3
Plant Water Relations

1. Introduction

Although water is the most abundant molecule on the Earth's surface, the availability of water is the factor that most strongly restricts terrestrial plant production on a global scale. Low water availability limits the productivity of many natural ecosystems, particularly in dry climates (Fig. 1). In addition, losses in crop yield due to water stress exceed losses due to all other biotic and environmental factors combined (Boyer 1985). Regions where rainfall is abundant and fairly evenly distributed over the growing season, such as in the wet tropics, have lush vegetation. Where summer droughts are frequent and severe, forests are replaced by grasslands, as in the Asian steppes and North American prairies. Further decrease in rainfall results in semidesert, with scattered shrubs, and finally deserts. Even the effects of temperature are partly exerted through water relations because rates of evaporation and transpiration are correlated with temperature. Thus, if we want to explain natural patterns of productivity or to increase productivity of agriculture or forestry, it is crucial that we understand the controls over plant water relations and the consequences for plant growth of an inadequate water supply.

1.1 The Role of Water in Plant Functioning

Water is important to the physiology of plants because of its crucial role in all physiological processes and because of the large quantities that are required. Water typically comprises 70–95% of the biomass of nonwoody tissues such as leaves and roots. At the cellular level, water is the major medium for transporting metabolites through the cell. Because of its highly polar structure, water readily dissolves large quantities of ions and polar organic metabolites like sugars, amino acids, and proteins that are critical to metabolism and life. At the whole-plant level, water is the medium that transports the raw materials (carbohydrates and nutrients) as well as the phytohormones that are required for growth and development from one plant organ to another. Unlike most animals, plants lack a well-developed skeletal system; especially herbaceous plants depend largely on water for their overall structure and support. Due to their high concentrations of solutes, plant cells exert a positive pressure (**turgor**) against their cell walls, which is the basic support mechanism in plants. Turgor pressures are typically of the order of 1.0–5.0 MPa, similar to the pressure in nuclear steam turbines. Large plants gain additional structural support from the lignified cell walls of woody tissues. When plants lose turgor (**wilt**), they no longer carry out certain physiological functions, in particular cell expansion and to a lesser extent photosynthesis. Prolonged periods of wilting usually kill the plant.

A second general reason for the importance of water relations to the physiological ecology of plants is that plants require vast quantities of water. Whereas plants incorporate more than 90% of

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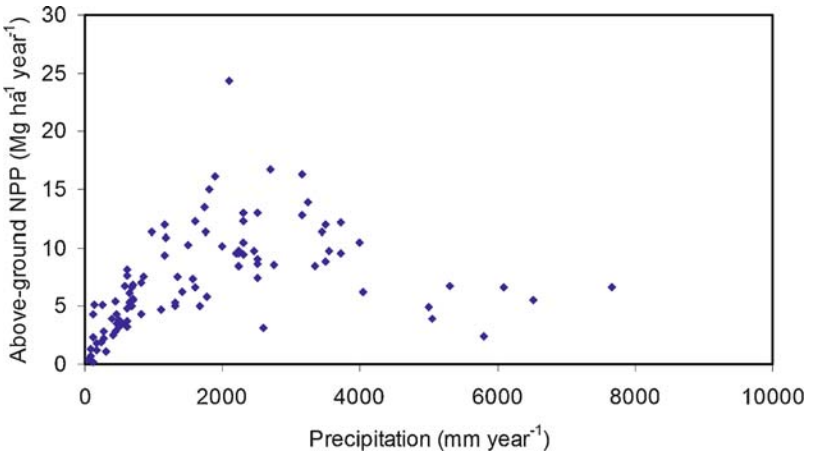

FIGURE 1. Correlation of above-ground net primary production (NPP, in units of biomass) with precipitation. NPP declines at extremely high precipitation (>3 m yr^{-1}) due to indirect effects of excess moisture, such as low soil oxygen and nutrient loss by leaching (Schuur 2003). Copyright Ecological Society of America.

TABLE 1. Concentration of major constituents in a hypothetical herbaceous plant and the amount of each constituent that must be absorbed to produce a gram of dry biomass. The values only give a rough approximation and vary widely among species and with growing conditions, indicated in Sect. 4.3 of Chapter 6 on mineral nutrition for nutrients, and in Sect. 6 for water.

Resource	Concentration (% of fresh mass)	Quantity required (mg g^{-1})
Water	90	500,000
Carbon	4	40
Nitrogen	0.3	3
Potassium	0.2	2
Phosphorus	0.02	0.2

TABLE 2. The ratio of the surface area of mesophyll cells and that of the leaf (A_{mes} / A) as dependent on species and growing conditions.*

Leaf morphology/habitat	A_{mes}/A
Shade leaves	7
Mesomorphic leaves	12–19
Xeromorphic sun leaves	17–31
Low altitude (600 m)	37
High altitude (3000 m)	47
Species	A_{mes}/A
Plectranthus parviflorus	
High light	39
Low light	11
Alternanthera philoxeroides	
High light	78
Low light	50

*The data on leaves of species with different morphologies are from Turrel (1936), those on low-altitude and high-altitude species from Körner et al. (1989), those on *Plectranthus parviflorus* from Nobel et al. (1975), and those on *Alternanthera philoxeroides* (alligator weed) from Longstreth et al. (1985).

absorbed N, P, and K, and about 10–70% of photosynthetically fixed C into new tissues (depending on respiratory demands for carbon), less than 1% of the water absorbed by plants is retained in biomass (Table 1). The remainder is lost by **transpiration**, which is the evaporation of water from plants. The inefficient use of water by terrestrial plants is an unavoidable consequence of photosynthesis. The stomates, which allow CO_2 to enter the leaf, also provide a pathway for water loss. CO_2 that enters the leaf must first dissolve in water on the wet walls of the mesophyll cells before diffusing to the site of carboxylation. This moist surface area of mesophyll cells exposed to the internal air spaces of the leaf is about 7–80 times the external leaf area, depending on species and plant growth conditions (Table 2). This causes the air inside the leaf to be saturated with water vapor (almost 100% relative humidity) which creates a strong gradient in water vapor concentration from the inside to the outside of the leaf.

1.2 Transpiration as an Inevitable Consequence of Photosynthesis

Transpiration is an inevitable consequence of photosynthesis; however, it also has important direct effects on the plant because it is a major component of the leaf's energy balance. As water evaporates from mesophyll cell surfaces, it cools the leaf. In the absence of transpiration, the temperature of large leaves can rapidly rise to lethal levels. We

further discuss this effect of transpiration in Chapter 4A on the plant's energy balance. The transpiration stream also allows transport of nutrients from the bulk soil to the root surface and of solutes, such as inorganic nutrients, amino acids, and phytohormones, from the root to transpiring organs. As will be discussed later, however, such transport in the xylem also occurs in the absence of transpiration, so that the movement of materials in the transpiration stream is not strongly affected by transpiration rate.

In this chapter, we describe the environmental factors that govern water availability and loss, the movement of water into and through the plant, and the physiological adjustments that plants make to variation in water supply over diverse timescales. We emphasize the mechanisms by which individual plants adjust water relations in response to variation in water supply and the adaptations that have evolved in dry environments.

2. Water Potential

The status of water in soils, plants, and the atmosphere is commonly described in terms of **water potential** (ψ_w) [i.e., the chemical potential of water in a specified part of the system, compared with the chemical potential of pure water at the same temperature and atmospheric pressure; it is measured in units of pressure (MPa)]. The water potential of pure, free water at atmospheric pressure and at a temperature of 298 K is 0 MPa (by definition) (Box 3.1).

In an isothermal two-compartment system, in which the two compartments are separated by a **semipermeable membrane**, water will move from a high to a low water potential. If we know the water potential in the two compartments, then we can predict the direction of water movement. It is certainly *not* true, however, that water invariably moves down a gradient in water potential. For example, in the **phloem** of a source leaf, the water potential is typically more negative than it is in the phloem of the sink. In this case, water transport is driven by a difference in hydrostatic pressure, and water moves up a gradient in water potential. Similarly, when dealing with a nonisothermal system, such as a warm atmosphere and a cold leaf, water vapor may condense on the leaf even though the water potential of the air is more negative than that of the leaf.

Water potential in any part of the system is the algebraic sum of the **osmotic potential**, ψ_π, and the **hydrostatic pressure**, ψ_p (the component of the water potential determined by gravity is mostly ignored):

$$\psi_w = \psi_\pi + \psi_p \quad (1)$$

where water potential is the overall pressure on water in the system. The **osmotic potential** is the chemical potential of water in a solution due to the presence of dissolved materials. The osmotic potential always has a negative value because water tends to move across a semipermeable membrane from pure water (the standard against which water potential is defined) into water containing solutes (Box 3.1). The higher the concentration of solutes, the lower (more negative) is the osmotic potential. The **hydrostatic pressure**, which can be positive or negative, refers to the physical pressure exerted on water in the system. For example, water in the turgid root cortical cells or leaf mesophyll cells is under positive **turgor pressure** exerted against the cell walls, whereas water in the dead xylem vessels of a rapidly transpiring plant is typically under **suction tension** (negative pressure). Large negative hydrostatic pressures arise because of capillary effects, i.e., the attraction between water and hydrophilic surfaces at an air–water interface (Box 3.2). Total water potential can have a positive or negative value, depending on the algebraic sum of its components. When dealing with the water potential in soils, an additional term is used: the **matric potential**, ψ_m. The matric potential refers to the force with which water is adsorbed onto surfaces such as cell walls, soil particles, or colloids, similar to the forces in xylem vessels. As such it is actually a convenient *alternative* to hydrostatic pressure for characterizing the water status of a porous solid. The hydrostatic pressure and the matric potential should therefore never be added! The matric potential always has a negative value because the forces tend to hold water in place, relative to pure water in the absence of adsorptive surfaces. The matric potential becomes more negative as the water film becomes thinner (smaller cells or thinner water film in soil).

Now that we have defined the components of water potential, we show how these components vary along the gradient from soil to plant to atmosphere.

3. Water Availability in Soil

The availability of soil water to plants depends primarily on the quantity of water stored in the soil and its relationship to soil water potential. Clay and organic soils, which have small soil particles, have more small soil pores; these small capillaries generate very negative pressures (large suction tensions)

Box 3.1
The Water Potential of Osmotic Solutes and the Air

We are quite familiar with the fact that water can have a potential: we know that water at the top of a falls or in a tap has a higher potential than that at the bottom of the falls or outside the tap. Transport of water, however, occurs not invariably as a result of differences in hydrostatic pressure, but also due to differences in vapor pressure (Sect. 2.2.2 of Chapter 2A on photosynthesis) or due to differences in the amount of dissolved osmotic solutes in two compartments separated by a semipermeable membrane. In fact, in all these cases, there is a difference in water potential, which drives the transport of water. For a full appreciation of many aspects of plant water relations, we first introduce the concept of the chemical potential of water, for which we use the symbol μ_w.

By definition, the chemical potential of pure water under standard conditions (298 K and standard pressure), for which the symbol μ_w^0 is used, is zero. We can also calculate the chemical potential of water under pressure, of water that contains osmotic solutes, or of water in air. This can best be explained using a simple example, comparing the chemical potential of water in two sealed containers of similar size (Fig. 1). One of these containers (A) contains pure water under standard conditions: $\mu_w = \mu_w^o = 0$. Of course, the gas phase is in equilibrium with the liquid pure water, and the vapor pressure is p_o. The second container (B) contains a 1 M sucrose solution in water. The gas phase will again be in equilibrium with the liquid phase; the vapor pressure is p. The vapor pressure, however, will be less than p_o because the sucrose molecules interact with the water molecules via hydrogen bonds, so that the water molecules cannot move into the gas phase as readily as in the situation of pure water. How large is the difference between p and p_o?

To answer this question, we use Raoult's law, which states that

$$p/p_0 = N_w \qquad (1)$$

where N_w is the mol fraction [i.e., the number of moles of water divided by the total number of moles in container B; in the case of 1 mole of sucrose in 1 L water (55.6 moles of water), N_w = 55.6/56.6 = 0.982]; p_o is the vapor pressure (in Pa) above pure water, at standard pressure and temperature. We can calculate the difference in potential between the two containers $(\mu_w - \mu_w^o)$ by considering the amount of work needed to obtain the same (higher) pressure in container B as in container A. To achieve this, we need to compress the gas in container B until the pressure equals p_o:

$$\mu_w - \mu_w^0 = \int_{p_0}^{p} V \quad dp = RT \ln\left(\frac{p}{p_0}\right) \qquad (2)$$

where V is the volume (m^3) of container B, which is compressed until p_o is reached, R is the gas constant (J mol^{-1} K^{-1}), and T is the absolute temperature (K).

Combination of Equations (1) and (2) yields

$$\mu_w - \mu_w^o = RT \ln(1 - N_w) \qquad (3)$$

Because N_w is the mole fraction of water and N_s is the mole fraction of the solute (in our example, 1/56.6 = 0.018), we can write Equation (3) as

$$\mu_w - \mu_w^o = RT \ln(1 - N_s) \qquad (4)$$

As long as we consider solutions in a physiologically relevant range (i.e., not exceeding a few molar) Equation (4) approximates

$$\mu_w - \mu_w^o = RT\, N_s \qquad (5)$$

[as can readily be calculated for our example of a 1 M solution of sucrose, N_s is 0.018 and $\ln(1 - N_s)$ = –0.018].

Dividing N_s by the molar volume of pure water (V_w^o m^3 mol^{-1}), we arrive at the concentration of the solute, c_s (in mol m^{-3}):

$$N_s/V_w^o = c_s \qquad (6)$$

We make one further change, by introducing the molar volume of pure water (m^3 mol^{-1}; at 273 K) in Equation (5):

$$\frac{\mu_w - \mu_w^o}{V_w^o} = -RTcs = \Psi \qquad (7)$$

continued

Box 3.1. *Continued*

Ψ is the water potential. Because we are dealing with the water potential of a solution in this example, we refer to this potential as the osmotic potential of water(Ψ_π). The dimension is Pascal (Pa). It is often more convenient, however, to use megapascal (MPa = 10^6 Pa) instead (1 MPa = 10 bars, a unit used in the literature, or 10 atm, a unit that is no longer used).

We can therefore calculate that our 1 M sucrose solution has an osmotic potential of –2.4 MPa, which approximates a pressure of a water column of about 250 m! In equilibrium, the water potential of the gas phase above the 1 M sucrose solution also equals –2.4 MPa. In the case of electrolytes, the calculation is slightly more complicated in that the dissociation of the solute has to be taken into account.

By modifying Equation (7), we can also calculate the water potential of air that is not in equilibrium with pure water [i.e., with a relative humidity (RH) of less than 100%]:

$$\frac{\mu_w - \mu^{o_w}}{V_w^o} = \frac{RT}{V_w^o}\ln\left(\frac{p}{p_o}\right) \qquad (8)$$

For air of 293 K and a RH of 75%, Ψ equals –39 MPa [to calculate this, you need to know that the molar volume of water (molecular mass = 18) at 293 K is $18.10^{-6}m^3mol^{-1}$]. Values for Ψ of air of different RH are presented in Table 1. Note that even when the water vapor pressure is only marginally lower than the saturated water vapor pressure RH = 100% , the water potential is rather negative.

Table 1. The water potential (MPa) of air at a range of relative humidities and temperatures. *

Relative humidity (%)	-Ψ (MPa) at different temperatures (°C)				
	10	15	20	25	30
100	0	0	0	0	0
99.5	0.65	0.67	0.68	0.69	0.70
99	1.31	1.33	1.36	1.38	1.40
98	2.64	2.68	2.73	2.77	2.81
95	6.69	6.81	6.92	7.04	7.14
90	13.75	13.99	14.22	14.45	14.66
80	29.13	29.63	30.11	30.61	31.06
70	46.56	47.36	48.14	48.94	49.65
50	90.50	92.04	93.55	95.11	96.50
30	157.2	159.9	162.5	165.2	167.6
10	300.6	305.8	310.8	316.0	320.6
RT/V_w	130.6	132.8	135.0	137.3	139.2

***Note*: The values were calculated using the formula: $\Psi = -RT/V_w^0$ ln (% relative humidity/100).**

*** Note that all values for Ψ are *negative* and that the effect of temperature is exclusively due to the appearance of temperature in the equation given in the last line of this table, rather than to any effect of temperature on p_o.**

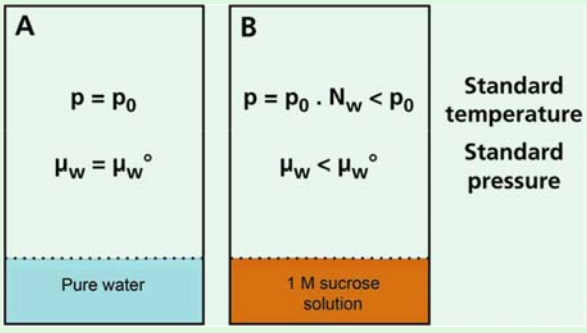

Figure 1. The difference in water potential between two systems. The system at the left is a sealed container with pure water at standard temperature and pressure; the partial water vapor pressure in this container is p_o and the chemical potential of water in this system is μ_w^o. The system at the right is a container with a solution of 1 M sucrose at the same temperature and pressure; the water vapor pressure can be calculated according to Raoult's law ($p = p_o.N_w$) and the chemical potential of water in this system is μ_w. The difference in chemical potential between the two systems can be calculated as explained in the text.

Box 3.2
Positive and Negative Hydrostatic Pressures

Positive values of hydrostatic pressure in plants are typically found in living cells and are accounted for by high concentrations of osmotic solutes. Large negative values arise because of capillary effects (i.e., the attraction between water and hydrophilic surfaces at an air–water interface). It is this attraction that explains the negative matric potential in soil and the negative hydrostatic pressure in the xylem of a transpiring plant.

The impact of the attraction between water and hydrophilic surfaces on the pressure in the adjacent water can be understood by imagining a glass capillary tube, with radius a (m), placed vertically with one end immersed in water. Water will rise in the tube, against the gravitational force, until the mass of the water in the tube equals the force of attraction between the water and the glass wall. A fully developed meniscus will exist (i.e., one with a radius of curvature equal to that of the tube). The meniscus of the water in the glass tube is curved because it supports the mass of the water.

The upward acting force in the water column equals the perimeter of contact between water and glass ($2\pi a$) multiplied by the surface tension, γ(N m^{-1}), of water; namely, $2\pi a\gamma$ (provided the glass is perfectly hydrophilic, when the contact angle between the glass and the water is zero; otherwise, this expression has to be multiplied by the cosine of the angle of contact). When in equilibrium, there must be a difference in pressure, ΔP (Pa) across the meniscus, equal to the force of attraction between the water and the capillary wall (i.e., the pressure in the water is less than that of the air). The downward acting force (N) on the meniscus is the difference in pressure multiplied by the cross-sectional area of the capillary tube (i.e., $\pi a^2 \gamma P$). Thus, because these forces are equal in equilibrium, we have

$$\pi a^2 \Delta P = 2\pi a\gamma \quad (1)$$

and

$$\Delta P = 2\pi a\gamma / \pi a^2 = 2\gamma / a \quad (2)$$

The surface tension of water is 0.075 N m^{-1} at about 20°C, so ΔP = 0.15/a (Pa). Thus a fully developed meniscus in a cylindrical pore of radius, say 1.5 μm, would have a pressure drop across it of 1.0 MPa; the pressure, P, in the water would therefore be –0.1 MPa if referenced to normal atmospheric pressure, or –0.9 MPa absolute pressure (given that standard atmospheric pressure is approximately 0.1 MPa).

This reasoning also pertains to pores that are not cylindrical. It is the radius of curvature of the meniscus that determines the pressure difference across the meniscus, and this curvature is uniform over a meniscus that occupies a pore of any arbitrary shape. It is such capillary action that generates the large negative pressures (large suction tension) in the cell walls of leaves that drive the long-distance transport of water from the soil through a plant to sites of evaporation. The pores in cell walls are especially small (approximately 5 nm) and are therefore able to develop very large suction tensions, as they do in severely water-stressed plants.

(Box 3.2). Pores larger than 30 μm hold the water only rather loosely, so the water drains out following a rain. Pores smaller than 0.2 μm hold water so tightly to surrounding soil particles that the drainage rate often becomes very small once the large pores have been drained. As a result, most plants cannot extract water from these pores at sufficiently high rates to meet their water needs. It is thus the intermediate—sized pores (0.2–30 μm diameter) that hold most of the water that is tapped by plants.

In friable soil, roots can explore a large fraction of the soil volume; hence, the volume of water that is available to the roots is relatively large. Upon soil compaction, roots are unable to explore as large a fraction of the soil volume; the roots then tend to be clumped into sparse pores and water uptake is restricted. Compacted soils, however, are not uniformly hard and usually contain structural cracks and biopores (i.e., continuous large pores formed by soil fauna and roots). Roots grow best in soil with an intermediate density, which is soft enough to allow

good root growth but sufficiently compact to give good root–soil contact (Stirzaker et al. 1996).

Water movement between root and soil can be limited by incomplete root–soil contact, such as that caused by air gaps due to root shrinkage during drought. It can also be influenced by a **rhizosheath** (i.e., the soil particles bound together by root exudates and root hairs) (McCully & Canny 1988). Rhizosheaths are limited to distal root regions, which generally have a higher water content than do the more proximal regions (Huang et al. 1993) in part due to the immaturity of the xylem in the distal region (Wang et al. 1991). The rhizosheath virtually eliminates root–soil air gaps, thus facilitating water uptake in moist soil. On the other hand, bare roots restrict water loss from roots to a drier soil (North & Nobel 1997).

3.1 The Field Capacity of Different Soils

Field capacity is defined as the water content after the soil becomes saturated, followed by complete gravitational drainage. The water potential of nonsaline soils at field capacity is close to zero (–0.01 to –0.03 MPa). There is a higher soil water content at field capacity in fine-textured soils with a high clay

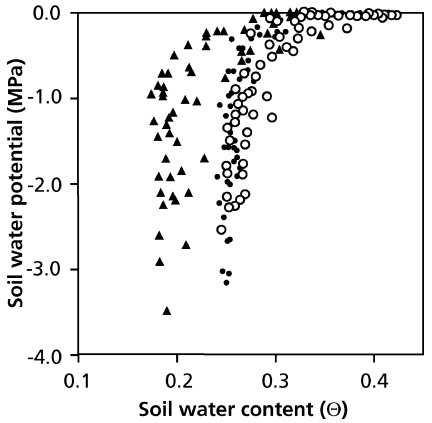

FIGURE 2. **Relationship between soil water potential and volumetric soil water content (ratio of volume taken up by water and total soil volume,) at different soil depths: 25 cm, *solid triangles*; 50–80 cm, *open circles*; 110–140 cm, *filled circles*. The top horizon was a silty clay loam; the middle layer was enriched with clay, and in the deepest soil layer, the clay content decreased again. Soil water potential was measured with tensiometers and micropsychrometers, and soil water content with a neutron probe. Data were obtained over 1 year while water content fell during drought (Bréda et al. 1995).**

TABLE 3. **Typical pore-size distribution and soil water contents of different soil types.**

	Soil type		
	Sand	Loam	Clay
Parameter			
Pore space (% of total)			
>30 m particles	75	18	6
0.2–30 m	22	48	40
<0.2 m	3	34	53
Water content (% of volume)			
Field capacity	10	20	40
Permanent wilting point	5	10	20

or organic matter content (Fig. 2). The lowest water potential at which a plant can access water from soil is the **permanent wilting point**. Although species differ in the extent to which they can draw down soil water (e.g., from –1.0 to –8.0 MPa), as discussed later, a permanent wilting point of –1.5 MPa is common for many herbaceous species. The **available water** is the difference in the amount of soil water between field capacity and permanent wilting point, –1.5 MPa (by definition). The amount of available water is higher in clay than it is in sandy soils (Fig. 2, Table 3).

In a moist soil, the smallest soil pores are completely filled with water and only the largest pores have air spaces. As soil moisture declines, the thickness of the water film surrounding soil particles declines, and remaining water is held more tightly to soil particles, giving a low (negative) matric potential. Finally, the hydrostatic pressure (reflecting gravity or the mass of the water column) is generally negligible in soils. In nonsaline soils, the matric potential is the most important component of soil water potential.

In **saline soils**, the osmotic potential adds an additional important component. If plants are well watered with a saline solution of 100 mM NaCl, then the soil water potential is –0.48 MPa. As the soil dries out, the salts become more concentrated and further add to the negative value of the soil water potential. When half of the water available at field capacity has been absorbed, the osmotic component of the soil water potential will have dropped to almost –1 MPa. Under such situations, the osmotic component of the soil water potential, clearly, cannot be ignored.

Soil **organic matter** affects water **retention** because of its hydrophilic character and its influence on soil structure. Increasing the organic matter content from 0.2 to 5.4% more than doubles the water-holding capacity of a sandy soil–from 0.05 to 0.12

(v/v). In silty soils, which have a larger water-holding capacity, the absolute effect of organic matter is similar, but less dramatic when expressed as a percentage; it increases from about 0.20 to less than 0.30 (v/v). Effects on plant-available water content are smaller because the water content at field capacity as well as that at the permanent wilting point is enhanced (Kern 1995). Roots, especially mycorrhizal roots (Sect. 2.5 of Chapter 9A on symbiotic associations), may promote the development of soil aggregates, through the release of organic matter, and thus affect soil hydraulic properties. **Organic matter** may also have the effect of **repelling** water, if it is highly hydrophobic. Such situations may arise when plant-derived waxy compounds accumulate on the soil surface. These reduce the rate at which water penetrates the soil so that much of the precipitation from a small shower may be lost through runoff or evaporation rather than becoming available for the plant. Some roots release surfactants, which may counteract the effect of water-repelling compounds in soil (Read et al. 2003).

3.2 Water Movement Toward the Roots

Water moves relatively easily through soil to the roots of a transpiring plant by flowing down a gradient in hydrostatic pressure. If the soil is especially dry (with a water potential less than –1.5 MPa), then there may be significant movement as water vapor. Under those conditions, however, transpiration rates are very low. Gradients in osmotic potential move little water because the transport coefficients for diffusion are typically orders of magnitude smaller than for flow down a hydrostatic gradient. Movement across the interface between root and soil is more complicated. There may be a mucilaginous layer that contains pores so small that the flow of water across it is greatly hindered. There may also be a lack of hydraulic continuity between root and soil if the root is growing in a pore wider than itself or if the root has shrunk. A root has, generally, access to all available water within 6 mm of the root. As the soil dries and the matric forces holding water to soil particles increases, movement of liquid water through soils declines (Fig. 3).

In a situation where the soil is relatively dry and the flow of water through it limits water uptake by the roots, the following equation approximates water uptake by the roots:

$$\mathrm{d}\theta'/\mathrm{d}t = D(\theta' - \theta_a)/2b^2 \qquad (2)$$

where $\mathrm{d}\theta'/\mathrm{d}t$ is the rate of fall of mean soil water content, θ', with time, t; D is the diffusivity of soil water, which is approximately constant with a value of 2×10^{-4} m^2 day^{-1} (0.2×10^{-8} m^2 s^{-1}), during the extraction of about the last third of the available water in the soil (Fig. 3), when the flow is likely limiting the rate of water uptake; θ_a is the soil water content at the surface of the root; and b is the radius of a putative cylinder of soil surrounding the root, to which that root effectively has sole access, and can be calculated as $b = (\pi L)^{-1/2}$, where L (m m^{-3}), the rooting density, is the length of root per unit volume of soil (m^3) (Passioura 1991).

Under the reasonable assumption that θ_a is constant, as it would be if the root were maintaining a constant water potential of, say, –1.5 MPa at its surface (Fig. 3), the equation can be integrated to give

$$(\theta' - \theta_a)_d = (\theta' - \theta_a)_0 \exp(-Dt/2b^2) = \theta_{d0} \exp(-t/t^*) \qquad (3)$$

where $(\theta' - \theta_a)_0$ is $(\theta' - \theta_a)$ when $t = 0$, and t^* (equal to $2b^2/D$) is the time constant for the system: the time taken for the mean soil water content to fall to 1/e (i.e., 0.37) of its initial value. If D is 2×10^{-4} m^2 day^{-1}, then t^* is simply $b^2 \times 10^{-4}$ days. If the roots are evenly distributed in the soil, then, even at a low rooting density, L, of 0.1 m m^{-3}, t^* (calculated from

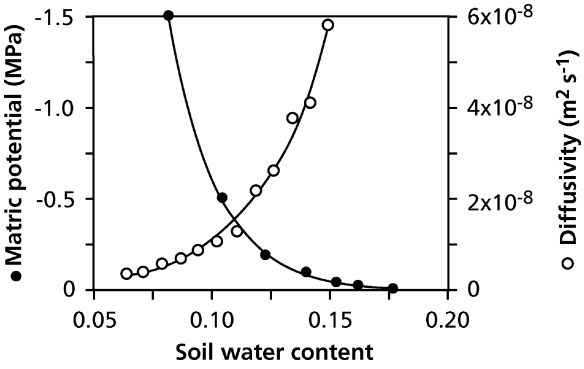

Figure 3. The matric potential and diffusivity of soil water as a function of the volumetric water content (ratio of volume taken up by water and total soil volume) of a sandy loam soil (55% coarse sand, 19% fine sand, 12% silt, and 14% clay) (after Stirzaker & Passioura 1996).

