

# 1 The Environment of Plants

In the distant geological past, the first plants evolved in environments consisting of water, air and rock. Later, soil systems, i.e., the pedosphere, formed with the assistance of microorganisms and animals and served as the principal substrate for plants to grow. Hydrosphere, atmosphere and pedosphere together constitute the *spatial environment* of plants. However, a plant's environment is determined also by all the physical and chemical factors characterizing habitats, and by the influences of other co-occurring organisms, which either favor or harm plant survival and success. *Environment*, thus, is the combination of all biotic and abiotic external conditions acting upon individual living organisms or a community of organisms (biocenosis) in their habitats (biotopes).

## 1.1 The Surroundings of Plants

### 1.1.1 The Atmosphere

The most sensitive region of the global environment is the atmosphere, a thin layer of air enveloping the earth (Fig. 1.1). The innermost layer of the

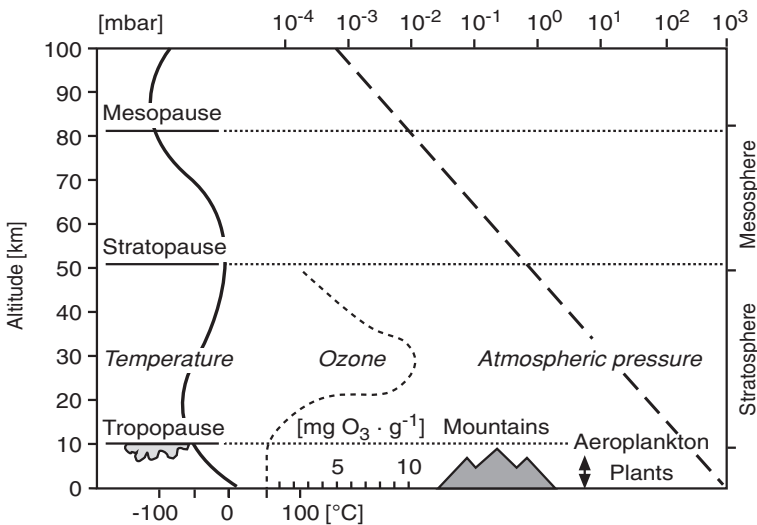


Fig. 1.1. Structure of the atmosphere. (After Häckel 1990)

atmosphere is the *troposphere*, i.e., the weather zone. In that layer, air pressure drops with increasing distance from the earth (decrease in air pressure:  $10\text{--}12\text{ Pa m}^{-1}$ ), for example, at an altitude of 5500 m it is only half that at sea level. Similarly, the air temperature also decreases until it reaches a minimum at the so-called tropopause, at altitudes ranging between 10 km (at mid-latitudes) and 18 km (over subtropical and equatorial regions). The extreme stability of the temperature inversion right above the tropopause prevents any air exchange between the troposphere and the *stratosphere*, the layer above the troposphere. Thus, all water vapor deriving from evaporation and other emitted gases and substances accumulate primarily in the troposphere. The stratosphere extends from 25–50 km altitude; in that layer, air pressure drops to less than one-tenth of the value at sea level. In this rarefied layer of the atmosphere, intense UV radiation induces the formation of ozone, which is a powerful absorber of ultraviolet radiation. It was only after the formation of this ozone filter that the lethal shortwave UV radiation reaching the earth dropped to low intensity levels allowing life on land.

The air enveloping the globe provides carbon dioxide for plants and oxygen for all living organisms. The primaeval atmosphere contained large quantities of carbon dioxide, ammonia and methane. Today, the air of the troposphere consists of 78 vol.% nitrogen, 21 vol.% oxygen, rare gases (0.95 vol.%), and carbon dioxide (0.035 vol.%). Other constituents of the troposphere are water vapor, trace gases such as methane, sulfur dioxide, halides, volatile nitrogen compounds, ozone and photooxidants, as well as aerosols, ash, dust and soot. Substances entering the atmosphere are dispersed rapidly over great distances; within a few weeks or even days, and emissions are transported across entire continents and oceans via air currents. Striking examples of long-distance airborne particle movements can be observed after severe volcanic eruptions.

The atmosphere contains roughly  $1200 \times 10^{12}$  t of oxygen, most of which has been formed by autotrophic organisms and has accumulated over aeons of time (see Fig. 2.1). Oxygen losses are continuously replaced by photosynthesis of phytoplankton in the oceans, and by terrestrial plants, mostly of forests. However, oxygen released by terrestrial ecosystems does not yield a long-term net gain in the global atmospheric oxygen budget, as most of the photosynthetically released oxygen is re-consumed in roughly the same amounts in the course of microbial breakdown of organic matter. The oxygen consumed by respiring living organisms and by combustion processes can only be replaced by the activity of phytoplankton. In aquatic environments, sinking organic detritus is largely decomposed by anaerobic processes, i.e., without the use of oxygen. The atmosphere contains  $720 \times 10^9$  t of carbon in the form of  $\text{CO}_2$ . In the lower atmosphere, the average concentration of carbon dioxide is at present  $350\text{ }\mu\text{l l}^{-1}$  (equivalent to 35 Pa partial pressure); however, the  $\text{CO}_2$  concentration is increasing continuously (see Box 2.3).

