2.1

Thermal Balance of Plants

Formation of ice on the branches of beech. Formation of ice crystals is due to freezing of super-cooled water from clouds onto the surface of the vegetation. The "ice beard" grows against the direction of the wind (hoar frost) and can reach such a volume that the crown of the tree may break (ice damage). In contrast to this, rime is composed of ice crystals which are formed from vapour. Solling IBP Beech-area B1. Photograph E.-D. Schulze

Recommended Literature

The most comprehensive book on whole plant ecology was by Lange, Nobel, Osmond and Ziegler in the Encyclopaedia of Plant Physiology, Part Physiological Plant Ecology, vols. 12 A–D (Springer, 1982). Despite being published 20 years ago it is still a landmark in providing understanding of whole plant ecology. The textbook by W. Larcher *Ecophysiology of Plants* (Springer 4th ed. 2003) and Lambers and Chapin: *Plant Physiological Ecology* (Springer, 1998) are recommended for further reading.

The thermal relations of plants deal with the balance of radiation energy. Only slightly more than 1% of the incident solar energy is used for photosynthetic metabolism. The remainder of the energy (about 700–1000 $W\,m^{-2}$ at full sun light near the ground) has to be released again because the plant is fixed at the site and absorbs short-wave radiation dependent on its **albedo** (reflectivity). The energy balance can only be regulated by release of heat to the surrounding air (**sensible heat**) or by evaporation of water (**latent heat**). The flow of heat into the soil is too slow to regulate the thermal balance in a leaf or plant organ, with rapidly changing incident radiation. The **temperature of organs** (particularly of leaves and flowers) or the **temperature of surfaces** (stems, flowers) results from the energy balance. The temperature must be kept within certain physiological limits, to avoid damage, and energy balance must be regulated by the plant in such a way that damaging temperatures do not occur, even for short periods. Moreover, the temperature should rather be within the range of the physiological optimum of metabolic processes, which could be above or below the general temperature of the habitat. Plants are able to influence their organ temperatures over a wide range. For example, in the inflorescences of the Araceae, temperatures of ca. 17 K greater than the ambient air are produced via cyanide-resistant electron transport in respiration in order to entice pollinators. In arid climates leaf temperatures may be ca. 17 K below the ambient temperature because of evaporation, thus avoiding heat damage. The temperature of the plant thus is a result of the energy balance and is connected within a certain range to edaphic and climatic conditions.

In the following, the atmosphere and air layers near the ground will be considered as part of the habitat followed by the analysis of the energy balance of a leaf and its effects on plant responses. Ecophysiological responses of plants at extreme temperatures were discussed in Chapter 1.3.

Box 2.1.1 Atmospheric composition

Chemical composition of the lower atmosphere

78% N_2, 21% O_2, 0.6–4% H_2O, 0.03% CO_2, noble and trace gases of natural and anthropogenic origin.

Water vapour pressure: The maximum amount of water vapour that can be held by the atmosphere is termed saturation pressure (e_o), and which depends on temperature and pressure. The pressure of the atmosphere without water vapour, P_a, is derived from the measured pressure of the atmosphere, P, and the actual vapour pressure, e ($P_a = P - e$). At a constant air pressure the vapour pressure rises exponentially with a linear increase in temperature. For exact data on the composition of air, see List (1971).

Note: humid air is lighter than dry air, determined by the relationship between the molecular weights of H_2O and N_2, which is 0.62 (18/36). Hence, humid air in the lower atmosphere rises until it condenses on cooling, and forms fog or clouds. For the same reason, condensation forms on the ceilings of humid rooms or on the lids of Petri dishes.

The atmosphere is only rarely saturated with water vapour. The actual vapour pressure of the atmosphere (e) is generally lower than the saturation value (e_o). There are a number of terms that are used to describe the humidity of air (Fig. 2.1.1):

- **absolute vapour pressure:** $c_w = (2.17/T)\ e$, unit: g m^{-3} (Note: volume of air is temperature and pressure dependent);
- **relative humidity:** $H = e/e_o$, unit % (Note: at constant vapour pressure this is dependent on T);
- **water vapour saturation deficit of the atmosphere:** $D_a = (e_o - e)/p_a$, unit Pa Pa^{-1} (often shortened to VPD: vapour pressure deficit). Note: the value is independent of temperature and pressure;
- **water vapour saturation deficit between leaf and atmosphere:** $D_l = (e_{oL} - e)/p_a$, where e_{oL} is the vapour pressure deficit at leaf temperature and e the actual vapour pressure in the atmosphere; this term is important as it is the driving force for transpiration in plants (used to be abbreviated as WD: water vapour deficit);
- **dew point temperature °C:** T_d for $e = e_o$ (temperature, t, below which condensation temperature is reached and therefore condensation follows);
- **wet bulb temperature T_w:** This unit is used to measure the actual vapour pressure (psychrometer)

$$e = e_{o(Tw)} - \gamma(T_a - T_w)$$

where γ, the psychrometric constant, is 66.1 Pa K^{-1} for a ventilated thermometer at 100 kPa air pressure and 20 °C.