$b^2 = 1/[\pi L])$ is only about 3 days. Roots, therefore, should readily be able to extract all the available water from the soil. When the soil is compacted, roots are not distributed so evenly through the soil (Sect. 5.5 of Chapter 7 on growth and allocation), and Equations (2) and (3) are no longer applicable. Under those conditions, t^* could become of the order of weeks. The parameter t^* changes with soil type and soil depth, but is not strongly affected by the nature of the plant extracting the water (Passioura 1991).

If a plant does not absorb all the ions arriving at the surface of its roots, the osmotic potential will drop locally, either only in the apoplast of the roots or possibly in the rhizosphere as well. This is more pronounced in fertilized or saline soils than in nutrient-poor, nonsaline soils. The effect is that plants have greater difficulty in extracting water from soil than expected from the average soil water potential (Stirzaker & Passioura 1996).

3.3 Rooting Profiles as Dependent on Soil Moisture Content

As long as the upper soil is fairly moist, plants tend to absorb most of their water from shallower soil regions, which is where roots are concentrated. As the soil dries out, relatively more water is absorbed from deeper layers. Water from the deepest layers, even from those where no roots penetrate, may become available through capillary rise (Fig. 4; Bréda et al. 1995). The actual **rooting depth** varies greatly among species, with some chaparral shrubs [*Adenostoma fasciculatum* (chamise), *Quercus dumosa* (California scrub oak), and *Quercus chrysolepis* (canyon live oak)] growing in the San Gabriel and San Bernardino mountains in southern California reaching depths of **8** m in fractured rock structures (Hellmers et al. 1955). Maximum rooting depths are found in deserts and tropical grasslands and savannas (Canadell et al. 1996). On the Edwards Plateau of central Texas, United States, rooting depths of a range of species were determined by using DNA sequence variation to identify roots from caves 5 to 65 m deep. At least six tree species in the system produced roots deeper than 5 m, but only the evergreen oak, *Quercus fusiformis*, was found below 10 m. The maximum rooting depth for the ecosystem was approximately 25 m (Jackson et al. 1999). In the Kalahari Desert, well drillers must bore to great depths in very dry sand to reach water, and drillers reported some of the deepest roots thus far recorded in the world at 68 m. In the Kalahari sands, the annual precipitation of less than 300 mm can only penetrate a couple of meters at most. Below this wetting front, roots must grow in very dry sand for tens of meters before they can reach deep geologic water (Jennings 1974, as cited in Schulze et al. 1988). A potential mechanism that would facilitate this growth in very dry sand is through hydraulic redistribution (Sect. 5.2; Schulze et al. 1988).

The root-trench method, in combination with measurements of volumetric soil water content (Fig. 4), is a laborious and expensive method to obtain information on where most of the water comes from that a tree transpires. If the **isotope signature** of water differs among soil layers, then

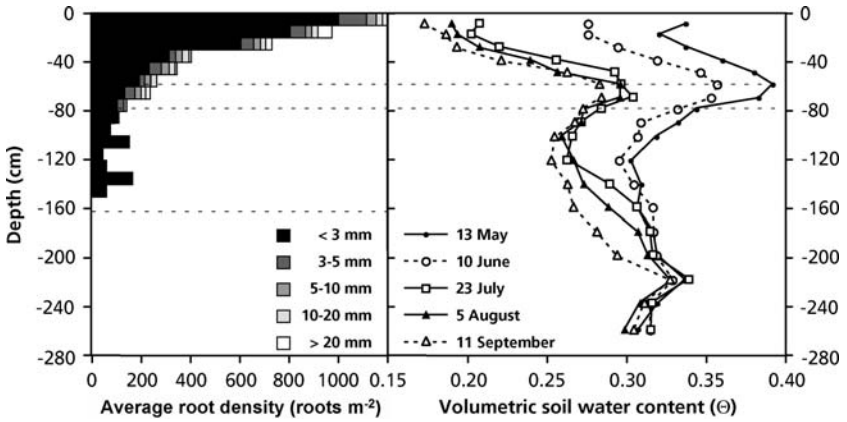

FIGURE 4. (*Left*) Rooting profile of *Quercus petraea* (sessile oak) as dependent on soil depth. Roots are divided in different diameter classes. (*Right*) Volumetric water content of the soil in which the oak tree was growing, as dependent on depth and time of the year. A clay-enriched horizon at around 50 cm depth is indicated by the two *broken lines*. The third *broken line* at 160 cm depth indicates the depth of the trench that was dug to make the measurements (Bréda et al. 1995).

this value can be used to obtain information on which soil layers and associated roots provide the water that is transpired (Box 3.3). This technique has shown that perennial groundwater sources can be important (Thorburn & Ehleringer 1995, Boutton et al. 1999). For example, in a Utah desert scrub community, most plants use a water source derived from winter storm recharge for their early spring growth (Ehleringer et al. 1991). As this water source is depleted, however, only the deep-rooted woody perennials continue to tap this source, and more shallow-rooted species such as annuals, herbaceous

Box 3.3
Oxygen and Hydrogen Stable Isotopes

Small fractions of the elements H and O occur as their heavy stable isotopes ^{2}H (also called deuterium; D) and ^{18}O (0.156 and 1.2‰, respectively). Their abundances in water (and CO_2) in the immediate environment of the plant, and in water, metabolites, and macromolecules in the plant itself vary as a result of fractionation processes operating in these two compartments. Isotopic composition, which can be measured with high precision, provides information about environmental and physiological parameters that is otherwise difficult to obtain. Isotopes in xylem water, for instance, can yield information on the source of water tapped by a plant, and isotopes in leaf water are influenced by stomatal conductance and humidity. Isotopes in plant dry matter can give a time-integrated and time-resolved historical record of environmental and physiological processes, as in tree rings (Dawson et al. 2002). A problem, however, with interpreting isotopic composition of plant dry matter or of specific compounds (e.g., cellulose) in field studies is that it is simultaneously influenced by many factors. Models have been developed to resolve these problems as much as possible (Farquhar et al. 1998, Roden et al. 2000, Gessler et al. 2007).

Isotopes are measured as atomic ratios (R = rare isotope/common isotope) using mass spectrometers and are expressed relative to a standard (Standard Mean Ocean Water; SMOW; see also Box 2A.2 and Box 2B.1):

$$\delta^2\mathrm{H} \text{ or } \delta^{18}\mathrm{O}(‰) = (R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1) \times 1000 \quad (1)$$

The $\boldsymbol{\delta}^2$H and $\boldsymbol{\delta}^{18}$O of precipitation water and other water bodies that are regularly involved in the global water cycle (meteoric waters) vary as a result of fractionation during evaporation and condensation in a temperature-dependent manner. Tropical regions are characterized by $\boldsymbol{\delta}$-values close to ocean water, and these values decrease toward the poles, particularly in winter. Depleted values are also found at higher altitudes and further inland on continents. Fractionation processes in meteoric water operates similarly for ^{2}H and ^{18}O, and the $\boldsymbol{\delta}$-values are linearly related. This is known as the global meteoric water line [$\boldsymbol{\delta}^{18}\mathrm{O} = (\boldsymbol{\delta}^2\mathrm{H} - 10)/8$]. Fractionation processes in more closed compartments result in deviations from this line.

Soil moisture in surface layers is typically isotopically enriched as a result of evaporation (Fig. 1). Different isotopic compositions of precipitation events can further add to a profile of $\boldsymbol{\delta}^2$H and $\boldsymbol{\delta}^{18}$O in the soil (Midwood et al. 1998). Since fractionation does not normally occur during uptake of water, the $\boldsymbol{\delta}$-value of xylem water may contain information about the depth of water uptake or source of water (e.g., ground or stream water). Once in the leaf, the water is isotopically enriched as a result of transpiration. The ultimate $\boldsymbol{\delta}^2$H and $\boldsymbol{\delta}^{18}$O of leaf water is influenced by stomatal and boundary layer conductances, vapor pressure difference, transpiration rate and the $\boldsymbol{\delta}$-values of water vapor around the leaf.

The H in photoassimilates stems from water and carries its isotopic composition during assimilation. That is also the case with O, although in an indirect manner. Assimilated O is derived from CO_2, but its O is exchanged with H_2O in the reaction $CO_2 \leftrightarrow HCO_3^-$ catalyzed by carbonic anhydrase. Assimilates thus carry the isotopic signal of leaf water. During CO_2 assimilation, substantial fractionation occurs for ^{2}H (–117‰), whereas fractionation during further metabolism works in the opposite direction (+158‰). There is also isotopic enrichment of ^{18}O during assimilation and metabolism (+27‰). However, the environmental effect on these fractionation processes is limited. During synthesis of macromolecules from assimilates exchange of H and O with water occurs (Fig. 1). This applies only for part of the atoms. The

continued

Box 3.3 *Continued*

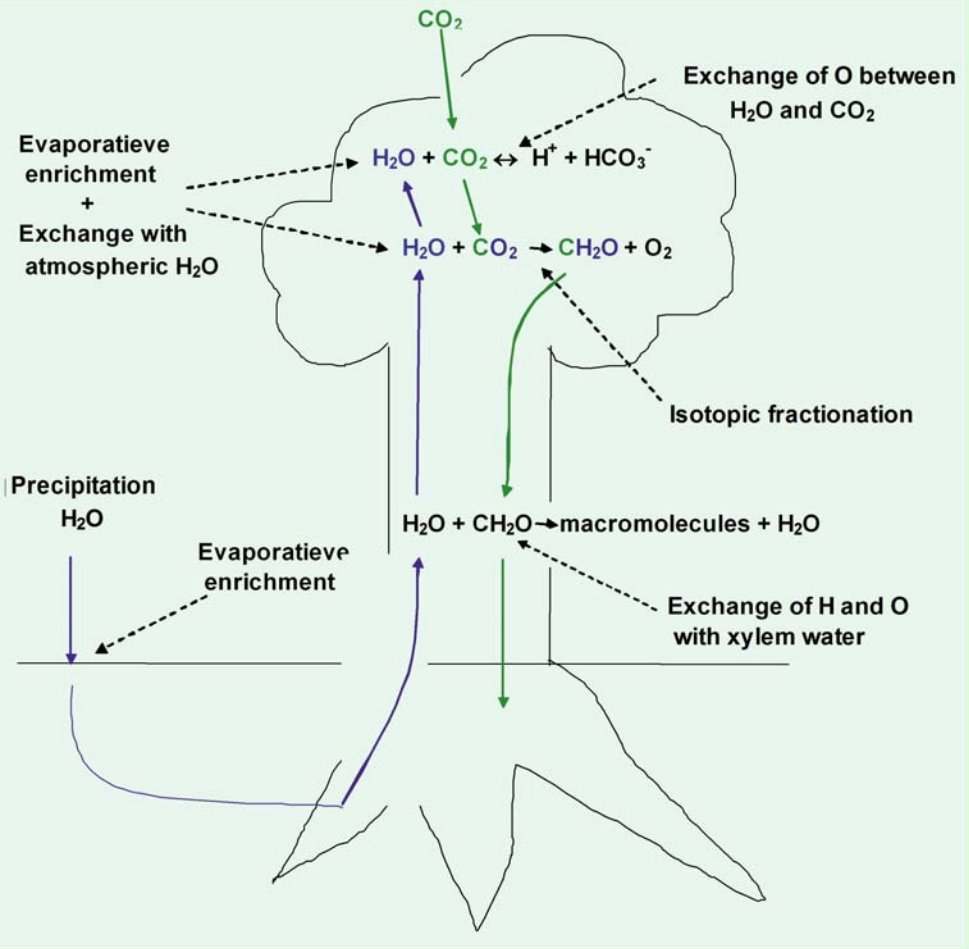

FIGURE 1. Isotopic fractionation and exchange processes of H and O in a tree and its environment.

fraction of exchange during cellulose synthesis in tree rings was estimated at 0.36 for H and 0.42 for O (Roden et al. 2000). Intramolecular positions have different degrees of exchange (Sternberg et al. 2006) which can be used for specific purposes.

The above qualitatively described reactions have been formalized in quantitative models that give good predictions of measured values. When information is available about sufficient environmental variables, unknowns can be calculated on the basis of δ-values.

perennials, and succulent perennials depend on summer rains (Fig. 5). Plants that have an isotopic composition of their xylem water that is representative of deep water are less water stressed and have higher transpiration rates and lower **water-use efficiency** (Sect. 6) than do species with a shallow-water isotopic signature.

3.4 Roots Sense Moisture Gradients and Grow Toward Moist Patches

As with so many other fascinating phenomena in plants, Darwin (1880) already noticed that roots have the amazing ability to grow away from dry sites and toward wetter pockets in the soil: They

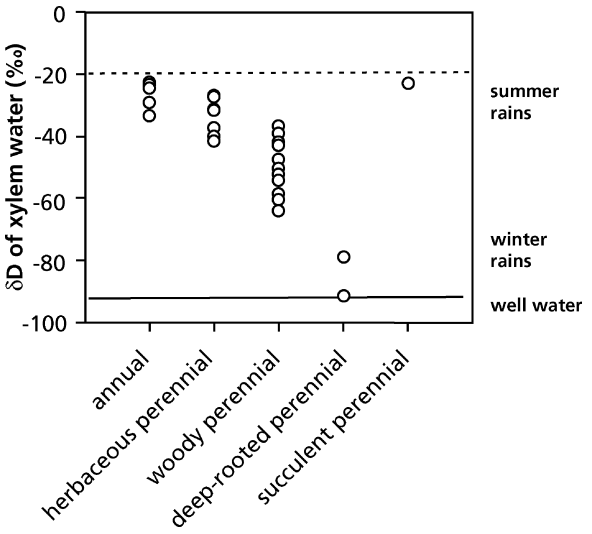

FIGURE 5. Hydrogen isotope ratios (δD) of xylem water during the summer from plants of different growth forms in a Utah desert scrub community. The mean winter precipitation δD was –88‰, whereas summer precipitation δD ranged from –22 to –80‰ (Ehleringer et al. 1991).

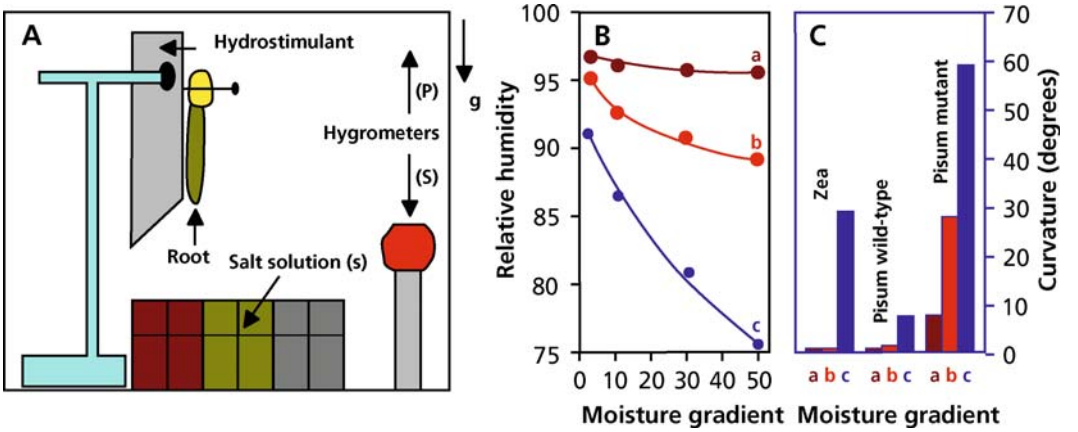

FIGURE 6. Hydrotropism in roots of *Zea mays* (corn) and of the wild type and the ageotropic mutant (*ageotropum*) of *Pisum sativum* (pea). (A) Diagram showing the humidity-controlled chamber. Roots were placed 2–3 mm from the "hydrostimulant" (wet cheesecloth). Saturated solutions of salts create the humidity gradient. Different salts (KCl, K_2CO_3) give different gradients. The relative humidity and temperature was measured with a thermohygrometer (P). A stationary hygrometer (S) measured the relative humidity in the chamber. The arrow and letter g indicate the direction of gravitational force. (B) Moisture gradients, between 0 and 50 mm from the hydrostimulant, created by using no salt (a), KCl (b), or K_2CO_3 (c). (C) Root curvature 10 hours after the beginning of hydrostimulation by the three moisture gradients shown in (B) (after Takahashi & Scott 1993).

are **hydrotropic**. Positive hydrotropism occurs due to inhibition of root cell elongation at the humid side of the root. The elongation at the dry side is either unaffected or slightly stimulated, resulting in a curvature of the root and growth toward a moist patch (Takahashi 1994, Tsuda et al. 2003). The root cap is most likely the site of **hydrosensing** (Takahashi & Scott 1993), but the exact mechanism of **hydrotropism** is not known. It involves an increase in cell-wall extensibility of the root cells that face the dry side (Sect. 2.2 of Chapter 7 on growth and allocation; Hirasawa et al. 1997). The hydrotropic response is stronger in roots of *Zea mays* (corn), which is a species that tolerates relatively dry soils, than it is in those of *Pisum sativum* (pea), and it shows a strong interaction with the root's gravitropic response (Fig. 6).

4. Water Relations of Cells

There are major constraints that limit the mechanisms by which plants can adjust cellular water potential. Adjustment of the water potential must come through variation in hydrostatic pressure or

osmotic potential. Live cells must maintain a positive hydrostatic pressure (i.e., remain turgid) to be physiologically active; in most plants, osmotic potential of the cell or apoplast is the only component that live cells can adjust to modify water potential within hours (Korolev et al. 2000). In the long term, plants can also adjust by changing the elasticity of their cell walls. By contrast with living cells, dead xylem cells have very dilute solutes, so their water potential can change only through changes in hydrostatic pressure.

Within a tissue, the water relations of individual cells may differ widely. This accounts for phenomena such as stomatal opening and closure (Sect. 5.4.2), leaf rolling and movements (Sect. 6.2), and **tissue tension**. Tissue tension plays a role in herbaceous stems (e.g., of Asteraceae), where the outer layers of the stem tissue are held in a state of longitudinal tension by more internal tissues that are held in a reciprocal state of compression (Niklas & Paolillo 1998). This can readily be demonstrated by cutting a stem of celery (*Apium graveolens*) parallel to its axis. Upon cutting, the stem halves curl outward, illustrating that the inner cells were restrained by outer cells and unable to reach their fully expanded size before the cut. Tissue tension plays a major role in the closing mechanism of the carnivorous plant *Dionaea muscipula* (Venus' fly trap) (Sect. 3.1 of Chapter 9F on carnivory).

4.1 Osmotic Adjustment

As the soil dries, causing soil water potential to decline, live cells may adjust their water potential by accumulating osmotically active compounds which reduce the osmotic potential (ψ_π), and, therefore, their water potential (ψ_w). As a result of an increased concentration of osmotic solutes, cells have a higher turgor (ψ_p) when fully hydrated, provided the cell walls maintain their original rigidity (Sects. 4.2 and 4.3). In addition, they lose their turgor at a more negative water potential compared with the turgor-loss point of nonacclimated plants (Rodriguez et al. 1993, Nabil & Coudret 1995), thereby enabling the plant to continue to acquire water from soil at low soil water potentials. The osmotic solutes in the vacuole, which constitutes most of the volume of the plant cell, are often inorganic ions and organic acids. Such compounds reduce the activity of cytoplasmic enzymes, and plants tend to synthesize other **compatible solutes** in the cytoplasm (i.e., solutes that do not have a negative effect on cell metabolism). Such compatible solutes include glycinebetaine, sorbitol, and proline. These compounds are not highly charged,

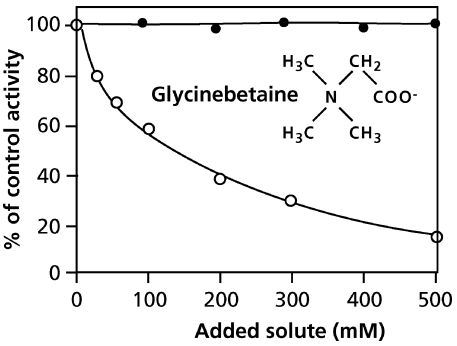

FIGURE 7. The effect of NaCl (*open symbols*) and glycinebetaine (*filled symbols*) on the activity of malate dehydrogenase from barley leaves (Pollard & Wyn Jones 1979). The chemical structure of glycinebetaine, a compatible solute in many higher plant species, is also given.

and they are polar, highly soluble, and have a larger hydration shell (the layer of water molecules surrounding each molecule) than denaturing molecules, like NaCl. Compatible solutes do not interfere with the activity of enzymes at a concentration where NaCl strongly inhibits them (Fig. 7). Transgenic *Nicotiana tabacum* (tobacco) plants that accumulate *D*-ononitol, because of insertion of the gene encoding *myo*-inositol *O*-methyltransferase, show less inhibition of photosynthesis by water stress and salinity than do wild-type plants (Sheveleva et al. 1997). Some compatible solutes (e.g., sorbitol, mannitol, and proline) are effective as hydroxyl radical scavengers in vitro, but this is not the case for glycinebetaine (Smirnoff & Cumbes 1989). A role as radical scavenger in vivo has been established for mannitol, using transgenic *Nicotiana tabaccum* (tobacco) plants that accumulate mannitol in their chloroplasts (Shen et al. 1997a). Polyols probably shield susceptible thiol-regulated enzymes from inactivation by hydroxyl radicals (Shen et al. 1997b).

Some plants accumulate fructans (i.e., one glucose molecule linked to two or more fructose molecules), when exposed to water stress. Fructan accumulation confers greater drought resistance, partly because these solutes play a role in osmotic adjustment, but presumably also because fructans protect membranes. Transgenic tobacco plants (*Nicotiana tabacum*) that contain the genetic information that enables them to accumulate fructans show greater desiccation resistance than wild-type plants (Pilon-Smits et al. 1995).

4.2 Cell-Wall Elasticity

When cells lose water, they decrease in volume until the turgor is completely lost. The extent to which the

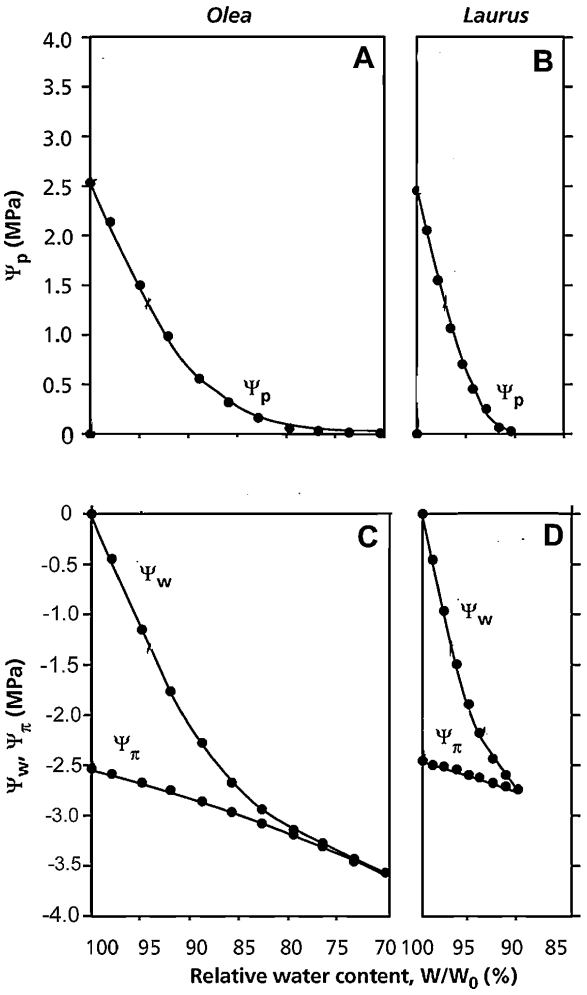

FIGURE 8. Höfler diagrams, relating turgor pressure (Ψ_p), osmotic potential (Ψ_π), and water potential (Ψ_w), to relative water content for leaves of two Mediterranean tree species. (A) *Olea oleaster* (olive) and (B) *Laurus nobilis* (laurel). The bulk elastic modulus, ε, is the initial slope of Ψ_p with relative water content (Lo Gullo & Salleo 1988). Copyright Trustees of The New Phytologist.

cells can decrease in volume and hence the extent to which their water potential can decrease until the turgor-loss point is reached depends on the **elasticity** of their cell walls. Cells with highly elastic walls contain more water at full turgor; hence, their volume can decrease more, before the turgor-loss point is reached. The elasticity of the cell walls depends on chemical interactions between the various cell-wall components. Cells with elastic walls can therefore store water that they accumulate during the night and gradually lose again during the day due to the leaf's transpiration. In this way, they can afford to lose more water temporarily than is imported from the root environment.

A greater elasticity of cell walls is expressed as a smaller **elastic modulus,** ε (MPa), which describes the amount by which a small change in volume (ΔV, m^3) brings about a change in turgor, $\Delta\psi_p$ (MPa) at a certain initial cell volume:

$$\Delta\Psi_p = \varepsilon\Delta V/V, \text{ or } \varepsilon = d\Psi_p/dV.V \qquad (4)$$

The **bulk elastic modulus** (ε) can be derived from **Höfler diagrams** (Fig. 8); they refer to an entire leaf, rather than individual cells. More commonly, ε is calculated from plots of –1/ vs. the relative water content (Schulte & Hinckley 1985). [Relative water content (RWC) is defined as the water content of the tissue, relative to that at full hydration.] At full turgor (RWC = 100%), the change in turgor for a change in volume is much greater for *Laurus nobilis* (sweet bay) than for *Olea oleaster* (olive) (i.e., ε is greater for *Laurus nobilis*) (Table 4). The greater elasticity of the leaf cell walls of *Olea oleaster* from drier sites, in comparison with species from moister sites, implies that its cells can lose more water before they reach the **turgor-loss point** (Table 4); they have cells that can shrink more during periods of water shortage without damage to the cytoplasm. In other words, they have a greater capacity to store water.

Table 4. The elastic modulus of 1-year-old leaves of three Mediterranean evergreen, sclerophyllous trees, growing in the same Mediterranean environment, but at locations differing in water availability*

Species	Elastic modulus, at full turgor (MPa)	
	Wet season	Dry season
Olea oleaster	19.5	19.3
Ceratonia siliqua	20.5	24.5
Laurus nobilis	28.1	40.7

***Source*: Lo Gullo & Salleo (1988).**
***Olea oleaster* (olive) is the most desiccation-tolerant, followed by *Ceratonia siliqua* (carob); *Laurus nobilis* (laurel) grows at somewhat wetter locations, near river banks. The elastic modulus was determined at full turgor, in both May (wet season) and September (dry season). Additional information about these trees is included in Figs. 8 and 28.**

The elastic modulus can also be determined for individual cells, by using a **pressure probe** (Tomos & Leigh 1999). It involves the insertion in a cell of a small glass microcapillary. The fluid in the capillary will then be pushed back by the turgor pressure. The force to push back the meniscus of the fluid to its position before insertion is then measured, using a sensitive pressure transducer. In this way, the pressure in individual cells, such as stomatal guard cells, can be measured very accurately (Sect. 5.4.2).

4.3 Osmotic and Elastic Adjustment as Alternative Strategies

Osmotic and **elastic adjustment** are alternative strategies for a species to acclimate to water stress. Osmotic adjustment and simultaneous increases in elasticity are not an option, because accumulation of solutes would cause cells to swell, and not lead to the same decrease in water potential (Fig. 9; White et al. 2000, Ngugi et al. 2003, Mitchell et al. 2008). An increase in elasticity (a lower elastic modulus) thus contributes to turgor maintenance in much the same way as a decrease in osmotic potential (greater osmotic adjustment).

In nonadapted species, leaves lose turgor ($\psi_p = 0$) at higher relative water content and higher leaf water potential (Table 4; Nabil & Coudret 1995). The protoplasm of the leaf cells of adapted species [e.g., *Olea oleaster* (olive), *Eucalyptus wandoo* (wandoo)] must have the capacity to tolerate more negative water potentials to survive the greater loss of water from their cells with more elastic cell walls (Lo Gullo & Salleo 1988, Mitchell et al. 2008).

