9 Temperature

Contents

Plants can survive the whole range of atmospheric temperatures from −89°C (recorded at Vostok in Antarctica www.ncdc.noaa.gov/oa/climate/globalextremes.html#sites) to 56.7°C (recorded in Death Valley, California; El Fadli *et al.*, 2012) that occur on the surface of the Earth, as well as the associated higher temperatures (up to about 70°C) that occur in the surface of desert soils and in the surface tissues of slowly transpiring massive desert plants such as cacti (Nobel, 1988). The even higher surface temperatures of up to 300°C that occur in bushfires can be survived by fire-tolerant plants. Seeds are particularly hardy, though other tissues of some species can also survive an extremely wide temperature range. Most plants can only grow, however, over a much more limited range of temperatures from somewhat above freezing to around 40°C, while growth approaches the maximum over an even more restricted temperature range that depends on species, growth stage and previous environment. Useful information on plants and temperature may be found in Larcher (1995) and Long and Woodward (1988).

In this chapter the physical principles underlying the control of plant temperatures are described and the physiological effects of high and low temperatures outlined. The final section considers the more ecological aspects of plant adaptation and acclimation to the thermal environment.

9.1 Physical basis of the control of tissue temperature

As outlined in Chapter 5, the temperature of plant tissue at any instant is determined by its energy balance. Neglecting any metabolic storage, the energy balance equation (Eq.(5.1)) reduces to:

$$\mathbf{R_n} - \mathbf{C} - \lambda\mathbf{E} = \mathbf{S} \tag{9.1}$$

where, as we have seen, $\mathbf{R_n}$ is the net radiation, $\mathbf{C}$ is the sensible heat transfer, λ is the latent heat of evaporation of water, $\mathbf{E}$ is the evaporative flux and $\mathbf{S}$ is the amount of energy going into physical storage. Any imbalance in the energy fluxes goes into physical storage, thus altering tissue temperature. Although what follows refers mainly to leaf temperatures, the same principles apply to all above-ground tissues. Further discussion of biophysical aspects of control of plant temperature may be found in appropriate texts (Campbell & Norman, 1998; Gates, 1980; Monteith & Unsworth, 2008).

9.1.1 Steady state

In the steady state, when leaf temperature is constant, Eq. (9.1) reduces to:

$$\mathbf{R}_n - \mathbf{C} - \lambda\mathbf{E} = 0 \tag{9.2}$$

This may be expanded by substituting the following versions of equations for the sensible heat (Eq.(3.29)) and latent heat (Eq.(5.20)) losses:

$$\mathbf{C} = \rho_a c_p (T_\ell - T_a)/r_{aH} \tag{9.3}$$

$$\begin{aligned}\lambda\mathbf{E} &= (0.622\rho_a\lambda/P)(e_{s(T\ell)} - e_a)/(r_{aW} + r_{\ell W})\\ &= (\rho_a c_p/\gamma)(e_{s(T\ell)} - e_a)/(r_{aW} + r_{\ell W})\end{aligned} \tag{9.4}$$

Using the resulting expanded equation, it is possible to determine leaf temperature when values for absorbed radiation, air temperature, humidity, and leaf and boundary layer resistances are known by means of an iterative computing procedure (Campbell & Norman, 1998; Gates, 1980; Jones & Vaughan, 2010; Monteith & Unsworth, 2008). A rather more convenient analytical expression for leaf temperature can be obtained by using the Penman linearisation as used for the combination equation for evaporation (Eq. (5.26)). The procedure is to use Eq. (5.21) to replace the leaf–air vapour pressure difference in Eq. (9.4) by the humidity deficit of the ambient air (D) and the leaf–air temperature difference. Subsequent combination of Eqs. (9.2) to (9.4) yields the following:

$$T_\ell - T_a = \frac{r_{aH}(r_{aW} + r_{\ell W})\gamma\mathbf{R}_n}{\rho_a c_p[\gamma(r_{aW} + r_{\ell W}) + s\,r_{aH}]} - \frac{r_{aH}D}{[\gamma(r_{aW} + r_{\ell W}) + s\,r_{aH}]} \tag{9.5}$$

This equation shows that the leaf temperature excess is given by the sum of two terms, one depending on net radiation and the other on the vapour pressure deficit of the air.

There are two important approximations involved in the derivation of Eq. (9.5). The first is the Penman linearisation, which assumes that the rate of change of saturation vapour pressure with temperature (s) is constant between T_a and T_ℓ. This introduces negligible error for normal temperature differences. The other approximation is that net radiation is an environmental factor unaffected by leaf conditions, but $\mathbf{R}_n$ is actually a function of leaf temperature itself. It is possible to allow for this effect by using the concept of isothermal net radiation that was introduced in Section 5.1.2. Replacing $\mathbf{R}_n$ in Eq. (9.5) by $\mathbf{R}_{ni}$ and replacing r_{aH} by r_{HR} gives:

$$T_\ell - T_a = \frac{r_{HR}(r_{aW} + r_{\ell W})\gamma\,\mathbf{R}_{ni}}{\rho_a c_p[\gamma(r_{aW} + r_{\ell W}) + s\,r_{HR}]} - \frac{r_{HR}\,D}{[\gamma(r_{aW} + r_{\ell W}) + s\,r_{HR}]} \tag{9.6}$$

Using Eq. (9.6) we can now investigate how the leaf–air temperature difference depends on environmental and plant factors. Although in practice there are complex feedback effects on r_ℓ (see Chapter 6), a useful summary of how the various factors in Eq. (9.6) affect leaf temperature can be obtained by varying each independently. The results of such an approach are shown in Figure 9.1 and summarised below.

Leaf resistance

Where the surface is dry so that there is no latent heat term in the energy balance (this is equivalent to $r_\ell = \infty$), Eq. (9.6) reduces to:

$$T_\ell - T_a = \mathbf{R}_{ni} r_{HR}/\rho_a c_p \tag{9.7}$$

In this case, $T_\ell - T_a$ is proportional to $\mathbf{R}_{ni}$, with the leaf being warmer than air when $\mathbf{R}_{ni}$ is positive (as it usually is during the day), and cooler than air when $\mathbf{R}_{ni}$ is negative. Because r_{HR} includes both a radiative and a convective component, $T_\ell - T_a$ is not linearly related to r_{aH}.

When the surface is perfectly wet, as might occur when it is covered in dew, $r_\ell = 0$. In this case the latent heat cooling is maximal for any boundary layer resistance. As r_a tends to 0, the value of $T_a - T_\ell$ tends to $D/(\gamma + s)$, the theoretical wet bulb depression.

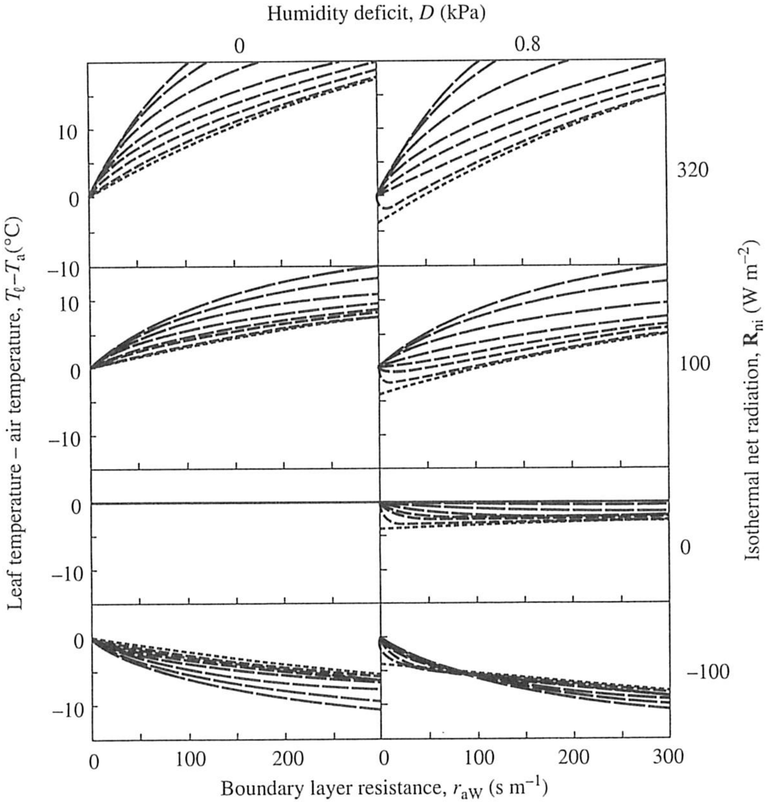

Figure 9.1 Calculated dependence of leaf–air temperature difference on D, $\mathbf{R}_{ni}$, r_a and r_ℓ for $T_a = 20$°C. The different lines represent r_ℓ ranging from 0 s m^{-1} with short dashes, through 10, 50, 100, 200, 500, 2000 to ∞ with the longest dashes.

When r_ℓ is finite, leaf temperature tends towards air temperature as the boundary layer resistance approaches zero. With normal values for the boundary layer resistance, the amount of transpirational cooling increases as r_ℓ decreases. Whether this transpirational cooling is adequate to cool the leaf below air temperature depends on other factors, particularly $\mathbf{R}_{ni}$ and D. Leaf temperature tends to rise as r_ℓ increases (see Figure 9.1); the anomalous behaviour in Figure 9.1, when net radiation is negative, arises when condensation (i.e. dewfall) is occurring. In this case the leaf resistance is zero so the calculated curves for higher values of r_ℓ are physically unrealistic.

