiration assessment. Field measurements and partitioning of ET in different ecosystems are methodologically complicated and therefore ground-based valid data are unfortunatelly still rather difficult to find in literature. Basic principles of both direct and indirect ground-based methods of measuring evapotranspiration were reviewed for example by Shutov et al. (2006). Transpiration and soil evaporation can be isolated either through a combination of stable isotope, sap flow, and eddy covariation techniques (Williams et al., 2004) or with porometer, lysimeter, and Bowen ratio techniques (e.g. Klocke et al., 1985; Herbst et al., 1996). Errors in ET partitioning calculated by any of these methods may be, however, large (Lawrence et al., 2007). In the context of the presented text, the most important ecosystem ET aspects are the yearly changes resulting from vegetation dynamics and interrelations of ET, actual water availability and actual incoming radiation in different ecosystems. The latter can be expressed by Bowen ratio ($\beta = C/LE$), which describes partitioning between LE and sensible C heat fluxes.

Wilson et al. (2002) studied Bowen ratio at 27 eddy covariance sites (FLUXNET) throughout the warm season (mid-June through late August). β was typically lowest at the agricultural and deciduous forest sites (0.25 – 0.50) probably due to relatively high stomatal conductance of crops and overall high water transport capacity of broad-leaved trees. Poplar forest in Iceland had β only 0.11. In unstressed conditions, β was similarly low at grassland sites, but tended to be sensitive to soil water content. Grasslands are highly sensitive to management practices and more sensitive to soil moisture than forests. Variability in β at coniferous sites was high, but the ratio was typically about twice the value compared to deciduous forests. Impacts of land cover conversion to different vegetation types on energy dissipation, surface temperature and water fluxes (including rainfall patterns) are discussed in a review by Pielke et al. (2006). These topics are also discussed in chapter 6. Temperature distribution as a result of incoming energy distribution in landscape is one of the parameters considered decisive for evaluation of ecosystem functioning within our Tokenelek project (NPV 2B06023) presented briefly in chapter 6.2.1.

Evapotranspiration changes throughout the season, especially with leaf-out of deciduous forests or herbal ecosystems, significantly impact the Bowen ratio. Generally, the presence of leaves causes Bowen ratio to drop (Baldocchi et al., 2001; Wu et al., 2007). The timing of leaf-out was also shown to have a distinct impact on the humidity and temperature of the planetary boundary layer (Schwartz, 1996; Baldocchi et al., 2001; Wilson et al., 2002) and the seasonal pattern of its maximum height (Wilson and Baldocchi, 2000; Yi et al. 2000). Therefore, when comparing ET differences at sites with different land use, we also have to take into account the phenological phase of the ecosystems in question.

When evaluating the impact of land use changes on landscape water resources it is very important to decide which conditions will be taken as initial (van Dijk and Keenan, 2007). ET rates often increase with transition from natural vegetation to agriculture, especially during dry periods of the year due to irrigation. This is, however, not true when the conversion is from intensively transpiring ecosystems, such as moist forests (in particular tropical forests) or wetlands (e.g. Douglas et al., 2006; Pielke et al., 2006). Haddeland et al. (2007) even suggested that conversion of forests and woodlands to croplands led between 1700 and 1992 to a historical increase of annual run-off by 2.5 and 6 % in North America and Asia respectively. As the author noticed, the estimated increase has, however, been canceled out by increased irrigation. Gordon et al. (2003) suggested an overall ET decrease on the Australian continent of about 10 % in the last 200 years due to vast decrease in woody vegetation and corresponding increase of croplands. The model-based estimates of ET decrease from historical times to present time were so large, that if the sum of the continent run-off and ET had been constant throughout the studied time period (as expected in the article), the run-off from the continent would have been almost non-existent 200 years ago. That does not seem very probable though, as the authors themselves admit. On a global scale Gordon et al. (2005) suggested that the decrease of ET as a consequence of deforestation is approximately balanced by increase of ET due to irrigation. These are, however, again large temporal and spatial scale estimates with many possible distortions and as such have to be assessed with a lot of caution. Water fluxes between the atmosphere and ecosystems and their possible consequences for climate are further discussed in chapter 6.

5.2.2 Transpiration and latent heat flux of trees and forests

In this section I would like to provide evidence about transpiration capacities of the largest terrestrial plants, i.e. trees. Water use of woody plants plays a particularly important role in energy budget of the Earth surface. Trees are capable of conducting large volumes of water from the soil to the atmosphere. Due to their size and the fact that they grow in both canopies and solitarily, trees are most suitable for studying variability of transpiration rates. The span of water volumes transferred by a single tree is enormous, depending on the species (Wullschleger et al., 1998), size and age of the tree (e.g. Martin et al., 1997; Martin et al., 2001; Ewers et al., 2005), position within the stand (Čermák et al., 2004) as well as actual environmental conditions. Dominant trees (commonly making up for one-third of trees in the canopy) are responsible for about two-thirds, medium trees for about one-quarter and suppressed trees only for about 5-10 % of the total stand water use (Čermák et al., 2004). Martin et al. (2001) even measured that the dominant trees in a 220-year-old *Abies amabilis* forest and demonstrated that they accounted even for over 83 % of stand transpiration while representing 77.7 % of the stand's leaf area. Small trees suffer from larger competion pressure which makes them due to their shallow roots more susceptible, especially during drought. Water use of solitary trees tends to be higher than that of trees within a canopy as their net radiation input is higher and they are more easily influenced by advection (e.g. Green, 1993; Hagishima et al., 2007).

Typically, the transpiration rate of plants increases in the morning with rising irradiance and VPD, peaks at about noon and decreases again during afternoon. In trees, the transpiration rate is reflected in the sap flow rate which can be measured and which represents a reliable value of integral plant transpiration. Similarly to the transpiration rate, sap flow increases sharply in the morning and decreases in the afternoon. However, the initial morning increase in basal sap flow lags behind that of branch sap flow. Consistently, the afternoon decrease in sap flow tends to occur earlier in branches than at the base of the stem while the internal water stores are apparently being recharged. The time lag between attainment of maximum sap flow rates in the upper branches and at the base of the stem ranged from 0.1 up to 4 to 5 h (in large trees) in five species of a seasonal tropical forest in Panama (Goldstein et al., 1998). This behaviour of trees is facilitated by large diurnal water storage capacity (mass of water that can be withdrawn from the main trunk and branches during the day and replaced over a 24 h cycle) of their shoots. Goldstein et al. (1998) showed that the total diurnal water storage capacity is determined primarily by the plant size. The water storage capacity of trees from the tropical forest increased linearly with increasing sapwood area, the increment being about 10 kg of stored water for every $0.1\,m^2$ increase in basal sapwood area. It also increased exponentially with the tree height. Phillips et al. (2003) confirmed that reliance of trees on stored water increases with tree size. For Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), water stored in xylem accounted for 20 to 25 % of total daily water use in 60-m trees, whereas stored water comprised 7 % of daily water use in 15-m trees. Similar results were found for Oregon white oak (*Quercus garryana* Dougl. ex Hook.) and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). Basal sap flow grows with increasing sapwood area in asymptotic relationship, i.e. the relationship is more significant for smaller trees (Goldstein et al., 1998). Measurements of the radial distribution of sap flux density are necessary to accurately estimate water flow in trees with large sapwood areas (e.g. Ford et al., 2004). Consequently, tree sapwood area and stand sapwood area were suggested to be major determinants of water use in a forest watershed (Kumagai et al., 2007).

Some authors have tried to find universal rules in plant kingdom, scaling functional and structural properties as a function of size, i.e. allometry (West et al., 1999; Magnani et al., 2000; Mencuccini, 2002). Meinzer et al. (2001) suggested that there exists a common relationship between diurnal stem water storage capacity and tree size and that allometric scaling of plant vascular systems, and therefore water use, is universal. The authors also showed the diameter at breast height (DBH) to be closely correlated with variation in sapwood area, sapwood depth as well as with the variation in the time of day at which maximum sap flow occurred (the larger the tree the later). Magnani et al. (2000) proposed that trees allocate carbon to leaves or sapwood in the most economical (i.e., optimal) way. When leaves are produced in excess, the xylem conductive capacity to each leaf decreases, thereby increasing the risk of hydraulic failure. As a result, more xylem is produced to restore the previous optimal equilibrium.

An overview of water use of several trees is presented in table 10. Although all the results have been obtained using the sap flow method, it is not possible to draw general conclusions about species specific or habitat specific water use trends simply by comparing all results. This is due to three levels of uncertainity in the data set. First, the trees differed markedly in their height, diameter, leaf area as well as sap wood area, position in the stand, age etc.

Second, the stands differed markedly in their history, density of trees, soil characteristics etc. And third, the conditions, i.e. water supply, temperature, VPD, irradiance, advection etc., of each tree differed to a large extent. Therefore the data gathered serve merely as an example of possible real values of transpiration per tree and day. To learn more about the importance of a particular tree for the energy budget of the ecosystem in question every situation would have to beproperly scrutinized. The only somewhat comparable interspecific values are those measured at the same site (i.e. Granier et al., 1996; Goldstein et al., 1998).

Table 10. Whole-plant water use and latent heat flux (0.682 kWh kg^{-1} H_2O, at 20 °C) of different trees larger than 10 cm in diameter. Daily rates of water use were measured by thermal balance or heat dissipation methods. The data set is based on a review by Wullschleger et al. (1998). Studies cited from that article are marked by *). Height (m), diameter (cm), leaf area (m^2) or LAI (if indicated), cross-sectional sapwood area (cm^2), and water use (kg day^{-1}) for trees are given. Maximal values are marked by **m**, values in brackets (if presented) are standard deviations.

Species	Height (m)	Diameter (cm)	Leaf area (m^2)	Water use (kg H_2O per day)	n	LE (kWh)	Comments	Reference
Abies amabilis	42	78	461	>100 (for 70% of days) 281**m**	1	>68, 192m	SE Seattle, U.S.	Martin et al., 2001
Abies amabilis	26	32	71	9**m**	1	6	SE Seattle, U.S.	Martin et al., 2001
Abies amabilis	18	40	151	98	1	67	Western Washington, U.S., dense stand	Martin et al., 1997
Acacia dealbata	-	25	-	59**m**	-	40	15 year old forest, Australia	Vertessy et al., 1995 *
Carapa procera	37	38	-	52**m**	-	35	*Rain* forest	Granier et al., 1996 *
Caryocar glabrum	27	26	-	48**m**	-	33	Rain forest	Granier et al., 1996 *
Cassipourea guianensis	18	17	-	24**m**	-	16	Rain forest	Granier et al., 1996 *
Cecropia longipes	18	20	-	47**m**	-	32	Seasonal tropical forest Panama	Goldstein et al., 1998*
Dicorynia guianensis	44	57	-	212**m**	-	145	Rain forest	Granier et al., 1996 *
Eperua falcata	35	45	-	166**m**	-	113	Rain forest	Granier et al., 1996 *
Eperua grandifolia	33	55	-	151**m**	-	103	Rain forest	Granier et al., 1996 *
Eucalyptus regnans	-	37	147	151	9	103	Australia, near Melbourne	Vertessy et al., 1997
Fagus sylvatica	35	54		137**m**	-	93	Highlands near Zurich, declining beech	Čermák et al., 1993*

							forest	
Ficus insipida	30	54	-	164**m**	-	112	Seasonal tropical forest Panama	Goldstein et al., 1998*
Hirtella glandulosa	31	32	-	62**m**	-	42	Rain forest	Granier et al., 1996 *
Larix gmelinii	20	25	-	67**m**	-	46	130-year-old, eastern Siberia, emergent trees	Arneth et al., 1996 *
Larix sp.	20	-	-	74m	-	50	CZ	Schulze et al., 1985*
Luehea seemannii	29	37		129m	-	88	Seasonal tropical forest Panama	Goldstein et al., 1998*
Nothofagus fusca	34	60	-	110**m**	-	75	Broad leaved forest, New Zealand	Kelliher et al., 1992*
Olea europea	-	12	29	23	1	16	Semi-trunk, Unirrigated, Spain	Moreno et al., 1996
Olea europea	-	13	21	35-39	1	24-27	Semi-trunk, Irrigated, Spain	Moreno et al., 1996
Picea abies	25	-	-	63**m**	-	43	CZ	Schulze et al. 1985*
Picea abies	11	10	-	10**m**	-	7	-	Granier and Claustres, 1989*
Picea abies	15	19	-	49**m**	-	33	Southern Sweden	Cienciala et al., 1992*
Picea abies	25	36	-	175**m**	1	119	220 year old tree, 1639 a.s.l., Davos, Switzerland	Herzog et al., 1995*
Picea abies	17	15	-	66**m**	-	45	Fichtelgebirge, Bavaria, Germany	Köstner et al., 1998*
Pinus pinaster	20	34	-	161**m**	8	110	Les Landes forest, SW France	Granier et al., 1990*
Pinus pinaster	26	35	-	125**m**	-	85	64-year-old stand Ribatejo, Portugal	Loustau et al., 1996*
Pinus ponderosa	36	75+-5	< 1 LAI	14 (4), 20 (6) **m**	5	10, 14 **m**	Pacific Northwest, forest	Phillips et al., 2003
Pinus ponderosa	12	27+-2	< 1 LAI	38 (11), 50 (20) **m**	5	26, 34 **m**	Pacific Northwest, forest	Phillips et al., 2003
Populus trichocarpa # P. deltoides	15	15	-	51**m**	1	35	4-year-old stand, Washington, U..S.	Hinckley et al., 1994*
Pseudotsuga menziesii	15	18+-3	11 LAI	14 (2), 22 (4) **m**	3	10, 15m	Pacific Northwest, forest	Phillips et al., 2003
Pseudotsuga menziesii	60	157	9 LAI	205 (41), 333 (35) **m**	1	140, 227m	Pacific Northwest, forest	Phillips et al., 2003
Quercus garryana	25	55+-5	3 LAI	84 (11), 97 (11) **m**	3	57, 66m	Pacific Northwest, forest	Phillips et al., 2003
Quercus garryana	10	23+-1	3 LAI	167 (16), 183 (16) **m**	3	114, 125m	Pacific Northwest, forest	Phillips et al., 2003
Quercus macrocarpa	-	83+-8	-	136+/-105	3	93+/-72	Restored Savanna Central Iowa, U.S.	Asbjornsen et al., 2007
Quercus	-	75+-5	-	75+/-18	2	51+/-	Woodland	Asbjornsen et al., 2007