Comparing hemiepiphytic *Ficus* (fig) species, which start their life as epiphyte and subsequently establish root connections with the ground, leaf cells have a less negative osmotic potential at full turgor (less osmotic adjustment) and lower bulk elastic modulus (more elastic cells) in the epiphytic stage than they do as terrestrial trees. Lower osmotic potentials (in the tree stage) should allow leaves to withstand greater evaporative demand without wilting, in order to mobilize water from deeper and/or drier soil layers. This strategy, however, requires that there be some substrate moisture in the first place. Given the substrate of the epiphyte which dries rapidly, frequently, and uniformly, a more favorable strategy is to gather water from the aerial rooting medium when it is readily available for storage in highly elastic leaf cells (Holbrook & Putz 1996).

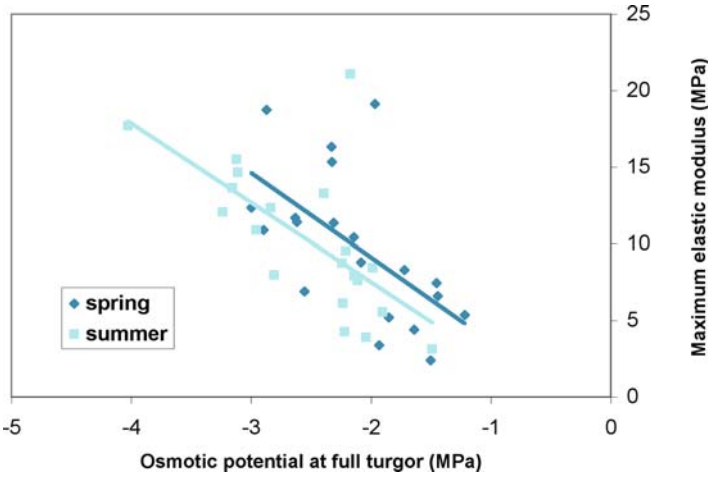

Figure 9. Osmotic potential at full turgor ($\Psi_{\pi\,100}$, MPa) vs. maximum bulk tissue elasticity (ε_{max}, MPa) for spring and summer for 20 species in their natural habitat, in the southwest of Australia, which is characterized by a Mediterranean climate (after Mitchell et al. 2008).

4.4 Evolutionary Aspects

The capacity to adjust the concentration of **osmotic solutes** and the **elasticity** of the leaves' cell walls are both under genetic control. There is a wide range of species of the genus *Dubautia* (Asteraceae), some of which are restricted to dry habitats and others to moister sites. They are therefore ideally suited to an analysis of the survival value of specific traits related to plant water relations. Individuals of the species *Dubautia scabra*, which is restricted to a relatively moist 1935 lava flow in Hawaii, have less negative water potentials, lower turgor, and a higher elastic modulus (less elastic cells) than those of *Dubautia ciliolata*, which is restricted to an older drier lava flow (Robichaux 1984). These differences in tissue elastic properties have a marked influence on diurnal turgor maintenance. Diurnal water potentials of *Dubautia ciliolata* from drier sites are more negative than those of *Dubautia scabra*, but the turgor pressures are very similar throughout the entire day.

A wider comparison of six other *Dubautia* species from Hawaii confirms the results obtained with *Dubautia scabra* and *Dubautia ciliolate* (Robichaux & Canfield 1985). The species from a wet forest (12300 mm rainfall per year) have larger leaves with a higher elastic modulus (lower cell-wall elasticity) than the ones from a dry scrub habitat (400 mm per year). The species in between these extremes show values for leaf size and wall elasticity that are intermediate. Cell-wall elasticity obviously allows maintenance of turgor without a major adjustment in osmotic potential.

As discussed in Sect. 4.1, **fructan accumulation** confers greater desiccation resistance. Some prominent fructan-accumulating families include Poaceae [*Triticum aestivum* (wheat), *Hordeum vulgare* (barley)], Liliaceae [*Allium cepa* (onion)], and Asteraceae [*Helianthus tuberosus* (Jerusalem artichoke), *Cichorium intybus* (chicory)]. In plants, the synthesis of fructans involves at least two enzymes. The first catalyzes the formation of a trisaccharide (one molecule of glucose and two fructose molecules); the second extends this trisaccharide with fructose residues (Pollock & Cairns 1991). Fructan-accumulating taxa increased some 30–15 million years ago, when the climate shifted toward seasonal droughts. The distribution of present-day fructan-accumulating species corresponds with regions of seasonal droughts. The appearance of the genes coding for fructan-synthesizing enzymes probably allowed the fructan flora to cope with seasonal droughts (Hendrey 1993). The deduced amino acid sequence of key enzymes in the formation of fructans shows a high homology with plant **invertases**, which are ubiquitous enzymes that hydrolyze sucrose, producing glucose and fructose (Sprenger et al. 1995, Vijn et al. 1997). Therefore, the genes in fructan-producing taxa may have emerged as a result of duplication of the invertase gene, followed by slight modification.

5. Water Movement Through Plants

5.1 The Soil—Plant—Air Continuum

Water transport from the soil, through the plant, to the atmosphere, takes place in a soil–plant–air continuum that is interconnected by a continuous film of liquid water (Fig. 10). Water moves through the plant along a **gradient**, either from high to low **water potential** (if transport occurs across a selectively permeable membrane), from high to low **hydrostatic pressure** (if no such membrane is involved), or from a high to a low **water vapor concentration**. The low concentration of water vapor in the air, compared with that inside the leaves, is the major driving force for water loss from leaves which, in turn, drives water transport along the gradient in hydrostatic pressure between the xylem in roots and leaves, and down a gradient in water potential between the soil and the cells in the roots (Fig. 10). As soils dry out, there are parallel decreases in soil water potential and plant water potential, both immediately before dawn (when water stress is minimal, and the water potentials of soil and plant are thought to be in equilibrium) and at midday (when water stress is maximal) (Fig. 11). The passive movement of water along a gradient differs strikingly from plant acquisition of carbon and nutrients which occurs through the expenditure of metabolic energy. The steepest gradient in the soil–plant–atmosphere continuum occurs at the leaf surface which indicates that the stomata are the major control point for plant water relations. There are substantial resistances to water movement in soil, roots, and stems, however, so short-term stomatal controls are constrained by supply from the soil and resistances to transfer through the plant. An appreciation of these controls that operate at different timescales is essential to a solid understanding of plant water relations.

Water flux, J ($mm^3\ s^{-1}$) (i.e., the rate of water movement) between two points in the soil–plant– atmosphere system, is determined by both the gradient between two points and the resistance to flow between these points. The **conductance**, L_p ($mm^3\ s^{-1}\ MPa^{-1}$) (i.e., the inverse of resistance), is often a more convenient property to measure. As pointed out

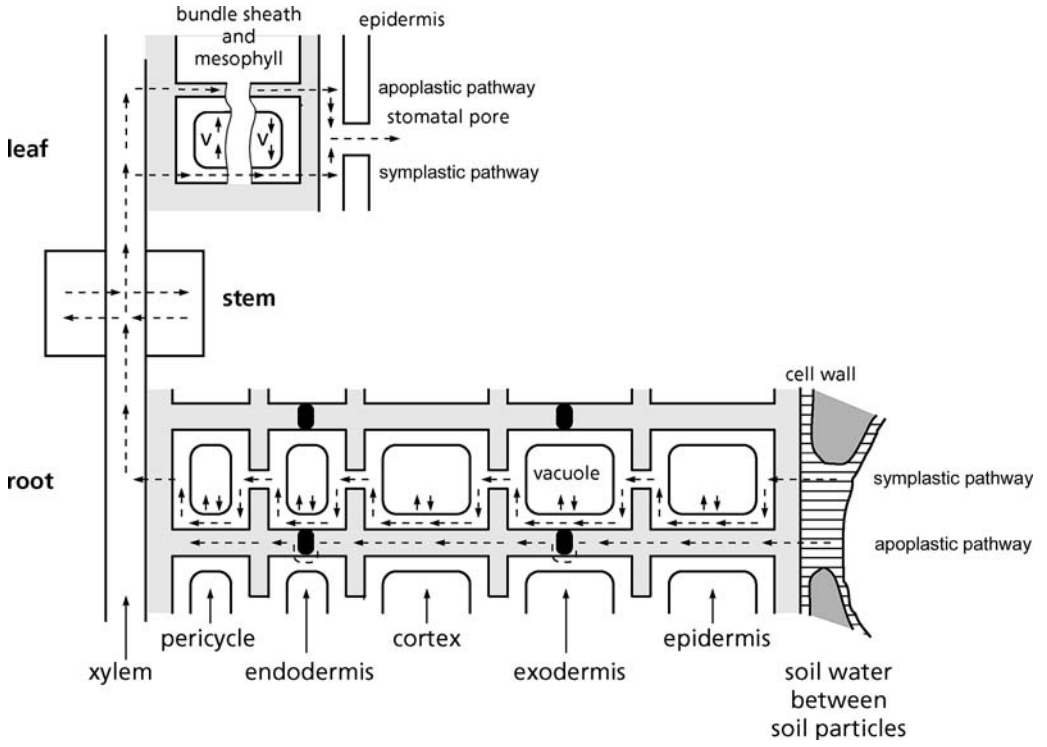

FIGURE 10. Water transport in the soil–plant–air continuum. Water can move through the cell walls (apoplast), or cross the plasma membrane and move through the cytoplasm and plasmodesmata (symplast). Water cannot move through the suberized Casparian bands in the wall of all endodermal and exodermal cells, including passage cells. Note that the exodermis is absent in some species, in which case water can move from the soil through the apoplast as far as the endodermis.

earlier, the gradient along which water moves is *not* invariably a gradient in water potential ($\Delta\psi_w$, MPa), but it may be a gradient in hydrostatic pressure ($\Delta\psi_p$, MPa), or in water vapor concentration (Δw, the difference in mole or volume fraction of water vapor in air in the intercellular spaces and in air; Equation (2) in Chapter 2A on photosynthesis). In the case of a gradient in water potential, we can write

$$J = L_p \Delta\Psi_w \qquad (5)$$

During the day, the water potential of leaves often declines, when the conductance of the roots or stems is too low to supply sufficient water to the leaves to meet their transpirational water loss. This is not invariably found, however, because roots in drying soil send signals to the leaves which reduce the stomatal conductance and hence water loss (Sect. 5.4.1).

5.2 Water in Roots

When plants are growing in moist soils, cell membranes are the major resistance to water flow through the roots. Water travels along three pathways from the outside to the inside of the root. If there is no **exodermis** (an outermost layer of root cortical cells adjacent to the epidermis with suberin-coated cell walls; Fig. 12A), then water may move through the **apoplast** (i.e., the cell walls and other water-filled spaces outside of living cells), or through the **symplast** (i.e., the space comprising all the cells of a plant's tissues connected by plasmodesmata and surrounded by a plasma membrane) (Fig. 10), or through the cells by crossing through the walls, cytoplasms, and vacuoles (and plasma membranes and tonoplasts). The latter is termed the **transcellular path** and, under normal conditions, is the main pathway used by water. Water must eventually enter the **symplast** at the **endodermis**, which is the innermost cortical layer of cells and has **Casparian bands**. The radial and transverse walls of the endodermal and exodermal cells are rich in cell-wall proteins, and impregnated with lignin, suberin, and wax (Zeier et al. 1999, Ma & Peterson 2003), which forms a **Casparian band** (Fig. 12A). These hydrophobic bands completely encircle each

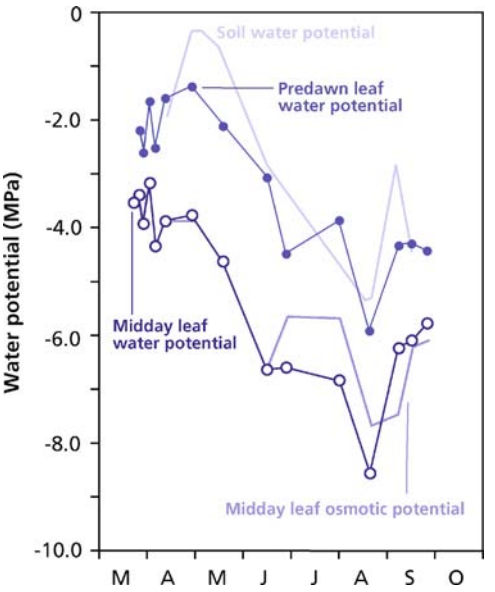

FIGURE 11. Seasonal changes in soil water potential, predawn leaf water potential, midday leaf water potential, and midday leaf osmotic potential in the C_4 plant *Hammada scoparia* (after Schulze 1991).

endodermal cell and prevent further transport of water through the apoplast. Even when the neighboring cortical and pericycle cells plasmolyze, the plasma membrane of the endodermal cells remains attached to the Casparian band. **Plasmodesmata**, which connect the endodermis with the central cortex and pericycle, remain intact and functional during the deposition of suberin lamellae. More importantly for the passage of water, the Casparian bands do not occur in the tangential walls of the endodermal cells, so water may pass through the plasma membranes lining these walls. **Passage cells** frequently occur in both the endodermis and the exodermis; in the endodermis, they are typically located in close proximity to the xylem (Fig. 12B). Passage cells have Casparian bands, but the suberin lamellae and thick cellulosic (often lignified) walls that characterize other endodermal and exodermal cells in some species are either absent or are formed at a much later stage of development. The passage cells become the only cells that present a plasma membrane surface to the soil solution once the epidermal and cortical cells die which occurs naturally in some herbaceous and woody species. Passage cells then provide areas of low resistance to water flow (Peterson & Enstone 1996).

In most plants, water entry into the symplast must occur at the **exodermis**, which has cell properties similar to the endodermis. Only 9% of all investigated species have either no exodermis or have a hypodermis without Casparian bands and suberin lamellae (Enstone et al. 2003). At the endodermis or exodermis, water must enter the cells, passing at least the plasma membrane, before it can arrive in the xylem tracheary elements (vessels or tracheids). Like other organisms, plants have a family of **water-channel proteins**, usually called "**aquaporins**", which are inserted into membranes and allow passage of water in a single file. Water-channel proteins in the plasma membrane play a vital role in water uptake by plants by reducing the resistance to water flow along the transcellular path (Daniels et al. 1994, Maggio & Joly 1995). The number of water-channel proteins decreases during the night and starts to increase again just before dawn which suggests rapid turnover. Water-channel proteins are also "gated", and affected by phosphorylation, cytosolic pH, Ca^{2+}, pressure, solute gradients, and temperature (Tyerman et al. 2002, Tournaire-Roux et al. 2003, Chaumont et al. 2005). Environmental factors that affect the roots' hydraulic conductance affect either the number or the status of the water channels.

At **low temperature**, when membrane lipids are less fluid and membrane proteins are somewhat immobilized, the resistance of the plasma membrane to water flow is high. Adaptation and acclimation to low temperature generally involves a shift to more unsaturated fatty acids which increases the fluidity of these membranes at low temperature. The resistance to water flow is also high in plants exposed to soil **flooding**, which results in a low oxygen concentration in the soil, followed by inhibition of the normal aerobic respiration and cytosol acidosis. This decreased pH reduces the activity of the water-channel proteins and hence the roots' hydraulic conductance (Sect. 5.6 of Chapter 7 on growth and allocation; Zhang & Tyerman 1999, Chaumont et al. 2005). An excess of water in the soil may, paradoxically, cause symptoms that also occur in water-stressed plants: wilting, accumulation of ABA, and stomatal closure (Sect. 5.6.2 of Chapter 7 on growth and allocation).

As the soil dries, roots and soils shrink which reduces the contact between roots and the soil water films, as well as the conductance of water flow into the root. In dry environments, the contact between roots and soil is the greatest resistance to water flux from soil to leaves. Plants increase root conductance primarily by increasing allocation to production of new roots. Root hairs may be important in that they maintain contact between roots and soil. The role of mycorrhizal associations in water transport is discussed in Sect. 2.7 of Chapter 9A on

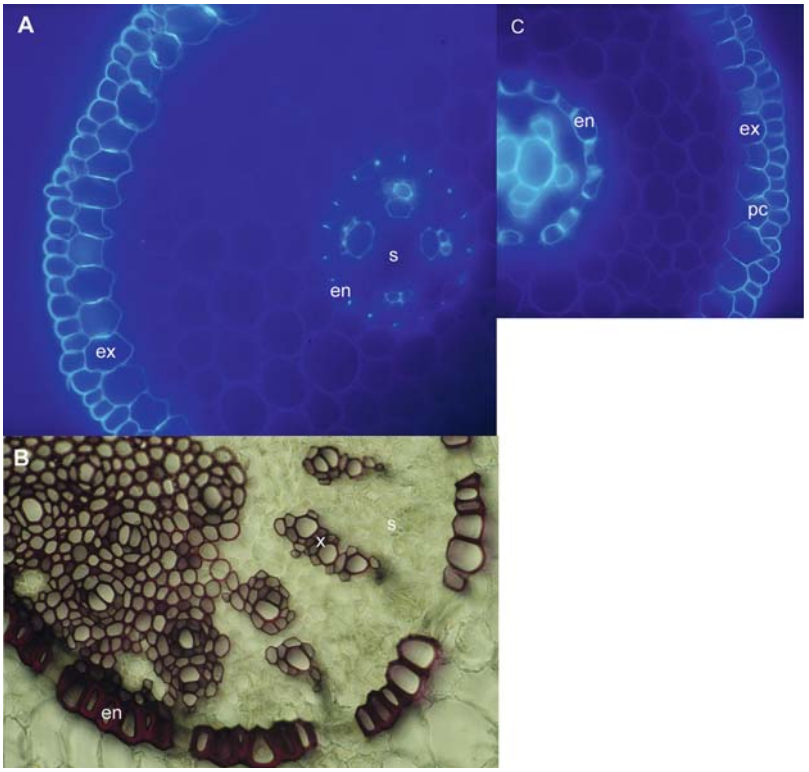

FIGURE 12. (A) Transverse section of an adventitious root of *Allium cepa* (onion). The endodermis (en) and exodermis (ex) both have a Casparian band. The cells of the exodermis also have suberin lamellae. The section has been stained with berberine-aniline blue and viewed with UV light. (B) Cross-section of an orchid (*Phalenopsis* sp.) aerial root showing the endodermis (en), several passage cells (pc), and the xylem (x) within the stele (s). Except for the passage cells, the endodermal cells have thick, lignified, tertiary walls. Application of phloroglucinol–HCl has stained lignified walls red. (C) Cross-section of an onion root (*Allium cepa*), stained with berberine–aniline blue and viewed with UV light, to show the walls of the epidermis and exodermis. Note the passage cell (pc) in the exodermis; it lacks fluorescence on its inner tangential wall (courtesy D.E. Enstone, Biology Department, University of Waterloo, Canada).

TABLE 5. Above-ground and below-ground biomass and the root mass ratio in various forest ecosystems, partly grouped by climate, climatic forest type, and species. *

Ecosystem	Above-ground biomass (g m^{-2})	Below-ground biomass (g m^{-2})	Root mass ratio (g g^{-1})
Boreal			
Broadleaf deciduous	50	25	0.32
Needle-leaf evergreen	30–140	7–33	0.20–0.30
Cold-temperate			
Broadleaf deciduous	175–220	25–50	0.13–0.19
Needle-leaf deciduous	170	40	0.18
Needle-leaf evergreen	210–550	50–110	0.14–0.28
Warm-temperate			
Broadleaf deciduous	140–200	40	0.21
Needle-leaf evergreen	60–230	30–35	0.15

Source: Vogt et al. (1996).
* RMR, ratio of root mass, and total plant mass.

symbiotic associations. A high root mass ratio (RMR, root mass as a fraction of total plant mass) is typical of any plant grown under dry conditions, and drought-adapted C_3 species typically have higher root mass ratios than do nonadapted C_3 species. The very few studies that compare the root mass ratio of C_3 and C_4 species suggest that RMR is lower in C_4 which correlates with their higher water-use efficiency (Sect. 9.4 of Chapter 2A on photosynthesis; e.g., Kalapos et al. 1996). When these adaptations and acclimations to low temperature or low water supply are combined in natural vegetation patterns, above-ground biomass declines dramatically along a gradient of increasing aridity, but root biomass often remains relatively constant (Table 5), as a result of an increased root mass ratio.

In extremely dry soils, where the soil water potential is lower than that of plants, and roots can no longer extract water from soil, it may be advantageous to increase root resistance. For example, cacti shed fine roots in summer and so prevent water loss to soil. The Sonoran Desert plant *Agave deserti* quickly produces new roots (**rain roots**) within 24 hour after a shower to exploit new sources of soil moisture (Nobel et al. 1990). Some plants have **contractile roots**. These decrease in length and increase in width, and so maintain hydraulic contact with the surrounding soil. During root contraction in *Hyacinthus oriemntalis* (hyacinth), mature cortical cells increase in diameter while decreasing in length, suggesting a change in wall extensibility in one or more directions (Sect. 2.2 of Chapter 7 on growth and allocation; Pritchard 1994). [Contractile roots also offer the explanation for why geophytes tend to pull themselves into the ground over the years (Pütz 1996).]

Many of the dominant woody species growing in arid and semi-arid conditions have **dual** or **dimorphic root systems**. Shallow, superficial roots operate during the wet season, and the deep-penetrating part of the root, which is usually located in relatively unweathered bedrock or deep sands, operates during the dry season. Because most of the nutrients tend to be in the superficial soil layers, most of the nutrients will be taken up by the shallow roots. Plants that grow on shallow soil or even bare rock in the Israeli maquis continue to transpire during the entire summer by growing roots in rock fissures. On such sites with shallow soil in semi-arid climate conditions, roots of some plants [e.g., *Arctostaphyllos viscida* (whiteleaf manzanita) and *Arbutus menziesii* (Pacific madrone)] of the Pacific Northwest in the United States, can utilize water from the bedrock. Roots of such plants occupy rock fissures as small as 100 μm. The cortex of such roots may become flat, with wing-like structures on the sides of the stele (Zwieniecki & Newton 1995).

Water in the xylem vessels of the roots is normally under tension (negative hydrostatic pressure). At night under moist conditions and low transpiration, however, the hydrostatic pressure may become positive. The widely held view is that under these conditions the loading of solutes into the xylem is sufficiently rapid to produce a very negative osmotic potential in the xylem. Water may then move osmotically into the xylem vessels and create a positive hydrostatic pressure, forcing water up through the xylem into the stem. This phenomenon is known as **root pressure**. Recent measurements, using cryo-analytical microscopy in situ, have shown that solute concentrations in the xylem sap of primary roots of *Zea mays* (corn) are fairly low, also when the hydrostatic pressure in the xylem is high (Enns et al. 1998). This suggests that the simple explanation for root pressure outlined above might not be correct. As an alternative, a mechanism similar to the putative mechanism for stem pressure (Sect. 5.3.4) has been suggested (McCully et al. 1998).

Whatever the exact mechanism that accounts for root pressure is, it can push xylem sap out through the leaf tips of short-statured plants: **guttation**, which is a phenomenon that contributes to the formation of "dew" on leaves. Root pressure is important in reestablishing continuous water columns in stems, after these columns break (see later). Using Equation (7) in Box 3.1, we can calculate that xylem sap containing 10–100 mM solutes can be "pushed" up the stem as high as 2.6–26 m. The liquid exuding from tree stumps and wounds in stems may also result from root pressure [e.g., in *Vitis vinifera* (grapevine) and *Betula nigra* (river birch)]; however, the xylem sap exuded by palms and several maples [e.g., *Acer saccharum* (sugar maple) and *Acer nigrum* (black sugar maple)] which is often tapped commercially to make sugar or syrup, results from stem pressure, and *not* from root pressure (Kramer 1969).

Hydraulic lift is the movement of water from deep moist soils to drier surface soils through the root system. In C_3 and C_4 species, this occurs primarily at night, when stomates are closed, so that the plant is at equilibrium with root water potential. In the CAM plant *Yucca schidigera* in the Mojave Desert, however, hydraulic lift occurs during the day (Yoder & Nowak 1999). This agrees with maximum stomatal conductance at night in CAM plants (Sect. 10.2 of Chapter 2A on photosynthesis). Under these circumstances, water will move from deep moist soils with a high water potential into the root and out into dry surface soils of low water potential. Although hydraulic lift was first

observed in dry grasslands (Caldwell & Richards 1989), it also occurs during dry periods in temperate forests, when high leaf area and high transpiration rates deplete water from upper soil horizons. For example, adult sugar maples (*Acer saccharum*) derive all transpirational water from deep roots. Between 3 and 60% of water transpired by shallow-rooted species without direct access to deep water, however, comes from water that is hydraulically lifted by sugar maple (Dawson 1993). Deep groundwater often has a different isotopic signature than does surface water, making it possible to determine the original source of water transpired by plants (Sect. 3.3).

Because water in soil can be redistributed via the roots from moist regions in either deep or shallow soil layers, the term **hydraulic redistribution** is now widely used (Burgess et al. 1998). Hydraulic redistribution can be measured using sap-flow sensors (Box 3.4). In large trees, this redistribution may also involve the stem, where, at night, water can flow upward in one sector of the stem, and downward in another (Burgess & Bleby 2006). This is due to the much greater axial conductance compared with the radial conductance for water movement in the stem.

Hydraulic redistribution occurs in Amazonian trees, and it has a major impact on climate over the Amazon. Model results show that hydraulic redistribution enhances photosynthesis and evapotranspiration significantly during the dry season. The water subsidy from hydraulic redistribution sustains transpiration at rates that deep roots alone cannot accomplish. The water used for dry-season transpiration is from the deep storage layers in the soil, recharged during the previous wet season. Hydraulic redistribution in the Amazon may increase dry season transpiration by 40%. Such an increase in transpiration over drought-stressed regions affects the seasonal cycles of temperature through changes in latent heat, thereby establishing a direct link between root functioning and climate (Lee et al. 2005).

Hydraulic redistribution can modify competitive interactions among plants in unexpected ways by resupplying water to shallow-rooted species during dry periods, thereby modifying both water supply and the conditions for nitrogen mineralization and diffusion in dry soils. For example, 20–50% of the water used by shallow-rooted *Agropyron desertorum* (crested wheatgrass) comes from water that is hydraulically lifted by neighboring sage brush (*Artemisia tridentata*) in the Great Basin desert of western North America (Richards & Caldwell 1987). We discuss hydraulic lift in this context in Sect. 5.2 of Chapter 9E on interactions among plants. Water flow into deeper soil layers via **hydraulic redistribution** has been demonstrated for several perennial grass species in the Kalahari Desert. Deuterium labeling shows that water acquired by roots from moist sand in the upper profile can be transported through the root system to roots deeper in the profile, and there released into the dry sand at these depths. This may serve as an important mechanism to facilitate root growth through the dry soil layers below the upper profile where precipitation penetrates, and allow roots to reach deep sources of moisture in water-limited ecosystems (Schulze et al. 1998). The same mechanism accounts for hydraulic redistribution, when water can be transported through roots at the break of the dry season. This phenomenon is probably significant to plant establishment and the reduction of waterlogging in certain soil types (Burgess et al. 1998, 2001a).

Fog can be an important source of moisture in many fog-inundated coastal ecosystems, for example in *Sequoia sempervirens* (coastal redwood) and species in the understory of coastal redwood forests of northern California. In summer, one fifth of the water in the trees and two-thirds of that in understory plants comes from inputs from fog. Fog water accounts for 13–45% of the trees' annual transpiration (Dawson 1998). It can also be a significant component for perennial grasses in northern California, where fog–water inputs can mitigate the summer drought for many species, likely giving an advantage to species that can use it over species that cannot (Corbin et al. 2005). The exact pathway via which water enters the leaf is not entirely clear, but it is unlikely to be via the stomata. **Hydathodes** on the leaf epidermis are probably involved in foliar water uptake in *Crassula* species in the Namib Desert in Southern Africa (Martin & Von Willert 2000).

5.3 Water in Stems

Ever since the phenomenon of atmospheric pressure was recognized, it has been evident that even a perfect vacuum pump cannot lift water any higher than 10 m. In addition, even a relatively small xylem vessel with a radius of 20 mm only accounts for about 0.75 m of sap ascent by capillary action; however, plants can pull water well beyond this limit. Some of them, like the giant redwood (*Sequoia gigantea*) in California or karri (*Eucalyptus diversicolor*) in Western Australia, lift substantial quantities of water close to 100 m daily. If a vacuum pump cannot lift water higher than 10 m, then the pressure in the xylem must be lower than that delivered by such a pump (i.e., it must be negative!).