Vapour pressure deficit

The effect of humidity deficit on T_ℓ depends on the total resistance to water vapour loss. Where the surface is dry (or where $r_\ell = \infty$) so no latent heat loss can occur, D is irrelevant to leaf temperature (Eq. (9.7)). In all other cases, any increase in D lowers T_ℓ especially when r_ℓ is low.

Net radiation

Increasing the radiative heat load on a leaf while maintaining other factors constant always tends to increase T_ℓ (Figure 9.1). When $\mathbf{R}_{ni}$ is negative (it is commonly as low as −100 W m^{-2} on a clear night) T_ℓ must be below T_a. The net radiation absorbed by a leaf is very dependent on the value of the reflection coefficient for solar radiation (ρ_S, see Chapter 2).

Boundary layer resistance

The effect of r_a on leaf temperature is complex, especially with low boundary layer resistances where evaporative cooling can lower leaf temperature below air temperature. Increasing r_a can increase or decrease T_ℓ depending on the environmental conditions and on r_ℓ. When T_ℓ is above T_a, increases in r_a always tend to increase T_ℓ. The value of r_a itself is dependent on wind speed and leaf size and shape as outlined in Chapter 3.

Air temperature (T_a)

The effect of ambient air temperature on leaf temperature is two-fold. First, it provides the reference temperature to which T_ℓ tends. Second, there are two major effects of T_a on the value of $T_\ell - T_a$: the value of s increases with temperature so that any leaf temperature excess decreases with increasing temperature (Eq. (9.6)), and for any given value of relative or absolute humidity, D increases with increasing temperature, therefore increasing latent heat loss and lowering T_ℓ with respect to T_a as shown in Figure 9.2. These two latter effects lead to large positive values of $T_\ell - T_a$ at low temperatures.

Water deficit

Because the leaf–air temperature differential is related to the leaf conductance, it has been suggested that T_ℓ or the leaf–air temperature differential can be used as a measure of the degree of water stress to which a plant is subject. Both empirical and theoretical approaches have been used to calculate a 'stress index', based on this property. The theoretical and practical basis of such a stress index is discussed in detail in Chapter 10.

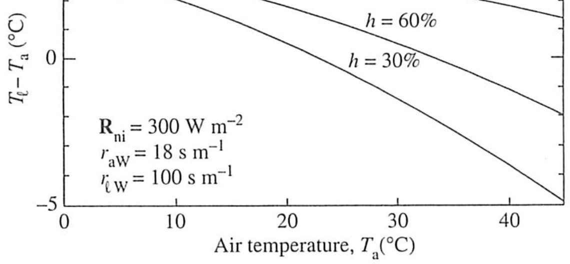

Figure 9.2 Effect of air temperature on leaf–air temperature difference at various constant relative humidities (h, %) according to Eq. (9.6).

9.1.2 Non-steady state

In a natural environment, irradiance and wind speed, particularly, are continually varying so that steady plant temperatures are rarely attained. When any component of the energy balance changes so that $\mathbf{S}$ is no longer zero, leaf temperature alters in the direction needed to return the net energy exchange to zero. For example, if $\mathbf{R}_n$ increases, leaf temperature also increases until the increased sensible and latent heat losses again balance the new value of $\mathbf{R}_n$.

The rate of change of leaf temperature depends on the heat capacity per unit area of the tissue ($\rho^* c_p^* \ell^*$):

$$\frac{\mathrm{d}T_\ell}{\mathrm{d}t} = \mathbf{S}/(\rho^* c_p^* \ell^*) = (\mathbf{R}_n - \mathbf{C} - \lambda\mathbf{E})/(\rho^* c_p^* \ell^*) \qquad (9.8)$$

where ρ^* and c_p^* are the density and specific heat capacity, respectively, of leaf tissue and ℓ^* is a volume to area ratio that equals the thickness for a flat leaf, $d/4$ for a cylinder or $d/6$ for a sphere (where d is the diameter). If the equilibrium temperature (T_e) for any environment is defined as that value of T_ℓ attained in the steady state, Eq. (9.8) (see Appendix 9) can be rewritten as:

$$\frac{\mathrm{d}T_\ell}{\mathrm{d}t} = \frac{\rho_a c_p (T_e - T_\ell)}{\rho^* c_p^* \ell^*}((1/r_{HR}) + [\mathsf{s}/\gamma(r_{aW} + r_{\ell W})]) \qquad (9.9)$$

Equation (9.9) is in the form of *Newton's law of cooling*, which states that 'the rate of cooling of a body under given conditions is proportional to the temperature difference between the body and the surroundings'. This is a first-order differential equation (like Eq. (4.31)) that after substitution of appropriate boundary conditions (i.e. the leaf is initially at equilibrium at T_{e1} and the environment is altered instantaneously at time zero to give a new equilibrium T_{e2}) can be solved by standard techniques to give:

$$T_\ell = T_{e2} - (T_{e2} - T_{e1})\exp(-t/\tau) \qquad (9.10)$$

where the time constant τ is given by:

$$\tau = \frac{\rho^* c_p^* \ell^*}{\rho_a c_p ((1/r_{HR}) + [\mathsf{s}/\gamma(r_{aW} + r_{\ell W})])} \qquad (9.11)$$

The time constant may readily be estimated in any situation by fitting Eq. (9.10) to any sequence of temperature measurements made following a step change in equilibrium 'environmental' temperature (e.g. caused by a change in absorbed radiation resulting from leaf shading). Any suitable curve-fitting routine can be used to estimate the three parameters (T_{e1}, T_{e2} and τ) in this equation, though I have found the use of the Solver Add-in in Microsoft Excel (Microsoft Corporation) to be particularly convenient for this purpose.

9.1.3 Thermal time constants for plant organs

The thermal time constant (τ) provides a measure of how closely tissue temperatures track T_e in a changing environment. The value of τ depends on the wind speed and on the size and shape of the organ (thickness affects heat capacity per unit area, while size, shape and wind speed affect r_a), on stomatal resistance and on air temperature (which affects the values of the constants, particularly s). Thermal properties of various materials are summarised in Appendix 5. If one assumes an average specific heat capacity of 3800 J kg^{-1} K^{-1} for leaves and fruits (this is close to the value for pure water (4180 J kg^{-1} K^{-1} at 20°C) because usually between 80 and 90% of tissue fresh mass is water), and an average leaf density of 700 kg m^{-3}, this gives $\rho^* c_p^*$ as $\simeq 2.7$ MJ m^{-3}.

Using this value for all plant tissues enables us to calculate approximate time constants for plant organs of different size and shape and for two wind speeds (Table 9.1). This table shows that τ is likely to be significantly less than a minute for all but the largest leaves. Stems and fruits have longer time constants than leaves because they have a larger mass per unit

Table 9.1 Thermal time constants for leaves, stems and fruits treated as simple geometric shapes at 20°C calculated using Eq. (9.11), where d is the breadth of a leaf (or diameter for a cylinder or sphere) and ℓ^* is the volume to area ratio. Values for τ are for non-transpiring organs except those in parentheses, which assume an r_ℓ of 50 s m^{-1} (Monteith, 1981).

	Dimensions		Calculated time constant (τ)	
	d (cm)	ℓ^* (cm)	$u = 1$ m s^{-1}	$u = 4$ m s^{-1}
Leaves				
Grass	0.6	0.05	0.18 (0.13)	0.09 (0.08)
Beech	6	0.10	0.94 (0.52)	0.55 (0.36)
Alocasia	60	0.15	2.90 (1.34)	2.00 (1.01)
Stems				
Small	0.6	0.15	1.4	0.68
Medium	6	1.5	31	16
Large	60	15	540	330
Fruits				
Rowan	0.6	0.1	0.71	0.33
Crab apple	6	1	16	7.7
Jack fruit	60	10	300	170

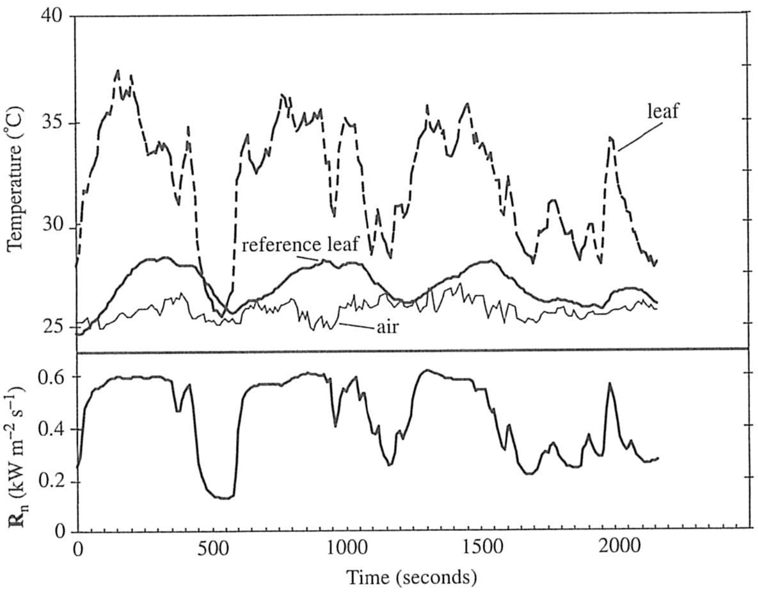

Figure 9.3 (*a*) Temperature fluctuations of a *Phaseolus* leaf (approximately 30 cm^2) in the field, together with simultaneous fluctuations of air temperature and the temperature of a relatively massive artificial wetted reference surface (aluminium covered with filter paper) and (*b*) the simultaneous fluctuations of net radiation. Temperatures measured with 42-gauge copper constantan thermocouples (H. G. Jones, unpublished data).

area, so that for the trunks of mature trees τ can be of the order of one day. The value of τ for leaves is significantly increased by stomatal closure. Figure 9.3 illustrates just how rapidly the temperature of medium-sized (*c.* 30 cm^2) transpiring leaves can fluctuate in the field, while the temperature changes of thicker and more massive artificial 'reference' leaves are much more heavily damped. Note that the air temperature itself also shows rapid changes that are not detected when using a measuring instrument with a long time constant such as a mercury-in-glass thermometer. Observed values of τ for leaves of different species are close to the values predicted in Table 9.1, ranging from about 0.15 to 0.45 min for species as diverse as vine, cotton, *Salix arctica* and *Pinus taeda* (Paw U, 1992) though reaching 7 min for the very thick leaves of *Graptopetalum* in a low wind (Ansari & Loomis, 1959; Linacre, 1972; Thames, 1961; Warren Wilson, 1957) and values in excess of 2 hours for a cactus stem (Ansari & Loomis, 1959).