macrocarpa						12	Central Iowa, U.S	
Quercus pyrenaica	7.4	11.7	3.4 LAI	15 (my estimate)	-	10	Spain	Hernández-Santana et al., 2008
Quercus rotundifolia	6.8	48	256	10-296 throughout a year	1	7-202	Sparse evergreen woodland, Southern Portugal	David et al., 2004
Salix fragilis	-	-	38-47	103	1	70	Solitary tree in a wet grassland	Čermák et al., 1984
Spondias mombin	23	44	-	80 **m**	-	55	Seasonal tropical forest Panama	Goldstein et al., 1998*
Ulmus americana	-	19+-3	-	21	4	14	Woodland Central Iowa, U.S	Asbjornsen et al., 2007
Vouacapoua americana	28	49	-	29 **m**	-	20	Rain forest	Granier et al., 1996 *
Dominant canopy trees	For details see the original study			80-120, 165 **m**	-	5-82, 113	Lower tropical montane forest Ecuador	Motzer et al., 2005
Suppressed mid-and subcanopy shaded trees	For details see the original study			1-10, 19 **m**	-	1-7, 13	Lower tropical montane forest Ecuador	Motzer et al., 2005

Transpirational behaviour of trees with different size or position within one stand may be seen in table 10 in studies of Martin et al. (2001), Phillips et al. (2003) and Motzer et al. (2005). Moreno et al. (1996) compared transpirational behaviour of trees with different irrigation treatments (see table 10). It is obvious that water use in trees may differ enormously. David et al. (2004) showed that daily water use of one tree may differ in order of magnitude throughout the year (see table 10). Values of water use presented in table 10 spann from 10 l per day for young *Picea abies* to 333 l per day for a large *Pseudotsuga menziesii* (60 m). Jordan and Kline (1977) estimated water use of a large overstory *Euperua purpurea* Bth. tree in the Amazonian rainforest to be as high as 1180 l day.

Variability of the transpiration rate of the same species growing on different soils is nicely documented in different studies by Čermák summed up in table 11. Transpiration is calculated for trees of unit size given by its length of circumference at height 1m and is therefore comparable. Water use of three broad-leaved species and two conifers from local flora are presented.

Table 11. Daily maxima of transpiration of three broad-leaved species (*Quercus petraea* (Mattusch) Liebl., *Quercus robur* L., *Betula alba* L.) and two conifers (*Picea abies* (L.) Karst and *Pinus sylvestris* L.) growing in different locations. Transpiration was calculated for trees

of unit size given by its length of circumference at height 1m above ground). Data have been kindly provided by the author (prof. Jan Čermák).

Species	Forest	Soil characteristics	Daily maxima (kg m^{-1})
Quercus petraea	Querceto-carpinetum	Medium depth loess	320
Quercus petraea	Quercetum	Sandy soil on clay	145
Quercus petraea	Quercetum	Oligotrof sandy loam	100
Quercus petraea	Quercetum	Oligotrof sandy loam	96
Quercus petraea	Querceto-carpinetum	Sandy loam	186
Quercus petraea	Querceto-carpinetum	Sandy loam	115
Quercus petraea	Fageto-quercetum	Oligotrof brown	78
Quercus robur	Fraxineto-quercetum	Deep alluvial soil	91
Quercus robur	Fraxineto-quercetum	Deep alluvial soil	241
Quercus robur	Fraxineto-quercetum	Deep alluvial soil	244
Betula alba	Querceto-carpinetum	Sandy loam	220
Betula alba	Querceto-pinetum	Sandy podsol	180
Betula alba	Querceto-carpinetum	Medium depth loess	204
Betula alba	Querceto-pinetum	Deep sandy loam	125
Picea abies	Fageto-quercetum	Brown oligotrof loam	78
Picea abies	Quercetum	Oligotrof sandy loam	69
Picea abies	Quercetum	Oligotrof sandy loam	33
Picea abies	Querceto-carpinetum	Sandy loam	69
Picea abies	Fageto-quercetum	Loamy soil	105
Picea abies	Fagetum	Brown podsol cambisol	51
Picea abies	Querceto-fagetum	Brown loamy soil	79
Picea abies	Querceto-carpinetum	Sandy loam	40
Picea abies	Fagetum	Loamy clayish soil	79
Picea abies	Fagetum	Loamy clayish soil	54
Picea abies	Fageto-quercetum	Brown oligotrof loam	58
Pinus sylvestris	Querceto-pinetum	Sandy podsol	114
Pinus sylvestris	Pinetum	Shallow sandy soil	58
Pinus sylvestris	Pinetum	Shallow sandy soil	47
Pinus sylvestris	Pinetum	Deep sandy soil	173

Variability in tree transpiration is reflected also in the variability of latent heat flux connected to different woodlands. Table 10 shows that the latent heat flux from trees differs substantially consuming from units to hunderds of kWh per day and tree. It is obvious, that large amounts of solar energy are used in the cooling transpirational process in trees. Green (1993) measured radiation balance of an isolated 3.5 m tall walnut tree. During the middle part of the day about 4300 W of radiant energy were absorbed by the rather small crown. The water use was almost 40 litres per day. Approximately 64 % of the total radiant energy absorbed by the tree was dissipated as latent heat. During the early part of the day transpiration was controlled mainly by radiation, during the later part of the day VPD became more important as a driver. Partitioning of incoming energy in a tree, however, depends on a whole range of factors.

Saugier et al. (1997) showed that only about one third of incoming energy was dissipated by latent heat flux in a stand of jack pines (*Pinus banksiana*) in a boreal forests. This was due to low transpiration rates which were caused by low stomatal conductances and a low leaf area index in the stand. It may be concluded that different trees react phenologically and physiologically differently to environmental factors in terms of water use (e.g. Fetene and Beck, 2004).

However, some average values of forest ET or whole canopy transpiration have been published. Köstner (2001) determined canopy transpiration by tree sapflow measurements scaled to the stand level combined with lysimeter and chamber measurements for determining understory transpiration and forest floor evaporation. The author stated that Central European spruce and beech forests have daily canopy transpiration of 1.5–3.0 mm and 2.6–6.4 mm respectively. Schipka et al. (2005) documented that canopy transpiration of mature beech forests in Central Europe showed rather similar rates across a broad range of precipitation regimes. Beech transpiration rates ranged from 210 to 350 mm per year, although precipitation varied between 550 and 1480 mm year^{-1}. According to this study it seems that beeches have the capacity to maintain controlled transpiration within a broad range of hydrologic regimes effectively regulating water transfer from soil to the atmosphere irrespective of water availability. As these results are again yearly averages it is difficult to identify the regulating mechanisms themselves. Differences in annual canopy transpiration of stands composed of different tree species under comparable climatic and soil conditions are thoroughly discussed by Schipka et al. (2005). In any case, in some areas, such as in semi-arid or arid climates, forests are exposed to so large weather and water supply fluctuations that their transpiration must change substantially throughout the year (e.g. Fetene and Beck, 2004). In these areas forest transpiration shows a strong precipitation dependency (Moreno et al., 1996; Hutley et al., 2001).

6. Vegetation and climate

It is obvious, that vegetation substantially influences our environment in countless biological, chemical and physical relations. Although some authors (e.g. Hayden, 1998) stated that the biosphere is an active agent in the control of local to global climate, there is still much doubt and controversy about vegetation impacts on climate. The importance of vegetation for carbon cycling has been largely acknowledged (e.g. Ruddiman, 2005). However, the impact of vegetation on energy and water cycling is still poorly understood. Although the impact of land use and land cover on the atmospheric concentration of carbon dioxide and methane, and on the global average surface albedo, have been included in international climate change assessments, the role of land use and land cover change and variability in altering regional temperature, precipitation, vegetation, and other climate variables is still often ignored (Pielke, 2005). Only lately has vegetation dynamics begun to be encompassed in the climate models of surface temperature and water cycling (Kabat et al., 2004).

Vegetation communicates with the atmosphere through exchange of gases, in particular CO_2 and water vapour. Both these gases are “greenhouse gases”, i.e. molecules that absorb radiation in approximately 8 to 14 μm wavelength of the infrared spectrum. Thus, by changing the concentrations of greenhouse gases, plants change the energy balance of the Earth. The impact of carbon assimilation and growth of vegetation on concentration of CO_2 can be nicely demonstrated on the annual fluctuating of CO_2 in the atmosphere related to vegetation growth dynamics. As 39 % of the Northern hemisphere is covered by land compared to only 19 % of land in the Southern hemisphere, it is the terrestrial vegetation of the Northern hemisphere which influences CO_2 concentration predominantly. Fluctuations of CO_2 concentration have been connected also to vast changes of land-use due to some historical changes (Ruddiman, 2005). Vegetation through transpiration processes also substantially influences the concentration of water vapour in the air. However, whereas rising CO_2 concentrations in the air may be seen clearly as a process which warms the near ground atmosphere layer through capturing part of long wave radiation emitted by the Earth’s surface (IPCC, 2007), the situation with water vapour is much more complicated because water is presented in the atmosphere in many forms which have different and sometimes even contradictory effects on actual energy balance of the Earth surface. The uncertainties about water incidence on atmospheric energy budget may be of great importance as a contribution of water vapour to longwave absorption of the atmosphere is of an order higher than the effect of CO_2 (Kiehl and Trenbeth, 1997). Water can be present in the atmosphere either as water vapour or it may form clouds which are highly variable and consequently differ in their optical features. Clouds, like water vapour, absorb the IR radiation, however, they also reflect radiation coming from the sun making the actual energy budget very dynamic and hard to determine.

Vegetation influences the energy budget of the Earth’s surface also directly by i) varying the albedo of the surface and ii) by influencing the distribution of net energy in sensible and latent heat. The temperature of land changes more rapidly than temperature of water surfaces because of the high heat capacity of water. Consequently a dry land surface generally heats and cools faster than a moist surface. As has been already discussed in chapter 4.2 vegetation through transpiration influences the rate of heating and cooling. Lowering evapotranspiration from the Earth surface increases surface temperature (e.g. Hayden, 1998; Kleidon et al., 2000). By shading the ground and influencing soil quality (especially organic matter content) and its water content, vegetation additionaly influences the intensity of ground heat flux (e.g. Zhou et al., 2007).

The statement that mean global temperature is increasing has evolved to be a commonly acknowledged fact (IPCC, 2007), although recently some authors have shown that periods of no trend or even cooling of the globally averaged surface air temperature have been recorded in the past decades and that periods of no trend in temperature or even slight cooling will be observable also in the course the 21st century (Easterling et al., 2009). Regardless which of these predictions is more probable, it is important to realize that mean temperature trends do not tell us much about climate itself. First, biota do not live in averaged conditions and the extremes of temperatures can be much more decisive than mean temperatures. Second, temperature dynamics throughout the season is important for plants development and successful reproduction. Third, vegetation and its diversity are preconditioned not only by energy but also by water availability (e.g. Clarke and Gaston, 2006). Unfortunately more detailed studies of global temperature do not make the situation any clearer. Diurnal range of surface air temperature has been observed to decrease worldwide from the 1950s to the 1990s, mostly on expense of an increase in nighttime minimum. This was related to intensification of water cycle due to increasing available energy and mean temperatures (see chapter 2.2) (Dai et al., 1999). Clouds, combined with secondary damping effects from soil moisture and precipitation, can reduce diurnal range of surface air temperature (DTR) by 25 % – 50 % compared with clear-sky days over most land areas (Dai et al., 1999). Clouds decrease the daytime surface solar heating and increase nighttime downward longwave radiation. Evapotranspiration associated with soil moisture and precipitation can also balance solar heating and reduce maximum temperature. However, observations showed, that DTR was reduced most in dry regions and especially in the West African Sahel during a period of unprecedented drought (Zhou et al., 2007), which seems to contradict the argument of higher cloud cover. Changes in DTR can result also from a number of other mechanisms, such as changes in atmospheric circulation, greenhouse gases, aerosols, and land cover/use, which are all connected to the surface energy balance. The authors hypothesized that in this case DTR was reduced due to night time release of heat as a consequence of the more intense heating of the soil uncovered by vegetation during the day. In the recent decades, however, a pan-European study revealed that the trend has reversed and DTR is increasing again (Makowski et al., 2008). The authors related this trend to a shift from “Global Dimming” to “Global Brightening” due to reduction of SO_2 emissions. As can be seen from this example, studying the temperature dynamics and the interpretation of the gathered data as well as using these results to predict actual trends is very complicated. The higher is our uncertainty the more we should be aware of possible roles and feedbacks of all components involved. Special attention should be paid to the role of biota, especially vegetation, as a dynamic and the only adaptable factor of the Earth climatic system with possible large feedback on climate.