Box 3.4
Methods to Measure Sap Flow in Intact Plants

Xylem sap-flow rates of whole plants, individual branches, or roots can be measured using a technique that uses heat as a tracer (Fig. 1). The stem, branch, or root is heated electrically, and the heat balance is solved for the amount of heat taken up by the moving sap stream which is then used to calculate the mass flow of sap in the stem. In the heat-pulse method, rather than using continuous heating, short pulses of heat are applied, and the mass flow of sap is determined from the velocity of the heat pulses moving along the stem. Alternatively, rates of sap flow can be determined from the temperature of sapwood near a continuously powered heater implanted in the stem (Smith & Allen 1996). Heat-based sap-flow techniques play a leading role in the study of transpiration and water relations of woody plants (e.g., Čermák et al. 1973, 2004, Wullschleger et al. 1998, Nadezhdina and Čermák 2003, Sakuratani).

Two of the techniques currently available to researchers are the compensation heat-pulse method and the heat-ratio method. Both use the heat-pulse principle, where the mass flow of sap is determined from the velocity of a short pulse of heat moving along xylem tissue through conduction and convection. The heat-ratio method was developed recently by Burgess et al. (2001b), whereas the compensation heat-pulse method has a long history. The theory of the compensation heat-pulse method is described in detail by Marshall (1958), Swanson & Whitfield (1981), and Smith & Allen (1996). Briefly, two temperature sensors are inserted to equal depths into the sapwood, and positioned above and below a similarly inserted line heater probe. The temperature probes are spaced asymmetrically from the heater such that the mid-point of the two probes is located at a fixed distance downstream (i.e., toward the crown) from the heater and all probes are in line with the axis of the plant stem. Following the release of a pulse of heat into the sap stream, heat moves toward the downstream temperature probe. Movement of the heat pulse to the mid-point between the temperature probes is indicated when both temperature sensors have warmed to the same degree. The time taken for the heat pulse to move this distance is used to calculate heat-pulse velocity:

$$\nu_h = \frac{x_d + x_n}{2fn} 3600 \qquad (1)$$

where v_h is heat-pulse velocity (cm h^{-1}), t_0 is the time to thermal equilibrium of the downstream and upstream temperature of the downstream and upstream temperature sensors, x_d and x_u are the distances (cm) from the heater probe of the downstream and upstream temperature sensors, respectively. A negative value is assigned to x_u because it is located on the opposite side of the heater from x_d (Bleby et al. 2004).

The theory of the heat-ratio method is described in detail by Burgess et al. (2001b). Briefly, temperature and heater probes are inserted into the sapwood in a similar manner to the compensation heat-pulse method, except that the heater probe is located at a point equidistant from the upstream and downstream temperature sensors (Fig. 1). Instead of a "distance-traveled-over time" approach to measuring v_h, the heat-ratio method measures the ratio of the increase in temperature at points equidistant upstream and downstream from a line heater, following the release of a heat pulse. Heat-pulse velocity is calculated as (Marshall 1958):

$$\nu = \frac{k \ln(\nu_1/\nu_2)}{x} 3600 \qquad (2)$$

where k is thermal diffusivity of wet (fresh) wood, x is the distance from the heater probe of either temperature probe, and v_1 and v_2 are increases in temperature at equidistant points (x cm) downstream and upstream, respectively (in relation to initial temperatures). Thermal diffusivity (k) is assigned a nominal value during measurements and is resolved empirically at a later stage using estimates of thermal conductivity, density, and specific heat capacity of fresh sapwood; variables are derived from simple measurements of the water content and density of sapwood (Bleby et al. 2004).

Heat-pulse methods can be used for accurate measurements of sap flow, provided a reliable calibration procedure is used to relate

continued

Box 3.4 *Continued*

the measured heat-pulse velocity to the actual sap flow. Correction factors are based on comparisons of heat-pulse measurements against actual rates of transpiration determined from measured weight loss of the trees growing in large lysimeters. The compensation heat-pulse method accurately measures flows down to a few cm h^{-1} (Green et al. 2003), but this method is unable to measure low rates of sap flow, due to its inability to distinguish heat-pulse velocities below a threshold velocity of 0.1 kg h^{-1} (3–4 cm h^{-1}). On the other hand, the heat-ratio method accurately describes sap flow at night when rates of flow are low (< 0.1 kg h^{-1}) or near zero (Bleby et al. 2004).

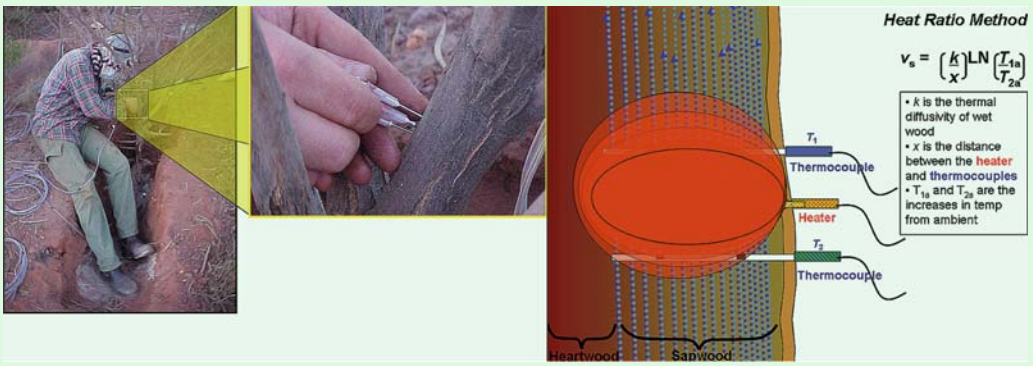

FIGURE 1. Sap-flow measurements using the heat-ratio method require insertion of probes in a stem, root, or branch (*left*). The middle probe is a heater, the other ones are thermocouples. If sap moves upward, then the heat pulse will reach the upper thermocouple before it reaches the lower one. The equation given in the figure (*right*) is used to calculate flow rates. Courtesy A. Grigg, School of Plant Biology, The University of Western Australia, Crawley, Australia.

Water in the xylem of the stem, in contrast to that in the live cells of the roots and stem, is under **tension** (negative hydrostatic pressure) in transpiring plants. As explained in Box 3.2, these suction tensions are due to interactions of water molecules with the capillaries in the cell walls of transport vessels. In fact, the water column in a 100 m tall tree is held in place by the enormous **capillary forces** in the xylem at the top of the tree. Due to the **cohesion** among water molecules from hydrogen bonding, the water column in the stem is "sucked upward" to replace water that is transpired from leaves. [This **cohesion theory** of water movement is generally ascribed to Böhm and Dixon and Joly (Böhm 1893, Dixon & Joly 1894, Dixon 1914, Steudle 1995), whereas, in fact, all of the elements of this theory were already described in 1727 by the English clergyman Stephen Hales (Floto 1999).] What is our evidence for such **suction tensions** or negative hydrostatic pressures and what exactly do they mean?

5.3.1 Can We Measure Negative Xylem Pressures?

Evidence for negative pressure in the xylem has been obtained using the **pressure chamber** (Scholander et al. 1965). A cut stem is placed in the chamber and sealed from the atmosphere, with the cut stem extending out (Fig. 13). A pressure is then applied just high enough to make the xylem sap in the stem appear at the cut surface. The positive pressure applied ("balancing pressure") is equal to the negative pressure in the xylem when the plant was still intact. Although there are problems using this technique when using plants with a low relative water content, the pressure chamber is widely used to assess the water potential in plants.

For a full appreciation of the ascent of sap in plants, we need to consider carefully the exact site the water is coming from that is pushed back into the xylem when pressure is applied to the pressure chamber (Box 3.2). This water is pushed out of the

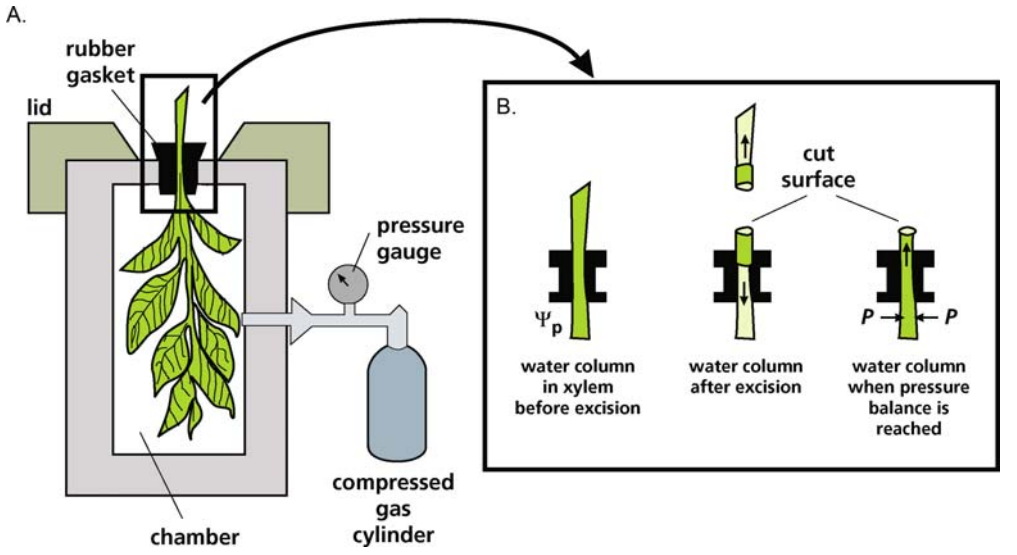

FIGURE 13. (*Left*) Schematic representation of the Scholander pressure chamber that is used for the measurement of negative hydrostatic pressures in the xylem (Ψ_p). A cut shoot, twig, root, or leaf is excised, and the negative Ψ_p in the xylem causes the water column to be drawn into, e.g., the leaf. (*Right*) A leaf (or other plant part) is mounted in a gasket and placed in the pressure chamber with the cut end protruding through the lid. The pressure in the chamber is increased, causing the xylem water column to be pushed upward in the xylem until it protrudes at the cut surface. At that point, the pressure inside the chamber (*P*) equals $-\Psi_p$. The osmotic potential of the xylem fluid is usually ignored, but can be determined by collecting sufficient xylem sap, avoiding contamination from surrounding cells.

many capillaries in the **walls** of the xylem vessels and adjacent cells, where it was held in place by strong **capillary forces** between the water molecules and the cell walls (Fig. 14). In a transpiring plant, water continuously moves from these capillaries to the intercellular spaces in leaves where the water potential is more negative, as long as the water vapor pressure is not saturated (Box 3.1). Due to the strong capillary forces, this water is replaced by water in the lumen of the xylem vessels. These strong capillary forces keep the entire water column in the xylem vessels in place and prevent it from retreating, such as that happens when the stem is cut. At physiological temperatures, the **cohesive forces** between the water molecules are so strong that the water column in the xylem will not break (but see Sect. 5.3.3).

The most compelling evidence in favor of the cohesion theory for the ascent of sap comes from measurements using a device that involves spinning a length of branch about its center to create a known tension based on centrifugal forces. Results of such experiments agree perfectly with those obtained with the pressure chamber (Holbrook et al. 1995). Tensions can, therefore, be created in xylem vessels and measured accurately by the pressure chamber; but what do these tensions really represent? When stating that the xylem is under tension, we do not actually mean the xylem conduit itself. Rather the suction tension, or negative hydrostatic pressure, refers to the **adhesive forces** that tightly hold the water in the small **capillaries** in the wall of the xylem conduits (Wei et al. 1999, Steudle 2001).

5.3.2 The Flow of Water in the Xylem

Hydraulic resistance in the shoot xylem accounts for 20–60% of the total pressure difference between the soil and the air in transpiring trees and crop plants (Sperry 1995). In woody plants, most of this pressure difference occurs in small twigs and branches, where the cross-sectional area of xylem is small (Gartner 1995). The water flow (J_v mm^3 mm^{-2} s^{-1} = mm s^{-1}) in xylem vessels is approximated by the **Hagen–Poiseuille equation**, which describes transport of fluids in ideal capillaries:

$$J_v = (\pi R_4 \Delta\Psi)/8\eta L \qquad (6)$$

where $\Delta\psi_p$ (MPa) is the difference in hydrostatic pressure, R (mm) is the radius of the single element with length L (mm) through which transport takes

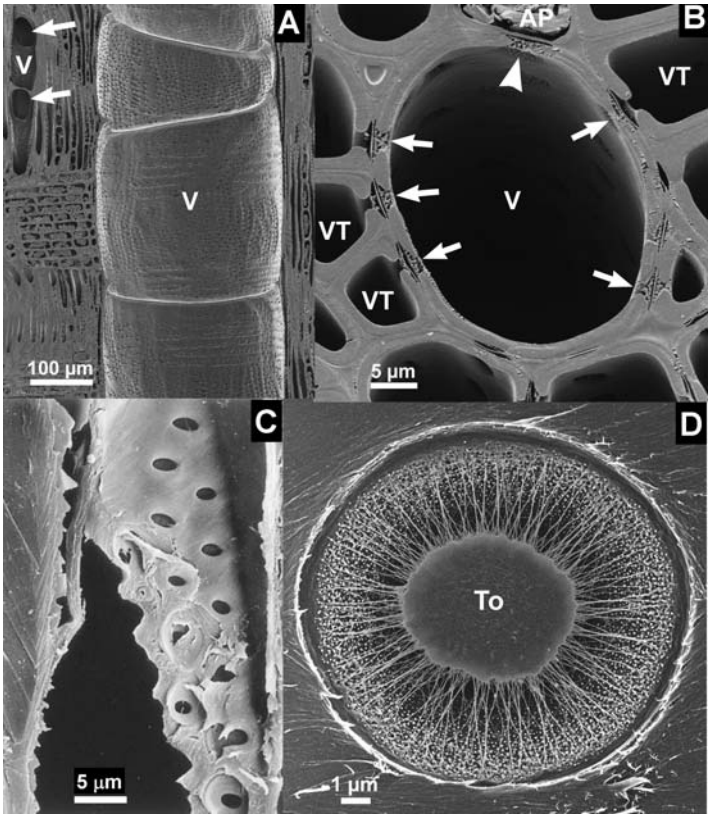

FIGURE 14. Field-emission scanning electron micrographs showing details of the xylem. (A) Radial section of the xylem of *Quercus crispula* (Mongolian oak), showing a wide vessel with numerous pits, and narrow vessel elements that are connected with simple perforations. (B) Transverse section of the xylem of *Eucalyptus camaldulensis* (river red gum), showing several vessel-to-vasicentric tracheid pits and vessel-to-axial parenchyma pits. (C) A scanning electron micrograph of the sapwood of *Populus nigra* (Lombardy poplar) hand-sectioned tangentially and slightly oblique. Bordered pits are shown between two adjacent vessels. Ray parenchyma cells are cut transversely in a vertical row to the right and left. Several pit apertures are seen (top central) in face view, with pit membranes visible through them. Lower down, the blade has removed the top borders of four pits, showing the interiors of the lower bordered pit chambers without any pit membranes. A pit can be seen centrally, half-closed by a torn pit membrane: The blade has folded the upper chamber above it revealing the inner cavity (indicated by arrow). The delicate pit membrane capillaries are sufficiently fine to filter fine carbon suspensions from Indian ink. They are normally supported from mechanical disruption by the borders if subjected to powerful pressure flow from liquids or gases. Gases can pass when the membranes are physically torn; alternatively, the suctions may be so great that air bubbles are pulled through the capillaries in the membranes initiating cavitation in the conduits in which the air bubble enters. (D) Intertracheary pit membrane of *Abies sachalinensis* (Sakhalin fir), a typical torus-bearing pit membrane of a gymnosperm. V, vessels; VT, vasicentric tracheids; AP, axial parenchyma; To, torus; arrows in A point to simple perforations; arrows in B point to vessel-to-vasicentric tracheid pits; the arrow head in B points to vessel-to-axial parenchyma pits (A, B, and D: courtesy Y. Sano, Hokkaido University, Sapporo, Japan; C: courtesy J.A. Milburn, University of New England, Australia).

place, and η (mm^2 MPa s) is the viscosity constant. This equation shows that the **hydraulic conductance** is proportional to the fourth power of the vessel diameter. The hydraulic conductance of a stem with only a few xylem vessels with a large diameter is, therefore, much higher than that of a stem with many more vessels with a small diameter, but the same total xylem area. In addition, the **pits** in the connecting walls of the tracheids impose a substantial resistance to water flow (Nobel 1991). Pits are narrow channels through the thick secondary walls of vessel elements (Fig. 14).

Plants differ widely with respect to the diameter and length of their xylem vessels (Table 6). Vessel

Table 6. Hydraulic conductance of xylem conduits, maximum velocity of water transport through the conduits and xylem diameter for stems of different types of plants.

	Hydraulic conductivity of xylem lumina ($m^2\ s^{-1}\ MPa^{-1}$)	Maximum velocity ($mm\ s^{-1}$)	Vessel diameter (m)
Evergreen conifers	5–10	0.3–0.6	<30
Mediterranean sclerophylls	2–10	0.1–0.4	5–70
Deciduous diffuse porous	5–50	0.2–1.7	5–60
Deciduous ring porous	50–300	1.1–12.1	5–150
Herbs	30–60	3–17	
Lianas	300–500	42	200–300

Source: Milburn (1979), Zimmermann & Milburn (1982).

length in trees varies from less than 0.1 m to well over 10 m or as long as the whole stem. There is no obvious advantage associated with either short or long vessels; it might be the accidental result of other variables of tree growth, such as mechanical requirement for fiber length (Zimmermann & Milburn 1982), or that small vessels are less prone to **freezing-induced cavitation**, the breakage of the water column in a transport vessel (Sect. 5.3.3). Vessel length tends to correlate with vessel diameter. In deciduous trees, xylem vessels produced early in the season tend to be longer and wider than the ones produced later in the year. The difference in xylem diameter between early and late wood shows up as **annual tree rings** of the trunk of these **ring-porous** trees. **Diffuse-porous** trees, on the other hand, with a random distribution of wide and narrow vessels throughout the year, such occur as in many tropical trees, do not always show distinct annual rings (Zimmermann 1983).

Vines, which have relatively narrow stems, have long vessels with a large diameter, compared with related species or with the species in which they climb (Sect. 5.3.6). Because the hydraulic conductance is proportional to the fourth power of the vessel diameter (Equation 6), the larger diameter compensates for the smaller total area. For example, the stem of the liana *Bauhinia fassoglensis* (creeping bauhinia) has a conductance equal to the tree *Thuja occidentalis* (white cedar) with a tenfold greater sapwood area (Ewers & Fisher 1991). Xylem vessels with a narrow diameter have the disadvantage of a low **hydraulic conductance**. Because more of the total xylem area is taken up by the xylem walls, they provide greater **mechanical strength**. The narrow xylem vessels, however, are also less vulnerable to freezing-induced cavitation (Sect. 5.3.6).

5.3.3 Cavitation or Embolism: The Breakage of the Xylem Water Column

Cavitation is not caused simply by breakage of capillary water columns which, at moderate temperatures, does not occur except at considerably higher tensions than ever occur in the xylem (i.e., in excess of 100 MPa) (Tyree & Sperry 1989). **Cavitation**, or **embolism**, however, does occur and leads to the filling of the xylem with water vapor and/or air, rather than water. Under water stress, when the tensions in the xylem become very high, cavitation is nucleated by the **entry of air** through the largest pores in the walls of the transport vessels, located in primary walls of the inter-conduit pits, the **pit membrane** (Figs. 14C,D and 15). Water then begins to evaporate explosively into the air bubble. Short acoustic pulses are registered during cavitation induced by water stress, allowing sound recordings to document cavitation rate. The bubble expands and interrupts the water column. Entry of air into the xylem conduit depends on the size of the pores in the pit membrane (Fig. 14C,D). The thin, porous areas in conduit walls allow passage of water between conduits, but not a gas–water meniscus. This minimizes the spread of air bubbles into neighboring conduits. The tension required to cause cavitation is a function of the permeability of the inter-conduit pits to an air–water interface, which depends on pore diameters (Pockman et al. 1995, Sperry 1995). Pore diameters range from less that 0.05 to more than 0.4 μm (as opposed to <0.01 μm in the cell wall proper), depending on species and location in the plant. Embolism reduces the ability to conduct water and, if severe enough, will limit growth.

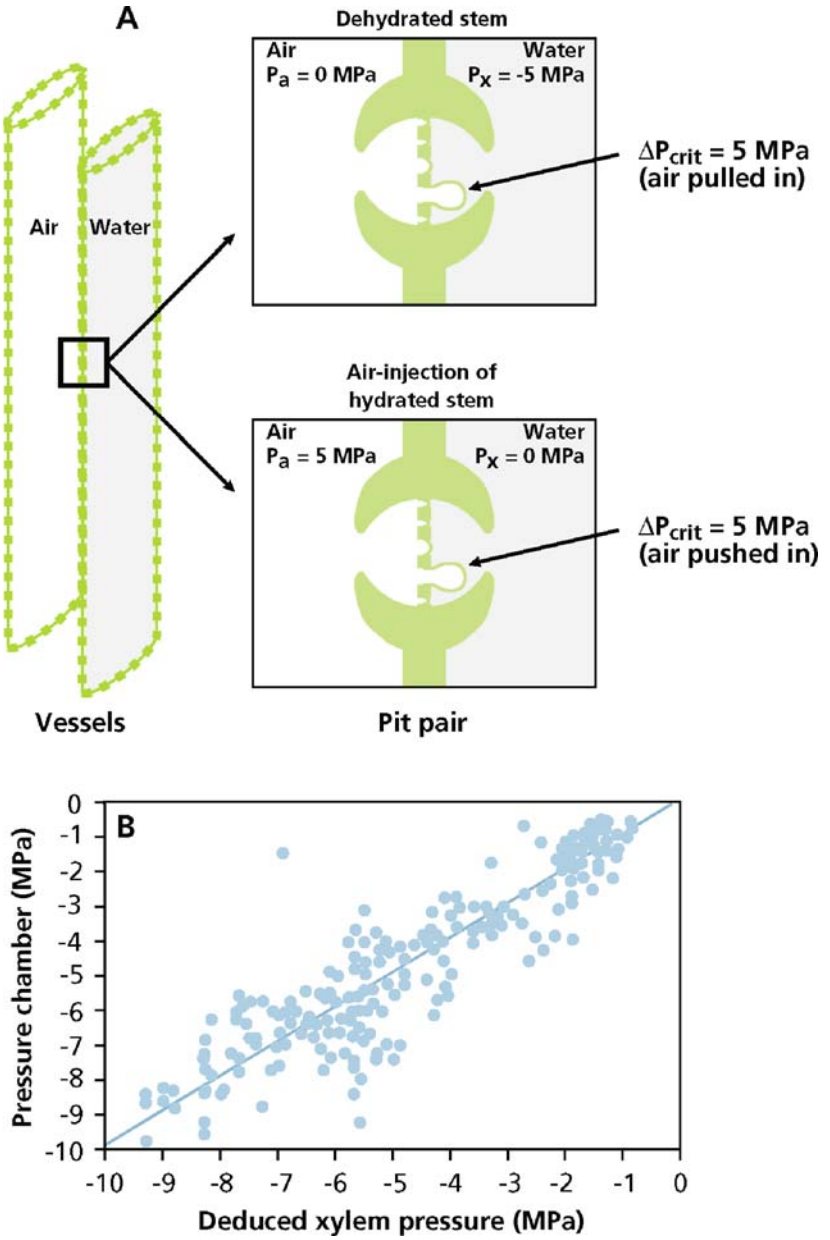

FIGURE 15. (A) Cavitation in dehydrating stems as affected by "air seeding". Two adjacent xylem vessels are shown. The one on the right is filled with xylem fluid; the one on the left has cavitated and is therefore filled with water vapor at a very low pressure, near vacuum: 0 MPa. Pits between the vessels allow water flow and prevent passage of an air–water meniscus in the event that one vessel becomes air-filled. The top part of the illustration shows how a small air bubble is pulled in through the pit membrane pores when the pressure difference between the two vessels exceeds a critical threshold. In the example shown, this occurs at a xylem pressure of –5 MPa. In the experimental design shown in the lower part of the illustration, the critical pressure difference is exceeded by pressurizing the air in the embolized vessel, while the fluid in the other vessel is at atmospheric pressure. Now an air bubble is pushed in. The top part illustrates what is happening in a real plant. (B) There is a very close agreement between pressure differences at which cavitation occurs in real plants, using the pressure chamber to determine the negative pressure in the xylem, and those achieved as illustrated in the bottom part of the top figure. This confirms that negative pressures occur in the xylem (after Sperry et al. 1996).

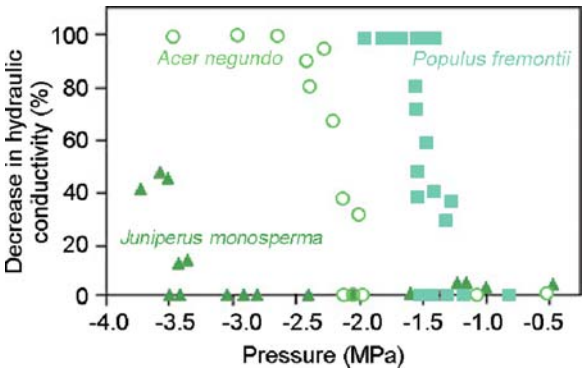

FIGURE 16. Decrease in hydraulic conductivity in the xylem of stems of *Populus fremontii* (poplar), *Acer negundo* (boxelder), and *Juniperus monosperma* (juniper) against xylem hydrostatic pressure. The hydrostatic pressure in the xylem was varied by centrifuging stems that were cut and then recut under water to a length of 260–400 mm (Pockman et al. 1995). Reprinted with permission from *Nature* 378: 715–716; copyright (1995) MacMillan Magazines Ltd.

Species differ considerably in their vulnerability to cavitation, with the less vulnerable species tending to be more **desiccation-tolerant** (Tyree & Sperry 1989). For example, stems of *Populus fremontii* (Fremont cottonwood) show complete cavitation at –1.6 MPa, whereas those of *Salix gooddingii* (Gooding's willow), *Acer negundo* (boxelder), *Abies lasiocarpa* (subalpine fir), and *Juniperus monosperma* (one-seed juniper) have a threshold at –1.4, –1.9, –3.1, and less than –3.5 MPa, respectively (Fig. 16). There are also phenotypic differences in vulnerability to cavitation which may be of similar magnitude as the differences between species. Root xylem in *Acer grandidentatum* (bigtooth maple) is more vulnerable when plants grow in wetter sites (Alder et al. 1996). Sun-exposed branches of *Fagus sylvatica* (beech) are less vulnerable than branches of the same tree that grow in the shade (Cochard et al. 1999). Because xylem conduits can only acclimate to new environmental conditions over prolonged periods, beech trees that are suddenly exposed to full light (e.g., after forest thinning) may experience xylem embolism if transpiration rates are not efficiently controlled.

The diameter of pores in pit membranes (Fig. 14A,B) determines the vulnerability of species to cavitation in response to water stress by determining the xylem tension at which an air bubble is sucked into the xylem lumen. It is not known whether pore diameter of the pit membrane also determines phenotypic differences in xylem vulnerability, but this is plausible. Because even the widest vessels in ring-porous trees are sufficiently narrow to prevent breaking of a water column other than by the mechanisms accounted for, conduit diameter has no relationship to the vulnerability to cavitation in response to drought stress (Fig. 17; Sperry 1995, Cochard et al. 1999).

Cavitation may also be caused by **freezing and thawing** of the xylem sap when it is under tension (Fig. 17). In this case, cavitation occurs at much lower tension and is induced by a different mechanism: dissolved gases in the sap are insoluble in ice and freeze out as bubbles. If these bubbles are large enough when tension develops during thawing, then they will grow and cause cavitation. When cavitation is caused by freeze-thaw cycles, we can predict that wide and long vessels will be more vulnerable than small ones. Differences in conduit diameter are the main factors that account for species differences in vulnerability to cavitation from

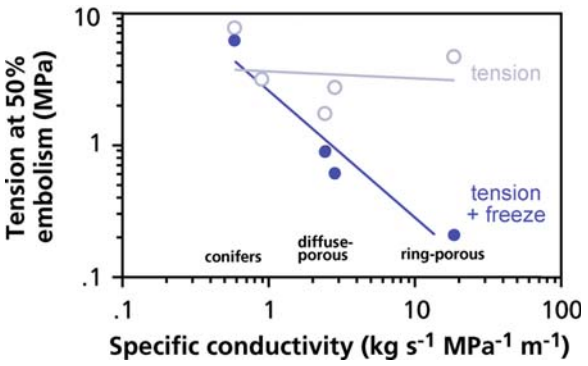

FIGURE 17. Tension at the time of 50% embolism as dependent on the size of the tracheids or vessels. The experiment was carried out with trees exposed to water stress (tension, *open circles*) and with trees exposed to a freeze-thaw cycle (tension + freeze, *solid circles*) (after Sperry & Sullivan 1992). Copyright American Society of Plant Biologists.

freeze-thaw events (Fig. 17). If the air freezes out as one large bubble, rather than a number of smaller ones, then the greater dissolved air content in larger conduits will give rise to larger bubbles that cause embolism at lower tensions (Sperry & Sullivan 1992). Most embolisms in temperate woody plants occur in response to freeze-thaw events during winter and during the growing season rather than in response to drought. Embolism correlates more closely with the number of freeze-thaw episodes than it does with degree of frost (Sperry 1995).