One approximation in the derivation of Eq. (9.9) is the assumption of a uniform surface temperature, a condition that is not usually satisfied in the field, though the error involved is usually small. A second problem is that with bulky tissue, the rate of heat conduction to the surface is important, because the thermal conductivity of plant tissues is quite low (being of the same order as water: Appendix 5). The lateral thermal conductivity of leaves, for example, ranges from about 0.24 to 0.50 W m^{-1} K^{-1} (Nobel, 2009) while the thermal conductivity of apple fruits is less than 0.9 W m^{-1} K^{-1} (Thorpe, 1974). This means that the temperature at the centre of large organs lags behind that at the surface, and that the time constant at the centre of stems may be longer that that given by Eq. (9.11), which may in turn be longer than that at the surface. The low thermal conductivity of plant tissue also means that unequal radiation absorption on different sides of large organs can lead to large temperature gradients. For example, temperature differences as large as 10°C between the two sides of an apple (Vogel, 1984) or a cactus (Thorpe, 1974) have been observed with high irradiance. Nobel (1988) has developed a model for calculating stem surface temperatures in different *Ferocactus* species that includes effects of plant size, apical pubescence and shading by spines. The results of the model were in close agreement with field observations and could be related to the natural distribution of the different species.

The actual temperature dynamics in any situation can be derived by solution of Fourier's equation for heat flow (see Section 3.2.2), which in one dimension is:

$$\partial T/\partial t = D_H \partial^2 T/\partial z^2 = (k/C_v)\partial^2 T/\partial z^2 \tag{9.12}$$

where D_H is the thermal diffusivity of the material ($m^2\ s^{-1}$), k is the thermal conductivity ($W\ m^{-1}\ K^{-1}$), and C_v is the volumetric heat capacity of the material ($J\ m^{-3}\ K^{-1}$). Note that C_v is the product of the density (ρ; $kg\ m^{-3}$) and the specific heat capacity (c_p; $J\ kg^{-1}\ K^{-1}$) of the material; these vary as a function of composition (the fractions of mineral content (for soils), organic matter, water and air) as shown in Appendix 5. Further details may be found in Campbell and Norman (1998) and Hillel (2004).

9.1.4 Particular cases of the time course of temperature changes

Step change

Where the equilibrium environmental temperature changes instantaneously from one value to another, the time course of leaf temperature, for example, is given by Eq. (9.10) and is illustrated in Figure 9.4(*a*).

Ramp change

Where the environment is changing at a steady rate, tissue temperature lags behind the equilibrium temperature, but when the time of the steady change exceeds about 3 × τ, the rate of increase of tissue temperature equals the rate of increase of equilibrium temperature (Figure 9.4(*b*)).

Harmonic change

Particularly important situations in environmental studies occur where the environmental temperature oscillates or where the energy input (e.g. solar radiation) oscillates. Both the diurnal and the seasonal changes in temperature, for example, can be approximated by sine waves so that we can write the notional variation of equilibrium temperature with time t ($T_{e,t}$) for a single cycle as:

$$T_{e,t} = T_{ave} + \Delta T_e \sin(\omega t) \tag{9.13}$$

where T_{ave} is the average temperature over the cycle, ΔT_e is the amplitude or half the peak to peak range

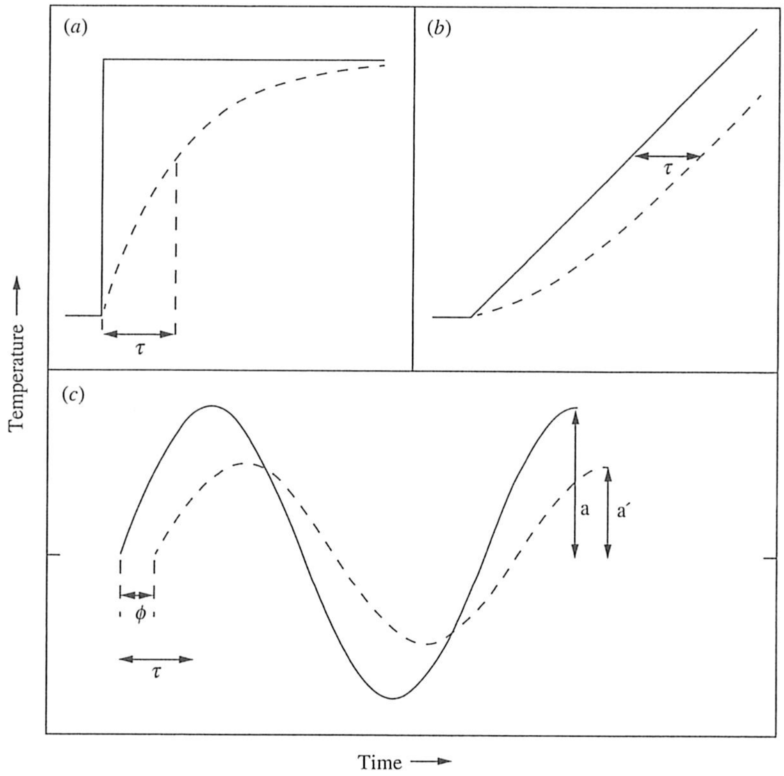

Figure 9.4 The change of surface temperature (broken line) in response to changing environmental temperature (solid line) (modified from Monteith & Unsworth, 2008). (*a*) Response to a step change, where τ is the t for a 63% change (see also Figure 4.14); (*b*) response to a ramp change, where τ is the constant time lag eventually established; (*c*) response to a sinusoidally varying environmental temperature (Eq. (9.13)).

of the cycle of the equilibrium temperature and ω is the angular frequency of the driving energy input ($= 2\pi/P$; where P is the period of oscillation, so that ω equals $7.27 \times 10^{-5}\ \mathrm{s}^{-1}$ for a diurnal cycle and $2 \times 10^{-7}\ \mathrm{s}^{-1}$ for an annual cycle). Using this harmonic input, Eq. (9.12) can be solved (see e.g. Monteith & Unsworth, 2008) to give the temperature at any time (t) and depth (z) as:

$$T_{\mathrm{s,t}} = T_{\mathrm{ave}} + \Delta T_{\mathrm{z}} \sin(\omega t - \phi) \tag{9.14}$$

where ΔT_{s} is the amplitude of the surface temperature and ϕ is the *phase lag* of the surface temperature behind the driving input (radian). The general effect is illustrated in Figure 9.4(c) for the same value of the time constant as in Figures 9.4(a) and (b). The effect of increasing τ is two-fold: first, it causes a damping of the amplitude of the oscillation and, second, it increases the magnitude of the phase lag between the driving temperature and the sample temperature. The phase lag, is related to the time constant by, $\phi = \tan^{-1}(\omega\tau)$, while the damping of amplitude ($\Delta T_{\mathrm{s}}/\Delta T_{\mathrm{e}}$) equals $\cos(\phi)$.

Temperature profile in massive tissues and soils

The analysis can be extended to allow prediction of variation in temperature with depth in soil or in massive tissues such as tree trunks (Campbell & Norman, 1998; Hillel, 2004). The finite thermal conductivity of soil or large plant organs leads to slow transfer of heat from the surface to the interior and an increase both of the lag and in the amount of damping that occurs. Solution of Eq. (9.12), assuming a constant temperature at infinite depth equal to T_{ave}, gives:

$$T_{\mathrm{z,t}} = T_{\mathrm{ave}} + \Delta T_{\mathrm{s}} \exp(-z/Z) \sin(\omega t - \phi - z/Z) \tag{9.15}$$

where $T_{\mathrm{z,t}}$ is the variation of temperature at depth, z, with time t, and Z is known as the *damping depth* and is given by:

$$Z = \sqrt{2\boldsymbol{D}_H/\omega} \tag{9.16}$$

Results from application of Eq. (9.15) to a typical soil are summarised in Figure 9.5. Although this adequately describes variation for many purposes it should be recognised that this represents a substantial simplification as both annual and diurnal cycles are superimposed, the rate of heat loss to the atmosphere varies with weather conditions and the thermal diffusivity depends on soil water content.

9.2 Physiological effects of temperature

9.2.1 Effect of temperature on metabolic processes

Although most metabolic reactions are strongly influenced by temperature, some physical processes such as light absorption are relatively insensitive, while the rate of diffusion is generally intermediate in sensitivity.