### 1.1.2 The Hydrosphere

The hydrosphere comprises the oceans, groundwater, inland waters, polar ice, and water in the atmosphere. The oceans cover 71% of the earth's surface and contain 74% of the world's total *water reserves*. These huge volumes of water store enormous quantities of energy and material thereby contributing significantly to the stability of geophysical and geochemical processes. The second largest reservoir of water is *groundwater* on the continents. However, only 1% of the groundwater is close enough to the surface to be accessed by plant roots; most of the water percolates to depths hundreds of meters below the surface. Surface water, i.e., lakes and rivers, accounts for only a small proportion of the hydrosphere, yet its contribution to the environment of plants is crucially important. The amount of water accumulated in *clouds*, *fog* and *water vapor* above continents and oceans is relatively small, amounting to only 0.001% of the total water on earth. However, water vapor in the atmosphere is crucially important in the global water and heat balance due to its high turnover rate (average residence time of water vapor in the atmosphere = 10 days). In quantitative terms, the global water cycle is the earth's largest flow of matter and the most important flow of energy, as the majority of the solar radiation that is absorbed by the earth's surface is actually dissipated through water evaporation. The hydrosphere plays a crucial role in the earth's climate system by balancing the heat (heat storage in water; global heat turnover in air; water vapor is most important greenhouse gas).

The various categories of water bodies differ considerably in their chemical composition. The principal constituent of seawater is NaCl (10.8 g l<sup>-1</sup> Na<sup>+</sup>, 19.4 g l<sup>-1</sup> Cl<sup>-</sup>, at a mean density of 1.027); the most important cations are Mg<sup>2+</sup> (1.3 g l<sup>-1</sup>), Ca<sup>2+</sup>, and K<sup>+</sup> (roughly 0.4 g l<sup>-1</sup> of each) and the most important anions are SO<sub>4</sub><sup>2-</sup> (2.7 g l<sup>-1</sup>), HCO<sub>3</sub><sup>-</sup> (0.14 g l<sup>-1</sup>), and Br<sup>-</sup> (0.09 g l<sup>-1</sup>). Numerous other elements in very low concentrations (a few mg l<sup>-1</sup> to µg l<sup>-1</sup>) occur either in ionic form or as compounds, e.g., silicates, organically bound nitrogen. Freshwater usually contains large quantities of Ca<sup>2+</sup> and HCO<sub>3</sub><sup>-</sup>. Wherever mineral solutes are imported into surface water either through inflows or through sediment erosion from shores, the water becomes eutrophic, i.e., high in nutrient concentration. In rivers and lakes, an excess of nutrients builds up as a result of inflowing nitrate- and phosphate-loaded wastewaters. In eutrophic lakes, the concentration of solid material and dissolved mineral substances is up to 300 times higher (from 0.03 to >5 mg P l<sup>-1</sup> and 0.5 to >15 mg N l<sup>-1</sup>) than in oligotrophic lakes.

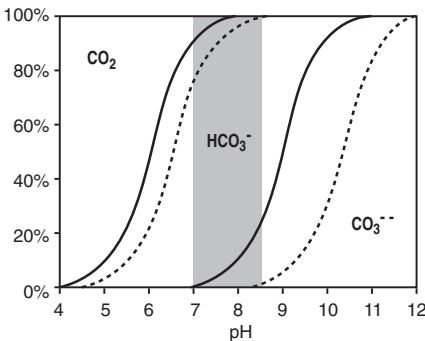
The solubility of *gases in water* rises with increasing pressure and decreasing temperature, yet it falls with increasing salt concentration. Carbon dioxide is readily soluble in water (Table 1.1). The proportion of free CO<sub>2</sub> depends on the pH-value of water; it is high in the acid range, whereas at pH-values above 9, only bicarbonate and carbonate ions are present (Fig. 1.2). Dissolved HCO<sub>3</sub><sup>-</sup> ions can be bound by cations, mainly by

**Table 1.1.** Solubility ( $\mu\text{M}$ ) and volume concentration (%) of  $\text{CO}_2$  and  $\text{O}_2$  in water at different temperatures, in equilibrium with the air. Partial pressure in the air: 35 Pa  $\text{CO}_2$ , 21 kPa  $\text{O}_2$ . (Šesták et al. 1971)