In this chapter impacts of vegetation on the local, regional as well as global climate are discussed, in particular in the context of surface temperature and water cycling. Controversy over the role of forests in energy and water cycling and a possible role of increased CO_2 concentration on vegetation and hydrology are commented on. Finally, I will reflect upon what we know and what we do not know about the importance of vegetation for the functioning of the cultural landscape.

6.1 Microscale, mesoscale and global impacts of vegetation on climate

The variability of conditions is high on all levels, from micro- to global scale, creating mosaics of patches characterized especially by distinct dynamics of humidity and temperature. The variability is caused by different factors, such as presence or absence of water, exposure to the sun, vegetation characteristics etc. The atmosphere near the ground surface is significantly influenced by dynamically changing land-surface characteristics, which may, particularly during conditions of high energy, input substantially influence humidity and temperature distribution (Kabat et al., 2004; McPherson, 2007).

The variability of temperature on the microscale level is to a large extent determined by factors related to the energy and water budget of leaves and vegetation stands discussed in the forgoing chapters. The actual conditions of microhabitats within a stand (even a low grassland) defined by different temperatures may vary to a large extent (personal observation). The distribution of temperatures, light and water within a stand is influenced by the vegetation structure, which predetermines also the readiness of the inner-stand environment to the impacts of the extra-stand environment (Stoutjesdijk and Barkmann, 1992). Under some conditions temperature as well as humidity within a canopy may thus substantially differ from the surroundings (e.g. Makarieva et al., 2006, see chapter 2.2.1). On bare land it is the soil optical characteristics and soil-surface wetness thet strongly affect the surface fluxes. If the surface is dry and bare, all R_n goes into ground heat flux and the turbulent sensible heat flux (Kabat et al., 2004).

Interactions and feedback loops between the atmosphere and the heterogeneous surface is dependent on many factors and variables, ranging from geomorphology of the studied area and its position within the global climatic system to the given meteorological situation and characteristics of the surface structure. To what extent heating of surface is manifested throughout the atmospheric planetary boundary layer depends a lot on the stability of the atmosphere (Kabat et al., 2004). The atmosphere near the ground is a very dynamic and complex system with the horizontal flows prevailing. Under common conditions it tends to stabilize vertical flow. The stability of the atmosphere depends on its lapse rate. The lapse rate defines the way in which temperature varies with altitude. The unsaturated atmosphere is considered stable when the environmental lapse rate (ELR, i.e. the actual variation of temperature with height at a certain time and place) is less than the dry adiabatic lapse rate (DALR; 9.8 ºC km^{-1}), i.e. when the rising air parcel cools through the process of expansion more rapidly than the surrounding air. In this case the density of the parcel becomes higher than that of the surrounding air and the air sinks back again. The air in the parcel does not reach the dew point and the only clouds likely to form are cumuli, which will not produce rain. The air in the parcel does not reach the lifting condensation level (i.e. dew point is not reached) and no clouds are formed. In summer, stable conditions suppress convection currents and bring dry and sunny weather. Under stable atmospheric conditions, stomatal conductance and leaf area index variability have the most significant effect on spatially integrated energy fluxes from vegetated land (Kabat et al., 2004).

The atmosphere is absolutely unstable when ELR is greater than DALR, i.e. when ELR > 9.8 ºC km^{-1}. This means that as the air parcel rises, it becomes warmer (and less dense) than the surrounding air and therefore rises further. When the lifting condensation level is reached, condensation warms the parcel and forces it to rise even more rapidly. Very high clouds evolve, such as cumulonimbus clouds, and thunderstorms may occur. When ELR is less than DALR but more than saturated adiabatic lapse rate (SALR), conditional instability occurs. The saturated adiabatic lapse rate is lower than DALR due to a release of latent heat as water vapour condenses. SALR is variable (between 3.9 ºC km^{-1} to 7.2 ºC km^{-1}) since it largely depends on how much latent heat is made available within the air parcel as its moisture condenses. The stability/instability of the atmosphere may be also largely influenced by orography of the surface as air is often forced to ascend up mountain slopes.

As follows from the above the heat energy for convective precipitation can be derived from sensible heating at the Earth’s surface and from the release of heat as water vapour condenses or freezes (Pielke, 2001). Convective precipitation is thus connected to both temperature and evapotranspiration of the surface. Any land use change, such as loss of vegetation due to overgrazing, increase/decrease of transpiration due to conversion of natural vegetation to agriculture, etc., affects the potential of thunderstorms (McPherson, 2007). The boundary layer structure, including its depth, is directly influenced by the surface heat and moisture fluxes. However, neither the nature of atmospheric flows (e.g. Nathan et al., 2005) nor the effect of landscape evaporation and transpiration on convective precipitation is a linear process (Pielke, 2001; Kabat et al., 2004). Whereas under some conditions, the surface moisture and transpiration are the major drivers of convective precipitation, under different circumstances the high sensible heat fluxes connected to dry surfaces determine the process. Because of this fact, higher convective precipitation in the mosaic of cultural landscape may be sometimes enhanced by native vegetation and sometimes by the man-introduced land use. Soil moisture conditions sometimes induce positive and sometimes negative feedback to rainfall occurrence (Alfieri et al., 2008). Pielke (2001), Kabat et al. (2004) and McPherson (2007) presented comprehensive reviews of studies dealing with this topic and drawing often controversial conclusions, which, however, demonstrate that the impact of vegetation, although not easily interpretable, is substantial. Differential heating caused by sensible heat gradients across adjacent regions of intensively transpiring vegetation and dry, bare soil can even generate a sea breeze-like circulation, called a "vegetation breeze" (Eltahir and Bras, 1996; Pielke, 2001; McPherson, 2007). An interesting example of vegetation influence on regional climate was presented by Lawton et al. (2001). The authors showed that land-use changes in tropical lowlands had serious impacts on ecosystems in the adjacent mountains. The Landsat and Geostationary Operational Environmental Satellite imagery showed that deforested areas of Costa Rica's Caribbean lowlands remained relatively cloud-free whereas forested regions had well-developed dry season cumulus cloud fields. Cloud base heights raised above the deforested lowlands, which may have negatively influenced the montane forests whose water and energy budget is tightly dependent on the presence of clouds.

Intense precipitation events correlated with higher frequency of cumulonimbus clouds have been lately documented to increase their frequency and intensity in mid-latitudes as well as elsewhere (Groisman et al., 2005). It has been suggested that this trend is related to climate warming which is responsible for increased energy and higher water vapour content in the atmosphere. As convective precipitation is influenced by surface structure, the role of water and vegetation distribution should also be considered. The climate system is through feedback and synergism processes interconnected into a web of complex dynamics and regulation mechanisms. The feedback loops depend strongly on the region under consideration. Different variables may dominate in different biotopes depending on circumstances (Kabat et al., 2004). A climatic system may show multiple equilibria, i.e. the same initial conditions may result in more than one stable state, which may sometimes even exist next to each other (Zeng et al., 2004). For example, atmosphere–biosphere interactions in the Sahel region of West Africa lead to multiple stable equilibria. It seems that either wet or dry climate equilibria can occur under otherwise identical forcing conditions. The equilibrium reached is dependent on the past history (i.e. initial conditions), and relatively small perturbations to either climate or vegetation can cause switching between the two equilibria. Crossing thresholds can lead to unpredictable or irreversible changes (Higgins et al., 2002). Changes in regions which tend to have more equilibria can be more rapid or less predictable than those in other regions. It seems that in some cases relatively small areas of changed land cover can determine the equilibrium state of the atmosphere–biosphere system of an entire region (Higgins et al., 2002).

Land use changes on a large scale may modify local climatic conditions more than the climate change itself (Shaver et al., 2000; McPhearson, 2007). Vast land-cover changes may result in teleconnections, i.e. land-cover changes expressed remotely on climate of other regions of the globe (Pielke, 2001). This may be true in particular when the surface changes influence convection in tropical regions, which may remotely affect weather and climate regimes both in the tropics and at high latitudes analogous to the effects of El Niño-Southern Oscillation (Kabat et al., 2004). Changes in tropical and mid-latitude vegetation cover appear to play a significant role in the strength and positioning of tropical monsoon circulations. The response of the atmosphere to a perturbation in the distribution of vegetation is site specific (Zheng and Eltahir, 1998). Our understanding of the relation between land use changes, hydrological cycle and climate is still so limited that we are not able to predict which changes would lead to which consequences and which feedback loops would be induced. However, it is clear from many examples that the consequences can be significant. To mention just some of the most obvious: run-off from the continents has been changed in many places due to land use changes (Aral sea reduced because of water extractions for agriculture, (e.g. Micklin, 1988) etc.) and many rivers are used so extensively that little or no water reaches the sea (Murray-Darling river, Huang He, Indus and others) with consequences for the local, regional and most likely also global climate.

6.1.1 Moisture feedback

DeGroen and Savenije (1995) began their paper with an anecdote: When in Africa we explain to people that we are trying to investigate whether the rigorous land use changes have influenced the rainfall, the most frequent answer is “Hasn’t that already been proved? The answer is still negative.” Scientists hesitate where common people in their straightforward answers draw on their feelings or experience. Questions such as what is the contribution of land-recycled water to precipitation of different areas or whether there is higher precipitation in areas with higher soil moisture content have not been satisfactorily answered yet. The understanding of vegetation (and consequently land use) impact on local water cycling is still very limited.

All terrestrial life depends on local water resources. To maintain hydrologic balance on land, the water flowing into oceans by the discharge of rivers must be compensated for by the water vapour brought with the atmospheric masses from the oceans. However, every single water molecule, which originated in the oceans, may take multiple “cycles” of precipitation and evaporation before it reaches its final terrestrial destination (Dirmeyer and Brubaker, 2007). The atmosphere can only generate rainfall downwind (i.e. further from the oceans) if the precitable moisture is at least partly replenished by evaporation from the land surface (de Groen and Savenije, 1995). In many regions a substantial fraction of the rainfall results from upstream evapotranspiration rather than from oceanic evaporation (Hayden, 1998). Letteau et al. (1979) calculated that 88 % of water vapour in the atmosphere of the upper reaches of the Amazon Basin was transpired into the air by vegetation in the basin (Hayden, 1998). Also Moreira (1997) measured forest vapour in the Amazon basin and showed that it was mostly, if not completely, generated by plant transpiration. The fraction of precipitation over a defined area that originated as evapotranspiration from the same area is called the recycling ratio. In the simplest sense one could imagine that a change to evaporation over the area under review has a direct and predictable impact on local precipitation (Dirmeyer and Brubaker, 2007). The recycling ratio may be interpreted as a variable relating the evapotranspiration rate to the rate of moisture convergence (i.e. transport of water by horizontal winds) in the area in question (Eltahir and Bras, 1996). In reality, although the land–atmosphere coupling plays an important role in the dynamics of the hydrologic cycle, it is still unclear how soil moisture conditions affect rainfall occurrence as both positive and negative feedback (due to increased supply of water vapour to the atmosphere on the one hand, and cooled down surface on the other hand) between soil moisture and precipitation has been described (for recent literature review see Alfieri et al., 2008; Bisselink and Dolman, 2009). Which of the two processes prevails on a given day and at a given place depends probably on many factors influencing the net energy contributions impacting the atmosphere. The recycling ratio depends on the geographical location, the temporal scale and the spatial scale considered. The question of scale is fundamental as for the global scale recycling ratio is 1 and for any point on Earth it equals 0 and we are interested in what is between the extremes (Eltahir and Bras, 1996). Long time and large area scales mask key relationships between recycling and other variables that occur at shorter time and smaller space scales (Bisselink and Dolman, 2009). The relative importance of the recycling ratio may also vary seasonally or according to the actual climatic and large-scale meteorological conditions (Eltahir and Bras, 1996; Costa and Foley, 1999; Zhang et al., 2008; Bisselink and Dolman, 2009). Its importance commonly grows during the warm season when soil moisture and vegetation can affect energy and water exchange between the land surface and the atmosphere through the process of evapotranspiration (Alfieri et al., 2008). As the recycling ratio is a relative variable, the actual values of recycled precipitation may vary substantially in different regions according to precipitation inputs.