Temperature dependence arises where the process requires that the molecules involved have a certain minimum energy (usually in the form of kinetic energy). In general, a high minimum energy requirement leads to greater temperature sensitivity. The reason for this temperature effect may be discussed in relation to a simple chemical reaction where, before the reaction can take place, the molecule or molecules involved must be raised to a state of higher potential energy (Figure 9.6). The energy involved in this reaction 'barrier' is called the activation energy (E_{a}). How the value of the activation energy affects the temperature response can be seen if one considers the distribution of energies between different molecules in a population of similar molecules at a given temperature. Although the mean kinetic energy increases with temperature, the number in the 'high-energy tail' of the frequency distribution increases more rapidly. The number ($n(E)$) that have an energy equal to or greater than E_{a} is given by the Boltzmann energy distribution, which can be expressed on a molar basis in the following form:

$$n(E) = n \exp(-E/\mathscr{R}T) \tag{9.17}$$

where n is the total number, $\mathscr{R}$ is the gas constant and T is the absolute temperature. The rate of a reaction that has a particular activation energy would be expected to be proportional to the number of

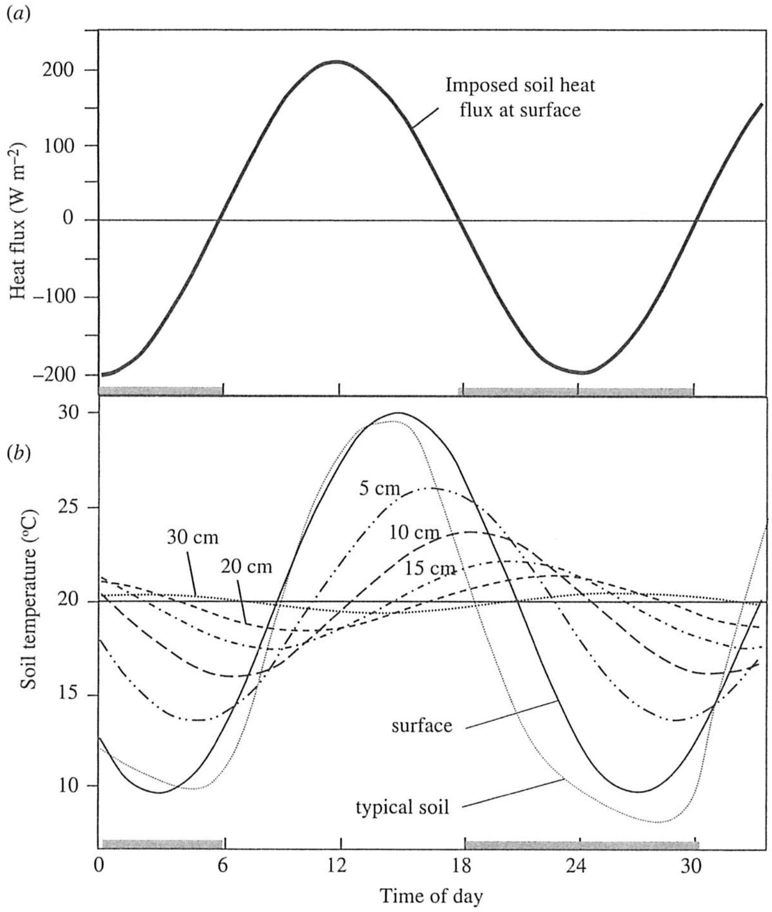

Figure 9.5 Diurnal trends in (*a*) imposed soil heat flux at the soil surface resulting from solar energy input on a clear day (with positive values corresponding to a positive flux, **G**, into the soil) and (*b*) the corresponding fluctuations in soil temperature at various depths in the soil. A typical actual diurnal trend of soil surface temperature for a representative soil is also shown (after Jones & Vaughan, 2010).

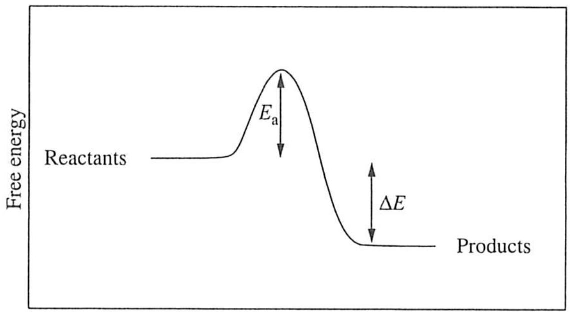

Figure 9.6 The energy threshold for a chemical reaction showing the activation energy (E_a) of the reaction and the net free energy change (ΔE).

molecules with the appropriate energy so that the rate constant (k) is given by:

$$k = A\exp(-E_a/\mathscr{R}T) \tag{9.18}$$

where A is approximately constant and depends on the type of process. If one takes logarithms of this equation, which is known as the *Arrhenius equation*, one obtains:

$$\ln k = \ln A - E_a/\mathscr{R}T \tag{9.19}$$

which predicts that the natural logarithm of the rate constant should be linearly related to $1/T$ with a slope of $-E_a/\mathscr{R}$.

Another way of describing the temperature sensitivity of biochemical processes is in terms of the temperature coefficient, Q_{10}, which is the ratio of the rate at one temperature to that at a temperature ten degrees lower. This coefficient is somewhat arbitrary and potentially misleading, especially when applied outside the rather limited range of conditions where the temperature response is exponential, but as long as its limitations are remembered it can be useful, and is widely used. The equations that follow can readily be reformulated for coefficients over temperature ranges other than 10°C. Therefore from Eq. (9.18):

$$\begin{aligned} Q_{10} &= \frac{A\exp[-E_a/\mathscr{R}(T+10)]}{A\exp(-E_a/\mathscr{R}T)} \qquad (9.20) \\ &= \exp[10E_a/\mathscr{R}T(T+10)] \end{aligned}$$

From this it can be shown that, at 20°C, a Q_{10} of 2 arises where the activation energy is 51 kJ mol^{-1} (i.e. $2 = \exp[(10 \times 51\,000)/(8.3 \times 293 \times 303)]$). The rate of respiration, for example, often has a Q_{10} of 2 at normal temperatures (Figure 9.7), though it varies with the state of the tissue and also decreases at high temperatures that damage tissues. Where the activation energy is lower, as for example for the diffusion of mannitol in water where $E_a = 21$ kJ mol^{-1}, the Q_{10} is lower: in this case 1.3.

In practice the Q_{10} may be obtained from the reaction rates k_1 and k_2 at any two temperatures T_1 and T_2, by using the approximation:

$$Q_{10} \simeq \left(\frac{k_1}{k_2}\right)^{[10/(T_2 - T_1)]} \qquad (9.21)$$

Although the rates of simple chemical reactions increase exponentially with increasing temperature, most biological reactions show a clear optimum temperature, with reaction rates declining with any temperature increase above the optimum. There are several reasons why the rates of biological reactions do not continue to increase indefinitely with increasing temperature. One factor is that the rate limiting reactions for any process may change, as rates increase, from highly temperature-sensitive ones to those such as diffusion, which have lower temperature coefficients. Another factor is that many processes are the net result of two opposing reactions with different temperature responses. The most important reason, however, is that most biological reactions are enzyme catalysed. Enzymes act to lower the activation energy, and hence to decrease temperature sensitivity and to increase the rate at any given temperature. However, as temperatures rise the catalytic properties of most enzymes are harmed and the total amount of enzyme present may fall as a result of increased rates of denaturation. These factors are discussed below in relation to net photosynthesis.

It is particularly notable that the rates of many plant processes, such as development, which integrate many individual components, are frequently approximately *linearly* related to temperature over a wide range of normal temperatures, though an optimum with a subsequent decline is reached at high temperatures.

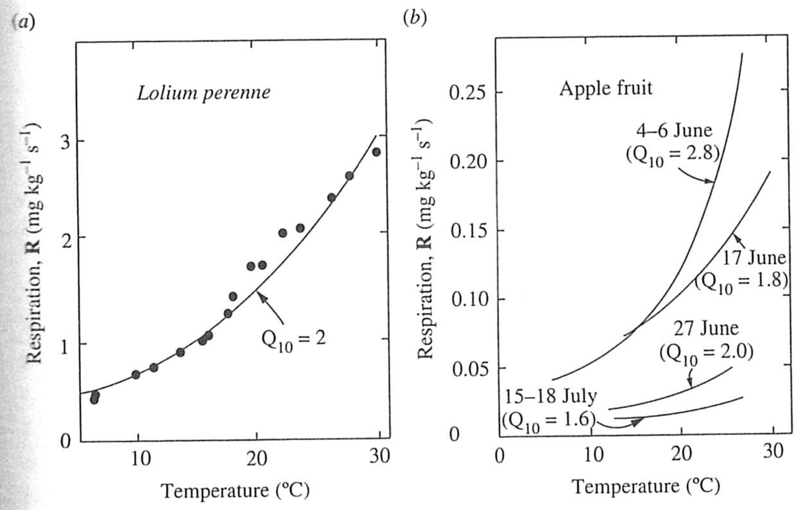

Figure 9.7 Temperature response of respiration for (*a*) simulated sward of ryegrass (*Lolium perenne*) together with the curve for $Q_{10} = 2$ (data from Robson, 1981); (*b*) fitted exponential curves for respiration from apple fruits on different dates (data from Jones, 1981a).