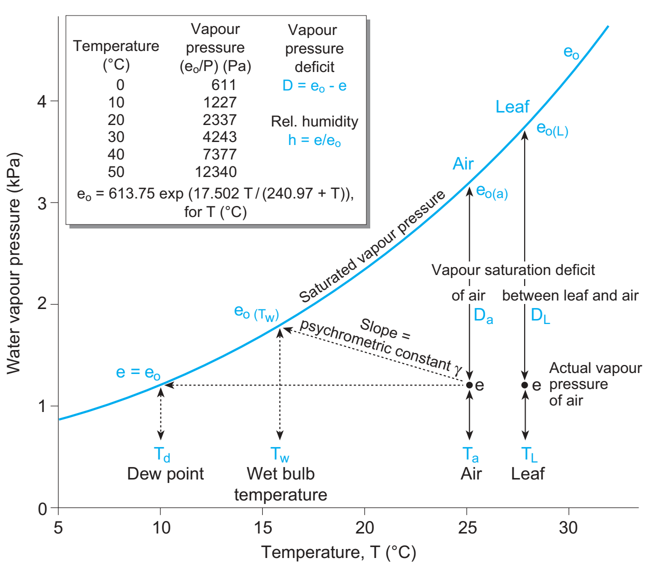

Fig. 2.1.1. Dependence of saturated vapour pressure, e_o, on temperature, T, and the graphical explanation of the various terms needed to define vapour pressure. T_a Air temperature; T_L leaf temperature; T_w wet bulb temperature; T_d dew point temperature; γ the psychrometric constant; *e* actual vapour pressure of the atmosphere; D_a saturation deficit of air; $e_{o(a)}$ saturation vapour pressure at leaf temperature, where e_o is calculated from $e_o = 613.75\ \exp(17.502\ T/(240.97+T))$, with T in °C

2.1.1

The Atmosphere as Habitat

The thermal balance of plants is closely connected to the chemical composition of and the physical transport processes in the atmosphere, which are part of the discipline of meteorology (textbooks: Lutgens and Tarbuck 2000; Wallace and Hobbs 1977). Variations in solar energy balance are responsible for the climatic conditions in the boundary layer near the ground, compared to the free atmosphere. Gregor Kraus (1911) was the first scientist to describe this phenomenon quantitatively on limestone sites near Würzburg, Germany, and thus founded a new discipline of micrometeorology (textbook: Jones 1994).

Water vapour, CO_2 and O_2 are the most important gases for the plant, independent of several other trace gases (ozone, nitric oxide, ammonia, methane and others) which influence the plant (see Chap. 1.9). Here, we discuss the energy balance in the context of water vapour and CO_2 in the atmosphere. Both gases are important for the existence and growth of plants.

Through the formation of clouds, **water vapour** influences

- absorption and reflection in the atmosphere and thus the solar radiation reaching the earth's surface;
- evaporation from the earth's surface as being dependent on the saturation deficit and on the plant cover;
- density of the atmosphere and the transport processes in it (formation of clouds) via the temperature dependence of saturation, which is the basis for precipitation.

Carbon dioxide influences

- the thermal balance of the lower atmosphere by absorption and radiation of long-wave radiation;
- photosynthesis, as it is the substrate for the process.

The interaction between the optical characteristics of the atmosphere and its constituent gases is explained in Fig. 2.1.2 A (Mitchell 1989; IPCC 1996). The solar radiation entering the earth's atmosphere occurs in the short-wave range at about 6000 K with maximum radiation at about 0.6 µm wavelength (visible light). Mean radiant energy at the upper limit of the atmosphere is 1370 W m^{-2} (**solar constant**, measured in the stratosphere). Because the earth is not flat, but a sphere, the mean radiation flux during the day, averaged over the illuminated hemisphere, is about 340 W m^{-2} (WBGU 1997). This radiation is balanced by the long-wave radiation (**thermal radiation**, I_1), which by itself is a balance between thermal radiation of the atmosphere and thermal radiation from the stratosphere which operates at a temperature of 255 K. Long-wave radiation follows the **Stefan-Boltzman** law:

$$I_1 = \sigma T^4, \qquad (2.1.2)$$

where $\sigma = 5.67 \times 10^{-8}$ (W m^{-2} K^{-4}), the Stefan-Boltzman constant, and T the temperature in Kelvin. Without an atmosphere, there would be no re-radiation from the atmosphere and thus the average temperature on earth would be −18 °C.