Dynamic movement of omnipresent water molecules throughout changing phases and different milieus is methodologically difficult to determine. Lately the composition of stable isotopes ^{2}H and ^{18}O has been used for studies of the hydrological cycle. The liquid-vapour phase transition is connected with isotopic fractionation. The heavier isotopes accumulate preferentially in the liquid water, be it in the ocean, lakes, rain droplets in clouds, or leaves of plants. Water around the world has varying isotopic composition (West et al., 2006). Dansgaard (1964) described four major parameters of variation in precipitation stable isotope ratios: altitude, latitude, distance from coast, and amount of precipitation. As heavier isotopes tend to precipitate as soon as possible, the isotope composition of the rain depends also on the duration and strength of the raining event (Dansgaard, 1964). The maps of spatial distribution of water isotopes in precipitation are available at http://waterisotopes.org/. There is no fractionation of water in roots and stems, therefore the isotopic composition of the source is reflected in the sap flow stream (Ehleringer et al., 1991; Flanagan and Ehleringer, 1991). Contrary to roots and stems, water in leaves is markedly enriched by heavy isotopes as lighter isotopes are transpired more quickly (Flanagan and Ehleringer, 1991). Some attempts have been made to study movement of water through ecosystems with the help of stable isotopes methods. Based on isotopic measurements Moreira et al. (1997) evaluated relative proportion of water vapour generated by plant transpiration and by soil evaporation at two sites in the Amazon basin. Isotopic studies of transpiration and soil evaporation components of evapotranspiration showed that soil evaporation contributed only little (<10 %) to total evapotranspiration of forest ecosystems (Flanagan and Ehleringer, 1991; Lai et al., 2006). Some authors used isotopic methods to differentiate water sources of different plant life forms (trees vs. shrubs, understory, vs. overstory etc.) or species (e.g. Jackson et al., 1995; Yepez et al., 2003; Yepez et al., 2005). However, despite some success in this field of study, we are still far from proper understanding of the movement and cycling of water through different types of ecosystems and the processes behind them, as isotopic analysis of precipitation can provide only the proportions of likely sources differentiated into broad categories (Dirmeyer and Brubaker, 2007; Rahn, 2007; Bowen, 2008).

Most of the results gathered so far in this topic are model based. Dirmeyer and Brubaker (2007) used a back-trajectory method which traced the air motion back in time to identify the evaporative sources of vapour contributing to precipitation events for all land areas of the world. The authors computed overall recycling ratios on a monthly basis for a 25- years period to be 4.5 % for the 10^5 km^2 spatial extent. On both the annual and seasonal bases minimum recycling was observed in regions with strong advection from adjacent waters (i.e. the Northern Amazon basin, the Mississippi basin, and coastal monsoon regions in South Asia and North-Western Mexico). Recycling appeared to be relatively high over much of South America south of the Amazon river through La Plata basin, much of subtropical southern Africa, interior China, southern Europe, North Western America, and a broad swath of the high latitudes of the Northern Hemisphere, especially over eastern Siberia. The model of Zhang et al. (2008) showed corresponding trends of strong summer land-atmosphere coupling (positive soil moisture feedback accounts for typically 10 – 20 %) of the Northern hemisphere to be mainly in arid to semiarid transition zones or in semihumid forest to grassland transition zones of central Eurasia, the region from Mongolia to northern China, southwest China, the northern part of continental United States, Sahel and southern Europe. According to Dirmeyer and Brubaker (2007), the high-latitude regions of the Northern Hemisphere, especially in the Pacific region, showed a very strong annual cycle as measured by the amplitude. Regions with very low seasonal variations in recycling included: the Amazon Basin and adjacent Atlantic coastal regions of equatorial South America, the southern coast of Australia and Great Australian Bight, areas to the west and northwest of the Persian Gulf and two regions of the Nile basin, including the delta and parts of Ethiopia. What seems to be rather surprising is the relatively low recycling ratio over the forested basins of the main tropical rivers which had been earlier shown to be higher. Precipitation recycling of 25-35 % with some estimates reaching even 50 % was suggested for the Amazon basin (for review of literature see Eltahir and Bras, 1996). Also the estimates for the Mississippi river varied between 10 and 41 % (for citations see Eltahir and Bras, 1996 and Kabat et al., 2004). Another possible role vegetation plays in precipitation recycling is the production of biogenic aerosols that may serve as condensation and ice nucleation particles and play an important role in precipitation formation (Andreae and Crutzen, 1997; Barth et al., 2005; Andreae and Rosenfeld, 2008; Junkermann et al., 2009).

The recycling of precipitation on land remains still controversial, with arguments spanning from statements that recycled water vapour from evaporation and transpiration is a major component of the continental precipitation (Pielke, 2001) to those indicating that this process is of a negligible effect. It is obvious that to understand these processes better we need to study them on a shorter time scale than on a monthly or even a longer scale examined by most precipitation recycling studies so far (Bisselink and Dolman, 2009).

Bisselink and Dolman (2009) applied the dynamic precipitation recycling model of Dominguez et al. (2006) to daily meteorological processes of Central Europe. In Central Europe, precipitation originates mostly from oceanic sources. However, the authors concluded that recycling becomes important during periods of reduced total precipitation when moisture of advective origin diminishes (Bisselink and Dolman 2008, 2009). As the moisture fluxes diminish, the air has more time to traverse the region and capture moisture from land evaporation. The authors studied heat spells of 2003 and 2006. When a lack of water in the landscape was most serious, the air was too dry to generate precipitation with the exception of the mountainous regions (due to orographical lifting). However, where there was enough moisture storage in the soil, evaporation continued to feed the atmosphere with water vapour and recycling was enhanced. Moreover, the authors suggested a precipitation triggering mechanism. Areas that still had enough moisture storage induced via evapotranspiration enhanced the instability of the atmosphere supporting precipitation falling. Thus it seems that in this region evaporation from the surface is an important driver in the recycling ratio variability. Water becomes most important when there is a lack of it under high temperatures. The enhanced recycling ratio during dry periods is thus of high importance. It follows from the above that the recycling capacity of Central Europe during hot spells depends on water availability in the soil. Therefore it is highly important to manage the landscape so that water retention is supported during wet periods to create reserves for dry periods. As was discussed in chapter 5, vegetation substantially influences evapotranspiration rates, especially if it is deep-rooted. Therefore its distribution and status may play a very important role in moistening the air and enhancing near surface wetness.

As presented by Bisselink and Dolman (2009), the enhanced instability of the atmosphere induced by evapotranspiration may support precipitation falling. Eltahir and Bras (1996) suggested that the reduction of evapotranspiration, related for example to deforestation, may reduce atmospheric humidity and surface moist static energy (i.e. the thermodynamic variable calculated by hypothetically lifting air adiabatically to the top of the atmosphere and allowing all water vapour present in the air to condense and release latent heat), which may consequently lead to a reduction of local rainfall. A strong land-atmosphere coupling effect via high evapotranspiration was hypothetized for large forested areas by Makarieva et al. (2009) and Makarieva and Gorshkov (2007, 2008). The authors argue that the dependence of annual precipitation on distance from the ocean differs markedly between the world's forested and non-forested continent-scale regions. Whereas in the non-forested regions, precipitation declines exponentially with distance from the ocean, in the forest-covered regions precipitation does not decrease and may even grow along several thousand kilometers inland. The authors assigned this to a physical process in which natural forests are claimed to "suck in" moist air from the ocean and called this process the "biotic pump of atmospheric moisture". The authors hypothetized that the large evapotranspiration rates of vast forests cause the air to be out of the hydrostatic equilibrium. The cumulative pressure of the moist air exceeds the weight of atmospheric column, which leads to an upward-directed force (evaporative force), i.e. air and water vapour to ascend. On the surface the ascending air volumes must be replaced by the air flowing horizontally from the neighbouring areas where this force is weaker forming horizontal fluxes of air and water vapour from areas with weak evaporation to areas with intense evaporation.

This theory has been heavily criticized as flawed with regard to the inappropriate use of certain fundamental principles of atmospheric physics. The disequilibrium effect on the transport of water vapour was shown to be negligible (Meesters et al., 2009). Nevertheless, even though the physical principles might have been simplified by the authors, the value of this theory is definitely in bringing new ideas to the relation between (forest) vegetation and precipitation, which has to be better understood, as this knowledge could be the basis for water and land-use management policies.

Another even more theoretical concept ofthe role of vegetation in Earth climate functioning was modelled by Kleidon et al. (2000). Based on the Gaia hypothesis according to which "homeostasis by and for the biosphere" (Lovelock and Margulis, 1974), the authors modelled conditions in a "desert world" and a fully "green planet". The "desert world" was characterized as relatively smooth with higher reflectance (albedo) and strongly reduced capacity of storing and thus recycling water. The green planet was characterized by the presence of maximum vegetation. This rougher and darker world had much higher ability of water recycling due to good access to water stored in the soil. Consequently the atmosphere in the green world was more humid over most continental parts of the summer hemisphere and the tropics and latent heat flux was higher. These processes led to cloud cover increase in the green world, which apart from other effects overcompensated the effect of a lower albedo of the dark surface. In comparison to the desert world, the authors showed that maximum vegetation cover of the green world resulted in considerably lower air temperatures of up to 8 K.

6.2 Forests – controversy over their role in hydrological and energy cycles

Trees are the largest plant forms on the Earth and as such have a great potential to influence the environment. The extent to which they impact terrestrial fluxes of water and energy is proportional to their size. Large amounts of water can be transpired from the dark and rough forests crediting huge portions of incoming energy to latent heat flux. Interception within the trees' crowns is higher than that in other vegetation types, contributing to high evaporation. Infiltration tends to be high in the forests and many trees have been described as capable of water redistribution in the soil as well. It is thus obvious that forests represent an important component in landscape hydrology.

Although the science has made enormous progress in encoding many secrets originally undetectable because of their scales, either too small or too big, we have to acknowledge that we still do not understand some fundamental processes in ecosystem functioning. In forest ecosystems the uncertainty continues to be immense. Scientists argue whether forests due to their low albedo contribute to warming or cooling of the surface (see chapter 5). And a great controversy is present in the discussions about forests' functioning in the hydrological cycle as we still do not know whether and under which circumstances forests multiply or diminish water yields in catchments. As the processes that determine the functioning of forests in the climatic system are interconnected in a web of direct and indirect feedback, it is difficult to decipher the relations. Moreover, it is obvious that environmental functions of forests have to be studied and assessed with respect to the region in question. As shown in the foregoing chapters forest physiology is to a large extent dependent also on species composition, broadleaved vs. needle leaved species presence, age-class distribution as well as canopy structure. The response of a forest to existing environmental conditions is to a large extent influenced by the degree of adaptation or acclimation of the stand to the long-term conditions (root distribution in the soil layer, structure of the stand etc.). Different species and stands differ in their capacity to acclimate as a consequence of their species composition, structure and life history (prof. Jan Čermák, personnal communication).

6.2.1 Controversy I. – do forests warm up or cool down the Earth surface?

It is summer. I am walking in the late morning or maybe it is already the lazy time right after lunch. The sun is shining and the air above pastures is quaking with heat. There is a forest. I enter it and breath the coolness of still lasting dew and smell of wet mosses and soil. The shadow of trees is so soothing. Is this a memory based on real experience? Sometimes I am beginning to wonder when I read scientific articles that try to make me believe in relations so absurd such as that deforestation might mitigate global warming (e.g. Bala et al., 2007). I am aware of the fact that my attitude to forests is biased by subjective emotions but still it seems to me that the scientific approach to forests' importance in energy and water cycling is somewhat strange in the way it differs from our common experience. As this is first of all due to a lack of holistic understanding of the ecosystem functioning, it is science itself that has to bridge this gap.

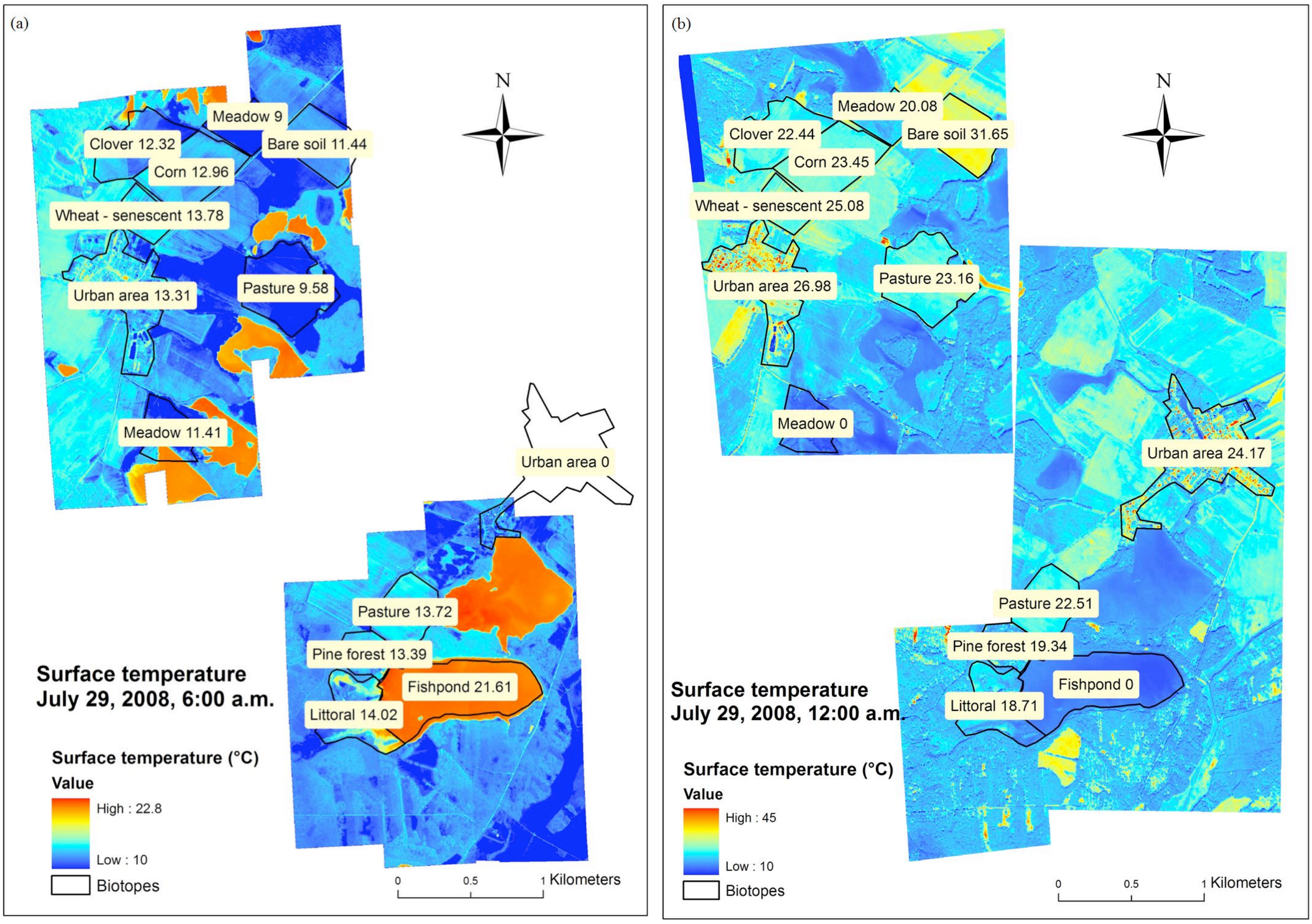
Actual temperature of forests may deviate substantially from ambient atmospheric conditions measured by weather stations (Leuzinger and Korner, 2007). As forests are tall stands, they may be in many aspects largely decoupled from the atmosphere. When discussing their temperature we should be therefore aware of which temperature we are talking about. In a mature forest stand the effective surface - where radiation is absorbed and emitted and wind influences the energy fluxes - is situated at the top of the crown (Geiger, 2003). The temperature of the canopy may substantially differ from the temperature near the ground (e.g Hojdová et al., 2005; Makarieva et al., 2006). This is determined first of all by the nature of solar energy distribution within the stand, but also by moisture distribution, transpiration rates of canopy as well as understorey plants and micrometeorological conditions influencing air movement. In a more dense forest, neither sunshine, nor wind can penetrate to a significant extent. Thus during the day the air in the trunk area remains cool and moist when compared to the crown area (Geiger, 2003).