A convenient empirical equation to simulate many temperature responses, such as photosynthesis (see below) is (for $0 \leq k \leq 1$):

$$k = \frac{2(T+B)^2(T_{\max}+B)^2 - (T+B)^4}{(T_{\max}+B)^4} \tag{9.22}$$

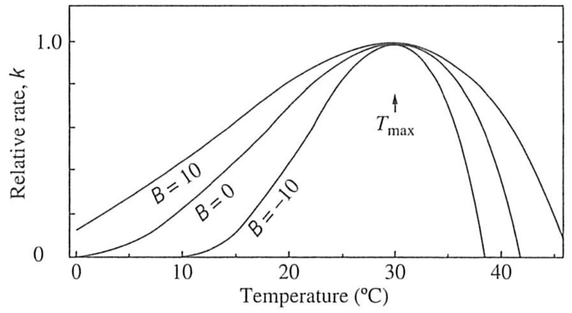

Figure 9.8 Simulation of temperature responses using Eq. (9.22), for $T_{\max} = 30$°C, and for different values of the constant B.

where $T_{\max}$ is the temperature at which the coefficient k reaches a maximum of 1.0 and B is a constant (Figure 9.8).

9.2.2 Temperature response of net photosynthesis

Photosynthesis is one of the most temperature-sensitive aspects of growth. Some photosynthetic temperature responses for species from different thermal environments are shown in Figure 9.9, illustrating the tendency for net photosynthesis of temperate zone plants to be maximal between about 20 and 30°C, with species from hotter habitats having higher temperature optima. In addition many species show marked temperature acclimation when grown in different temperature regimes, as illustrated for *Eucalyptus* and *Larrea*.

At higher temperatures the shapes of the temperature-response curves depend on the duration

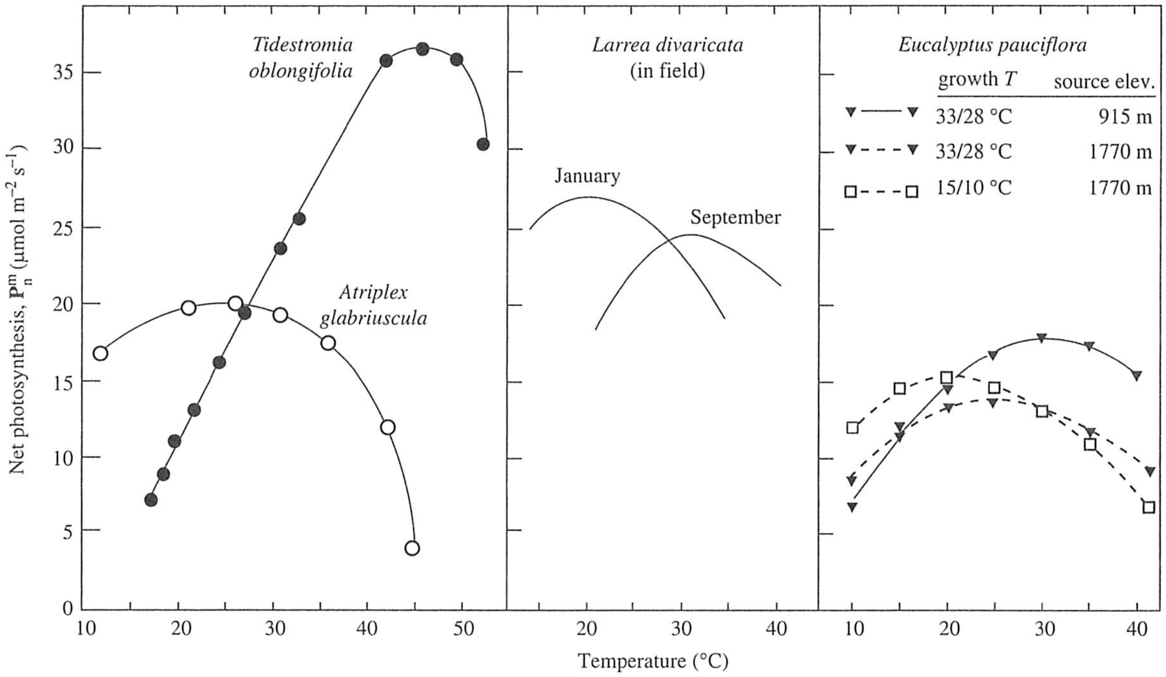

Figure 9.9 Photosynthetic temperature responses for *Tidestromia* and *Atriplex* (Björkman *et al.*, 1975), *Larrea tridentata* (Mooney *et al.*, 1978) and for *Eucalyptus pauciflora* (Slatyer, 1977), illustrating temperature acclimation in *Eucalyptus* and *Larrea*.

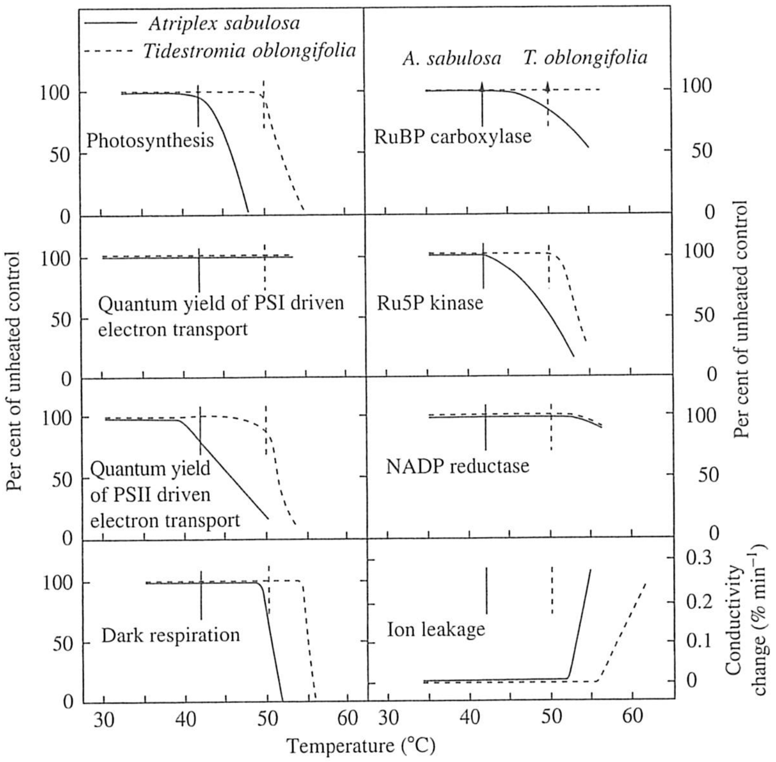

Figure 9.10 Time-dependent temperature inactivation of various photosynthetic components in *Atriplex sabulosa* and *Tidestromia oblongifolia* (see Björkman *et al.*, 1980 for data sources). Rates were measured at 30°C after 10 or 15 min pretreatment at the indicated temperature. Vertical lines indicate the temperatures at which time-dependent inactivation of photosynthesis sets in for the two species. PSI and PSII represent photosystems I and II, respectively.

of exposure to these temperatures, because thermal instability leads to time-dependent inactivation of the photosynthetic system. There are species differences in the temperature at which this inactivation occurs. For example, thermal inactivation occurs when leaf temperatures exceed about 42°C in *Atriplex sabulosa* (a C_4 species from a cool coastal environment), but does not occur in the desert species *Tidestromia oblongifolia* until about 50°C (Figure 9.10).

Some results from an extensive series of experiments investigating differences between *A. sabulosa* and *T. oblongifolia* in photosynthetic stability at high temperatures are presented in Figure 9.10. Some processes, such as photosystem I driven electron transport and activity of enzymes such as NADP reductase, showed little sensitivity to short exposures to high temperatures. Other features, such as membrane permeability (measured by ion leakage), dark respiration and carboxylase activities, were sensitive to high temperatures, with species differences being apparent. However, the inhibitory temperatures for these processes were significantly higher than those damaging photosynthesis. The temperature sensitivity of photosynthesis was most closely related to that of the quantum yield of photosystem II driven electron transport and some photosynthetic enzymes (such as ribulose 5-phosphate kinase). Other evidence indicated that species differences did not result from differences in stomatal behaviour. Overall, the available evidence supports the conclusion that much of the difference in thermal stability between species results from differences in thermal stability of the chloroplast membranes, and in particular the integrity of photosystem II. The involvement of primary damage at the photosystem II system is particularly clearly demonstrated by the sharp increase in basal level of chlorophyll fluorescence (F_o) above a threshold temperature that corresponds to the onset of leaf necrosis (Bilger *et al.*, 1984).

In contrast, there is evidence that differences between species in their photosynthetic rate at low

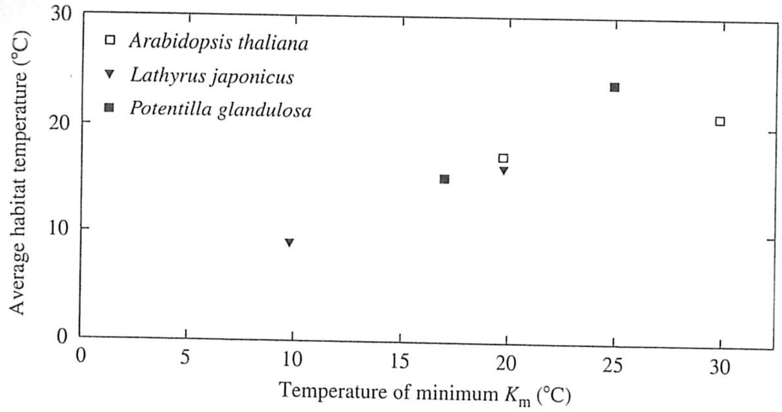

Figure 9.11 The relationship between the assay temperature giving the minimum K_m and the average habitat temperatures for two populations of each of three species. The enzymes studied were glucose 6-phosphate dehydrogenase for *Arabidopsis* and malate dehydrogenase for the other species. (Data from Teeri, 1980.)

temperatures is strongly correlated with the capacity of specific rate-limiting enzymes such as RuBP carboxylase and fructose bis-phosphate phosphatase. There is also evidence, at least for some enzymes, that their kinetic properties may be adapted to the normal environmental temperature of that ecotype. The assay temperature giving the minimum Michaelis constant (K_m) can be closely related to the habitat temperature (Figure 9.11). Small changes in K_m of about two-fold over the normal temperature range may provide a mechanism for maintaining the rate of the catalysed reaction relatively insensitive to temperature fluctuation. In some cases at least, thermal acclimation is based on changes in the profile of the isoenzymes synthesised (Scandalios *et al.*, 2000) with much of this protein diversity resulting from alternative splicing (Syed *et al.*, 2012).