The capacity of xylem to withstand freeze-thaw embolisms has important consequences for the evolution and distribution of woody plants. Evergreen trees from cold climates are more likely to be actively transpiring (and therefore developing negative xylem potentials) when freeze-thaw events occur. It is probable for this reason that they have small tracheids that are less likely to cavitate and easier to refill (see later). The disadvantage of narrow conduits is a low conductance. Among deciduous woody plants there are ring-porous trees that produce large vessels during rapid growth in early spring and diffuse-porous species that have smaller diameter conduits. Ring-porous species cannot refill overwintering xylem, so their transpiration is entirely supported by current year's xylem, which therefore requires large-diameter vessels with high conductance. These species leaf out at least 2 weeks later than co-occurring diffuse-porous species, presumably because of their greater vulnerability to spring frosts (Sperry 1995). Some diffuse-porous species can refill embolized, overwinter conduits and are particularly successful in cold climates, whereas other diffuse-porous species cannot.

Embolism can also be induced by **pathogens**. Although it has been known for quite some time that vascular diseases induce water stress in their host by reducing the hydraulic conductivity of the xylem, embolism as a cause for this has received very little attention. In the case of Dutch elm disease, however, embolism precedes any occlusion of vessels by other means. The exact cause of embolism remains unclear. It might be due to a pathogen-induced increase in stomatal conductance or decrease of water uptake by the roots. Pathogens might also change the xylem sap chemistry. For example, millimolar concentrations of oxalic acid, which is produced by many pathogenic fungi, lower the surface tension of the xylem sap. In *Acer saccharum* (sugar maple) and *Abies balsamea* (balsam fir), **oxalic acid** reduces the tension at which air can enter the xylem (Tyree & Sperry 1989). Xylem conductivity can also change in response to the concentration of **cations** in the xylem fluid (Van Ieperen 2007).

Can embolism also be brought about by xylem-feeding **spittlebug nymphs** (*Philaenus spumarius*)? Frothy white "spittle" deposits of feeding spittlebug nymphs are familiar to all who have walked through fields and gardens in late spring and early summer. The water of the spittle comes from the xylem sap that is sucked up through the insect's stylet that is inserted into a single xylem conduit. Because the concentration of nutrients in the xylem sap is very low, these tiny insects pump huge quantities of liquid against a strong pressure gradient, and excrete up to 280 times their body mass in 24 h. How does the spittlebug avoid inducing cavitation? Saliva secreted by the insect forms a hardened lining between the stylet bundle and the plant tissues. This **salivary sheath** is continuous through the hole made by the stylet as it enters a vessel, and it extends into the vessel along the periphery beyond the breach. It allows the insects to feed from functioning vessels, without embolizing them. Embolized vessels, which are basically filled with water vapor, would be of no use for the spittlebug nymphs (Crews et al. 1998).

5.3.4 Can Embolized Conduits Resume Their Function?

Cavitated conduits can refill by **dissolution** of the bubble which can occur at moderately negative xylem pressures. Dissolution of bubbles under tension may require narrow conduits (Sperry 1995) which perhaps explains the tendency of desert plants and plants from cold environments to have narrow conduits (Sect. 5.3.5). When such a moderately negative water potential cannot be reached, the xylem remains filled with water vapor and the conduit no longer functions in water transport (Yang & Tyree 1992). Failure to refill cavitated vessels can sometimes be advantageous. For example, conduits of cactus xylem cavitate when soil gets extremely dry, preventing water from being lost from the body of the plant to the soil.

Functioning of the embolized vessels can be resumed upon refilling the vessel with water. This can occur at night under moist conditions, when **root pressure** builds up a positive xylem pressure. In more extreme cases, this may not occur until it rains (Fig. 18). When roots grow in wet soil, a solute concentration in the xylem sap of 100 mM exerts just enough positive pressure to balance a water column of about 35 m (0.25 MPa plus 0.1 MPa of ambient pressure; Sect. 5.2); therefore, it is unlikely that cavitated conduits in the top of a tall tree are ever refilled by root pressure. In *Fraxinus americana* (white ash),

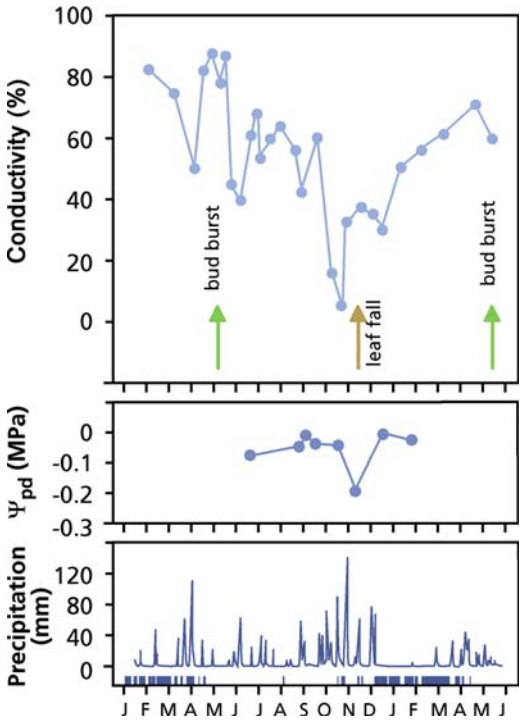

FIGURE 18. Seasonal changes of xylem embolism in apical twigs, expressed as percentage of hydraulic conductivity (*top*); predawn water potential (*middle*); precipitation at the site of the studied tree *Fagus sylvatica* (beech). The occurrence of subzero temperatures is marked by bars at the bottom of the lower graph. Arrows in the top figure indicate bud burst and leaf fall (after Magnani & Borghetti 1995).

Acer rubrum (red maple), and *Picea rubens* (red spruce) embolisms are repaired at night, however, despite the existence of tension in the xylem (Zwieniecki & Holbrook 1998).

Trees can also build up **stem pressure**. It is quite possible that stem pressure can also restore cavitated xylem conduits in stems. The exact mechanism that accounts for stem pressure is unknown. Canny (1997) has found evidence for **refilling** of embolized vessels in petioles of *Helianthus annuus* (sunflower) during the day, when transpiration rates are high. Refilling concurrent with transpiration appears to be quite common, raising the question of how embolized vessels can be refilled while the majority of the water in the xylem remains under tension (Tyree et al. 1999). Refilling of embolized conduits requires that water enter the vessel lumen while pressurizing the gas phase until it is forced back into solution (Fig. 19). This requires a local input of energy that may come from the activities of living cells adjacent to the xylem. It is hypothesized that water is released into the vessel lumen from these adjacent living cells in a manner similar to the process that leads to root exudation (Sect. 5.2). Water will move from living cells to the embolized vessel if an adequate driving gradient is present, e.g., involving active secretion of solutes by the living cells. Measurements of the osmotic concentration within repairing vessels, however, suggest that osmotic forces may not be adequate to explain the observed exudation (Canny 1997, Tyree et al. 1999). Further studies of water exudation from living cells and the potential involvement of aquaporins are needed to understand exactly how water enters embolized conduits (Holbrook & Zwieniecki 1999).

5.3.5 Trade-off Between Conductance and Safety

Species differences in xylem anatomy and function reflect the **trade-off** between a large xylem diameter, which maximizes **conductance**, and a small diameter, which increases the **strength** of the wood and minimizes the chances of **cavitation** due to freeze-thaw events. For example, **vines**, which have a small stem diameter, have large vessels with a high conductance and rapid water movement through the vessels, compared with other species (Table 6). Their stem does not have the strength of that of a tree with similar leaf area, however. Many plants, including herbs and crop plants, function close to the water potential where cavitation occurs. This suggests that the investment in transport conduits is such that it is only just sufficient to allow the required rate of water transport during the growing season (Tyree & Sperry 1989).

Woody species function close to the theoretical limit of the hydraulic conductance of their xylem conduits, and loss of xylem conductance due to embolism is a regular event. Species differ enormously in their vulnerability with respect to water-stress induced cavitation (Fig. 16). In general, the vulnerability of a species correlates negatively with the xylem tensions it experiences in the natural habitat (Fig. 20). The risk of cavitation plays a major role in the differentiation between drought-adapted and mesic species. On the one hand smaller inter-conduit pores confer resistance to cavitation. On the other hand, they may reduce the hydraulic conductivity of the xylem. The **safer** the xylem, the **less efficient** it may be in water conduction.

Cavitation induced by freezing stress occurs at less negative water potential in wide and long xylem conduits than it does in shorter and narrower

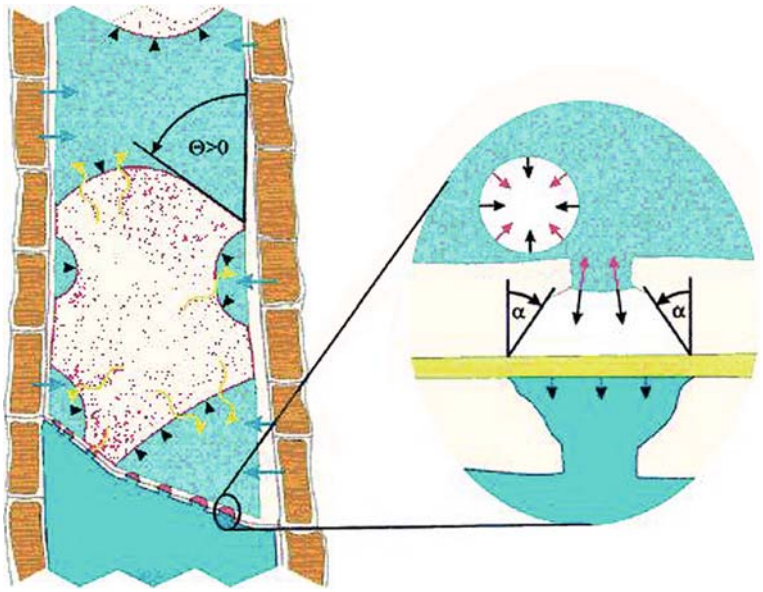

FIGURE 19. Hydraulic compartmentalization of hypothesized vessel refilling. (A) Living cells adjacent to the embolized vessel create a driving gradient that draws water into the vessel lumen (*blue arrows*). Droplets are retained on the wall due to the nonzero contact angle (Θ). Low permeability of the secondary wall prevents tension in adjacent vessels from being transmitted. Influx of water into the lumen compresses the gas phase (*black arrows*), forcing it into solution (*yellow arrows*). The dissolved gas then diffuses away from the refilling vessel, where it may be carried off by the transpiration stream. (B) Bordered pit geometry (inverted funnel with angle a) prevents water from entering the pit channel before the lumen is entirely filled. The upper conduit is actively refilling and the water is under positive pressure; the lower vessel is under tension. Arrows indicate the effects of hydrostatic pressure (*black*) and surface tension force (*red*) on the gas/liquid interface. After Holbrook & Zwieniecki (1999). Copyright American Society of Plant Biologists.

ones (Fig. 17). This may explain why xylem diameters are less in species from high latitude or altitude (Baas 1986). It may also account for the rarity of woody vines at high altitude (Ewers et al. 1990); however, if, as discussed above, the breaking of the water column in the xylem at moderate temperatures is *not* related to conduit size (Fig. 17), then why do **desert plants** tend to have narrow vessels? Conduits with a small diameter also tend to have smaller pit membrane pores than do wide ones, and this

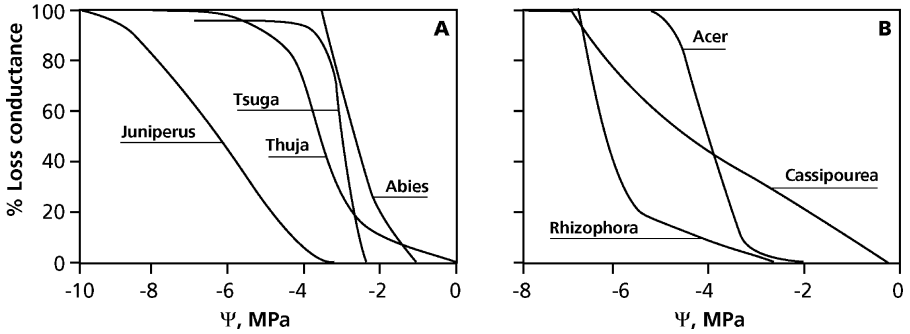

FIGURE 20. Vulnerability of various species to embolism, measured as the loss of hydraulic conductance vs. water potential in the xylem. (A) Coniferous species (*Juniperus virginiana, Thuja occidentalis, Tsuga canadensis*); (B) hardwood species (*Rhizophora mangle, Acer saccharum, Cassipourea elliptica*) (Tyree & Sperry 1989). With kind permission, from the Annual Review of Plant Physiology and Plant Molecular Biology, Vol. 40, copyright 1989, by Annual Reviews Inc.

probably explains why desert plants have small xylem diameters. That is, the correlation does *not* reflect a direct causal relation. Pits may differ widely in different species, however, and the correlation between pit membrane pore size and xylem diameter is not very strict which accounts for the generally poor correlation between xylem diameter and vulnerability to cavitation in different taxa (Sperry 1995). The length of the xylem conduit is also important, and this is often correlated with conduit diameter. Many short and narrow xylem conduits (such as those concentrated in the nodes or junctions of a stem segment) may be of ecological significance in that they prevent emboli from traveling from one internode to the next or from a young twig to an older one, thus acting as "safety zones" (Lo Gullo et al. 1995).

TABLE 7. Typical ratios of foliage area (A_f) to sapwood area (A_s) of conifers.

Species	Common name	$A_f A_s$ (m^2 m^{-2})
Mesic environments		
Abies balsamea	Balsam fir	6700–7100
A. amabilis	Pacific silver fir	6300
A. grandis	Grand fir	5100
A. lasiocarpa	Subalpine fir	7500
Larix occidentalis	Western larch	5000
Picea abies	Norway spruce	4600
P. engelmanni	Engelmann spruce	2900–3400
P. sitchensis	Sitka spruce	4500
Pseudotsuga menziesii	Douglas fir	3800–7000
Tsuga heterophylla	Western hemlock	4600
T. mertensiana	Mountain hemlock	1600
Average		5000 ± 500
Xeric environments		
Juniperus monosperma	One-seeded juniper	800
J. occidentalis	Western juniper	1800
Pinus contorta	Lodgepole pine	1100–3000
P. edulis	Pinyon pine	2500
P. nigra	Austrian pine	1500
P. ponderosa	Ponderosa pine	1900
P. sylvestris	Scotch pine	1400
P. taeda	Loblolly pine	1300–3000
Average		1800 ± 200

Source: Margolis et al. (1995).

5.3.6 Transport Capacity of the Xylem and Leaf Area

In a given stand of trees, there is a strong linear relationship between the cross-sectional area of **sapwood** (A_s), that part of the xylem that functions in water transport, and the foliage area (A_f) supported by that xylem. Given that hydraulic conductance of stems differs among species and environments, however, it is not surprising that the ratio of foliage area to sapwood area (A_f:A_s) differs substantially among species and environments (Table 7). Desiccation-resistant species generally support much less leaf area per unit of sapwood than desiccation-sensitive species (Table 7). This is logical because vessels are narrower in species from dry habitats; hence more sapwood is needed for a similar transport capacity (Zimmermann & Milburn 1982). Any factor that speeds the growth of a stand (i.e., higher "site quality") generally increases A_f:A_s because it increases vessel diameter (Fig. 21A). For example, nutrient

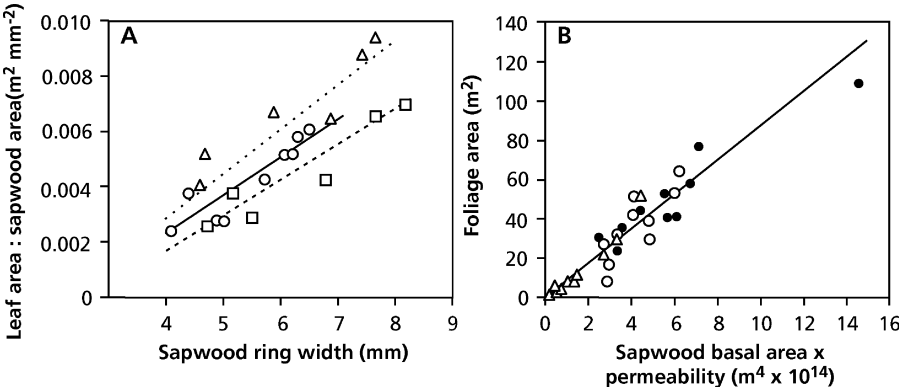

FIGURE 21. (A) Leaf area:sapwood area ratio (A_f:A_s) in relation to sapwood ring width (a measure of growth rate) in Douglas fir (*Pseudotsuga menziesii*) growing in plantations of slow (*squares*), medium (*circles*), and fast (*triangles*) growth rate. (B) Relationship of foliage area to sapwood area adjusted for permeability (unit area conductance) in fertilized (*solid circles*) and control (*open circles*) trees of *Picea sitchensis* (Sitka spruce) and control trees of *Pinus contorta* (lodgepole pine) (*open triangles*) (after Margolis et al. 1995).

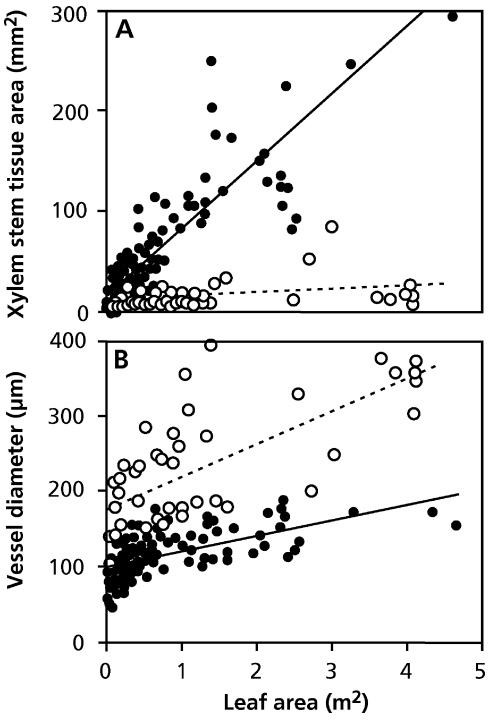

FIGURE 22. Xylem area (A) and maximum diameters of vessels (B) of contrasting *Bauhinia* species. Values are plotted as a function of the leaf area distal to the investigated stem section for stems of lianas (*dashed line*, open symbols) and congeneric trees and shrubs (*solid line*, closed symbols) (Ewers & Fisher 1991).

addition and favorable moisture status enhance A_f:A_s, and dominant trees have greater A_f:A_s than do subdominants (Margolis et al. 1995). When conductance per unit sapwood is also considered, there is a much more consistent relationship between foliage area and sapwood area (Fig. 21B).

Vines have less xylem tissue area per unit of distal leaf area (i.e., per unit leaf area for which they provide water). Their stems are thin relative to the distal leaf area, when compared with plants that support themselves. Vines compensate for this by having vessels with a large diameter (Fig. 22). It is interesting that the correlation between sapwood area and distal leaf area also holds when the leaf area is that of a **mistletoe** tapping the xylem, even when there is no host foliage on the branch (Sect. 2.3 of Chapter 9D on parasitic associations). Because there are no phloem connections between the xylem-tapping mistletoe and its host tree, the correlation cannot be accounted for by signals leaving the leaves and traveling through the phloem. This raises the intriguing question on how leaf area controls sapwood area (or vice versa).

5.3.7 Storage of Water in Stems

Plants store some water in stems, which can temporarily supply the water for transpiration. For example, water uptake and stem flow in many trees lags behind transpirational water loss by about 2 hours (Fig. 23) because the water initially supplied to leaves comes from parenchyma cells in the stem. [Stem flow can be measured using sapflow equipment (Box 3.4).] Withdrawal of stem water during the day causes stem diameter to fluctuate diurnally, being greatest in the early morning and smallest in late afternoon. Most **stem shrinkage** occurs in living tissues external to the xylem, where cells have more elastic walls and cells decrease in volume when water is withdrawn. In trees, the stem

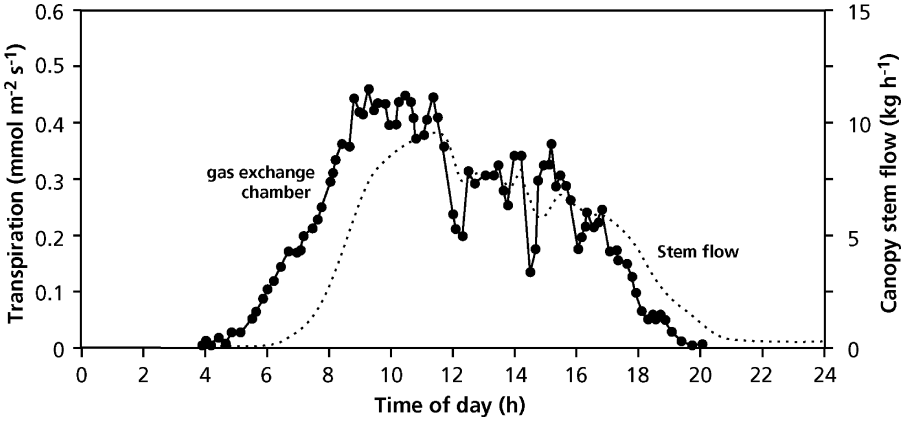

FIGURE 23. Diurnal pattern of water flow in the stem and water loss from transpiring leaves of a *Larix decidua* x *leptolepis* (larch) tree. The difference between the two lines represents stem storage (Schulze et al. 1985).

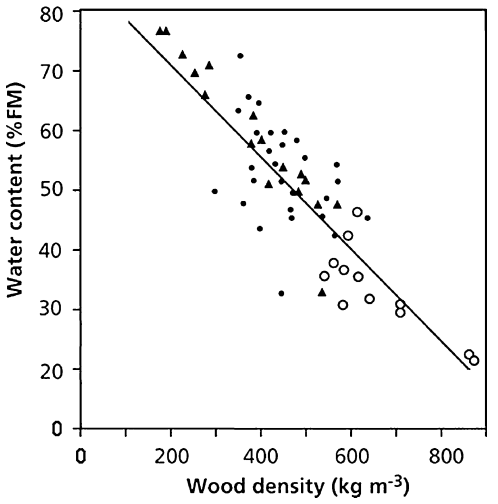

FIGURE 24. Relationship between stem water content and wood density in 32 species of deciduous trees from a dry tropical forest in Costa Rica (after Borchert 1994). Copyright Ecological Society of America.

water provides less than 10–20% of the daily water transpired in most plants, so it forms an extremely small buffer. In addition, if this water becomes available as a result of cavitation, which stops the functioning of the cavitated conduit, then the benefit of such a store is questionable.

Under some circumstances, however, stem water storage is clearly important. For example, in tropical dry forests, the loss of leaves in the dry season by drought-deciduous trees eliminates transpirational water loss. Stem water storage makes an important contribution to the water required for flowering and leaf flushing by these species during the dry season (Borchert 1994). Water storage in these trees is inversely related to wood density (Fig. 24). Early successional, shade-intolerant species grow rapidly, have low wood density, and, therefore, high water storage that enables them to flower during the dry season and to reflush leaves late in the dry season. By contrast, slow-growing deciduous trees with high wood density and low water storage remain bare to the end of the dry season (Borchert 1994). Storage of water in stems is also important in reducing winter desiccation [e.g., of the needles of *Picea engelmannii* (Engelmann spruce) that grow at the timberline]. Water in the stem may become available when the soil is frozen and air temperatures are above –4°C (Sowell et al. 1996).

In herbaceous plants and succulents, which have more elastic cell walls than those of the sapwood in trees, storage in the stem is more important. Small herbaceous plants also transpire water made available by cavitation of some of the conduits in the stem. They refill the xylem by root pressure during the following night. *Hylocereus undatus* (red pitaya), a hemiepiphytic cactus, has fleshy stems whose water storage is crucial for surviving drought. Under wet conditions, the turgor pressure is 0·45 MPa in its **chlorenchyma**, but only 0–10 MPa in its water-storage parenchyma. During 6 weeks of drought, the stems lose one-third of their water content, predominantly from cells in the **water-storage parenchyma** (hydrenchyma), which decrease by 44% in length and volume, whereas cells in the adjacent chlorenchyma decrease by only 6%; the osmotic pressure concomitantly increases by only 10% in the chlorenchyma, but by 75% in the water-storage parenchyma (Nobel 2006).

5.4 Water in Leaves and Water Loss from Leaves

The earliest known measurements of stomata were made in 1660 by Mariotte, a French mathematician and physicist who earned his living as a clergyman in Dijon. Fifteen years later, Malpighi, who was a professor of medicine at Bologna and Pisa, mentioned porelike structures on leaf surfaces (Meidner 1987). It is now an established fact that leaves inexorably lose water through their stomatal pores, as a consequence of the photosynthetic activity of the mesophyll leaf cells. Stomates exert the greatest short-term control over plant water relations because of the steep gradient in water potential between leaf and air. There are two major interacting determinants of plant water potential: soil moisture, which governs water supply, and transpiration, which governs water loss. Both of these factors exert their control primarily by regulating stomatal conductance. Stomatal conductance depends both on the availability of moisture in the soil and on vapor pressure in the air, as will be outlined shortly.

5.4.1 Effects of Soil Drying on Leaf Conductance

Leaves of "isohydric" species, which control gas exchange in such a way that daytime leaf water status is unaffected by soil water deficits, must control stomatal conductance by messages arriving from the root. This is an example of **feedforward control**. That is, stomatal conductance declines before any adverse effects of water shortage arise in the leaves. Isohydric species include *Zea mays* (corn) and *Vigna sinensis* (cowpea). The

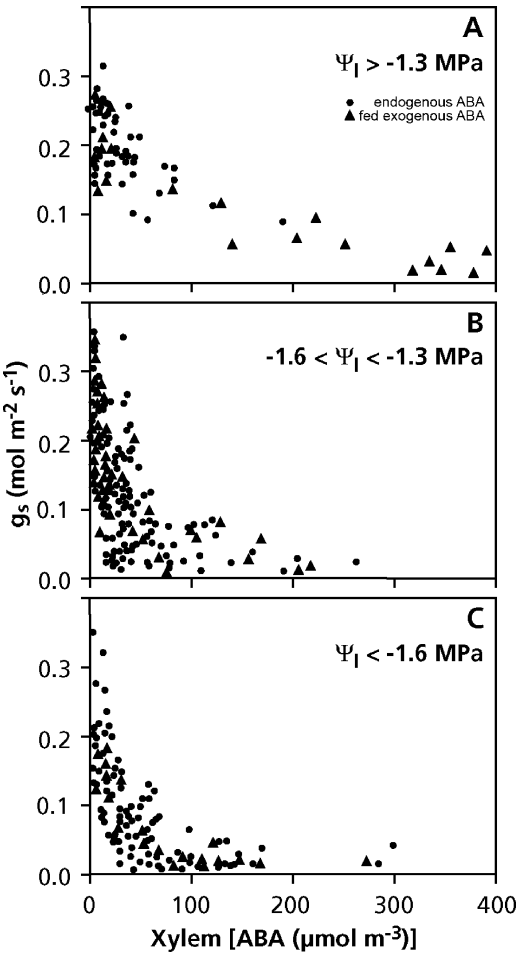

FIGURE 25. Leaf conductance (g_s) as a function of the concentration of ABA in the xylem sap of field-grown *Zea mays* (corn) plants. Measurements were made over three ranges of leaf water potential ($_l$). ABA concentrations varied either due to variation in plants producing different amounts of ABA, or because ABA was injected into the stem (after Davies et al. 1994). Copyright American Society of Plant Biologists.

phytohormone abscisic acid (**ABA**) is the predominant chemical message arriving from roots in contact with drying soil (Schurr et al. 1992, Dodd 2005). Soil drying enhances the concentration of this hormone in the xylem sap as well as in the leaves (Tardieu et al. 1992, Correia et al. 1995). Another chemical change related to soil drying is an increase in the pH of the xylem sap flowing from the roots (Gollan et al. 1992, Wilkinson et al. 1998). Injection of ABA in the stem of corn plants has fairly similar effects on the ABA concentration in the xylem sap and on stomatal conductance as exposure to a drying soil. The stomata of desiccated plants become more "sensitized" to the ABA signal, however, possibly by a combination of other chemical signals (e.g., pH) transported in the xylem and the low water potential of the leaf itself (Fig. 25). The mechanism by which a high pH in the xylem sap affects the stomata is that the mesophyll and epidermal cells have a greatly reduced ability to sequester ABA away from the apoplast when the pH in that compartment is increased by the incoming xylem sap. This follows from the fact that weak acids such as ABA accumulate in more alkaline compartments (Wilkinson & Davies 1997, Jia & Davies 2007). Among trees, isohydric species are those that generally occur in mesic habitats and operate at water potentials extremely close to potentials causing complete cavitation (Sect. 5.3.3; Sperry 1995). These species seldom experience more than 10% loss in conductance due to cavitation because their effective control of stomatal conductance minimizes diurnal variation in leaf water potential.