Atmospheric gases, particularly water vapour and CO_2, have the effect that part of the incoming solar radiation in the short-wave and near-IR range is absorbed and reflected (Fig. 2.1.2 B). In the atmosphere the short-wave solar radiation (UV radiation) is absorbed particularly by ozone. H_2O and CO_2 absorb in the near-IR, thus limiting the incoming radiation to a narrow **radiation window** with a maximum in the visible range. The incoming energy is balanced by emission of long-wave IR from the earth's surface; this is limited by water vapour and CO_2. There is only a narrow **emission window** between 8 and 14 µm wavelength in which the earth's surface absorbs or emits heat.

Reflection and absorption processes are additive in determining the **energy balance** of the earth (Fig. 2.1.2 C; Mitchell 1989). Short-wave radiation is absorbed in the molecules of the atmosphere and clouds and reflected. Some of the short-wave radiation is reflected from the earth's surface, dependent on the type of vegetation cover.

The thermal balance is determined by the sum of processes of reflection and absorption (Table 2.1.1). A distinction is made between the **radiation balance** and the **energy balance**. The radiation balance comprises the sum of short- and long-wave radiation fluxes and their reflection whilst the energy balance of radiation is the sum of all thermal fluxes and incorporates thermal transport, latent heat of evaporation and the fluxes of heat into the soil. The radiation balance is normally not at equilibrium (i.e. it differs from zero), but the energy balance must be zero as the sum of all processes.