9.3 Effects of temperature on plant development

9.3.1 Thermal time

The rates of many plant developmental processes, and hence the timing of phenological stages, are strongly temperature dependent. If under a particular set of conditions a particular developmental stage takes t days, the corresponding rate of development (k_d) is $1/t$; this implies that the time taken to complete the developmental stage is inversely proportional to k_d.

The rate of development is usually a strong function of temperature, so that in a constant environment:

$$1/t = k_d = f(T) \tag{9.23}$$

We can denote the state of plant development at any time t (measured from a suitable starting date such as sowing) as $S(t)$, where S is a fractional state of development on a zero to one scale. In a fluctuating environment where T is a function of time (written as $T(t)$), $S(t)$ is given by:

$$S(t) = \int_{t=0}^{t} k_d \mathrm{d}t = \int_{t=0}^{t} T(t)\mathrm{d}t \tag{9.24}$$

In practice it is often found that, between a threshold temperature for development to occur known as the base temperature (T_{base}) and an optimum temperature (T_o), the rate of development is approximately linearly related to temperature so that between these temperatures:

$$k_d = a(T - T_{base}); \text{ for } T_{base} \le T \le T_o \tag{9.25}$$

where a is a constant. Temperatures below T_{base} therefore do not contribute to development. Thus if temperature remains constant over time one can substitute into Eq. (9.24) to get:

$$S(t) = a(T - T_{base})\int_{t=0}^{t} \mathrm{d}t = a(T - T_{base})t \tag{9.26}$$

It follows that the value of the temperature integral, $(T - T_{base})t$, that is required to complete the developmental stage being considered (i.e. $S(t) = 1$)

is equal to $1/a$. For convenience this temperature integral is given the symbol D and measured in day-degrees. Under fluctuating temperature conditions we can write:

$$\begin{aligned} S(t) &= a\int_{t=0}^{t}(T(t)-T_{base})\mathrm{d}t \\ &= (1/D)\int_{t=0}^{t}(T(t)-T_{base})\mathrm{d}t \end{aligned} \qquad (9.27)$$

Calculation of this integral requires a knowledge of the relationship between temperature and time. For convenience the temperature sum (D) is often obtained by summing for each day the excess of the daily mean temperatures (T_m) above the threshold according to:

$$D = \sum_{d=1}^{n}(T_m - T_{base});\ \text{for } T_{base} \le T_m \le T_o \qquad (9.28)$$

Completion of the developmental stage ($S = 1$) requires that this temperature sum, D, often incorrectly referred to as a 'heat sum', equals or exceeds $1/a$. D is known as the *thermal time* or the accumulated temperature required for completion of the developmental stage being considered. Other terms such as growing degree days (GDD) or even, unfortunately, 'heat' units (HU) are frequently used as synonyms for thermal time. It is worth noting in passing that this recommended method of calculation uses the daily average temperature ($T_m = (T_{max} + T_{min})/2$, irrespective of whether or not T_{min} falls below T_{base}).

Estimates of the appropriate threshold or base temperature can be obtained in two main ways. Where studies can be made in controlled environments at constant temperature, it is possible to plot rate of development against temperature and T_{base} is given by the intercept on the x-axis. Where temperatures are fluctuating, as in the field, it is necessary to calculate D with different thresholds and determine which gives the best linear fit to Eq. (9.26) across a number of different years or sites. In practice the base temperature varies with species, with calculations for some temperate crops such as wheat, barley and *Brassicas* often using 0°C as a threshold, while others such as peas and forage often use 5°C. For maize, soybeans and tomato a value of 10°C is often used while thresholds for some tropical crops such as cowpea often reach around 15°C. Many published calculations of GDD (e.g. for maize) use 10°C as a standard base temperature value, but it is important to remember that this may not be appropriate for all crops. Some typical values for thresholds and GDD are shown in Table 9.2; information on specific crop

Table 9.2 Some published values of the number of growing degree days (GDD) required for different growth stages for different plants.

	T_{base} (°C)	GDD to flowering (°C d)	GDD to maturity (°C d)	Reference
Pea	3.0		824–926	(Bourgeois *et al.*, 2000)
Cherry	4.0	243 (from 1 Mar)		(Zavalloni *et al.*, 2006)
Rice	10.0	1350–1484	1810–1915	(Islam & Sikder, 2011)
Pearl millet	10.0	667–944	1150–1220	(Cardenas, 1983)
Barley	0.0	738–936	1269–1522	(Miller *et al.*, 2001)
Brassica rapa	0.0	630–726	1152–1279	(Miller *et al.*, 2001)
Maize (OCHU)[a]	5.0 (night) 10.0 (day)		2500–3500	(Ma & Dwyer, 2001)

[a] Ontario corn heat units.

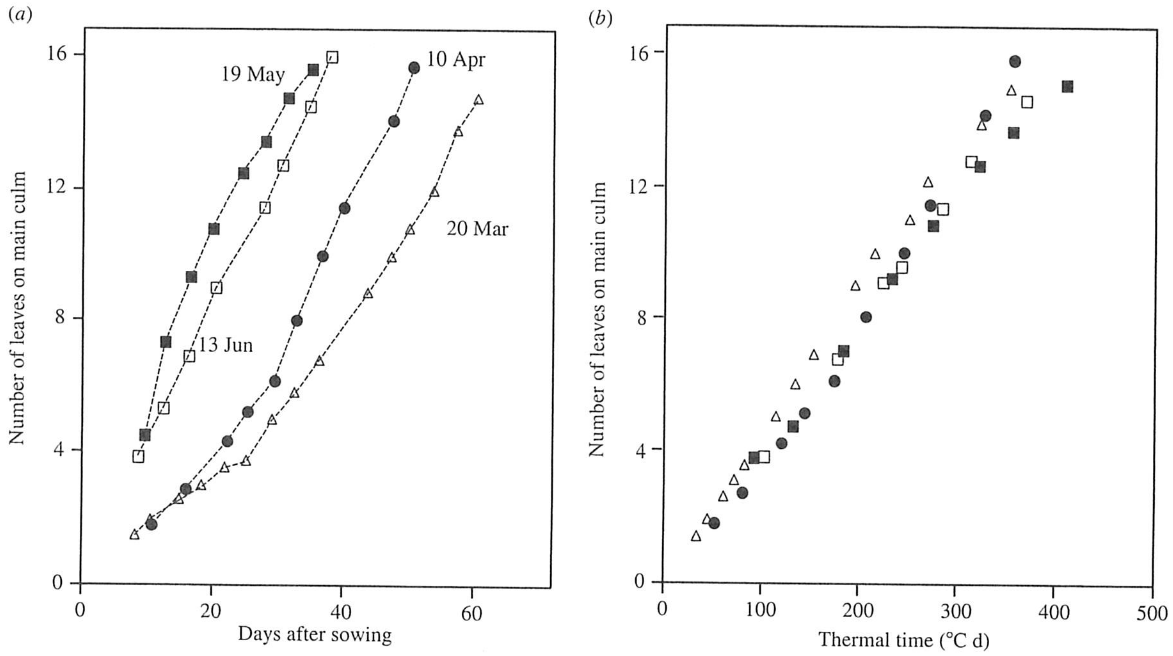

Figure 9.12 (*a*) Time course of appearance of leaves on the main stem of *Pennisetum typhoides* for four different sowing dates. (*b*) The same data plotted against thermal time calculated for soil temperature at 5 cm depth and using a threshold temperature of 12.4°C. (Data from Ong, 1983.)

requirements together with calculations of GDD for local climatic data helps farmers to determine which crops will grow successfully in any area.

An example of the effectiveness of thermal time as a tool for the study of plant development is presented in Figure 9.12; this figure shows the dependence of a plant's rate of development on the sowing date, with more rapid development occurring for later sowings because of the higher temperatures. When, however, the rate of leaf appearance along the main stem, in this case for pearl millet, is expressed as a function of thermal time rather than real time it is clear that the rate of appearance of leaves falls on one line.

Extensions of thermal time

The concept of thermal time as a replacement of chronological time has been in use for phenological studies for over 200 years (Wang, 1960). Although the simple formula is adequate for most purposes, non-linearities in the temperature responses and interaction with other environmental factors have been incorporated into a number of more sophisticated equations. For example, polynomial or other functions of T can be substituted for the linear form used in Eqs. (9.25) and (9.26), while the 'Ontario corn heat unit' accumulates maximum and minimum temperatures separately (Dwyer *et al.*, 1999).