We may assume that high radiation absorption (due to low albedo) by forests results in higher sensible or latent heat fluxes (Hutjes et al., 1998). Which of the fluxes will become prevalent depends above all on the stand water supply. As already mentioned in chapter 4.3, during the heat wave spell of summer 2003 in Europe, temperate forests were found to be the least sensitive of all low elevation vegetation types in terms of canopy temperature (Zaitchik et al., 2006). Their temperature characteristics were relatively balanced compared to other types of vegetation such as grassland and crops. According to Zaitchik et al. (2006) the absolute sensible heat flux from agriculture land was estimated to exceed that from forests during the 2003 heat wave and crops and pastures contributed most to the radiative heating of the planetary boundary layer. This was most probably due to the fact that the forests were not so dependent on short-term variation in soil moisture, as their roots usually reach to deeper soil layers (Leuzinger and Korner, 2007). Using remote sensing methods we showed that the forest dominated by spruce and beech had the lowest surface temperature and sensible heat flux and the highest humidity and latent heat flux when compared with other vegetation types (mowed meadows, pastures, wetlands, ruderal and degraded vegetation, xerophytic communities) in two small catchments in the Šumava Mountains, Czech Republic (Brom et al., accepted, see attachment). Similarly, dieback of mountain spruce forests in the central Šumava Mountainsled to a significant increase in land cover relative temperatures of the site (Hais and Kučera, 2008). Hojdová et al. (2005) using remote sensing also demonstrated that the surface temperature of living forest canopy was lower than surface temperature of a dry forest, peat bog and a clearing. The authors measured also temperature and humidity gradients (15cm under the ground, at the ground level, above the herbal floor and 2 m above the ground) within the studied sites. Temperature dynamics differed markedly in forests in comparison with the other three observed sites. Fluctuations of temperatures were far the lowest in the living forest as a consequence of a combined effect of lower day maximums and higher night minimums. Better temperature balance was correlated with increased humidity in a living forest throughout the day. Likewise, Ripl et al. (2004) studied temperatures (measured in -10, 0, 10 and 200 cm above ground) in a virgin forest (Albert Rothschild Wildnisgebiet Rothwald) in the Kalkenalpen Austrian National parc. When compared with a glade, the temperature within the forest reached lower maximum temperatures and differed also in the temperature daily course. In forests temperature increased more slowly in the morning whereas evening cooling was more rapid than in the glade. The morning trend was similar to the results of Hojdová et al. (2005). Hojdová et al. (2005) showed that evening cooling was slower in the living forest than at the other sites. This might have been caused by release of heat accumulated in dry trunks during the day or by advection of hot air into the forest from its surroundings. Areas which transform large amounts of energy into sensible heat may influence the neighbouring moist areas also during other parts of the day by enhancing their latent heat flux (Ripl et al., 2004).

Ripl et al. (2004) suggested that due to the high moisture content (RH=80-100 %) in the air from evapotranspiration, the dew point in the virgin forest was reached usually a couple of times during a day. When this happens, the somewhat cooler places, such as transpiring leaves or needles, serve as condensation zones. This process supports effective balancing of temperature and it represents an extremely quick clompletion of micro water cycles (see chapter 2.2.1). The loss of water vapour from the system is thus minimized and temperature extremes reduced. According to Kedziora and Olejnik (2002) this water surplus income can reach 20 to 50 mm per year and in some cases, for example in dense meadows, as much as 100 mm.

Forests as well as other ecosystems with more balanced temperature dynamics are thought to be less sensitive to disturbances than areas of high temperature amplitudes. This assumption was one of the crucial starting points of the Tokenelek project (funded by the Ministry of Education, Youth and Sports of the Czech Republic, National research programme II, 2B-Health and Quality of Life, project No. 2B06023), which is being carried out by our research team in ENKI o.p.s., Třeboň. The project deals with development of methods for determining energy and substance flows in selected ecosystems and tries to propose and verify the evaluation criteria for economic intervention with the aim of creating conditions for self-regulation and the enhancement of biodiversity. In figure 6 morning (a) and noon (b) values of remotely sensed temperature of the studied ecosystems are presented. In the morning the temperature of different vegetation types was relatively balanced compared to differences measured in the afternoon. However, also in the morning we may see some interesting trends. The temperatures were scanned in strips from east to west. The temperatures in the western part of the morning scene might be therefore somewhat higher due to a certain time lag of several minutes which may be responsible for a measurable temperature difference in the early morning hours when surfaces warm up quickly. An interesting trend may be seen in the eastern part of the morning scanning series. Whereas the mean temperature of the meadow, bare soil and pasture areas set in the northern part of the scene is 10.01 +/- 1.27 °C, the mean temperature of the pasture, litoral and pine forest situated in the southern part of the scene around the Ruda fishpond is 13.71+/-0.32 °C. This difference cannot be explained by the time lag of measurement. It must therefore result from some local characteristics having an impact on temperature. The vegetation types in the southern part are probably influenced by the fishpond, which does not cool that much during night due to high heat capacity of water and in the morning is thus much warmer than the surrounding landscape. Apart from the direct effect of the fishpond temperature, a higher release of heat due to condensation is another possible process which can influence the temperature of the fishpond surrounding. Although three values cannot serve as significant indications, the lower standard deviation of the latter vegetation types may indicate more balanced temperature in the habitats near the fishpond.

Figure 6 a,b. Map of surface temperature distribution (space resolution = 2m) generated by remote sensing using IR camera (Therma CAM^{TM} PM695) for morning (a) and noon (b) hours of July 29th 2008. The temperatures are average values for marked polygons. The polygons mark areas of described vegetation types.



In the noon hours the temperatures of different vegetation types varied significantly. The coolest vegetation types were the forest together with the litoral area of the Ruda fishpond. Also the other cooler vegetation areas on figure 6b represent mainly forests of various composition. On the contrary, the hottest area was the plowed field with bare soil due to its dark colour and possibly also low water supply. The second hottest areas were the urban areas with substantial percentage of the surface covered with concrete or other artificial materials which warm intensely when irradiated. Also other represented field areas covered with senescent wheat and corn were relatively warm due to low latent heat flux. Pastures and clover were somewhat warmer than the meadow. This was probably due to different LAI and the fact that the meadow was set near another fishpond. All of these measurements will be supplemented by the ground-based measurements. However, the results presented here already support our assumption that places covered with closed canopy in the vicinity of lakes (i.e. supported by enough water and possibly usually subjected to higher air humidity) show the lowest diurnal temperature amplitudes in the studied cultural landscape, i.e. their temperature is most balanced and the temperature extremes are minimized. Thus plants with sufficient water supply use incoming solar energy for mitigating local temperature extremes.

6.2.2 Controversy II. Do forest multiply or minimize water reserves on the Earth surface?

The most often challenged argument is that of forest being able to improve hydrological balance of catchments, a topic that has been making fur fly for a long time. The controversy over this argument may be traced throughout centuries back in time in scientific as well as in lay disputations (Andréssian, 2004; Bruijnzeel, 2004). I have asked many of my friends with no scientific background “What would happen with the hydrological cycle if we cut down forests on a large scale?” They all answered: “There would be less water.” However, the problem is not that clear as scientific findings bring evidence challenging these common convictions and experience.

With only a slight simplification we may distinguish two opposing parties. The first party could be called “forests defenders”, i.e. those who believe that forests give us water by attracting rain, and by retaining water make hydrological conditions more balanced during both dry and flooding periods and consequently regulate climate in a positive way. The other party, we may call “the forest sceptics” for the way they think of hydrological functioning of landscape. Representatives of this side of the ideological spectrum have often been presented as engineers (Andréssian, 2004) because of their tendency to take into account only the quantifiable hydrometric and meteorological data and because of their preference for the technical solutions to problems. The supporters of the latter platform point out that forests tend to deplete water reserves in landscape due to their high transpiration rates.

It is not surprising that many studies working solely with the assumption that both transpiration and interception of forests are commonly high have shown that forests use more water and locally produce less run-off than shallow rooted forms of vegetation such as crops, pastures, grasslands or shrub lands. This effect is undoubtedly enhanced also by higher infiltration enabled by the characteristics of forest soil, which is usually richer on organic matter and less compacted (van Dijk and Keenan, 2007). Deforestation increases the amount of water retained by a dam catching water from the catchment in question. The run-off is unstable, fluctuating with actual precipitation events. The peak flow from the catchment is enhanced while low river flows (flow of water in a stream during prolonged dry weather) may be reduced (Geiger, 2003). Although the regulating influence of forests on the stream flow is obvious (retarded floods, more uniform ground water recharge) (Geiger, 2003), both increase and decrease in low flows after deforestation are theoretically possible. This is because the low-flow regime of the river includes the distribution and infiltration characteristics of soils, the hydraulic characteristics and size of the aquifers, the rate, frequency and amount of recharge, the evapotranspiration rates from the basin, distribution of vegetation types, topography and climate and is therefore influenced by many factors simultaneously (Smakhtin, 2001).

Andréssian (2004) in his comprehensive overview of paired-watershed experiments showed that according to many authors, deforestation increased the annual flow of the catchment while reforestation decreased it. The paired-watershed method is regarded the most objective method of studying water relations of catchments in relation to their different land-use. It is based on comparing two catchments as similar as possible in terms of their size, morphology, geology, climatic forcing and land use. After preliminary calibrating observations, land use of one of the basins is modified (deforestation), while the other one remains untouched as a 'reference' watershed. Afterwards the changes in hydrological behaviour of the modified basin are observed and confronted with the reference basin. For obvious technical reasons most experiments have covered very small watersheds, with the majority being smaller than 2 km^2 (Andréssian, 2004). In my opinion the scale may be the largest source of possible errors in the interpretation of the role of forests in the landscape. Consequently, these studies have been opened to doubt. Is it possible to achieve better water yields also from large-scale deforestation? Wilcox et al. (2006), who estimated that conversion from woody to herbaceous vegetation at upland sites where deep drainage occurs may result in a water saving on a yearly basis, mentioned that until further work was done it was uncertain whether these savings could materialize on larger scales. But is science able to pursue further experimental work and manage it properly in this context? A small deforested basin cannot be decoupled from its surroundings. Therefore its hydrology is likely to remain interconnected with a much larger area of the surrounding catchments. Precipitation input and water retention capacity of the area are therefore likely to remain stable. There where the hydrology of the whole region is not disturbed yet deforestation leads to advanced run-off due to decrease in the evapotranspiration of the local stand (Andréssian, 2004). Would this however hold true if large areas of forests were to vanish and the created space remained scarcely vegetated? Would it have no consequences on hydrological input of the area? I truly believe it would bring deterioration to the whole area. Not only in terms of soil erosion and nutrients loss, but in a longer term also in water yield. However, how can we prove it? Apart from modelling activities we can rely only on historical evidence of once flourishing civilizations, which ran dry after large areas had been deforested or observations which, however, have not been scientifically documented as they were happening and are therefore difficult to use to convince the scientific public.