In "anisohydric" species, such as *Helianthus annuus* (sunflower), both the leaf water potential and stomatal conductance decline with decreasing soil water potential. In these species, both root-derived ABA and leaf water status regulate stomatal conductance. A controlling influence of leaf water status on stomatal conductance need not be invoked. Rather leaf water status is likely to vary as a consequence of water flux through the plant which is controlled by stomatal conductance. Correlations between stomatal conductance and leaf water status are only observed in plants where leaf water status has no controlling action on the stomata (Tardieu et al. 1996).

The spectrum in stomatal "strategy" between isohydric and anisohydric plants is determined by the degree of influence of leaf water status on stomatal control for a given concentration of ABA in the xylem. There are also effects that are not triggered by ABA arriving from the roots, mediated via ABA produced in the leaf. In addition, both electrical and hydraulic signals control stomatal conductance in response to soil moisture availability (Sect. 5.1 of Chapter 2A on photosynthesis).

The mechanism by which roots sense dry soil is not clear. ABA, like any other acid, crosses membranes in its undissociated form. It therefore accumulates in soil, especially when the rhizosphere is alkaline. Because the concentration of ABA in soil increases when water is limiting for plant growth, it has been speculated that roots may sense drying soils through ABA released into the soil. Because the presence of NaCl inhibits the microbial degradation of ABA, the concentration of ABA also tends to be

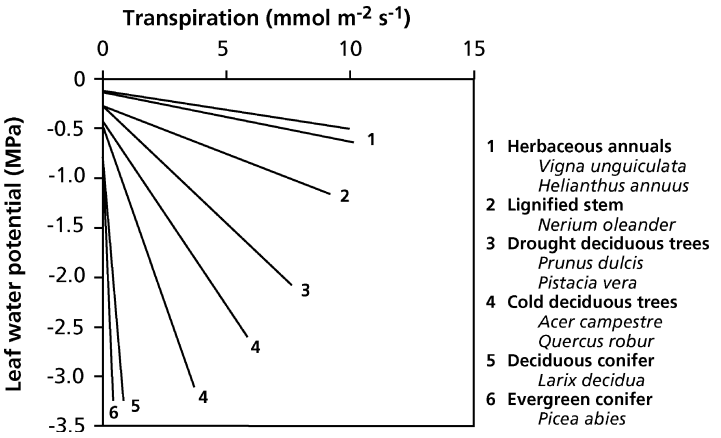

FIGURE 26. The leaf water potential reached at different transpiration rates in various life forms, when exposed to the same water supply (after Schulze 1991).

higher in saline soils. This might offer a mechanism for the roots to sense a low osmotic potential in the soil (Hartung et al. 1996). On the other hand, roots might also sense a decrease in turgor using **osmosensors** that measure the change in concentration of osmotic solutes; such osmosensors have been extensitvely studied in yeasts (Shinozaki & Yamaguchi-Shinozaki 1997). More recently, it has been discovered that the activity of a specific plant response to cytokinin is also regulated by changes in turgor pressure (Reiser et al. 2003, Bartels & Sunkar 2005). The topic of sensing dry soil is further discussed in Sect. 5.3.1 of Chapter 7 on growth and allocation.

The relationship between stomatal conductance (and hence transpiration) and leaf water potential differs strikingly among growth forms (Fig. 26). Because the difference in leaf water potential and soil water potential is the driving force for water transport in the plant, the relationship in Fig. 26 gives the conductance for water transport of the entire system. This conductance is greatest in herbaceous annuals and smallest in evergreen conifers. Herbaceous species like *Helianthus annuus* (sunflower) change stomatal conductance and transpiration dramatically in response to small changes in leaf water potential. By contrast, stomatal conductance and transpiration are insensitive to progressively larger changes in water potential as we go from herbaceous annuals to woody shrubs to deciduous trees to conifers. There is a corresponding decrease in conduit diameter and increase in the margin of safety against cavitation (Sect. 5.3.3). These patterns demonstrate the close integration of various parameters that determine plant "strategies" of water relations.

Among trees, anisohydric species maintain a larger safety margin against cavitation, but they also experience more cavitation (up to 50% loss of conductance), compared with isohydric species. In anisohydric species, the closure of stomates in response to declines in leaf water potential is essential; otherwise, effects of declines in soil water potential would be augmented by those of cavitation which would cause further declines in leaf water potential, and lead to runaway cavitation (Sperry 1995).

How do we know that the decreased stomatal conductance is really accounted for by signals from the roots in contact with drying soil, rather than by the low water potential in the leaf itself? To address this question, Passioura (1988) used a pressure chamber placed around the roots of a *Triticum aestivum* (wheat) seedling growing in drying soil. As the soil dried out, the hydrostatic pressure on the roots was increased so as to maintain shoot water potential similar to that of well-watered plants. Despite having the same leaf water status as the control plants, the treated wheat plants showed reductions in stomatal conductance similar to those of plants in drying soil outside a pressure chamber. Additional evidence has come from experiments with small apple trees (*Malus* x *domestica*) growing in two containers (split-root design). Soil drying in one container, while keeping water availability high in the other, restricts leaf expansion and initiation, with no obvious effect on shoot water relations. These effects on leaves of wheat seedlings and apple trees must therefore be attributed to effects of soil drying that do not require a change in shoot water status (Davies et al. 1994). They are a clear example of **feedforward** control. In other species [e.g., *Pseudotsuga menziesii* (Douglas fir) and *Alnus rubra* (red alder)], however, stomata do not respond to soil drying according to a feedforward model. When their leaf water status is manipulated in a pressure chamber, stomatal conductance responds to turgor in the leaves within minutes. In these species,

stomatal control is hydraulic and no chemical signal from the roots appears to be involved (Fuchs & Livingston 1996).

5.4.2 The Control of Stomatal Movements and Stomatal Conductance

How do signals discussed in Sects. 5.4.1 and 5.1 of Chapter 2A on photosynthesis affect stomatal conductance? To answer this question, we first need to explore the mechanism of opening and closing of the stomata.

Although the anatomy of stomata differs among species, there are a number of traits in common. First, there are two **guard cells** above a **stomatal cavity** (Fig. 27A1–3). Because the cell walls of these adjacent cells are only linked at their distal end, they form a pore whose aperture can vary because of the swelling or shrinking of the guard cells (Fig. 27A,B). Next to the guard cells, there are often a number of lateral and distal **subsidiary cells** (Outlaw 2003, Franks and Farquhar 2007). Stomatal closure occurs when solutes are transported from the guard cells, via the apoplast, to the subsidiary cells, followed by water movement along an osmotic gradient. Stomatal opening occurs by the transport of solutes and water in the opposite direction, from subsidiary cells, via the apoplast, to the guard cells (Fig. 27C).

The stomatal pore becomes wider when the guard cells take up solutes and water due to the special structure of the cells, which are attached at their distal ends, and the ultrastructure of their cell walls. The **ultrastructural features** include the radial orientation of rigid microfibrils in the walls which allow the cells to increase in volume only in a longitudinal direction. In addition, the guard cells of some species show some thickening of the cell wall bordering the pore. This may help to explain the movement of the guard cells, but the radial orientation of the microfibrils is the most important feature. The combination of the structural and ultrastructural characteristics forces the stomata to open when the guard cells increase in volume. This can happen in minutes and requires rapid and massive transport of solutes across the plasma membrane of the guard cells (Nilson & Assmann 2007).

Which solutes are transported and how is such transport brought about? The major ion that is transported is K^+, which is accompanied, immediately or with some delay, by Cl^-. On a cell volume, basis KCl transport represents a change which is equivalent to 300 mM in osmotically active solutes. As an alternative to the transport of Cl^-, the charge may be (temporarily) balanced by negative charges that are produced inside the guard cells, the major one being malate produced from carbohydrate inside the guard cell (Blatt 2000). Guard cells also accumulate sucrose during stomatal opening (Nilson & Assmann 2007). A **H^+-ATPase** and several **ion-selective channels** play a role in the transport of both K^+ and Cl^-, in the opening as well as the closing reaction. The channels responsible for the entry of K^+ are open only when the membrane potential is very negative (Fig. 27C). A very negative membrane potential results from the activation of the H^+-pumping ATPase in the plasma membrane of the guard cells. Activation may be due to **light**, involving a blue-light receptor (Sect. 5.4.4). The ion-selective channels responsible for the release of K^+ open when the membrane potential becomes less negative (Hedrich & Schroeder 1989).

ABA affects some of the K^+- and Cl^--selective channels, either directly or indirectly, via the cytosolic Ca concentration or pH; the decrease in stomatal conductance as affected by ABA involves both an inhibition of the opening response and a stimulation of the closing reaction. Stomatal closure is a consequence of the stimulation, possibly by ABA directly, of the channel that allows the release of Cl^-, which depolarizes the membrane and generates a driving force for K^+ efflux. ABA inactivates the channel that normally mediates K^+ entry and activates the channel that determines K^+ release. This picture of events pertains to the plasma membrane; however, since much of the solute lost during stomatal closing originates from the vacuole, equivalent events must occur at the tonoplast. Ca plays a role as "second messenger" in the inhibition of the inward-directed K^+-channel and stimulation of the outward-directed Cl^- channel. ABA enhances the Ca concentration in the cytosol which in its turn inhibits the inward K^+-selective channel and stimulates the outward Cl^--selective channel. The outward K^+-selective channel is unaffected by $[Ca^{2+}]$. The Ca that accumulates in the cytosol arrives there via Ca^{2+}-selective channels in the tonoplast and, probably, the plasma membrane (Fig. 27C; Mansfield & McAinsh 1995, Blatt 2000).

Irradiance, the **CO_2 concentration** and **humidity** of the air as well as **water stress** affect stomatal aperture. There are **photoreceptors** in stomatal cells that perceive certain wavelengths, thus affecting stomatal movements. We know little about the exact mechanisms and the transduction pathways between perception of the environmental signal and the ultimate effect: stomatal opening and closing, and diurnal variation in stomatal conductance. Even within a single species, there can be drastically

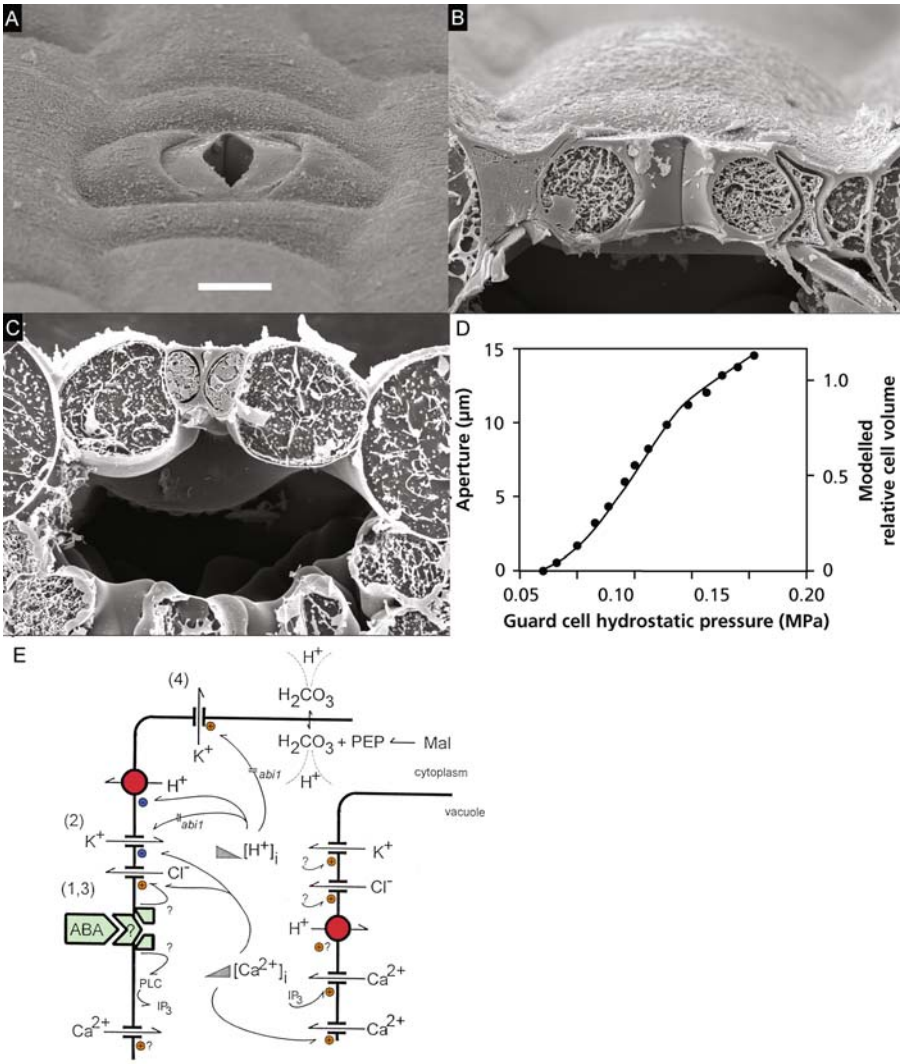

FIGURE 27. (A) Stomata of *Tradescantia virginiana* (Virginia spiderwort) sampled by snap freezing an intact leaf. 1. View of an open stoma from the top, showing the stomatal pore, two guard cells, and two adjacent subsidiary cells. 2. Cross-section showing an open stoma, large guard cells, small subsidiary cells, a stomatal pore, and a substomatal cavity. 3. Cross-section showing a closed stoma, small guard cells, large subsidiary cells, no stomatal pore, and a substomatal cavity (courtesy P.J. Franks, School of Tropical Biology, James Cook University, Australia). (B) Stomatal aperture and cell volume as a function of the guard cell hydrostatic pressure. The pressure in the cells of *Tradescantia virginiana* was controlled with a pressure probe after the guard cells had been filled with silicon oil (after Franks et al. 1995). (C) Effects of ABA on ion fluxes in guard cells. ABA leads to a concerted modulation [(+) = increase or activation, (–) = decrease or inactivation] of at least three subsets of plasma-membrane ion channels. ABA first binds to a plasma-membrane receptor, possibly both from the outside and from the inside (not shown). This triggers the formation of inositol 1,4,5-triphosphate (IP_3), catalyzed by phospholipase C (PLC). IP_3 facilitates the release of Ca^{2+} from intracellular stores, and the consequent rise in cytosolic $[Ca^{2+}]$ affects a number of channels and, possibly, the plasma-membrane H^+-ATPase. ABA also triggers a rise in pH, which affects a number of channels and depletes the substrate for the H^+-ATPase. Modified after Blatt & Grabov (1997).

different diurnal courses of stomatal conductance at different times of year (associated with very different relative water contents and leaf water potentials). In addition, the leaf water potential at which leaf cells start to lose turgor can change through a season (Fig. 28). Such a change in **turgor-loss point** must be associated with changes in elastic modulus (Table 4, Fig. 8; Sect. 5.4.6).

5.4.3 Effects of Vapor Pressure Difference or Transpiration Rate on Stomatal Conductance

Exposure of a single leaf or a whole plant to dry air is expected to increase transpiration because of the greater vapor pressure difference between the leaf and the air. Such a treatment, however, may also decrease stomatal conductance and hence affect transpiration. These effects on transpiration are readily appreciated when considering the Equation introduced in Sect. 2.2.2 of Chapter 2A on photosynthesis:

$$E = g_w(w_i - w_a) \quad (7)$$

where g_w is the leaf conductance for water vapor transport, and w_i and w_a are the mole or volume fractions of water vapor in the leaf and air, respectively. Which environmental factors affect Δw, the

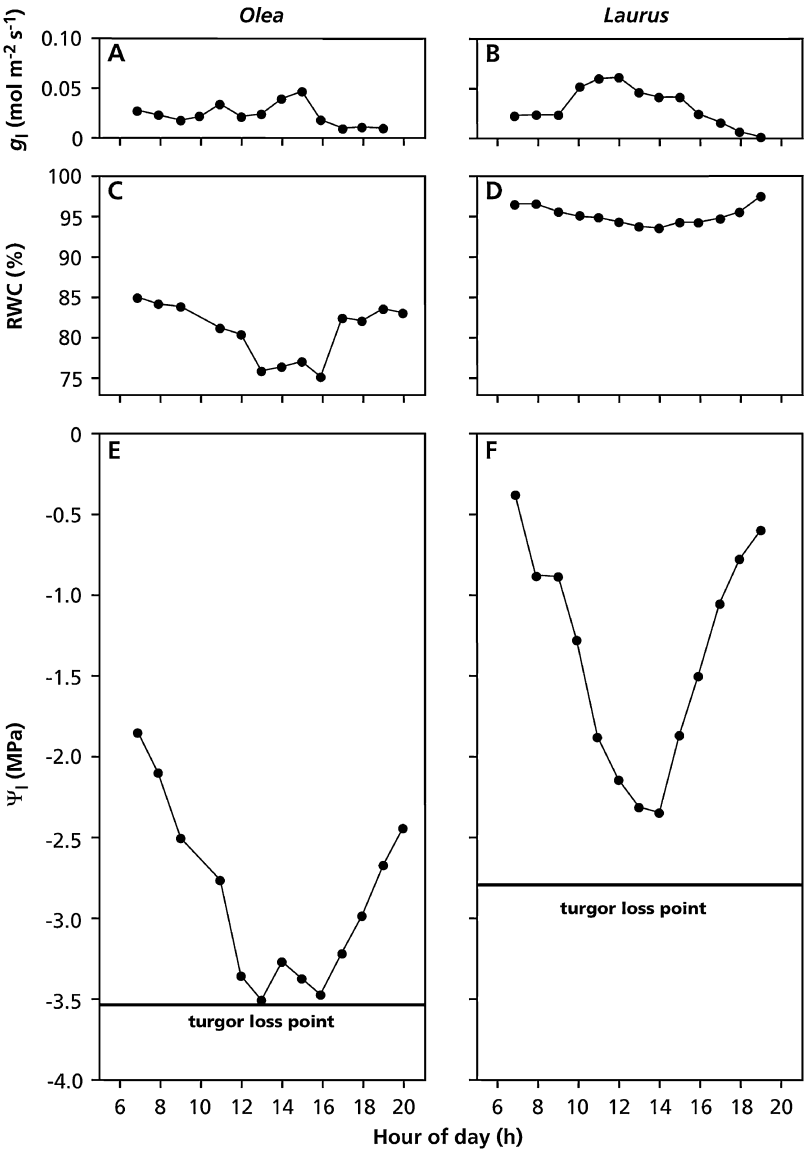

FIGURE 28. Time course of the leaf conductance to water vapor (A, B), the relative water content (RWC) of the leaves (C, D), and the leaf water potential (E, F) for two Mediterranean tree species, the relatively drought-tolerant *Olea oleaster* (olive) and the less tolerant *Laurus nobilis* (laurel). RWC is defined as the amount of water per unit plant mass relative to the amount when the tissue is fully hydrated. Measurements were made in September (dry season) (after Lo Gullo & Salleo 1988). Additional information about these trees is presented in Table 4 and Fig. 8. Copyright Trustees of The New Phytologist.

difference in water vapor concentration between leaf and air and how can stomata respond to humidity?

The water vapor concentration inside the leaf changes with leaf temperature. As temperature rises, the air can contain more water vapor, and evaporation from the wet surfaces of the leaf cells raises the water vapor concentration to saturation. This is true for leaves of both well-watered and water-stressed plants. The air that surrounds the plant can also contain more humidity with rising temperature, but water vapor content of the air typically rises less rapidly than that of the leaf. If the water vapor concentration outside the leaf remains the same, then Δw increases. This enhances the leaves' transpiration in proportion to the increased Δw, as a result of increasing vapor pressure deficit (VPD), unless stomatal conductance declines. However, as VPD increases, stomata generally respond by partial closure (Lange et al. 1971). The stomatal closure response to increasing VPD generally results in a nonlinear increase in transpiration rate to a plateau and in some cases a decrease at high VPD. By avoiding high transpiration rates that would otherwise be caused by increasing Δw, stomatal closure avoids the corresponding decline in plant water potential. The closure response presumably evolved to prevent excessive dehydration and physiological damage. Responses of stomatal conductance to increasing VPD generally follow an exponential decrease, but the magnitude of the decrease, the **stomatal sensitivity**, varies considerably both within and among species. Stomatal sensitivity at low VPD ($\leq$1 kPa) is proportional to the magnitude of stomatal conductance (Fig. 29). Individuals, species, and stands with high stomatal conductance at low VPD show a greater sensitivity to VPD, as required by the role of stomata in regulating leaf water potential (Oren et al. 1999).

Note that as in Sect. 2.3 of Chapter 2A on photosynthesis, we use absolute values of water vapor in the air, rather than relative humidity or water potential. The relative humidity of the air is the absolute amount of water vapor (partial pressure is p) in the air as a proportion of the maximum amount of water vapor that can be held at that temperature (partial pressure is p_o). The water potential of the air relates to the relative humidity as (Box 3.1):

$$\Psi_{air} = RT/V_w^o . \ln p/p_o \qquad (8)$$

where $V_w{}^o$ is the molar volume of water. For air with a temperature of 293 K and a relative humidity of 75%, the water potential ψ_{air} = –39 MPa (using the value for the molar volume of water at 293 K of 18×10^{-6} m^3 mol^{-1}). Air with a lower RH has an even more negative water potential. This shows that water potentials of air that contains less water vapor than the maximum amount are extremely negative (Box 3.1). This negative water potential of the air is the driving force for transpiration. When describing the transport of water in different parts of the soil– plant–atmosphere continuum, it is essential to use the concept of water potential. For an analysis of leaf gas exchange, however, it tends to be more convenient to express the driving force for transpiration in terms of Δw, the difference in water vapor concentration between leaf and air, as is done for the diffusion of CO_2 from air to the intercellular spaces inside the leaf (Sect. 2.2.2 of the Chapter 2A on photosynthesis).

To further elucidate the mechanism that accounts for stomatal responses to humidity, transpiration was measured in several species using normal air and a helium:oxygen mixture (79:21 v/v, with CO_2 and water vapor added) (Mott & Parkhurst 1991). Because water vapor diffuses 2.33 times faster in the helium/oxygen mixture than it does in air, Δw between the leaf and the air at the leaf surface can be varied independently of the transpiration rate, and vice versa. The results of these experiments are consistent with a mechanism for stomatal responses to humidity that is based on the rate of water loss

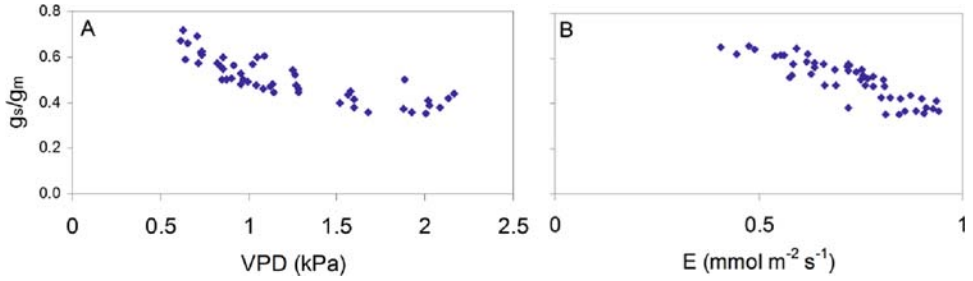

FIGURE 29. Average canopy stomatal conductance relative to the maximum value in relation to (A) vapor pressure deficit (VPD) and (B) canopy transpiration per unit of leaf area (after Oren et al. 1999).

from the leaf. It suggests that stomata do not directly sense and respond to either the water vapor concentration at the leaf surface or Δw.

The mechanism that accounts for the stomatal **response to humidity** of the air or **transpiration rate** is unknown (Eamus & Shanahan 2002), but it does not involve ABA because both ABA-deficient and ABA-insensitive mutants of *Arabidopsis thaliana* (thale cress) respond the same as wild-type plants (Assmann et al. 2000). It can even be demonstrated in epidermal strips, isolated from the mesophyll. It is not universal, however, and it may even vary for one plant throughout a day (Franks et al. 1997). The consequence of this phenomenon is that a decrease in water vapor concentration of the air has less effect on the leaf's water potential and relative water content than expected from the increase in Δw. Stomatal response to humidity therefore allows an apparent **feedforward response** (Cowan 1977, Franks et al. 1997). It enables a plant to restrict excessive water loss before it develops severe water deficits and may enhance the ability of plants to use soil water supplies efficiently. The stomatal response to humidity inevitably reduces the intercellular CO_2 pressure in the leaf, C_i, in response to low humidity, and hence the rate of CO_2 assimilation. A compromise, somehow, has to be reached, as discussed in Sect. 5.4.7.

5.4.4 Effects of Irradiance and CO_2 on Stomatal Conductance

About a century ago, Francis Darwin (1898) already noted that the surface of a leaf facing a bright window had open stomata, whereas the stomata on surface away from the window were closed. When he turned the leaf around, the stomata, which were closed before, opened. The ones that were open, then closed. Since Darwin's observation, an overwhelming amount of evidence accumulated showing that stomata respond to light (Assmann & Shimazaki 1999). In Sect. 4.2 of Chapter 2A on photosynthesis, we discussed the rapid response of stomata in plants exposed to sunflecks. The response to light ensures that stomata are only open when there is the possibility to assimilate CO_2. In this way, water loss through transpiration is minimized.

How do stomata perceive the light and how is this subsequently translated into a change in stomatal aperture? There are basically two mechanisms by which stomata respond to light. The *direct* response involves specific pigments in the guard cells. In addition, guard cells respond to C_i, which will be reduced by an increased rate of photosynthesis. This is the *indirect* response.

The light response of guard cells is largely to **blue light** (with a peak at 436 nm) mediated by **phototropin** (Shimazaki et al. 2007). Stomata also open in response to **red light** (with a peak at 681 nm). Since *Paphiopedilum harrisianum*, an orchid species that lacks chlorophyll, has guard cell sensitivity only to blue light, the red-light response is most likely mediated by chlorophyll (Kinoshita & Shimazaki 1999). The blue-light receptor (phototropin) affects biochemical events, such as an enhancement of PEP carboxylase, which catalyzes malate formation. Blue light also affects K^+ channels in the plasma membrane of the guard cells, allowing massive and rapid entry of K^+ into the guard cells which is the first step in the train of events that lead to stomatal opening (Blatt & Grabov 1997, Blatt 2000).

Stomata can respond to CO_2, even when isolated or in epidermal peels, but the sensitivity varies greatly among species and depends on environmental conditions. If stomata do respond, then the response is found in both light and dark conditions. Mott (1988) used leaves of amphistomatous species (i.e., with stomates on both the upper and lower leaf surface) in a gas-exchange system that allows manipulation of C_i, while keeping the CO_2 concentration at one surface of he leaf constant (Sect. 5.4.3). In this way, it was shown that stomata sense the **intercellular CO_2concentration** (C_i), rather than that at the leaf surface. Although the mechanism that accounts for the stomatal response remains unclear, it does play a major role in plant response to elevated atmospheric CO_2 concentrations (Assmann 1999). Under these conditions, stomatal conductance is less than it is under present atmospheric conditions, enhancing the plant's photosynthetic water-use efficiency (Sect. 10.2 of Chapter 2A on photosynthesis).