For seed germination studies it is common to assume that germination rate increases linearly with temperature between T_{base} and T_o, and then decreases linearly above T_o (see Figure 9.13), so that above the optimum:

$$k_d = (T_{\max} - T)/D_2; \text{ for } T_o \leq T \leq T_{\max} \qquad (9.29)$$

where $T_{\max}$ is the upper limit for germination and D_2 is an appropriate temperature sum. The behaviour at

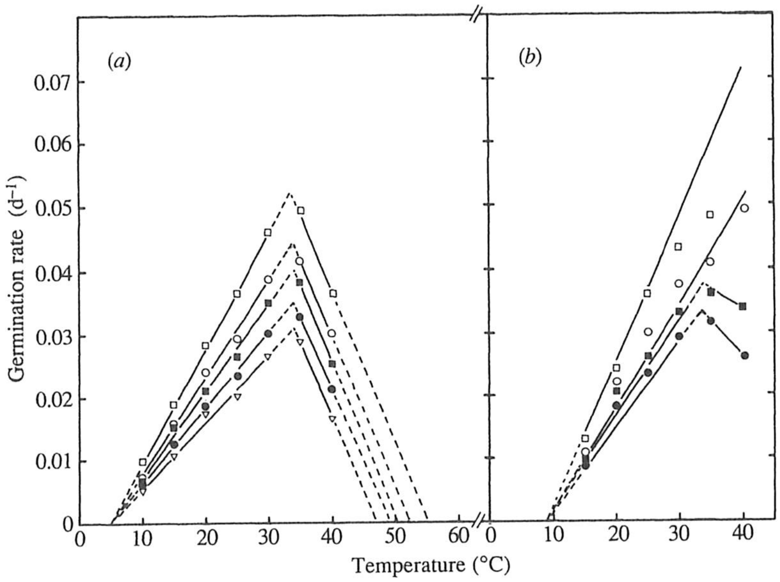

Figure 9.13 The relation between temperature and rate of progress to germination (at constant temperature) for (*a*) soybean and (*b*) cowpea. Broken lines represent extrapolation beyond experimental values, and the different symbols represent various percentage germination: 10% (□), 30% (○), 50%, (■) 70% (●) and 90% (▽). (Data from Covell *et al.*, 1986.)

supraoptimal temperatures, however, is complicated by the fact that there is a time × temperature dependency. Although high temperatures may damage the seed there can still be an underlying tendency for germination to be speeded up by higher temperatures. This is illustrated for the cowpea data in Figure 9.13 where the earliest germinating seeds emerged before high temperature damage became apparent.

Effective day-degrees

Inclusion of other environmental variables enables one to describe development where temperature is not the only environmental variable affecting the process. A particularly useful approach is the definition of what have been called 'effective day-degrees' (D_{eff}) (Scaife *et al.*, 1987) to include effects of radiation and temperature. In this approach D is replaced by D_{eff}, defined by:

$$D_{eff}^{-1} = D^{-1} + b\mathbf{I}^{-1} \qquad (9.30)$$

where b is a constant describing the relative importance of irradiance ($\mathbf{I}$) and temperature. Where b is zero, D_{eff} becomes equal to conventional day-degrees.

9.3.2 Dormancy, chilling, stratification and vernalisation

Temperature shows marked seasonal fluctuation, particularly at higher latitudes, and although there may be considerable short-term variability these seasonal changes are a major factor in the control of flowering, often interacting with photoperiodic control. Many perennial species show a well-marked period of dormancy, usually during the winter in temperate species, but in the summer in many Mediterranean species. A characteristic of dormant tissues is that their meristems are not able to initiate growth even in favourable conditions. A feature of winter dormancy is that it also involves hardening of tissues in a way that enhances cold tolerance.

Seasonal temperature fluctuation plays an important role in the induction of dormancy and leaf abscission in autumn, and in the subsequent release from dormancy after the winter, in each case often acting in conjunction with daylength effects. Similarly, biennial species usually require exposure to a period of low temperatures before they can flower. For example 'winter' varieties of wheat must be exposed to several months of low temperatures to permit flowering. If sown in the spring (rather than the autumn), they remain vegetative as a consequence of failure to satisfy their vernalisation requirement. Spring varieties, on the other hand, have only a minimal or no vernalisation requirement so they can be successfully sown in the spring. The requirement for a period of low temperatures can ensure an adequate period of growth before flowering, otherwise, in natural situations seeds that germinate in late summer might flower in the same year and fail to mature. Similarly, release from dormancy in many perennial plants, including most temperate fruit species, also requires a period of cold (chilling) to break dormancy and as a prerequisite for effective and synchronous bud break.

Vernalisation

As with photoperiodic responses (Section 8.4.3), vernalisation requirements vary from obligate to quantitative, with the rate of vernalisation being a variable function of temperature according to the species. Vernalisation is required for the meristem to change from a vegetative state (producing leaves) to a floral state (producing flowers). Unfortunately the effect of temperature on this transition confounds the effect of temperature on vernalisation with the effect of temperature on meristem development (as discussed above). It is therefore difficult to isolate the true temperature response of vernalisation: the common interpretation of the vernalisation response for wheat is illustrated in Figure 9.14 where the rate is very slow at 0°C or below, reaches a maximum at about 2 to 4°C, and has an upper limit of about 11°C (Evans *et al.*, 1975). It has been argued, however, on the basis of a developmental analysis (where rate of vernalisation is defined as the reciprocal of the number of days of treatment until achievement of the minimum number of leaf primordia) that the rate of vernalisation in wheat actually increases linearly from 0°C to about 11°C, declining thereafter (Brooking, 1996). Plants may be vernalised as seeds (a process known as stratification) or may achieve adequate chilling when exposed as leafy plants to low temperatures.

Although the pathway of vernalisation is complex, there appears to be substantial similarity between the genetic control of vernalisation in monocots and dicots, with the central *FLOWERING LOCUS C* (*FLC*) gene in *Arabidopsis* (or the *VRN2* homologue in wheat) acting to suppress flowering. Exposure to extended periods of low temperature, however, leads in *Arabidopsis* to a stable repression of *FLC*, and in wheat to stimulation of *VRN1*, which represses *VRN2*; these changes then set off subsequent genetic cascades leading to floral development. An interesting feature is that repression is maintained even after the temperature increases through epigenetic modification of the histones in the appropriate part of the DNA (Dennis & Peacock, 2007).

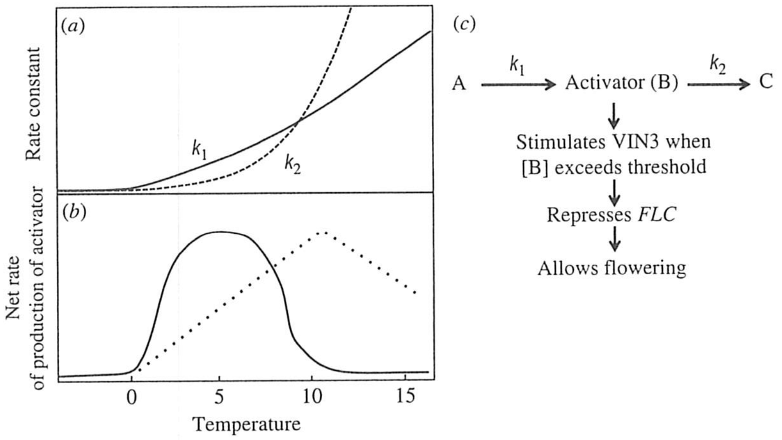

Figure 9.14 A hypothetical mechanism for vernalisation. (*a*) Shows the temperature responses of the rate of synthesis (k_1) and degradation (k_2) of an activator (B), (*b*) the resulting temperature dependence of the rate of net synthesis of B and (*c*) a schematic of the role of this in vernalisation response in *Arabidopsis* when enough B accumulates after prolonged exposure to vernalising temperatures (see text for further detail). The dotted line in (*b*) shows the temperature sensitivity of the 'rate of vernalisation' for wheat proposed by Brooking (1996).

An interesting feature of vernalisation is the very low temperature optimum, which is unusual for biological processes. Very little is known of how the plant senses the low temperature exposure, though it is possible that some component of the cold-acclimation process (e.g. modification of membrane lipids and membrane fluidity or changes in protein phosphorylation patterns in response to low temperatures) may be involved. There is evidence that cold acclimation and vernalisation involve independent pathways (Bond *et al.*, 2011). What is known is that in *Arabidopsis* the *VIN3* gene appears to be the gene most closely linked to signalling of the cold exposure. A hypothetical scheme (see e.g. Sung & Amasino, 2005 for a different variant) that could give rise to such a response would be a two-stage reaction where upregulation of *VIN3* would occur when the concentration of an activator exceeds a threshold as a result of a period of exposure to permissive temperatures, with the concentration of the activator at any time depending on the competing processes of synthesis and degradation each having different temperature responses as indicated in Figure 9.14.

Many seeds also have a requirement for a period (often extensive) of low temperature before they can germinate. These low temperatures are most effective at overcoming seed dormancy if given when the seeds are moist.

Chilling and winter dormancy

Woody perennial plants, such as temperate fruit trees, that enter a dormant period during the winter require exposure to adequate chilling for breaking the 'endodormancy' and to ensure synchronous bud break. It has been noted in some cases, however, that it is possible partly to substitute the cold requirement by drought or by defoliation; for example Jones (1987b) was able to initiate in apple trees a second phase of flowering within one year by drought treatments that were severe enough to cause defoliation on re-watering.