Deforestation may negatively impact some ecosystems in both humid temperate or maritime and predominantly dry climates also due to increasing water tables. For example Díaz et al. (2007) described hydrological changes on Chiloe´ Island in Chile where over 40 % of the land has been cleared and converted into sparse shrub cover since the 19th century. It was estimated, that as a consequence of this land use change evapotranpiration decreased from 53 % (forest) to only 9 % (shrub vegetation) of the incoming rainfall mainly because of a marked reduction in interception surfaces and canopy transpiration as well as a reduction in extracting of advective energy due to decreased roughness. This change in water distribution has led to an increase of the water table and consequently to poor tree regeneration on waterlogged sites, which are quite common here due to poor drainage of local soils. The adverse effects of increased water table as a consequence of forest depletion have been suggested also for Australia (Ruprecht and Schofield, 1991; Schofield, 1992). Here, the effects are intermingled with the threat of salt rising from the lower soil layers as salinization has become a nationwide problem in Australia. Planting trees in salt-affected areas has been proposed as one strategy of controlling rising saline groundwater (Schofield and Bari, 1991; Schofield, 1992).

Another snag in the argument concerns afforestation effects on catchment hydrology. Although afforestation may increase groundwater recharge and low flows due to improved infiltration and improve soil prevention, and although it influences surface-atmosphere transfers of heat and moisture with a potentially positive feedback on precipitation (van Dijk and Keenan, 2007), it has been shown that it may negatively impact on water resources, especially in places where these are already under pressure due to stream flows and water reserves reduction (Bosch and Hewlett, 1982; Farley et al., 2005; Calder, 2007; van Dijk and Keenan, 2007). This is connected especially with high water use of rapidly growing woody species in forest plantations as well as young seedlings in new forests (van Dijk and Keenan, 2007). Water use in new or rejuvenated stands typically gradually decreases with age (van Dijk and Keenan, 2007; Vanclay, 2009). However, this stage is often not at all materialized because the forest is cut. Therefore it is likely that the possible positive effects of new forests on catchment hydrology (von Glasow and Bott, 1999; Makarieva et al., 2006; Vanclay, 2009) cannot be recognized at all due to their short period management.

Generally, the functioning of forests in hydrological cycle is discussed under three fields of impact:

a) release of water from the soil to the air via transpiration, together with interception
b) possible improving of water budget of the landscape via precipitation enhancement
c) retention of water and its influence on water run-off connected with soil conservation due to erosion and nutrient leakage prevention

Transpiration characteristics of trees and forests are discussed in chapter 5. Interception is influenced by canopy structure and species composition. Measuring interception is a complicated task (Muzylo et al., 2009). Interception generally increases with increasing biomass (Geiger, 2003). It is usually smaller in deciduous forests than in needle forests, particularly where most interception falls in winter (e.g. Roberts, 1999; Kedziora and Olejnik, 2002). Interception is most intense in montane cloud forests due to high air humidity and high potential water storage capacity of the canopy supported also by the presence of epiphytes, especially bromeliads and mosses (Bruijnzeel, 2005; for further details see chapter 2.2.1.1). Interception of air humidity is also enhanced at vegetation edges, i.e. ecotones (Kedziora and Olejnik, 2002). Deforestation results in interception reduction (e.g. Díaz et al., 2007). High interception in combination with changed atmospheric turbulence could present two mechanisms backing enhanced precipitation on forested islands in comparison to the deforested ones (Ponting, 1993; Hayden, 1998; Diamond, 2005). Possible principles of water conservation within forests canopy (von Glasow and Bott, 1999; Makarieva et al., 2006) are described in chapter 2.2.1. Possible roles of forests in moisture recycling are discussed in chapter 6.1.1.

Retention of water by forests is a topic, which is periodically hotly debated mainly when large floods occur (Laurance, 2007). Recently, some evidence has been collected which emphasizes the impact of natural forests on flood prevention. Bradshaw et al. (2007) published results of a comprehensive study based on 10 years' data collected in 56 developing countries. The authors offer ample evidence that with a 10 % decrease of natural forest area flood frequency increases by 4 to 28 % (in different countries). Similarly, the same hypothetical decline in natural forest area resulted in a 4-8 % increase in total flood duration. The study's geographical scope and statistical rigour make it a strong argument for large-scale forest protection and more reforestation as a means of flood prevention (Laurance, 2007). Non-native vegetation may have different impact on catchment hydrology which in turn may lead to less effective or even negative impacts on the flood events compared to native forests (Bruinzeel, 2004; Bradshaw et al., 2007).

Run-off from a catchment depends on the intensity and volume of the precipitation event on the one hand, and on surface characteristics on the other hand. In this context both abiotic and biotic characteristics are important. The abiotic factors are a result of surface morphology of the basin, in particular its hill slope, and soil and subsoil structure. The biotic factors result from vegetation characteristics, i.e. canopy structure, species composition, proportion of broad-leaved to needle-leaved tree species, age structure as well as health conditions. Canopy structure influences interception. By dividing precipitation between throughfall and stemflow, vegetation also influences the distribution of rain on the forest floor (e.g. Crockford and Richardson, 2000) while by modifying the kinetic energy of drops it changes the erosional power of rain (Geiger, 2003). Vegetation influences also the composition, thickness and structure of the litter layer which is an important retention factor (e.g. Guevara-Escobar et al., 2007). Soil properties are only to a certain extent dependent solely on abiotic factors. The soil structure, the number of macropores and the number and orientation of preferential flow paths in the soil (along the roots for example) are influenced by plants (Dekker et al., 2007; Dijk and Keenan, 2007). Soil infiltration capacity is lowered by both chemical and physical aspects changing soil pH, hydrophobic properties of the soil, soil microbiological communities, soil mechanical properties such as soil compaction and surface sealing etc. (Scherrer et al., 2007; Bens et al., 2007). Infiltration capacity depends also on the soil surface moisture. Although relations between dryness of different kinds of soils and water infiltration are not well understood, most studies indicate that infiltration decreases with increasing dryness of the soil (e.g. Doerr and Thomas, 2000). Soil repellence (hydrophobicity) may be also changed by fires due to volatilization and condensation of hydrophobic substances during soil heating (e.g. DeBano, 2000; Martin and Moody, 2001). Reduced infiltration and soil water holding capacity lead to increased water runoff and erosion (Bruijnzeel, 2004; van Dijk and Keenan, 2007).

6.3 Vegetation in hydrological cycle under elevated CO_2 concentrations

Photosynthesis is not saturated under current CO_2 concentrations. Therefore it is demanding to investigate plants' response to the increasing concentrations of CO_2. Although the original concept of more intense growth of plants with increasing CO_2 supply is likely to be limited in natural mature ecosystems due to other environmental constraints – space, light, nutrients etc. (Körner et al., 2005), increased CO_2 concentrations may still result in overall changes in plant physiological processes with some large scale consequences. Körner (2006) in his review of plant CO_2 responses warned against overstating the beneficial effects of a CO_2-rich world for plant growth. Under natural conditions, in which plant growth is coupled to the nutrient cycle, and particularly those in which plants have reached a steady-state canopy development, the impact of elevated CO_2 on standing crop biomass is much smaller (often zero) than expected from field experiments (Körner, 2006) because of simultaneous resource and space limitations. Whereas young intensively growing stands function as temporary sinks of carbon, mature ecosystems have usually balanced CO_2 budget (Körner, 2006). Only those ecosystems where accumulation of biomass exceeds biomass decomposition, such as undisturbed peatlands, may serve as longterm carbon sinks, actively decreasing CO_2 concentration in the air (e.g. Turetsky et al., 2002). Although the responses to elevated CO_2 do not seem to be vegetation type specific, as Poorter and Pérez-Soba (2001) found no systematic difference in response between herbaceous and woody species while studying a whole range of environmental constraints, they are markedly species specific (Keel et al., 2007) and thus the behaviour of one species cannot be applied to plants in general.

As CO_2 uptake is through stomatal conductance related to water use of plants, we have to ask first of all, what changes in gas exchange can be expected with elevated concentration of CO_2. There has been evidence gathered that stomatal conductance is lowered by rising CO_2 concentrations in the air by adjusting stomatal apertures and/or decreasing stomatal density (Miyazawa et al., 2006; Medlyn et al., 2001; Ainsworth and Long, 2005). Extensive studies of many species showed that stomatal density decreases with increasing CO_2 concentration (Woodward, 1987; Woodward and Kelly, 1995). Consequently, predictions have been made that in the future lowered stomatal conductance will result in decreased conductance of water vapour, improved plant water status, altered seasonal evapotranspiration dynamics, and periodic increases in soil water content (Pospíšilová and Čatský, 1999; Morgan et al., 2004; Gedney et al., 2006; Bernacchi et al., 2007; Keel et al., 2007), especially in plant systems with high stomatal control over transpiration. Although other studies found no significant (e.g. Curtis and Wang, 1998) or less significant than expected (Keel et al., 2007) CO_2 effect on stomatal conductance, it seems that higher CO_2 concentration could have a significant impact on water balance in ecosystems, especially in those limited by low water supply. Based on these assumptions Gedney et al. (2006) and Betts (2007) concluded that down regulation of transpiration as a consequence of decreased stomatal conductance would have a large-scale impact on landscape hydrology. Gedney et al. (2006) using mechanistic land surface model stated that global runoff of water from vegetated lands (i.e. the difference between precipitation and evapotranspiration) has increased by 6 % over the twentieth century as a result of reduced plant transpiration, despite a decreasing trend in precipitation. The authors thus suggested that freshwater resources may be less limited than previously proposed under the scenarios of future global warming.

However, recent results gained for *Arabidopsis* have shown that stomatal density changes also according to the water status of plants under increased CO_2 concentration. Lake and Woodward (2008) showed that stomatal density of new leaves was determined by transpiration rate and ABA concentration in mature leaves. The mechanism by which transpiration rate of grown up leaves changes the stomatal density of developing leaves is not known. However, it is obvious that changes in stomatal density as a consequence of high CO_2 concentrations are dependent also on air humidity, indicating that in this process water status might be an environmental factor more influential than CO_2 concentration. Moreover, water scarcity may lead to non-linear changes in stomata density. Xu and Zhou (2008) showed that stomatal density in leaves of a perennial grass, *Leymus chinensis*, increased with decreasing water potential under moderate water deficit but declined under severe drought. Simultaneously stomatal size decreased with increasing water stress. There is also little available information on the combined effects of temperature and CO_2 enrichment on stomata anatomical characteristics of plants. Studying rose leaves (*Rosa hybrida*) under elevated CO_2 concentrations, Pandey et al. (2007) observed significant increases in stomatal density in plants grown at high temperature. These results indicated that also temperature may, at least in some cases, represent a more important factor in terms of stomatal density and anatomy than the increased CO_2 concentration. As follows from the above we still do not understand well enough the relationship between stomatal density, air CO_2 concentration and water status of plants.

In my opinion, our knowledge is far from sufficient to predict implications of plant responses to increased CO_2 concentration for water cycle. There are several reasons why we have to be cautious when making these predictions. First, plants are integrated within a system, which is limited by a myriad of relations and plenty of feedback, which all influence plants' physiology and it is difficult to determine the behaviour of the whole ecosystem when one of the variables changes. Second, in most places on the Earth water is already limited to the extent that plants have to regulate its release and therefore I don't think the down regulation due to CO_2 concentration could make much difference. Third, plants that have sufficient water supply would most likely use this luxury for cooling down, especially if the temperatures were to rise, to defend themselves against negative impacts of overheating. Though also this tendency is definitely species specific, this type of behaviour may be nicely documented in some wetland plants, which do not regulate their transpiration rate even under high irradiance and VPD (Rejšková et al., subm.; see attachement). Moreover, some recent research in mature tall trees has indicated that these trees are not limited by carbon supply (Körner, 2003b). This would mean that stomatal conductance and hence the transpiration flux might, in this case already under existing conditions, be regulated preferentially by other feedbacks than CO_2 demand.

6.4 Do we want the landscape to evaporate?

YES, with a but… as is common in all living systems. I have tried to gather evidence showing that plants play a crucial role in influencing the Earth's surface temperature. Vegetation has a substantial impact on the energy fluxes via regulating consumption and release of energy in evaporation and condensation processes thereby mitigating temperature extremes. BUT only if it is sufficiently supplied with water and, as it seems, only when the landscape is suitably structured so that the loss of water vapour from it is minimized. The evaporated water serves the region only if the structure of local vegetation and morphology of the region allow that. If the conditions are not suitable, most of the evaporated water is lost from the area and the high evapotranspiration rate may be seen as a process whose impact on catchment hydrology is rather negative. Thus in prevailing parts of habitats in our cultural landscape increased evapotranspiration per se cannot be seen as an indicator of well functioning local water cycle and it always needs to be judged in the context of landscape context as a whole.

The importance of canopy arrangement for whole-canopy water use has been acknowledged in agroforestry. Agroforestry is an integrated approach using the interactive benefits from combining trees and shrubs with crops and/or livestock. Shading crops by trees can help reduce soil evaporation and improve micro-climate around crops including radiation, humidity and temperature (Wallace, 2000). Fernández et al. (2008) showed that roots of *Ponderosa* pines and grasses behaved complementarily while using water resources in the soil. Their roots tend to occupy different areas of soil. The roots of pines extracted more water from the deeper soil layers than the same trees growing in a monoculture. The authors suggested also soil water redistribution via the tree roots, which improved moisture availability for grass. Suitable choice of crop and tree species for agroforestry is likely to enhance water use efficiency of the crop (Wallace, 2000) provided there is no competition for water between crops and trees. Although direct shading of crops by trees (agroforestry) may usually be beneficial only in areas where high energy input is common, in other parts of the world, such as Central Europe, water, energy and nutrient cycling may be improved by suitable arrangement of shelterbelts in farmland (e.g. Ryszkovski and Kedziora, 1987; 2007).