5.4.5 The Cuticular Conductance and the Boundary Layer Conductance

In this chapter, we have so far mainly dealt with stomatal conductance (Sect. 2.2.2 of Chapter 2A on photosynthesis). The **cuticular conductance** for CO_2 and water vapor is so low that it can be ignored in most cases, except when the stomatal conductance is extremely low. It is widely believed that thick cuticles are better water barriers than thin ones, but all the experimental evidence shows this to be wrong. Cuticles are formed of three main constituents: waxes, polysaccharide microfibrils, and cutin, which is a three-dimensional polymer network of esterified fatty acids. The main barrier for diffusion is located within a waxy band, called the "skin", whose thickness is much less than 1 μm (Kerstiens 1996).

In the continuum from the cell walls in the leaf, where evaporation takes place, to the atmosphere, there is one more step that cannot be ignored under many conditions. This is the leaf **boundary layer conductance**. We have already dealt with this in Sect. 2.2 of Chapter 2A on photosynthesis and will come back to it in Chapter 4A on the plant's energy balance. A special case where boundary layer conductance is expected to be very low is that of **sunken stomata**, where stomata are concealed in a **stomatal crypt**, rather than be exposed at the leaf surface (Fig. 30). Sunken stomata are relatively common in scleromorphic leaves of plants on nutrient-poor soils in (semi-)arid climates (Grieve & Hellmuth 1970, Sobrado & Medina 1980). Because of their effect on boundary layer conductance, sunken stomata will reduce transpiration, but they will have a similar effect on photosynthesis, and hence water-use efficiency is expected to be the same as that of plants with stomata on the leaf surface, instead of in stomatal crypts. The ecophysiological significance of sunken stomata is therefore not immediately obvious. Perhaps the sunken stomata are protected, e.g., against the abrasive effects of sand blown in strong winds, which might damage epidermal cells and hence interfere with stomatal opening. Or sunken stomata may be exposed to more humid air than that above the leaf, allowing them to remain open despite the high VPD (Sect. 5.4.2). This topic clearly needs further investigation.

5.4.6 Stomatal Control: A Compromise Between Carbon Gain and Water Loss

As first discussed in Sect. 5 of Chapter 2A on photosynthesis, leaves are faced with the problem of a compromise between maximization of photosynthesis (A) and minimization of transpiration (E). At a relatively high leaf conductance (g_l; note that leaf conductance includes stomatal conductance, mesophyll conductance as well as boundary layer and cuticular conductance), A no longer increases linearly with C_i (Figs. 6 and 28; Sects. 2.2.1 and 4.1 of Chapter 2A on photosynthesis). On the other hand, E continues to increase with increasing g_l because it depends on the gradient in water vapor, and not on the biochemical machinery of photosynthesis (Fig. 29, Sect. 5.1 of Chapter 2A on photosynthesis). As explained, the intrinsic water-use efficiency (A/g_l) declines with increasing g_l. As can be seen from Fig. 29 of Chapter 2A, the ratio of the *change* in E and the *change* in A (termed λ) also increases with increasing leaf conductance (Cowan 1977).

Figure 31 gives the rate of transpiration as a function of the rate of assimilation and the time of the day, assuming different values for leaf conductance or for λ. If we assume that stomata are regulated only to *maximize* carbon gain, then this produces a transpiration curve with one diurnal peak on the contour of the surface. The peak is due to the high difference in water vapor concentration between the leaf and the atmosphere when the radiation level is high

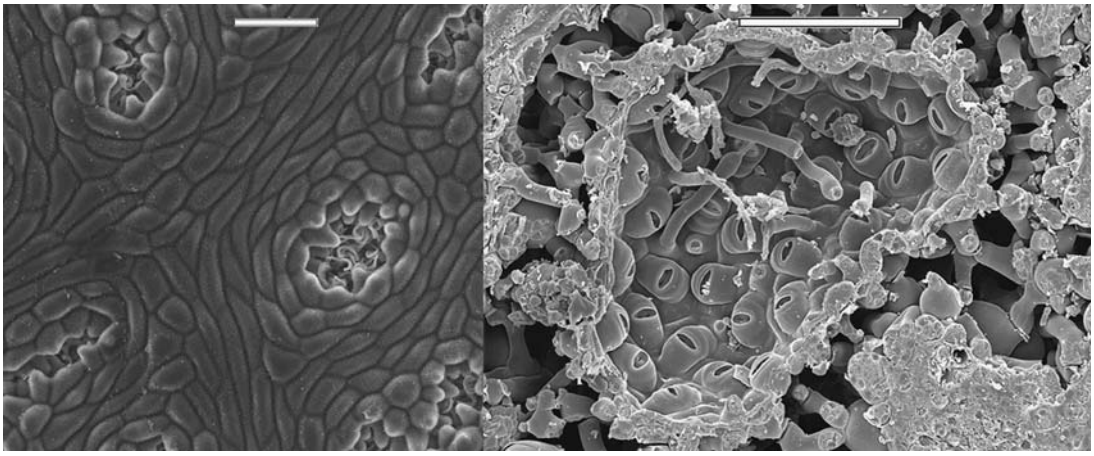

FIGURE 30. Sunken stomata and stomatal crypts in leaves of *Banksia* species. (*left*) Abaxial leaf surface of *Banksia quercifolia* (oak-leaved banksia) showing stomatal crypts with trichomes. Scanning electron micrograph; scale bar 100 m (courtesy F. Hassiotou, School of Plant Biology, The University of Western Australia, Australia). (*right*) Paradermal section of abaxial leaf surface of *Banksia elderiana* (swordfish banksia) showing a stomatal crypt with a few trichomes and many stomata. Stomata are restricted to the stomatal crypt. Cryoscanning electron micrograph; scale bar 100 m (courtesy F. Hassiotou, School of Plant Biology, The University of Western Australia, Australia, and C. Huang, Research School of Biological Sciences, Australian National University, Australia).

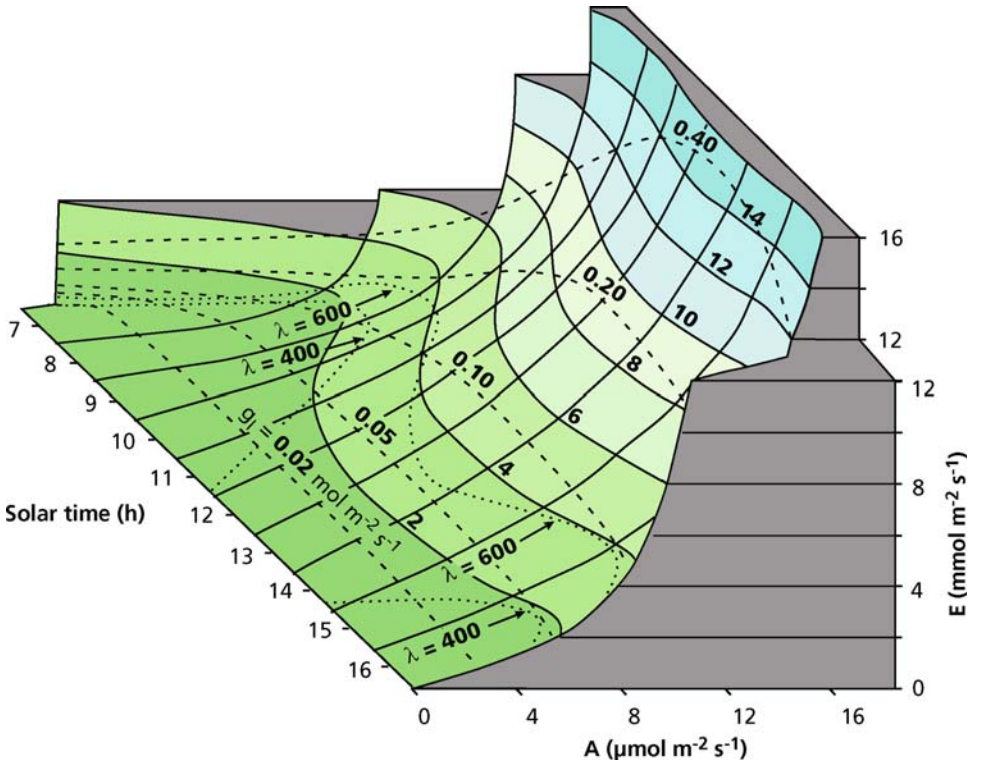

FIGURE 31. Calculated rates of transpiration (*E*), as a function of the rate of photosynthesis (*A*), and time of the day, assuming certain characteristics of leaf metabolism and environment. The magnitudes for *E* are given on the contours of the surface. The *broken lines* are diurnal trajectories on the surface giving the diurnal variation in *E* and *A* for particular constant magnitudes of leaf conductance (g_l; 0.02, 0.05, 0.10, 0.20, or 0.40 mol m^{-2} s^{-1}). The *broken lines* are diurnal trajectories for which is constant (400 or 600) (Cowan 1977). Copyright Australian Academy of Science.

during the middle of the day. Assuming **optimization** of stomatal regulation (i.e., constant λ) gives a curve with two peaks, when λ is small (i.e., when carbon assimilation is an important criterion for optimization). When rates of transpiration change to a lot, relative to assimilation, i.e., λ is large (greater than in the two examples in Fig. 31, but stomatal conductance is regulated to optimize carbon gain and water loss), a curve with only one diurnal peak is found. In summary, the optimization model predicts that plants in a water-limited environment should show morning and late-afternoon peaks in transpiration rate and **midday stomatal closure**, whereas plants well supplied with water would perform optimally with a single **midday peak in transpiration**. The two-peak curve may be achieved by (partial) closure of the stomata during that time of the day when the evaporative demand is highest, due to a large difference in water vapor concentration between the leaf and the air.

How should stomata be regulated so as to maximize the fixation of CO_2 with a minimum loss of water? The optimization theory for stomatal action is based on the following assumption: stomatal action is such that for each amount of CO_2 absorbed, the smallest possible amount of water is lost. The mathematics to solve such a problem requires a sophisticated approach, which will not be included here (Cowan 1977). The solution, however, can be presented very briefly: For each infinitesimally small change of *E* at a certain *E*, the change in *A* is constant, λ (Fig. 31).

The theoretical curves of Fig. 31 agree with observations on both C_3 and C_4 plants in dry environments, where curves with two peaks are quite common. When the water supply is favorable and VPD is moderate, however, curves with only one peak are found (i.e., there is no partial midday stomatal closure) (Fig. 32). This has led to the conclusion that stomatal conductance is regulated so as to optimize carbon gain and water loss. It should be kept in mind, however, that this optimization

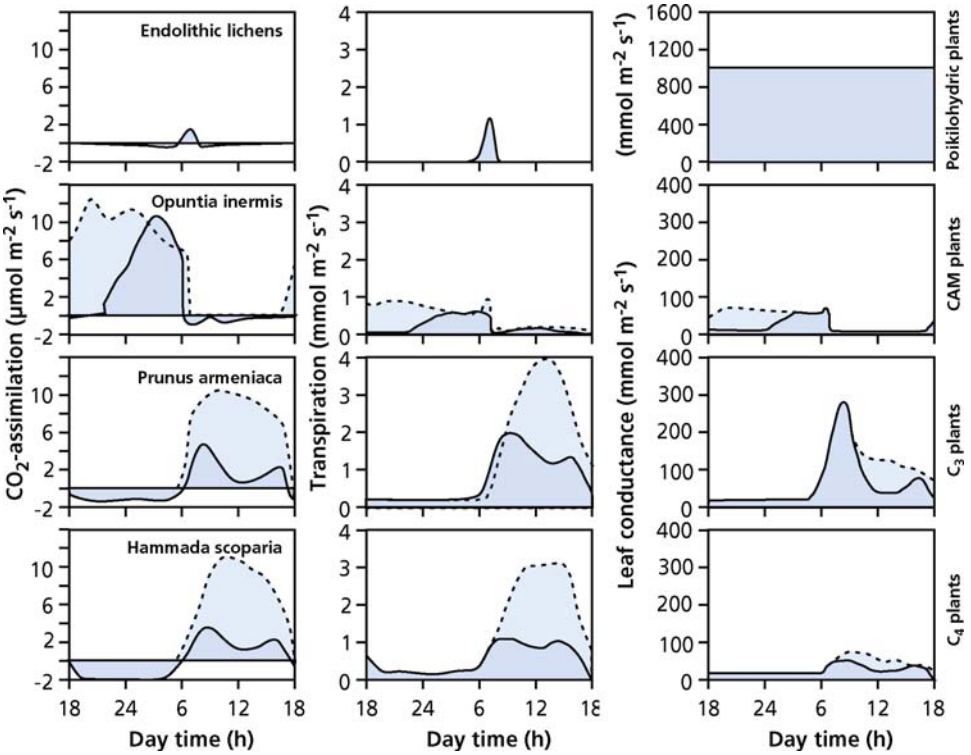

FIGURE 32. Diurnal variation in the rate of CO_2 assimilation (*left*), transpiration (*middle*), and leaf conductance (*right*) for four different plant types. Light shading (*dashed line*) shows wet season; dark shading (*solid line*) shows dry season (Schulze & Hall 1982).

approach, while very attractive for explanation of stomatal behavior, is teleological in nature; it has no mechanistic basis and is not easily used for predictive purposes.

Constancy of λ does not have to be the result of the action of stomata, but it may also be achieved by a specific leaf orientation. For example, vertical leaves absorb least radiation during the middle of the day as opposed to horizontal ones. A vertical orientation of leaves is typically associated with hot and dry places close to the equator. A horizontal leaf orientation is common in temperate regions, further away from the equator. Some leaves have the ability to orientate their leaves in response to environmental factors, including the angle of the incident radiation and leaf temperature. Such **heliotropic leaf movements** may also lead to the constancy of λ (Sect. 2.2 of Chapter 4A on leaf energy balance).

6. Water-Use Efficiency

Water-use efficiency (WUE) refers to the amount of water lost during the production of biomass or the fixation of CO_2 in photosynthesis. It is defined in two ways. First, the **water-use efficiency of productivity** is the ratio between (above-ground) gain in biomass and loss of water during the production of that biomass; the water loss may refer to total transpiration only, or include soil evaporation. Second, as explained in Sect 5.2 of Chapter 2A on photosynthesis, the **photosynthetic water-use efficiency** is the ratio between carbon gain in photosynthesis and water loss in transpiration, A/E. Instead of the ratio of the rates of photosynthesis and transpiration, the ratio of photosynthesis (A) and leaf conductance for water vapor A/g_w can be used (**intrinsic water-use efficiency**) (Comstock & Ehleringer 1992). As expected, there is generally a good correlation between the WUE of productivity and the photosynthetic WUE. Variation in intrinsic WUE is due the way stomata are controlled, as discussed in Sect. 5.4.6.

6.1 Water-Use Efficiency and Carbon-Isotope Discrimination

As explained in Box 2A.2, the carbon-isotope composition of plant biomass is largely determined

by the biochemical fractionation of Rubisco and the fractionation during diffusion of CO_2 from the atmosphere to the intercellular spaces. The higher the stomatal conductance, relative to the activity of Rubisco, the less $^{13}CO_2$ ends up in the photosynthates and hence in plant biomass. This is the basis of the generally observed correlation between $\delta^{13}C$-values and both the intercellular CO_2 concentration (C_i) and photosynthetic WUE (Fig. 30 in Chapter 2A on photosynthesis). As a result, **$\delta^{13}C$-values** can be used to assess a plant's WUE; however, differences in WUE determined at the leaf level may be reduced substantially at the canopy level, as further explained in Sect. 4 of Chapter 5 on scaling-up.

A plant's WUE depends both on stomatal conductance and on the difference in water vapor pressure in the leaf's intercellular air spaces and that in the air. Because temperature affects the water vapor concentration in the leaf, temperature also has a pronounced effect on plant WUE, A/E. Therefore, the intrinsic water-use efficiency, A/g_w, is a better indicator for a plant's physiological WUE (Comstock & Ehleringer 1992).

There are major differences in photosynthetic WUE (A/g_w) between C_3, C_4, and CAM plants, as well as smaller differences among species of the same photosynthetic pathway (Sect. 5.2 of Chapter 2A on photosynthesis). Xylem-tapping hemiparasitic plants have the lowest WUE, as discussed in Sect. 3 of Chapter 9 on parasitic associations (Table 8).

Table 8. The photosynthetic water-use efficiency* of plants with different photosynthetic pathwayand belonging to different functional groups. *****

Functional group	Water-use efficiency (mmol mol^{-1})
CAM plants	4–20
C_4 plants	4–12
Woody C_3 plants	2–11
Herbaceous C_3 plants	2–5
Hemiparasitic C_3 plants	0.3–2.5

***Source*: Kluge & Ting (1978), Osmond et al. (1982), Shah et al. (1987), Ehleringer & Cooper (1988), Morison (1987), Marshall & Zhang (1994), and Yu et al.(2005).**

***Because A/g_w (intrinsic water-use efficiency) is difficult to compare between CAM plants and other plants, A/E (photosynthetic water-use efficiency) was used instead.**

****C_3, C_4, and CAM; for CAM plants, the high values refer to gas exchange during the night and the low values to the light period.**

*****All species are nonparasitic, unless stated otherwise, grown at an ambient CO_2 concentration of around 350 mol mol^{-1} and not exposed to severe water stress.**

6.2 Leaf Traits That Affect Leaf Temperature and Leaf Water Loss

As discussed in Sect. 5.4.3, leaf temperature affects the water vapor concentration inside the leaf; therefore, it is expected to affect transpiration. At increasing irradiance, leaf temperatures may rise and enhance transpiration enormously. Plants have mechanisms to minimize these effects, however. For example, water stress may cause **wilting** in large-leaved dicots even in moist soils (Chiariello et al. 1987) or **leaf rolling** in many Gramineae (Arber 1923). The latter is associated with the presence of **bulliform** or **hygroscopic** cells in grasses and sedges which are large epidermal cells with thin anticlinal walls (Beal 1886). A decline in relative water content reduces the volume of these cells to a greater extent than that of the surrounding cells, so that the leaves roll up. As a result, less radiation is absorbed, the boundary layer conductance of the adaxial surface is decreased, and further development of water stress symptoms is reduced (Sect. 2 of Chapter 4A on the plant's energy balance). Leaf rolling is probably a consequence of the relatively large elasticity of the cell walls and associated water relations of the bulliform cells compared with other epidermal leaf cells.

Leaf movements (heliotropisms) may also reduce the radiation load, as discussed in Sect. 2.2 of Chapter 4A on the plant's energy balance. Such leaf movements require a leaf joint, or **pulvinus** at the base of the petiole or leaf sheath (Satter & Galston 1981). Solutes, especially K^+, are actively transported from one side of the pulvinus to the other (Fig. 33). Water follows passively, through **aquaporins** (Uhlein & Kaldenhoff 2008), and the turgor is increased which causes movement of the petiole or leaf sheath.

Leaf movements have been studied in detail in *Glycine max* (soybean) (Oosterhuis et al. 1985) and in *Melilotus indicus* (annual yellow sweetclover) (Schwartz et al. 1987). In these plants, as in some other Fabaceae and in *Mimosa* species, the (blue) light stimulus that gives rise to leaf movement is perceived in the pulvinus itself (Vogelmann 1984). In *Crotalaria pallida* (smooth rattlebox) (Schmalstig 1997) and in species belonging to the Malvaceae (Schwartz et al. 1987), perception occurs in the leaf lamina. In *Crotalaria pallida* the signal is transported to the pulvinus at a rate of 30–120 mm h^{-1}. Both the adaxial (upper) and the abaxial (lower) side of the pulvinus of *Melilotus indicus* perceive the light stimulus. Light perception at the adaxial side causes the pulvinus to move upward, whereas perception of light at the abaxial side induces the pulvinus to cause a downward movement (Fig. 34).

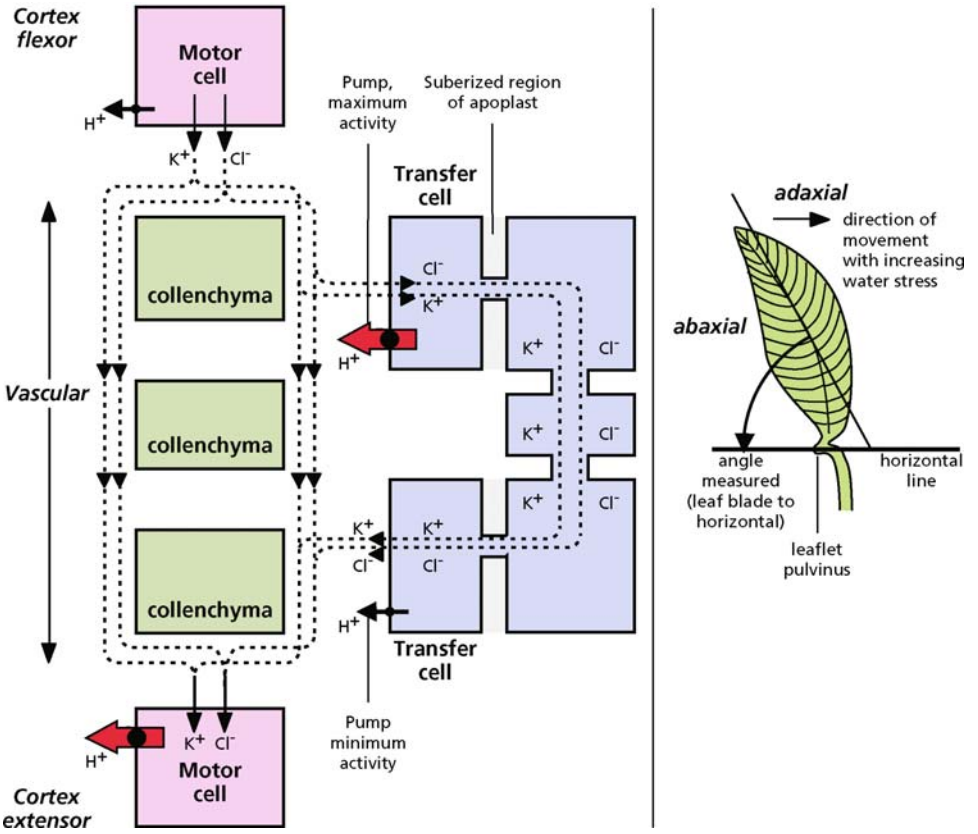

FIGURE 33. A flow diagram of the direction and pathways of net K^+, Cl^-, and H^+ movements in a pulvinus during leaflet opening (after Satter & Galston 1981; with kind permission, from the *Annual Review of Plant Physiology*, Vol. 32, copyright 1981, by Annual Reviews Inc.) and the location of the pulvinus in *Glycine max* (soybean) (after Oosterhuis et al. 1985).

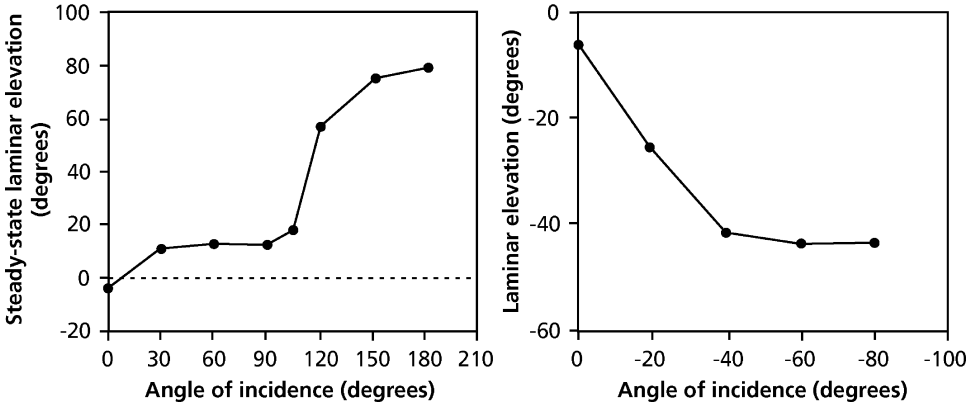

FIGURE 34. The orientation of the terminal leaf of a composite leaf of *Melilotus indicus* (annual yellow sweetclover), as dependent on the angle of the incident radiation. An angle of 0° and +180° of the light refers to light in the horizontal plane, from the tip to the base of the leaf, and from the base to the tip, respectively. An angle of +90° and –90° refers to light in the vertical plane, coming from above and below, respectively. For the leaf orientation, the same terminology is followed. (*Left*) The pulvinus is irradiated from above. (*Right*) The pulvinus is irradiated from below (after Schwartz et al. 1987). Copyright American Society of Plant Biologists.

Leaf movements of *Phaseolus vulgaris* (common bean) depend on air temperature (Fu & Ehleringer 1989). The effect of these leaf movements is that at a low air temperature the leaf is oriented in such a way as to enhance the incident radiation, whereas the opposite occurs at a high air temperature. As a result, the leaf temperature is closer to the optimum for photosynthesis (Fig. 35). The air temperature that induces the leaf movements in bean is perceived in the pulvinus, rather than in the leaf itself.

Other acclimations and adaptations that affect plant transpiration are discussed in Sect. 2.2 of Chapter 2A on the plant's energy balance.

6.3 Water Storage in Leaves

Many **succulents** store water in their leaves, often in specialized cells. For example, in the epiphytic *Peperomia magnoliaefolia* (desert privet), water storage occurs in a multiple epidermis (**hydrenchyma**), just under the upper epidermis which may account for 60% of the leaf volume (Fig. 36). The water-storage tissue of the epiphytic Bromeliad, *Guzmania monostachia* (strap-leaved guzmania), may amount to as much as 67% of the total leaf volume on exposed sites (Maxwell et al. 1992). The hydrenchyma in *Peperomia magnoliaefolia* consists of large cells with large vacuoles, but lacking chloroplasts. Their radial walls are thin and "collapse" when the cells lose water. Beneath the hydrenchyma is a layer of smaller cells that contain many chloroplasts: the

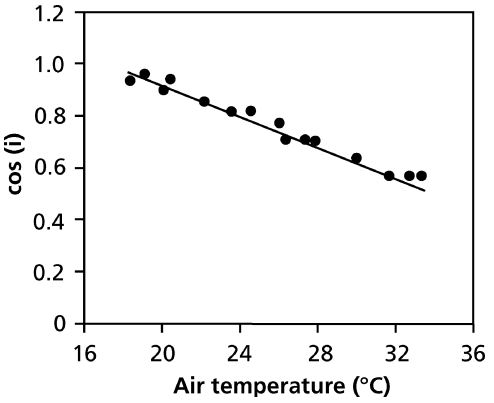

FIGURE 35. The correlation between the cosine of the angle between the incident light beam and the vector normal to the leaf lamina of *Phaseolus vulgaris* (common bean) as dependent on air temperature. Irradiance, atmospheric CO_2 concentration, and vapor pressure deficit were constant (after Fu & Ehleringer 1989). Copyright American Society of Plant Biologists.

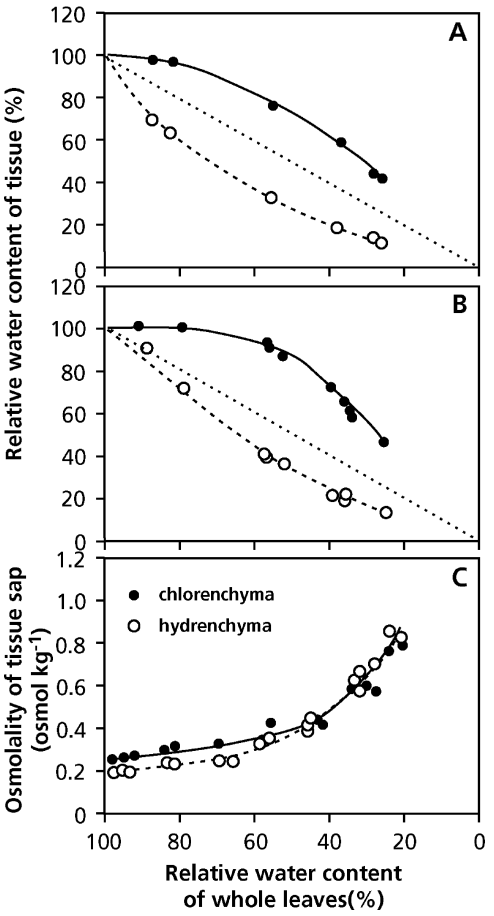

FIGURE 36. The relative water content (A, B) and the osmolality (C) of the hydrenchyma and chlorenchyma sap of *Peperomia magnoliaefolia* (desert privet) as dependent on the relative water content of whole leaves. The data in A and B refer to results obtained with detached and attached leaves, respectively; the *broken line* gives the relative water content if both tissues would lose water at the same rate (after Schmidt & Kaiser 1987). Copyright American Society of Plant Biologists.

chlorenchyma. Like in the stems of the hemiepiphytic cactus discussed in Sect. 5.3.7, when the leaves lose water, the dehydration of the chlorenchyma is much less than that of the hydrenchyma. The hydrenchyma functions as a reservoir for water lost through transpiration. This allows the chlorenchyma to remain photosynthetically active. During water loss, both solutes and water move from the hydrenchyma to the chlorenchyma. The total amount of water in the hydrenchyma of *Peperomia magnoliaefolia* exceeds 1 kg m^{-2} leaves. At an average transpiration rate of 0.2 mmol H_2O m^{-2} s^{-1} during 12 hours of the day, this stored water allows the plant

to continue to transpire at the same rate for about 1 week. The stored water allows the plant to maintain a positive carbon balance in the absence of water uptake from the environment for several days.