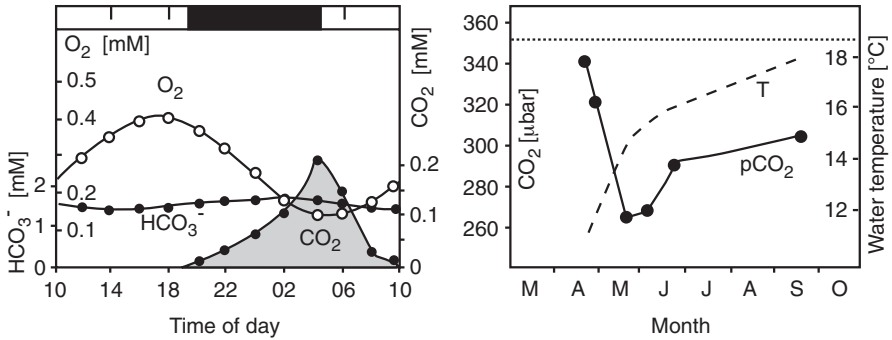
Temperature [°C]	Carbon [ $\mu\text{M}$ ]	Dioxide [%]	Oxygen		Mole ratio $\text{O}_2/\text{CO}_2$
			[ $\mu\text{M}$ ]	[%]	
0	26	0.059	458	1.02	17.6
10	18	0.041	356	0.79	19.8
15	15	0.035	318	0.72	21.2
20	13	0.030	291	0.66	22.4
25	11	0.026	263	0.59	23.9
30	9	0.023	245	0.55	27.2

$\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$ . The water of oceans and lakes contains 0.14% of all the carbon on earth in the form of bicarbonate and carbonate ions or as dissolved inorganic carbon (DIC). The majority of carbon occurs in deep waters of the oceans (about  $38000 \times 10^9$  t). The surface water contains a mere 0.2% of the organic carbon of the hydrosphere. The partial pressure of oxygen in surface waters is on average in equilibrium with the partial pressure of the atmosphere (see Table 1.1). The carbon dioxide and oxygen contents of the uppermost and best-illuminated layers of water (*euphotic zone*) fluctuate diurnally and seasonally due to the photosynthetic rhythm of the photoautotrophic organisms (Fig. 1.3). The oceans play an important role as buffering systems on account of the intensive exchange of  $\text{O}_2$  and  $\text{CO}_2$  between hydrosphere and atmosphere.

*Water currents* lead to both the mixing of surface water and the equilibration of surface water and water of greater depth. In poorly mixed waters, the oxygen concentration below the euphotic zone drops steadily with increasing depth; this is due to the oxygen consumption by animals, microorganisms and reducing substances in the detritus. Hence, deep waters may be completely anoxic, i.e., depleted of oxygen, where circulation is poor. This is frequently the case in basins of lakes and in constrained parts



**Fig. 1.2.** Effect of pH on the carbonate system in seawater (solid line) and freshwater (broken line). Shaded area: Average pH-values of seawater. The ordinate indicates the percent of the total  $\text{CO}_2$  or  $\text{CO}_3^{2-}$  present at particular pH-values



**Fig. 1.3a,b.** Fluctuations in the concentrations of dissolved inorganic carbon (DIC) and oxygen in different waters. **a** Changes in the concentrations of dissolved CO<sub>2</sub>, HCO<sub>3</sub><sup>-</sup> and O<sub>2</sub> at 20–22 °C and pH 7–8 through 24 h in a fish pond in central Europe on a sunny July day. (After Ondok et al. 1984; Pokorný and Ondok 1991). **b** Seasonal alterations in partial pressure of CO<sub>2</sub> (pCO<sub>2</sub>) and in temperature (T) of surface water in the NE Atlantic. (After Watson et al. as cited in Williamson and Platt 1991). Between fall and spring, the O<sub>2</sub> content of lakes may double or even triple within a month

of the oceans, e.g., in the Baltic or the Black Sea. In *upwelling regions* of continental shelves, vertical currents of convection move mineral substances from deeper layers to surface waters. By returning the products of inorganic breakdown back up to surface waters, the circulation of material is maintained.

Water currents also play an important role in *temperature equilibration*. This is clearly illustrated by the development of different strata of temperatures and densities when water currents are absent. Only the uppermost water body absorbs incoming radiation and increases in temperature while deeper waters remain cold. Warm water is less dense than cold water; the movement of water by wind and tides eliminates the density gradient until a certain depth, the so-called *thermocline*, which separates the water body into cold and warm water. In oceans, a permanent thermocline exists deep down below the euphotic zone. An additional seasonal thermocline occurs only at mid-latitudes. Near the poles and in equatorial regions, however, the water temperature of open oceans remains constant throughout the year. This explains why water bodies in tropical oceans do not mix and why the water of the uppermost, light-absorbing layers is permanently deficient in mineral substances. An exception to this is a considerable upwelling of nutrient-rich cold water on the west coast of South America near the equator. Density stratification also occurs in lakes, where warmer water on the surface floats on the cooler deeper water. Thorough mixing of the water body takes place only when surface water cools down sufficiently, i.e., in fall and spring, or in winter at mid- and high-latitudes, or diurnally in equatorial regions.

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