We still know very little about what kind of landscape organisation would be suitable to support the necessary processes. Nor do we know what scale is required for these processes to be able to occur. Moreover, even if we knew, we are seriously limited by population needs resulting in pressure on water reserves, especially in some, rather numerous, areas. However, there are still places where water is abundant at least during some parts of the year and landscape management could be much improved. Therefore searching for details in answering our questions is worth the effort. I am convinced that the Czech Republic and Central Europe fall within this category and I will therefore focus on the topic from the point of view of the local landscape.

Land use changes have led to decreased water retention in our landscape, and consequently the total amount of water present in the landscape has decreased (Kedziora and Olejnik, 2002). As has already been mentioned, ecosystems with more balanced temperature dynamics are thought to be less sensitive to disturbances than areas of high temperature amplitudes (Ripl et al., 2004). More balanced temperature dynamics is closely connected to balanced water supply as sufficient soil moisture is the most important condition for evapotranspiration. The conclusions presented in the foregoing chapters seems to suggest that vegetation with closed canopy is capable of conserving water. Also, at least under some conditions, it seems that vegetation may enhance convective precipitation by enriching the atmosphere by water vapour and influencing atmosphere stability and air movement (e.g. Foley, 2003; Bisselink and Dolman, 2009). According to Ripl (2003), a functioning landscape must meet three principles: cleaning water through evaporation (distilation) processes, using latent heat of water for determining the microclimate of habitats and sealing the landscape against matter losses through groundwater flow. In a functioning landscape components are structured in matter and heat chains, i.e. precipitation has to occur close to the evapotranspiration source (Ryszkowski and Kedziora, 2008). Although we still lack a lot of important information to be able to understand all the processes occuring in our landscape, we know enough to assume that our landscape would greatly benefit from water being more abundant. Regardless of reduced oxidation, CO_2 release and nutrient losses from the soil connected to the increased soil moisture content and reduced soil temperature, sufficient water supply would likely lead to more balanced temperature and humidity relations at least near the surface in the vegetation canopy. Vegetation maintains soil moisture more stable as it takes water from the deeper soil layers (Kedziora and Olejnik, 2002). Moreover, the evapotranspiration rate above vegetation can be lowered compared to ET above bare soil because of the decreased VPD above the plant canopy as a result of intensive cooling (Kedziora and Olejnik, 2002). Increased humidity of the air as a consequence of high transpiration from vegetation can support forming of radiation fog as described in chapter 2.2.1.1, which may improve the local water budget.

So, what shall we do? First of all, we should try to locally retain water within the landscape where and when possible to save it for warm and dry periods. The majority of natural gains to streamflow during low-flow periods is derived from releases from groundwater storage (Smakhtin, 2001). Therefore we should support water infiltration, a process tightly connected with vegetation (e.g. Scheffer et al., 2005; Dekker et al., 2007; Ryszkowski and Kedziora, 2008). Gains to low flows can be, however, also derived from the near surface storages where water is concentrated during and soon after precipitation events, such as more permanently wetted channel bank soils, alluvial valley fills and wetland areas. Also lakes and fishponds, which have direct hydraulic connection to streams and rivers may enhance low flows (Smakhtin, 2001). The ratio of water stored in the soil to water in the pond depends on the pond size, the smaller the pond the higher the ratio (Kedziora and Olejnik, 2002). Moreover, slowing down the surface run-off in surface water storages, shelterbelts, meadow strips, bushes etc. counteracts soil erosion, matter and nutrient losses (Kedziora and Olejnik, 2002). Therefore, although hydrology of catchments depends a lot on local geology, it is obvious that it may be improved through supporting vegetation and near surface water storages.

Agricultural activity dominates the use of freshwater and accounts for some 70 % of withdrawals from water resources globally (Morison et al., 2008). Therefore recent efforts have been focused on improving crop water use efficiency by adjusting crops to capture more of the water supply, exchange transpired water for CO_2 more effectively in producing biomass and convert more of the biomass into grain or other harvestable product (Passioura, 2004). Improved dehydration avoidance through breeding for earlier development, smaller leaves, and deeper roots seems to be more promising than improving dehydration tolerance (Morison et al., 2008). In any case, the breeding activities are directed to produce new varieties with improved water use efficiency. In other words we aim at making the landscape produce as much as possible while evapotranspiring as little as possible. This effort raises many questions in the context discussed. I will mention just some of them. First of all, could ecosystems with minimum transpiration really function similarly to those with high transpiration? In other words, is transpiration of plants actually essential for establishing plant communities of long-term high stability, variability and productivity? And should the highly evaporating plants and trees be really seen merely as water wasting? Are we not suppressing some life important functions of vegetation as defined for example in Lovelock's Gaia theory? To sum it up, is it right to regard transpiration as an inevitable evil? And are the artificial agriculture ecosystems with minimized evapotranspiration not actually malfunctioning in terms of landscape ecological functions?

Searching for answers to these questions we encounter practical problems. However, many problems ranging from local to regional may still be addressed by wise land-use management (Andrews, 2006) and that is what we strive for. Whereever possible we should try to shift our landscape or at least some parts of it to a community-based diversity of organisms producing sustainable structures by minimizing losses through closing matter cycles as the ecosystems dominated by r-strategists (pioneer organisms with high reproduction rate) are easily exhausted (Odum, 1983). In addition to all already mentioned principles, it seems that it is also the variability of landscape, which impacts its functioning and stability. According to Kedziora and Olejnik (2002) landscape with a more mosaic structure has a higher degree of landscape resistance, also because it has a higher total water income due to internal recycling. According to Kedziora and Olejnik (2002) the best way to improve landscape structure is the introduction of shelterbelts, strips or meadows and hedges, building of small ponds, and maintenance of wetlands and riparian ecosystems, i.e. filling the farmland with ecotones and small water storages. This landscape arrangement creates conditions in which plants can use solar energy with great efficiency and by doing so to improve local and regional climate.

7. Conclusions

Both the practical and the theoretical parts of my thesis show that plants possess structural adaptations and physiological mechanisms, which to a certain extent provide for thermoregulation. In my research I have shown that plants are capable of increasing or decreasing their temperature compared to the temperature of the ambient air in a measurable way. The temperature adjustment of plants is not as effective as that of animals, however, it may still be actively regulated in response to the existing conditions. Moreover, plants have a potential to regulate temperature of their surroundings thereby adapting the environment for other living organisms. The mechanisms of solar energy use in plants for warming up and cooling down are thus very important for ecosystem functioning. The consequences of these processes for organ, plant and ecosystems at all levels ranging from local to global, are discussed in the text.

It is important to note that vegetation presence or absence as well as change of one vegetation type for another may result in major changes of energy fluxes on the Earth's surface. These changes are by an order or even two orders of magnitude larger than the average changes considered a long-term consequence of increasing greenhouse gases concentration and other human caused changes in the atmosphere (IPCC, 2007). The energy flux changes caused by changes in land use are dynamic and fluctuate in time and space. Applying average values to these immensely important processes distorts the assessment of their impact on ecosystem and landscape functioning, resulting in a critical information loss with major consequences for the very interpretation of our findings. Processes in the biosphere are interconnected through many relations and various feedback. By regulating energy dissipation in time and space, vegetation substantially influences the existing surface temperature. Also water fluxes between land, ocean and the atmosphere are largely influenced by vegetation, its structure and other characteristics.

As the vegetation-mediated processes are closely connected to landscape management, adverse changes in energy and water fluxes are often predominantly caused by overexploitation of ecosystems rather than by climate change *sensu stricto*. Consequently, landscape drainage, deterioration of vegetation due to agricultural practices or soil erosion activities may lead to changes in temperature and hydrology with possible consequences for the environment on all scales. It is thus likely that humankind influences energy and water fluxes on the Earth's surface to a larger extent than has been acknowledged so far.

Although the ability to warm up may represent an important advantage for some plants growing in cold climates in terms of water and energy functioning of ecosystems within the climate system of the Earth, it is plants' ability to cool down via transpiration that is more important. We may regard vegetation in general as a system of individual components, which as a whole uses the incoming solar energy in an optimum way for cooling down to temperatures favourable for living processes. The process is, however, limited by water availability and different plants use different strategies to survive non-optimum proportion of incoming solar energy and water. When plants using large amounts of water for transpiration cooling are exposed to too dry and hot conditions, they are replaced by other plants. In natural ecosystems plants with different water demands are distributed in an optimum manner to use accessible water and energy resources effectively. However, it is a complicated task to determine what this means and to what extent plants are predetermined by the environmental conditions and to what extent plants may create their own environment. The debate challenges some basic concepts in biology as it questions the functioning of plants solely as individual competitors in the process of natural selection. A functioning mature ecosystem cannot be seen only as a sum of individuals. It represents a superorganism of a kind. In terms of environment functioning, vegetation has to be regarded as a holistic system. Physiological characteristics of individual plants do not provide information on the functioning of the whole ecosystem. In this context it is imperative that the selection process be studied on a larger than individual scale.

Processes within the biosphere vary in response to daily, seasonal and long-term changes. Everything in nature is striving for balance between and among all processes involved. Plants - due to their adaptivity and regeneration capacity – are very effective at striking balance. They can grow in a broad spectrum of environmental conditions. In our consideration of their role in the climate system of the Earth we must take into account that in different places plants have to be adapted to different conditions and we have to assess their functions locally.

It is obvious that our planet is influenced by humankind in such a manner that it is to date neither wise nor possible to rely exclusively on nature’s powers. Vegetation is no more distributed in an optimized manner according to nature’s laws; it is to a large extent distributed according to the human management practices. To be able to manage the cultural landscape effectively and in the long run we have to respect the principles essential for ecosystem functioning. Knowledge of plant physiological processes involved in energy and water fluxes in the biosphere is thus essential but so far often lacking. Many fundamental questions which would help us understand and manage the energetic and hydrological conditions of the landscape holistically and prevent it from the changing climate still remain unanswered. As a consequence erroneous political decisions may be made concerning global warming and water conservation strategies, especially when regulation is in the hands of politicians lacking the basic knowledge of landscape functioning. It seems that the role of vegetation and the whole biosphere for existing Earth energy budget is still largely underestimated.

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9. List of published and submitted papers

1. **Rejšková A.**, Pokorný J., Brom J., Korečko J., in press. Temperature distribution in flowers and inflorescences of vernal species measured by Infrared camera. Flora, 2010. *
2. Pokorný J., **Rejšková A.**, 2008. Water cycle management. In: Jorgensen S.E. and Fath B.D. (Eds.), Ecological Engineering, Encyclopedia of Ecology Vol. 5, Oxford, Elsevier. *
3. **Rejšková A.**, Patková L., Stodůlková E., Lipavská H., 2007. The effect of abiotic stresses on carbohydrate status of olive shoots (*Olea europaea* L.) under in vitro conditions. Journal of Plant Physiology 164, 174-184.
4. Pokorný J., **Rejšková A.**, Brom J., 2007. The role of macrophytes in the energy balance of wetlands. Bulletin of the Czech Botanical Society, Prague, Series 42 (22), 47-60. In Czech.
5. **Rejšková A.**, Čížková, H., Brom, J., Pokorný, J., submitted to Wetlands. Transpiration, evapotranspiration and energy fluxes in a temperate wetland dominated by *Phalaris arundinacea* under hot summer conditions. *
6. Brom J., Procházka J., **Rejšková A.**, accepted with minor changes in Soil and Water Research. Evaluation of functional properties of various types of vegetation using remotely sensed data analysis. *

* papers are presented in the attachment in full, other texts are presented as abstracts only. Czech translations of the abstracts are attached at the very end.

Třeboň, 10. 6. 2009

Prohlášení školitele o rozsahu podílu studenta na publikační činnosti

Prohlašuji, že Mgr. Alžběta Rejšková se podílela na společných publikacích přibližně v níže uvedeném rozsahu.

1. **Rejšková A.**, Pokorný J., Brom J., Korečko J., in press. Temperature distribution in flowers and inflorescences of vernal species measured by Infrared camera. Flora, 2010 **60%**
2. Pokorný J., **Rejšková A.**, 2008. Water cycle management. In: Jorgensen S.E. and Fath B.D. (Eds.), Ecological Engineering, Encyclopedia of Ecology Vol. 5, Oxford, Elsevier. **40%**
3. **Rejšková A.**, Patková L., Stodůlková E., Lipavská H., 2007. The effect of abiotic stresses on carbohydrate status of olive shoots (*Olea europaea* L.) under in vitro conditions. Journal of Plant Physiology 164, 174-184. **50%**
4. Pokorný J., **Rejšková A.**, Brom J., 2007. The role of macrophytes in the energy balance of wetlands. Bulletin of the Czech Botanical Society, Prague, Series 42 (22), 47-60. In Czech. **30%**
5. **Rejšková A.**, Čížková, H., Brom, J., Pokorný, J., submitted to Wetlands. Transpiration, evapotranspiration and energy fluxes in a temperate wetland dominated by *Phalaris arundinacea* under hot summer conditions. **40%**
6. Brom J., Procházka J., **Rejšková A.**, accepted with minor changes in Soil and Water Research. Evaluation of functional properties of various types of vegetation using remotely sensed data analysis. **10%**

Doc. RNDr. Jan Pokorný, CSc.