In a South African succulent, the facultative CAM plant *Prenia sladeniana*, during desiccation, water shifts from older leaves to younger ones. If this shift of water is prevented because the older leaves are removed, then the quantum yield of photosynthesis, as determined from fluorescence parameters (Box 2A.4), declines more during a 12-day drought period than it does when older leaves are present (Tüffers et al. 1996).

7. Water Availability and Growth

During incipient water-stress, specific genes are induced (Fig. 37). Some water-stress-induced gene products protect cellular structures from the effects of water loss, whereas others are involved in the regulation of genes for signal transduction in the water-stress response. The protective proteins include **water-channel** proteins (**aquaporins**) (Sect. 5.2), enzymes required for the biosynthesis of various **compatible solutes** (Sect. 4.1), proteins that may **protect** macromolecules and membranes, **proteases** for protein turnover, **detoxification enzymes** (e.g., catalase and superoxide dismutase) (Zhu 2002, Bray 2004). The protective proteins are predominantly hydrophilic and they are probably located in the cytoplasm where they are involved in the sequestration of ions, which become concentrated during cellular dehydration. They are amphiphilic α-helices (i.e., they contain both hydrophilic and hydrophobic parts). The hydrophilic part binds ions, thus preventing damage, whereas the hydrophobic part is associated with membranes. Other proteins have many charged amino acids and are thought to have a large water-binding capacity. Some of the proteins may protect other proteins, by replacing water, be involved in renaturation of unfolded proteins, or have a chaperon function (i.e., allow the transport of proteins across a membrane, on their way to a target organelle) (Bray 1993).

At a low soil water potential, the rate of photosynthesis decreases, largely due to a decline in stomatal conductance (Sec. 5.1 of Chapter 2A on photosynthesis). As pointed out in Sect. 5.3 of Chapter 7 on growth and allocation, however, effects of water stress on growth are largely accounted for by physiological processes other than photosynthesis. Many processes in the plant are far more sensitive to a low water potential than are stomatal conductance and photosynthesis. The growth reduction at a low soil water potential is therefore more likely due to inhibition of more sensitive processes such as **cell elongation** and **protein synthesis**; these processes are, at least partly, also controlled by **ABA** (Box 7.1).

Above-ground plant parts respond more strongly to a decreased soil water potential than do roots. Is this perhaps due to a much greater effect of the low water potential on growth of leaves, as compared with that of the roots, simply because they are closer to the source of water? Do roots and leaves, on the other hand, have a different

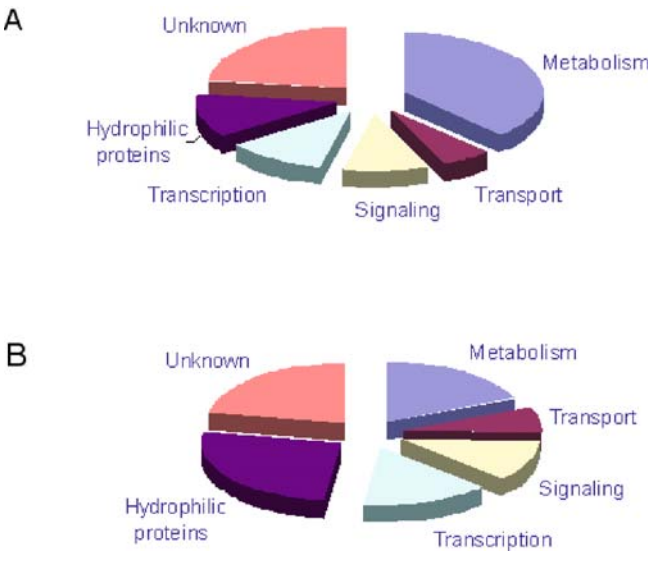

Figure 37. Functional categories of the genes induced in water-deficit experiments of *Arabidopsis thaliana* (thale cress), as observed in microarray experiments using different methods to impose water stress (A and B). The microarray technology allows the study of expression patterns of thousands of genes simultaneously, proving a comprehensive understanding of the types and quantities of RNAs that are present in a cell, in this example in response to water-deficit stress. There are 27 genes commonly induced and three commonly repressed (after Bray 2004).

sensitivity for the water potential? In *Zea mays* (corn), the soil water potential causing growth reduction is indeed lower (more negative) for roots than it is for leaves, but this does not provide a conclusive answer to our question. In Sect. 5.3 of Chapter 7 on growth and allocation, this problem is addressed more elaborately. Lowering the water potential enhances the transport of assimilates to the roots which is probably due to the growth reduction of the leaves. Because photosynthesis is less affected than leaf growth is, sugar import as well as root growth may be enhanced, with the overall effect that the leaf area ratio decreases in response to a decrease in soil water potential. That is, the evaporative surface is reduced, relative to the water-absorbing surface.

Aquatic angiosperms are perhaps comparable to whales: they returned to the water, taking with them some features of terrestrial organisms. In perennially submerged angiosperms, where the pressure in the xylem is never negative, the xylem is somewhat "reduced". The structure is like that of resin ducts. The xylem ducts in submerged aquatics often have thin walls, whereas "conventionally" thick-walled xylem cells are found in aquatics whose tops are able to emerge from the water.

It is well established that water transport from roots to leaves is possible in submerged aquatic angiosperms, and that it is important in the transport of nutrients and root-produced phytohormones to the stem and leaves. The roots of most aquatics serve the same role as those of terrestrial plants as the major site of nutrient uptake and in the synthesis of some phytohormones. In submerged angiosperms, the driving force for xylem transport cannot be the transpiration, and root pressure is the most likely mechanism (Pedersen & Sand-Jensen 1997).

8. Adaptations to Drought

Plants have adapted to a lack of water in the environment either by avoiding drought or by tolerating it. **Desert annuals** and drought-deciduous species **avoid** drought by remaining dormant until water arrives. Other plants in dry environments avoid drought by producing roots with access to deep groundwater (**phraetophytes**). The alternative strategy is to **tolerate** drought. Tolerance mechanisms are found in evergreen shrubs and in plants that can dry out in the absence of water and "resurrect" upon exposure to water. Many plants in dry habitats exhibit intermediate strategies. For example, succulents, especially those with the CAM pathway (Sect. 10 of Chapter 2A on photosynthesis), minimize effects of drought by opening their stomates at night and concentrating their activity in wet seasons, but they also have many characteristics typical of drought-tolerant species.

8.1 Desiccation Avoidance: Annuals and Drought-Deciduous Species

A large proportion of the plants in deserts are annuals with no specific physiological tolerance of desiccation. As is further discussed in Sect. 2.2 of Chapter 8 on life cycles, seeds of these species may germinate only after heavy rain. These species grow very fast following germination, often completing their life cycle in 6 weeks or less. These plants typically have high rates of photosynthesis and transpiration as well as a high leaf area ratio to support their rapid growth (Mooney et al. 1976).

The most obvious mechanism of acclimation to drought is perhaps a decrease in canopy leaf area. This can be rapid, through **leaf shedding**, or more slowly, through adjustments in allocation pattern (Sect. 5.3 of Chapter 7 on growth and allocation). In general, drought-deciduous species have high stomatal conductance and high rates of photosynthesis and transpiration when water is available, but lose their leaves and enter **dormancy** under conditions of low water potential. As with desert annuals, their leaves exhibit no physiological adaptations for drought tolerance or water conservation. The advantages of a drought-deciduous strategy (high rates of photosynthesis and growth under favorable conditions) are offset by the cost of producing new leaves in each new growth period. Some species [e.g., *Fouqueria splendens* (ocotillo) in the deserts of North America] produce and lose leaves as many as six times per year. There is typically a 2–4 week lag between onset of rains and full canopy development of drought-deciduous species. It is, therefore, not surprising that drought-tolerant evergreens displace drought-deciduous species as rains become more frequent and water availability increases (Fig. 38).

Some desert plants, known as **phreatophytes**, produce extremely deep roots that tap the water table. Like the desert annuals and drought-deciduous shrubs, these plants generally have high rates of photosynthesis and transpiration with little capacity to restrict water loss or withstand drought. For example, honey mesquite (*Prosopis glandulosa*) commonly occupies desert washes in the south-eastern United States, where there is little surface water but where groundwater is close enough to the surface that seedlings can occasionally produce deep

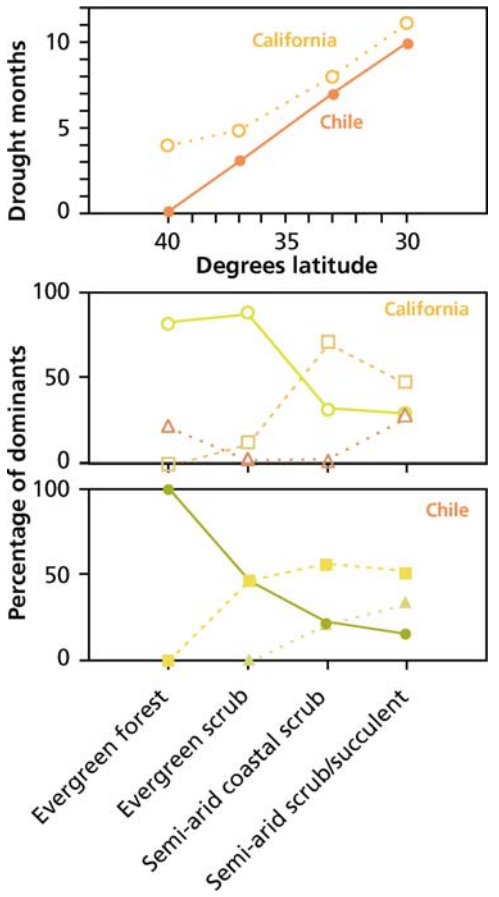

Figure 38. Leaf types of the dominant plants in major vegetation types along a latitudinal drought gradient in California and Chile. Leaf types are evergreen (*circles*), deciduous (*squares*), and succulent (*triangles*) (after Mooney & Dunn 1970).

enough roots to reach this groundwater in wet years. In the same area, *Tamarix chinensis* (saltcedar), which is an exotic phreatophyte, has lowered the water table sufficiently through its high transpiration rate that other species of intermediate rooting depth are being eliminated (Van Hylckama 1974).

8.2 Dessication Tolerance: Evergreen Shrubs

Most evergreen shrubs are exposed to water stress during part of the year, whether during the summer in a Mediterranean climate, or in winter in cooler climates.

Relatively drought-tolerant species [e.g., *Olea oleaster* (olive) in Fig. 28] withstand lower water potentials before stomatal closure and before loss of turgor because they have relatively elastic cell walls (low elastic modulus, ε) and a high resistance to cavitation of xylem. Natural selection leading to scleromorphic and evergreen growth habits is complex. Low P availability is a major environmental factor driving the evolution of evergreen, scleromorphic leaves (Loveless 1961, 1962).

Mediterranean shrubs are also characterized by **dual** or **dimorphic root systems**, having both deep taproots and shallow feeder roots. This architecture allows access to semi-permanent groundwater supplies as well as to surface precipitation (Rundel 1995). A large number of woody shrub and tree species [e.g., *Banksia prionotes* (acorn banksia) and*Banksia ilicifolia* (holly-leaved banksia)] of the nutrient-impoverished sandplains of southwest Australia possess dimorphic root systems. Superficial lateral roots exploit nutrient-enriched surface layers during the wet winter season (Sect. 2.2.5.2 of Chapter 5 on mineral nutrition), and a deeply penetrating sinker taps underground sources of water throughout the year, and especially during the prolonged dry summer. Sinkers may reach the water table at 2.5–2.9 m depth. They have xylem vessels with diameters ranging from 55 to 120 μm, as opposed to 30–70 μm for lateral roots. As a result, the hydraulic conductance (on the basis of organ transectional area) of sinker roots ranges from 30 to 780 $\times$ 10^{-3} m^2 MPa^{-1} s^{-1}, which is consistently greater than that of associated laterals (2–50 $\times$ 10^{-3} m^2 MPa^{-1} s^{-1}) or trunks (0.5–9 $\times$ 10^{-3} m^2 MPa^{-1} s^{-1}) (Pate et al. 1995).

8.3 Resurrection Plants

An extreme case of desiccation tolerance of whole plants is that of **resurrection plants** or "poikilohydric plants". Even after their protoplasm has dried out to the extent that the water potential of the cells is in equilibrium with dry air (with a relative humidity of 20–40%), they can almost fully restore their physiological activity (Gaff 1981). Their dry, shriveled, and seemingly dead leaves regain turgor in less than 24 hour after a shower which makes the term "resurrection" most appropriate. Many mosses and ferns and some angiosperms, including woody species [e.g., *Myrothamnus flabellifolius* (resurrection bush)] are characterized as resurrection plants. They are mostly found in Southern Africa, North America, Brazil, and Australia in environments where droughts occur regularly (e.g., on rocky substrates); there are only two

European genera of angiosperm resurrection plants, *Ramonda* and *Haberla* (Gesneriaceae).

There are two strategies among resurrection angiosperms:

1. Those that lose chlorophyll and break down their chloroplasts upon drying (**poikilochlorophyllous**)
2. Those that retain some or all of their chlorophyll and chloroplast ultrastructure (**homoiochlorophyllous**).

The poikilochlorophyllous species tend to take longer to recover than do the homoiochlorophyllous ones because they must reconstitute their chloroplasts (Sherwin & Farrant 1996). All poikilochlorophyllous species are monocots, but some of the grasses are homoiochlorophyllous. The two strategies may have evolved in response to light stress, which is exacerbated during dehydration and rehydration. While the leaf tissue is dehydrating, dry, or rehydrating, light absorption should be minimal and the energy that is absorbed must be dissipated. The leaves of homoiochlorophyllous plants tend to roll or curl and produce protective pigments (e.g., anthocyanins), which act as screens. The poikilochlorophyllous plants tend to have elongate leaves that can only fold, thus leaving a greater surface exposed to light (Sherwin & Farrant 1998).

The exact nature of the reactivation of the physiological processes is not yet fully understood. The following must generally hold

1. Any damage incurred during the drying phase is not lethal
2. Some of the metabolic functions are maintained in the dry state, to an extent that they can be deployed upon rewetting
3. Any damage incurred is repaired during or after rehydration

Even though the dehydrated homoiochlorophyllous resurrection plants may have lost most of their green color, their thylakoid membranes, chlorophyll complexes, mitochondria, and other membrane systems remain intact. Elements of the protein-synthesizing machinery, including mRNA, tRNA, and ribosomes, also remain functional. Using inhibitors of transcription and translation show that membrane protection and repair does not require transcription of new gene products or translation of existing transcripts. Full recovery of the photosynthetic apparatus in the homoiochlorophyllous *Craterostigma wilmsii* requires protein synthesis, but not gene transcription. On the other hand, for the poikilochlorophyllous *Xerophyta humilis* both transcription and translation are required for full recovery (Dace et al. 1998). *Myrothamnus flabellifolius* (resurrection bush) is a South African resurrection plant with a woody stem. Transpiration rates in well-watered plants are moderate, generating xylem water potentials of −1 to −2 MPa. Acoustic emissions indicate extensive cavitation events at xylem water potentials of −2 to −3 MPa. On re-watering, the root pressures are low (0.0024 MPa), but capillary forces are adequate to account for the refilling of xylem vessels and re-establishment of hydraulic continuity even when water was under a mild tension of –0.008 MPa (Sherwin et al. 1998). *Vellozia flavicans* in the cerrado in central Brazil takes up water via its shoot, as evidenced by sap-flow measurements (Oliveira et al. 2005).

A large number of enzymes associated with carbon metabolism remain intact in the dry state, as found for *Selaginella lepidophylla* (resurrection plant) from the Chihuahua Desert in Texas (Table 9). About 24 hours after rewetting, the plants have regained their green appearance, and rates of photosynthesis and respiration are again close to those of normal wet plants. At that time, the activity of many enzymes has increased, compared with that in dehydrated plants. On average, 74% of the enzyme activity remains in the dry phase; however, this value is only 27% for the NADPH-dependent triose-phosphate dehydrogenase in *Selaginella lepidophylla*. In addition, in a bryophyte, *Acrocladium cuspidatum*, the activity of this photosynthetic enzyme is reduced more than that of all other enzymes tested. It appears that enzymes involved in respiratory metabolism are conserved better than are those associated with photosynthesis. The increase in activity of the enzymes that are not fully conserved in the dry phase may involve de novo protein synthesis (NADP-dependent triose-phosphate dehydrogenase, Rubisco). Rapid de novo synthesis, in addition to the maintenance of functional enzymes, is clearly important in the reactivation phase after rewetting. Maintenance of the protein-synthesizing machinery, therefore, appears to be of vital importance.

During dehydration of the resurrection plants, as in "ordinary" plants, the phytohormone **ABA** accumulates. In resurrection plants, ABA induces the **transcription** of a number of genes, which code for proteins that are closely related to those that are abundantly induced during embryo maturation in the seeds of many higher plants or to some extent in water-stressed seedlings (Bartels & Salamini 2001). In the small, herbaceous, homoiochlorophyllous *Craterostigma plantagineum*, **sucrose** accumulates to high concentrations (up to 40% of the dry

Table 9. The activity of three enzymes associated with photosynthesis and three involved in respiration.*

	Enzyme activity enzyme units g^{-1} DM		Conservation
Enzyme	Desiccated	Hydrated	%
Photosynthetic enzymes:			
Ribose-5-phosphate isomerase	7.56	9.24	82
Rubisco	0.60	0.96	62
(NADPH)Triose-phosphate dehydrogenase	0.48	1.80	27
Respiratory enzymes:			
Citrate synthase	1.76	2.05	86
Malate dehydrogenase	2.89	2.97	97
(NADH)Triose-phosphate dehydrogenase	1.13	1.40	81

Source: Harten & Eickmeier (1986).
* They were isolated from the resurrection plant *Selaginella lepidophylla*, both from dehydrated plants and 24 hours after rehydration.

mass), while the concentration of the C8-sugar octulose declines; upon rehydration, sucrose is converted back into octulose (Bartels & Salamini 2001). In the European *Ramonda* and *Haberlea* species, sucrose is also the predominant sugar that accumulates upon desiccation (Müller et al. 1997). Sucrose and other solutes play a major role in stabilizing subcellular components, including membranes and proteins. The sugars ensure that the small amount of water left in the tissue occurs in a "glassy" state, like the glass in our windows, which is actually a fluid. Some of the gene products are proteins with both hydrophobic and hydrophilic zones; they may bind ions and be membrane-associated (Bartels & Salamini 2001). These probably have an "osmoprotective" function, reducing potential damage by high solute concentrations. Other gene products are likely involved in carotenoid biosynthesis (Alamillo & Bartels 1996).

The genes expressed upon dehydration of resurrection plants are similar to those expressed at the end of the ripening of the embryo in **ripening seeds**, described as **late embryogenesis abundant** genes, or *lea* genes. The proteins involved in the survival of dehydrated embryos in dry seeds are similar to those that protect resurrection plants in their dehydrated state (**LEA proteins** or **dehydrins**). Dehydrins are rich in polar and charged amino acids; their expression is induced by environmental stresses or the application of ABA (Bartels & Salamini 2001, Neale et al. 2000). Some of the genes that are expressed in resurrection plants during dehydration are also expressed in water-stressed leaves, and more so in the more desiccation-resistant *Populus popularis* (poplar) than in the less resistant *Populus tomentosa* (Chinese white poplar) (Pelah et al. 1997).

9. Winter Water Relations and Freezing Tolerance

As discussed in Sect. 5.3.2, subzero temperatures may lead to the formation of air bubbles in xylem conduits, hence to **embolism**. The water in the xylem generally freezes between 0 and –2°C. Some water transport may still continue after embolism has occurred, although at a very low rate (around 3% of normal rates). This slow movement probably occurs either through late-wood tracheids or through cell-wall cavities (Tranquillini 1982).

Frost damage is also associated with the formation of extracellular **ice crystals** that cause severe dehydration of the cytoplasm and the formation of crystals inside the cells, both being associated with damage to membranes and organelles. The cells become leaky and their water potential declines sharply. Resistance mechanisms predominantly involve the prevention of the formation of intracellular ice crystals, by restricting freezing to the extracellular compartment or by biochemical mechanisms to withstand dehydration (Thomashow 1999, Xiong et al. 2002, Shinozaki & Yamaguchi-Shinozaki 2000, Shinozaki et al. 2003). During cold acclimation, leaves of *Secale cereale* (rye) produce "**antifreeze proteins**" in their apoplast. These proteins interact directly with ice *in planta* and reduce freezing injury by slowing the growth and recrystallization of ice, but have no

specific cryoprotective activity (Griffith et al. 2005). At a molecular level, the responses to low temperature share major elements with plant responses to dehydration (Yamaguchi-Shinozaki & Shinozaki 2006).

Changes in the composition of cell walls play a major role in preventing ice formation. For example, deposition of **pectin** in the cell wall reduces the size of the microcapillaries in the walls, allowing a more negative water potential. Pectin formation in the pits between xylem and xylem-parenchyma cells (Fig. 14) closes these pores, so that water remains in the cells (Fig. 39). In spring, pectin is enzymatically removed again, coinciding with the loss of the capacity to tolerate deep supercooling (Wisniewski et al. 1991). Deep supercooling is only possible to temperatures around –40°C; below that temperature ice formation occurs in the absence of crystallization nuclei.

In subarctic trees, which tolerate temperatures below –40°C, supercooling does not play a role. Ice formation starts around–2 to –5°C, but only in the cell wall. The cold acclimation that occurs in autumn is triggered by photoperiod and exposure to cool temperatures. It involves synthesis of membrane lipids with less saturated fatty acids, so they remain flexible at low temperatures, and the production of osmotically active solutes. Cells that would freeze at –3 to –5°C in summer remain unfrozen to –40°C in winter. At subfreezing temperatures, ice forms first in cell walls, reducing the concentration of extracellular liquid water. Water moves out of cells along this water-potential gradient, increasing the

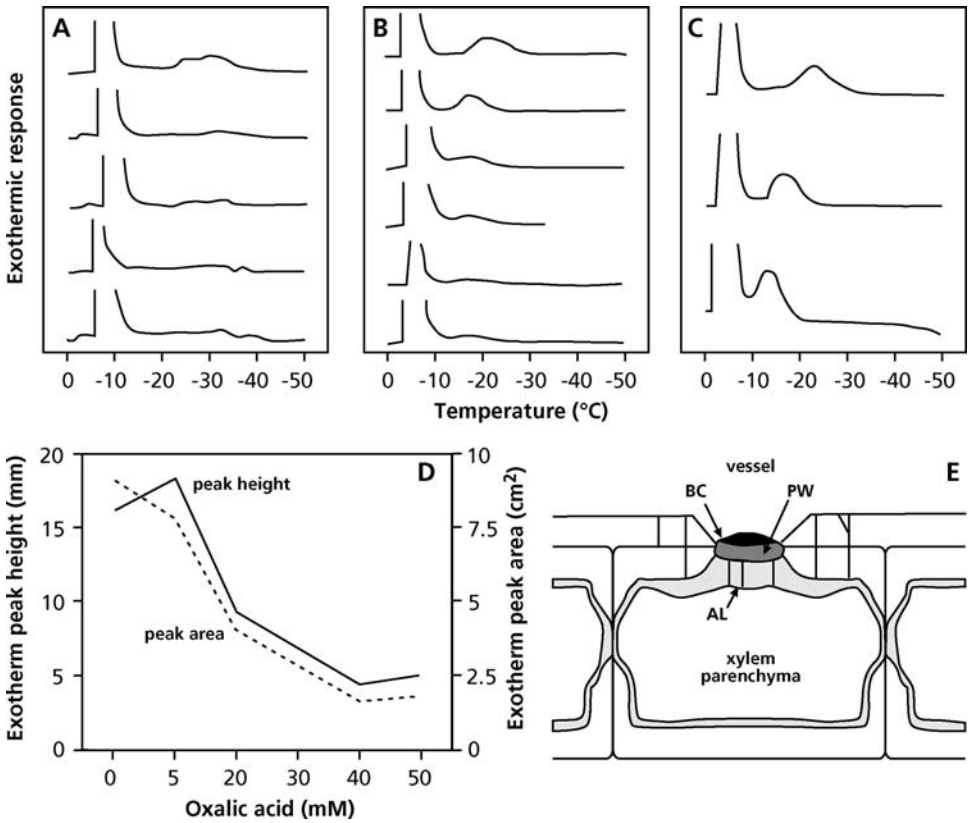

FIGURE 39. (A-C) The effect of macerase (an enzyme that hydrolyzes pectin), oxalic acid, and EGTA (both bind Ca^{2+}, responsible for "cross-linking" in pectin) on the exothermal response. The left peak (which is not relevant in the present context) is due to freezing of extracellular water. The peak to the right decreases, or shifts to lower temperatures, upon removal of pectin. The data in (B) have been replotted in (D), both as peak height and as peak area vs. the concentration of oxalic acid. (E) The structure of a pit between the xylem and a xylem-ray parenchyma cell of *Prunus persica* (peach). The pit membrane consists of three layers: an outermost black cap (BC) or toruslike layer, a primary wall (PM), and an amorphous layer (AL). The channels are meant to diagrammatically illustrate how pore size or continuity would affect the ability of a cell to exhibit deep supercooling (after Wisniewski et al. 1991). Copyright American Society of Plant Biologists.

intracellular solute concentration, which prevents intracellular freezing. The biochemical mechanisms to withstand this winter desiccation are identical to those caused by lack of water in deserts. It is therefore not surprising that species that tolerate extremely low temperatures are also highly desiccation-tolerant.

10. Salt Tolerance

Halophytes are species that typically grow in soils with high levels of NaCl and, hence, a low water potential. They accumulate NaCl in their vacuoles. By contrast, **glycophytes** have a limited capacity to transport NaCl into their vacuoles and are unable to tolerate high salinity levels. Cytoplasmic enzymes of glycophytes and halophytes are very similar with respect to their sensitivity to high concentrations of inorganic solutes (Fig. 6). Tolerance mechanisms of halophytes are discussed in Sect. 3.4 of Chapter 6 on mineral nutrition.

11. Final Remarks: The Message That Transpires

What have we finally learned from this chapter on water relations? First, that water is a major factor limiting plant growth in many ecosystems, and also that in different species fascinating mechanisms have evolved to cope with this limiting factor, ranging from **avoidance** to **tolerance**. Tolerance at one level (e.g., of the roots) may allow drought avoidance at another (e.g., of the leaves). Plants have adapted to a limiting supply of water in their environment, but all plants, to varying degrees, can also acclimate to an environment where water is scarce.

The characteristics that enable plants to tolerate drought are highly interdependent (Table 10). To appreciate these mechanisms, a full understanding of the biophysical, physiological, and molecular aspects of plant water relations is essential. Such an appreciation is pivotal, if we aim to improve the performance of crops in dry environments. This is not to say that other ecophysiological aspects are not of equal, or even greater, importance. In fact, vigorous early growth and early flowering may also greatly contribute to a greater water-use efficiency over the entire season, when evaporative demands are considerably less.

Resurrection plants offer one of the most remarkable examples of how plants cope with a shortage of water in their environment. At one stage, it may have been considered esoteric to study these peculiar plants, which would seem useless from an economic point of view. It now becomes increasingly clear, however, that resurrection plants show many similarities to ripening seeds and leaves that are able to cope with water stress. As such, resurrection plants offer a model system to study water-stress resistance, and they may also be a source of genes to be used to improve the performance of new crop varieties in dry environments. As so often in science, possibilities for applications emerge that are based on fascinating discoveries on fundamental aspects of plant biology.

Table 10. Summary of characteristics of drought-sensitive and drought-tolerant evergreen species.

Characteristic	Drought-sensitive species	Drought-tolerant species
Maximum transpiration rate	High	Low
Maximum photosynthetic rate	High	Low
Maximum stomatal conductance	High	Low
Specific leaf area	High	Low
Leaf size	Large	Small
Leaf longevity	Low	High
Potential growth rate	High	Low
Root mass ratio	Low	High
Leaf compatible solute concentration	Low	High
Water potential at turgor loss	High	Low
Stomatal regulation	Iso/anisohydric	Anisohydric
Safety margin for cavitation	Small	Large

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