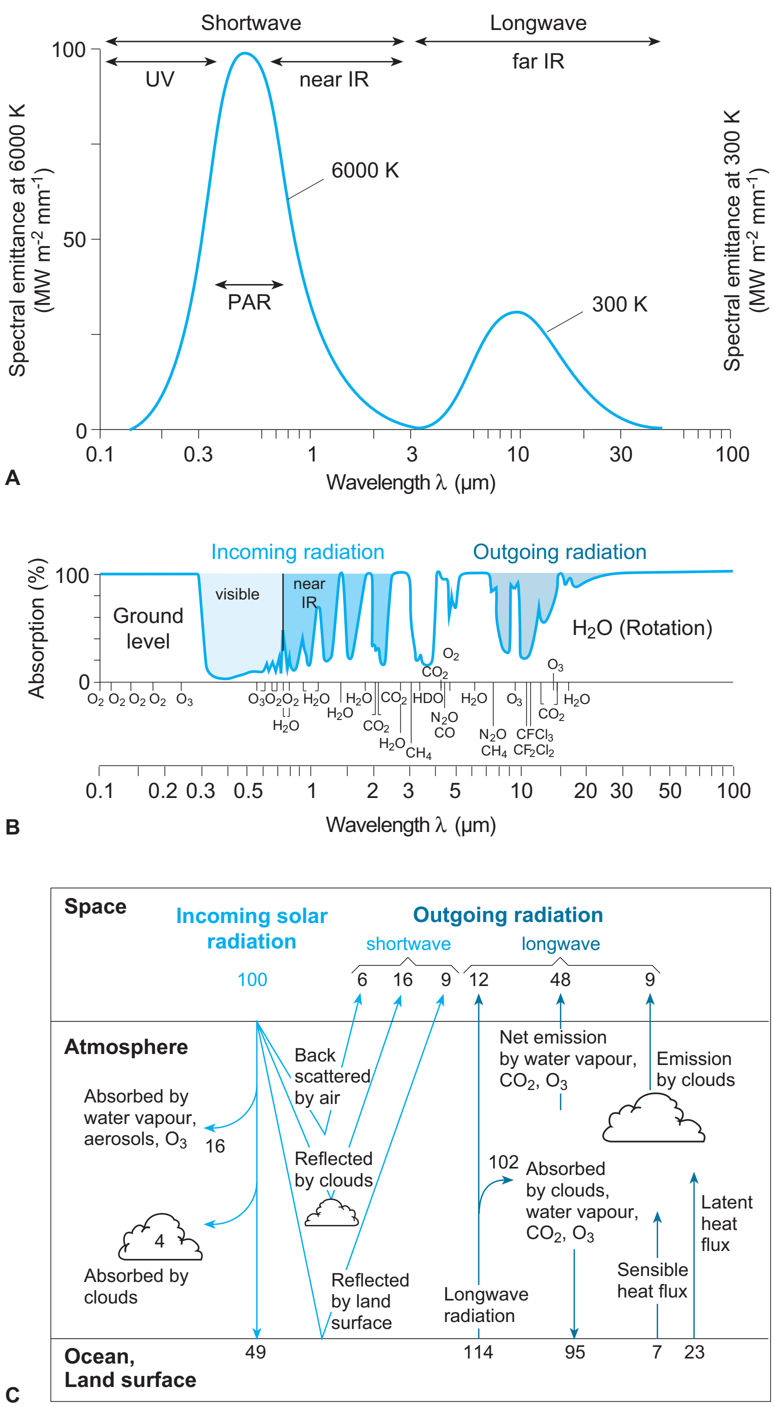

Fig. 2.1.2. Energy distribution and the incident radiation balance of the earth. A Spectral distribution of short wavelength incident solar radiation and the long wavelength heat radiation of the earth. B The spectral absorption of incident radiation by gases in the atmosphere. Note that ozone absorbs short wavelength radiation and CO_2 absorbs in the long wavelength range. In addition CO, N_2O and fluorochlorocarbons absorb incident radiation. C The transformation of incident radiation to heat radiation in the atmosphere. The percentages given are for the average global solar incident radiation of 342 W m^{-2}. (After Mitchell 1989; WBGU 1997)

Table 2.1.1. Energy balance[a] of the earth

Atmospheric radiation balance		**Turnover ($W\ m^{-2}$)**	**Relative contribution (%)**
Incident solar radiation (short-wave)	I_{sA}	+342	100
– reflection (short-wave)	$\rho_{sA}I_{sA}$	–106	–31
– of radiation	(–75 = 22%)		
– of aerosols and clouds	(–31 = 9%)		
– of the soil			
(= net radiation)			
– heat radiation	$\varepsilon_{lA}\ I_{lA}$	–236	–69
– of gases in the atmosphere	(–164 = 48%)		
– of clouds	(–31 = 9%)		
– of the soil to space	(–41 = 12%)		
Atmospheric radiation balance in the upper atmosphere	Q_{nA}	0	0
Radiation balance at the ground surface			
Incident solar radiation (short-wave)	I_{sA}	+342 100	
– reflection (short-wave)	$\rho_{sA}I_{sA}$	–106	–31
– of aerosols and clouds	(–75 = 22%)		
– of soil	(–31 = 9%)		
– absorption in the atmosphere		–68	–20
Short-wave radiation input to the ground surface		+168	+49
Long-wave radiation			
– heat loss by the ground surface	$\varepsilon_{lB}I_{lB}$	–390	–114
– heat re-radiation by clouds	$\varepsilon_{lA}I_{lA}$	+325	+95
Radiation balance of the ground surface	Q_{nB}	+103	+30
Energy losses of soils			
– conductance of sensible heat into the soil	H	–24	–7
– energy loss by vaporisation	λE	–79	–23
Energy balance of soil		0	0

[a] The energy conversion with reflection, absorption and long wavelength emission occurs in the atmosphere and at the ground surface. The solar constant (1370 $W\ m^{-2}$) is the amount of energy that arrives at a surface above the atmosphere vertical to the incident radiation from the sun. In contrast, the solar energy arriving at the earth's surface (342 $W\ m^{-2}$) is the average amount of energy falling on the half of the earth facing the sun. The parameters are equivalent to the transport equations given in the text

Generally, the net **radiation balance** of the earth (R_n; n = net) may be expressed in the following equation:

Radiation balance of the upper atmosphere (R_{nA})

$$R_{nA} = I_{sA} - \rho_{sA}I_{sA} - \varepsilon_{lA}I_{lA} \qquad (2.1.2)$$

radiation balance = incoming solar radiation – reflection – long-wave outgoing radiation

R_{nA} is the balance of radiation fluxes at the upper boundary of the atmosphere, I_{sA} the short-wave incoming solar radiation at the upper boundary of the atmosphere, ρ_{sA} the ability of the atmosphere (clouds, gases) and soil to reflect incoming solar radiation, ε_{sA} is the ability of the atmosphere to emit long-wave radiation and I_{lA} the long-wave emission of the atmosphere (clouds, gases) and soil.

The radiation balance near the soil may be expressed analogously. The radiation balance at the earth's ground surface (R_{nG}) is the sum of short-wave incoming and outgoing solar radiation.

$$R_{nG} = I_{sG} - \rho_{sA}I_{sG} + I_{lA} - \varepsilon_{lG}I_{lG} \qquad (2.1.3)$$

radiation balance = incoming short-wave radiation – reflection + incoming long-wave radiation – long-wave emission

The incoming short-wave radiation I_{sG} is called solar radiation. I_{sG}–$\rho_{sA}I_{sG}$ denotes the short-wave radiation balance measured by a radiometer with a glass dome and I_{lA}–$\varepsilon_{lG}I_{lG}$ is