Následující pasáž obsahuje utajované skutečnosti (publikace podléhající autorským právům) a je obsažena pouze v archivovaném originále disertační práce uloženém na UFB JU. Publikace jsou zde uvedeny pouze ve formě abstraktů.

Rejšková A., Pokorný J., Brom J., Korečko J., 2010. Temperature distribution in flowers and inflorescences of vernal species measured by Infrared camera./ Distribuce teplot v květech a květenstvích jarních druhů stanovená termovizní kamerou. Flora 205(5), in press.

Abstract

Temperature is a limiting factor for plant reproduction under harsh conditions. Using an infrared camera, we studied temperature distribution in three early flowering light-coloured species of markedly different morphology. The influence of three environmental factors (temperature of the ambient air, temperature of the ground and irradiance) on the temperature of the flowers and inflorescences was evaluated. White petals and yellow centres of sun tracking *Anemone nemorosa* (*Ranunculaceae*) were shown to be on average 1.6 °C and 3.4 °C warmer than the ambient air respectively. The surface temperature of the sun lit yellow discs of *Bellis perennis* (*Asteraceae*) was on average 7.4 °C warmer than the ambient air. Direct solar light was found to be responsible for large temperature differences between the discs and the marginal ray flowers. Bell-shaped white flowers of *Galanthus nivalis* (*Amaryllidaceae*) bent to the ground were on average 2.7 °C cooler than the surrounding air. The temperature relations of the different reproductive organs to the studied environmental factors are discussed. Temperature behaviour of the studied low land species is compared with the results previously gained for alpine and arctic species by other authors. Ecological importance of our conclusions is considered.

Abstrakt

Teplota je limitujícím faktorem pro rozmnožování rostlin. Pomocí termovizní kamery jsme měřili distribuci teplot ve třech raně kvetoucích druzích rostlin se světlými květy (květenstvími) a výrazně odlišnou morfologií reprodukčních orgánů. Hodnotili jsme vliv teploty vzduchu, teploty země a intenzity záření na teplotu květů (květenství). Bílé okvětní plátky a žluté středy *Anemone nemorosa* (*Ranunculaceae*) byly o 1.6 a 3.4 °C teplejší než vzduch. Povrchová teplota osluněných terčů *Bellis perennis* (*Asteraceae*) byla v průměru o 7.4 °C vyšší než teplota vzduchu. Zvonkovité květy sněženek, *Galanthus nivalis* (*Amaryllidaceae*) směřující k zemi byly v půměru o 2.7 °C chladnější než okolní vzduch. V článku se zabýváme teplotou reprodukčních orgánů rostlin ve vztahu k faktorům prostředí. Výsledky získané pro nížinné druhy

jsou srovnány s výsledky jiných autorů, které byly měřené v alpinských a arktických oblastech na jiných ale morfologicky podobných druzích.

Pokorný J., Rejšková A., 2008. Water cycle management./ Management koloběhu vody. In: Jorgensen S.E. and Fath B.D. (Eds.), Ecological Engineering, Encyclopedia of Ecology Vol. 5, Oxford, Elsevier.

Publikace neobsahuje abstrakt.

Rejšková A., Patková L., Stodůlková E., Lipavská H., 2007. The effect of abiotic stresses on carbohydrate status of olive shoots (*Olea europaea* L.) under in vitro conditions. Journal of Plant Physiology 164, 174-184.

Summary

Olive plants produce both sucrose and mannitol as major photosynthetic products. Contrary to previously studied celery [Vítová et al., Mannitol utilisation by celery (Apium graveolens) plants grown under different conditions in vitro. Plant Sci 2002; 163: 907–16], in vitro these carbohydrates were found to be able to sustain growth of olive shoots roughly to the same extent at all tested concentrations (1–9% w/v). We studied the involvement of the particular components of the endogenous carbohydrate spectrum in response to different abiotic stresses (osmotic stress, salinity, low temperature) in vitro. Salinity (100 mM NaCl) caused a decrease of total soluble carbohydrates, while an increase was observed during low-temperature treatment (0 and 4 1C). Mannitol accumulated primarily under salinity (up to 40% of total soluble carbohydrates compared to 10–20% in controls). Only a small (two-fold) increase of proline content in salinity stressed plants indicates proline does not play a significant role in olive stress response. Low temperature led to an increase of the raffinose family oligosaccharides (RFO) proportion in total carbohydrates. We conclude that olive plants exploit the high diversity of the carbohydrate spectrum in
specific response to different stresses.

Abstrakt

Oliva produkuje jako hlavní fotosyntetické produkty sacharózu a manitol. Na rozdíl od celeru in vitro pěstované olivy byly schopné růst na všech testovaných koncentracích těchto sacharidů (1-9 % w/v) srovnatelně. Studovali jsme úlohu jednotlivých složek endogenního sacharidového spektra v závislosti na různých abiotických stresech (osmotický stres, zasolení, nízká teplota) v podmínkách in vitro. Zasolení (100 mM NaCl) způsobilo pokles koncentrace celkových rozpustných sacharidů. Naopak při snížení teploty (0 a 4 °C) jsme pozorovali vzestup celkových rozpustných sacharidů. Manitol se hromadil zejména při zvýšené salinitě. Malý nárůst koncentrace prolinu v rostlinách stresovaných zvýšenou koncentrací solí naznačuje, že prolin nehraje výraznou roli ve stresové odpovědi oliv. Snížení teploty vedlo k navýšení zastoupení oligosacharidů rafinózového typu (RFO) v celkovém množství

sacharidů. Z našich pokusů vyplývá, že oliva využívá širokého spektra sacharidů specificky v odpovědi na různé druhy stresu.

Pokorný J., Rejšková A., Brom J., 2007. The role of macrophytes in the energy balance of wetlands./ Úloha makrofyt v energetické bilanci mokřadů. Bulletin of the Czech Botanical Society, Prague, Series 42 (22), 47-60. In Czech.

Abstract

Wetlands as ecosystems with sufficient water supply play an important role in the energy budget of a landscape due to their capability of shifting energy fluxes in favour of latent heat. Common rates of evapotranspiration in wetlands as high as 6–15 mm indicate that large amounts of energy are dissipated through this process. Wetland macrophytes substantially influence solar energy distribution by their high transpiration rate. Wetland ecosystems are also characterised by high primary production showing a relatively high efficiency in the use of solar energy in photosynthesis. Accumulation of biomass is however high only in wetlands with low decomposition, such as in marshes and peat bogs. An overview of methods to measure primary production and transpiration and evapotranspiration rates is presented. An example of energy fluxes in the course of a day in the wetland habitat Mokré Louky near Tøeboòisshown.Negativecon-sequences of losing wetlands for local and regional climates are discussed.

Abstrakt

Mokřady- jako ekosystémy dobře zásobené vodou- jsou významné pro energetickou bilanci krajiny, protože jsou schopné disipovat velké množství sluneční energie pomocí latentního toku výparu. Běžná rychlost evapotranspirace v mokřadech je 6-15 mm za den. Mokřadní rostliny ovlivňují výrazně vysokou transpirací distribuci sluneční energie v mokřadech. Mokřady jsou charakterizovány také vysokou primární produkcí, která je znakem relativně vysoké účinnosti využití sluneční energie v procesech fotosyntézy. Hromadění biomasy je nicméně značné pouze v mokřadech s nízkou mírou dekompozice jako jsou rašeliniště. V článku je uveden přehled metod pro měření transpirace a evapotranspirace a stanovení primární produkce. Uvádíme rovněž příklad denního průběhu toků energie na Mokrých Loukách u Třeboně. V závěru se zabýváme negativními dopady ztráty mokřadů pro fungování lokálního a regionálního klimatu.

Rejšková A., Čížková, H., Brom, J., Pokorný, J., submitted to Wetlands. Transpiration, evapotranspiration and energy fluxes in a temperate wetland dominated by *Phalaris arundinacea* under hot summer conditions./ Transpirace, evapotranspirace a toky energie v mokřadu mírného pásma s převahou *Phalaris arundinacea* za letních horkých podmínek.

Abstract

Transpiration, evapotranspiration and evaporative fraction were measured in a temperate zone wetland dominated by *Phalaris arundinacea* L. under extremely high temperature and intense irradiation conditions. The IR camera recorded no temperature extremes within the stand, indicating that the stand was capable of regulating the overheating by transpiration. The transpiration rate of individual leaves (measured by the gas exchange method) was positively correlated with the water vapour pressure deficit of the air ($R^2 = 0.56$, df = 1. 60, $p < 0.001$) reaching values of up to 7.8 mmol m^{-2} s^{-1} of leaf area. Evapotranspiration of the stand reached values of 4.8 and 5.3 mm.day^{-1}on the 27th and 28th July 2005, respectively. The evaporative fraction showed that more than one-half of the available energy was consumed in the evapotranspiration processes. In the afternoon the influence of hot air advection was obvious. A strong cooling effect of the wetland was shown. The results support the idea that wetlands sufficiently supplied with water are important in the energy and water budget of drained cultural landscapes.

Abstrakt

Měřili jsme rychlost transpirace, evapotranspirace a evaporativní frakci v mokřadu mírného pásma s převahou *Phalaris arundinacea* L. za extrémně vysokých teplot a intenzivního záření. IR kamera nezaznamenala žádné teplotní extrémy v porostu, z čehož můžeme usoudit, že rostliny byly schopné regulovat přehřátí transpirací. Rychlost transpirace jednotlivých listů stanovená gazometricky pozitivně korelovala s deficitem vodní páry ve vzduchu ($R^2 = 0.56$, df = 1. 60, $p < 0.001$) a dosahovala až 7.8 mmol m^{-2} s^{-1} listové plochy. Rychlost evapotranspirace porostu dosáhla 27.7.2005 hodnot 4.8 mm.den^{-1} a 28.7.2005 hodnot 5.3 mm.den^{-1}. Evaporativní frakce ukázala, že více než polovina dostupné energie byla využita na výpar. Mokřad se intenzivně chladil. Výsledky výzkumu podpořily naši představu, že mokřady dostatečně zásobené vodou jsou z hlediska toků energie a vody v krajině velmi důležité.

Brom J., Procházka J., Rejšková A., accepted with minor changes in Soil and Water Research. Evaluation of functional properties of various types of vegetation using remotely sensed data analysis.

Abstact

Photosynthetic Dissipation of solar energy and consequently forming of the hydrological cycle are largely dependent on the structural and optical characteristics of the land surface. In our study we chose seven units with different types of vegetation in the Mlýnský and Horský catchments (South-Eastern part of the Šumava Mountains, Czech Republic) in order to assess the differences in their functioning expressed through surface temperature, humidity and energy dissipation. For our analyses we used Landsat 5 TM satellite data from June 25th 2008. The results showed that the microclimatic characteristics and energy fluxes varied in different units according to their vegetation characteristics. A cluster analysis of mean values was used to divide vegetation units into groups according to their functional characteristics. The mown meadows were characterised by the highest surface temperature and sensible heat flux and the lowest humidity and latent heat flux. On the contrary, the lowest surface temperature and sensible heat flux and the highest humidity and latent heat flux were found in the forest. Our results showed that the climatic and energetic features of the land surface are related to the type of vegetation. We state that the spatial distribution of different vegetation units and the amount of biomass are crucial variables influencing the functioning of landscape.

Abstrakt

Disipace sluneční energie a utváření vodního cyklu jsou do značné míry závislé na strukturních a optických vlastnostech zemského povrchu. Vybrali jsme sedm jednotek různého vegetačního krytu v malých povodích Mlýnského a Horského potoka (v severovýchodní části Šumavy) a studovali jsme rozdíly v jejich fungování pomocí povrchové teploty, vlhkosti a disipace energie. Pro své analýzy jsme použili data z družice Landsat 5 TM z 25.6.2008. Výsledky ukázaly, že mikroklimatické podmínky a toky energie se lišily v různých vegetačních jednotkách v závislosti na vlastnostech vegetace. Kosené louky měly nejvyšší povrchovou teplotu a tok zjevného tepla a nejnižší vlhkost a tok latentního tepla. Naproti tomu nejnižší teplota povrchu a nejmenší tok zjevného tepla a nejvyšší vlhkost společně s největším tokem

latentního tepla byly naměřeny pro les. Naše výsledky ukázaly, že klimatické a energetické vlastnosti povrchu jsou závislé na typu vegetace a že rozmístění vegetace a množství biomasy jsou důležité faktory pro fungování krajiny.

FLORA

Plant Morphology, Distribution
and Functional Ecology

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Düsseldorf, 06.05.2009

Notification of acceptance

Dear Dr. Rejšková and coll.,

Herewith is confirmed that the paper

REJŠKOVÁ, A., BROM, J., POKORNÝ, J., KOREČKO J.

Temperature distribution in white flowers and inflorescences of early spring temperate species measured by Infrared camera.

approx. 11 pages

is accepted for publication in „Flora“. Formal date of acceptance is **3 May 2009.**

It is scheduled to appear printed in **Flora vol. 205, issue 5 (May 2010).**

signed:

Prof. Dr. Rainer Lösch, editor-in-chief