The amount and depth of chilling that is required to satisfy the chilling requirement varies substantially between species and even between cultivars. A number of models have been proposed to estimate the amount of physiologically significant chilling from meteorological data and have been used as an aid to the identification of genotypes appropriate for specific regions. The most common models for describing satisfaction of the chilling requirement are illustrated in Figure 9.15 and can be classified into (i) simple temperature accumulation models of which the commonest is the number of hours below an empirically derived threshold of 7.2°C (or the number of hours between 0°C and 7.2°C); (ii) more sophisticated temperature weighting models, such as the 'Utah' model for peach bud development (Richardson *et al.*, 1974), which includes a negative

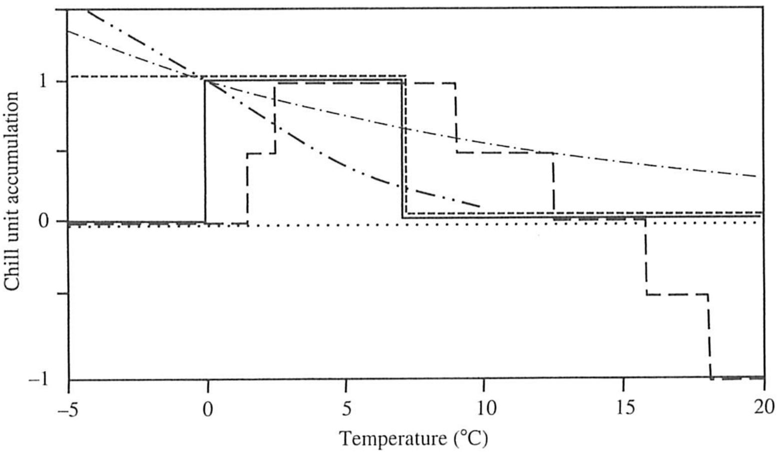

Figure 9.15 Various chilling functions for accumulation of chill units: these include those that are best suited to crops such as peach ('Utah' units, — — — —) and 0 to 7.2°C (——), and those that also respond to temperatures below 0°C including the <7.2°C units (-----), Bidabé's exponential function (– · – · – · –) and the best fit-curve for blackcurrant chilling requirement (– ·· – ·· – ·· –) (Jones *et al.*, 2012).

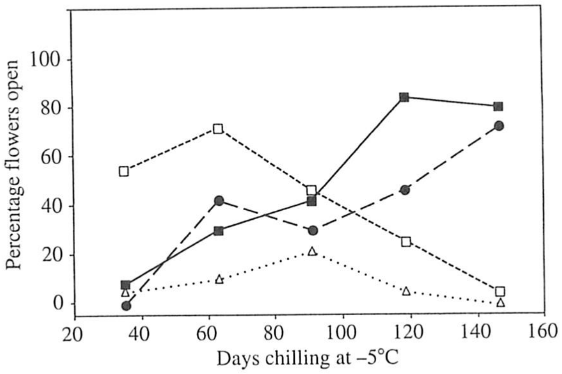

Figure 9.16 Effect of different periods of chilling at –5°C on flowering (recorded as % flowers open after 45 days in a permissive environment at 20°C) of typical blackcurrant cultivars that either require large amounts of chilling (Ben Avon, ——■——; Hedda, – – ● – –) and cultivars where flowering can be inhibited by excess chilling (Andega, ---□---; Amos Black, ···△···). (Data from Jones *et al.*, 2012.)

effect of higher temperatures, and models that assume that chilling 'effectiveness' increases exponentially (Bidabé, 1967) with decreasing temperature or according to some other function (Jones *et al.*, 2012). In deriving phenological models for predicting the dates of spring events such as bud burst and flowering it is usual to use sequential models that combine both the chill accumulation phase required to release endodormancy and a warming or 'anti-chill' phase (often referred to as the *forcing* phase) to describe the rate of release from dormancy and the actual date of flowering (see Jones *et al.*, 2012). This forcing phase is commonly calculated on the basis of a temperature summation (e.g. GDD above an appropriate base temperature). Because spring events may also be at least partially dependent on daylength, the best predictions of effects of climate change on developmental events may be achieved by incorporation of extra components such as daylength (Blümel & Chmielewski, 2012).

Although many chill models are based on hourly accumulation of chill, the necessary hourly temperature data are often not available, so Sunley *et al.* (2006) have shown that hourly temperatures may be estimated adequately from daily maximum/minimum data by assuming sinusoidal temperature variation according to Eq. (9.13), substituting $(T_{max} - T_{min})/2$ for T_{ave} in this equation.

The most appropriate function varies substantially between species and indeed within species, with more 'arctic' genotypes such as blackcurrant (*Ribes nigrum*) gaining most effect from chilling temperatures below 0°C. For blackcurrant, the number of chilling hours <7.2°C required to satisfy the chilling requirement varies from <1300 h to >2000 h for late flowering UK cultivars such as 'Ben Lomond' or Nordic cultivars. In some cases, excess chilling can even be inhibitory (Figure 9.16), with longer exposures to temperatures below –5°C reducing flowering in some cases (Jones *et al.*, 2012).

9.4 Temperature extremes

The ability of different plants to survive extreme temperatures depends both on their innate physiology and on the degree to which they have been acclimated by a process of 'hardening'. The survivable temperatures for fully hardened plants of different plant groups from different regions is summarised in Table 9.3. Although there are major differences between plant groups and provenances in their ability to tolerate low temperatures, the upper temperature limits are remarkably similar across the different groups.

9.4.1 High temperatures

High-temperature damage to cells and tissues normally involves loss of membrane integrity with consequent ion leakage, together with deactivation and denaturation of many enzymes. Cell death can readily be assessed by means of the ability of cells to take up a vital stain such as neutral red. On the tissue scale, high-temperature damage can usually be seen as tissue necrosis.

As has already been indicated (e.g. Figure 9.9), however, many plants have a great capacity to adapt to temperature extremes. This ability to acclimate is widespread: for example, Nobel (1988) has collated results from a number of experiments on 33 species

Table 9.3 Summary of temperature thresholds for survival of extreme temperatures by leaves of plants from different climatic regions, where thresholds are defined at the temperatures giving 50% damage after 2 h exposure to the given temperature (extracted from Larcher, 1995). Seeds are generally more tolerant of extremes.

	Threshold *T* for cold injury (hardened) (°C)	Threshold *T* for heat injury in summer (°C)
Tropics		
Trees	+5 to −2	45 to 55
Herbs	+5 to −3	45 to 48
Mosses	−1 to −7	–
Subtropics		
Evergreen woody plants	−8 to −12	50 to 60
Subtropical palms	−5 to −14	55 to 60
Succulents	−5 to −10 (−15)	58 to 67
C_4 grasses	−1 to −5 (−8)	60 to 64
Temperate		
Evergreen woody plants	−7 to −15 (−25)	46 to 50 (55)
Deciduous woody plants	(−25 to −35)[a]	c. 50
Herbaceous plants	−10 to −20 (−30)	40 to 52
Graminoids	(−30 to −196)[a]	60 to 65
Succulents	−10 to −25	(42) 55 to 62
Homoiohydric ferns	−10 to −40	46 to 48
Boreal		
Evergreen conifers	−40 to −90	44 to 50
Boreal deciduous trees	(−30 to −196)[a]	42 to 45
Arctic-alpine dwarf shrubs	−30 to −70	48 to 54
Arctic-alpine herbs	(−30 to −196)[a]	44 to 54
Mosses	−50 to −80	–

[a] Vegetative buds.

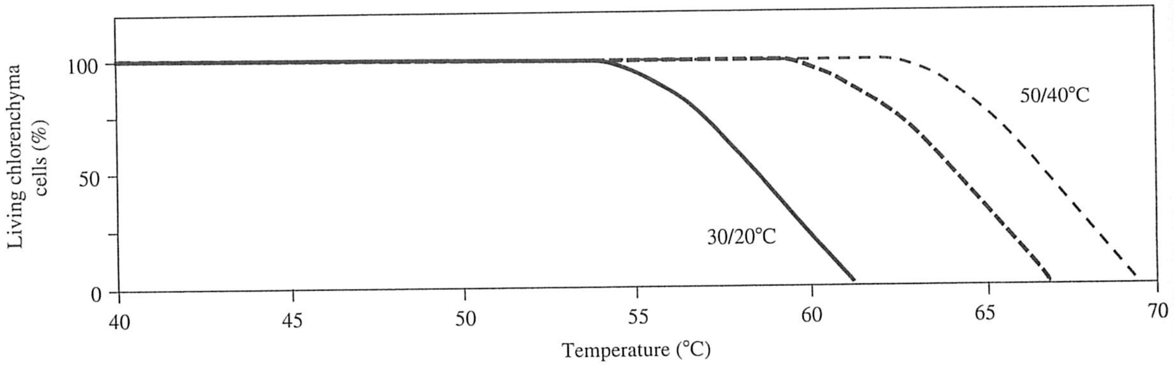

Figure 9.17 Influence of day/night growth temperatures on the high-temperature tolerance (measured as the % of chlorenchyma cells taking up vital stain) of *Opuntia ficus-indica*. The solid line is for plants grown at 30°C/20°C, the intermediate dashed line is for plants three days after shifting to a 50°C/40°C regime and the final dashed line is after three weeks at the higher temperature. (Data from Nobel, 1988.)

of agaves and cacti where it was shown that the temperature leading to 50% apparent cell death increased by between 1.6 and 15.8°C for different species when the growth temperature was raised from 30°C/20°C (day/night temperature) to 50°C/40°C. For nearly all species the temperature tolerated under the higher temperature growth regime was in excess of 60°C (Figure 9.17). Indeed a number of cacti including *Opuntia ficus-indica* (prickly pear) can tolerate temperatures in excess of 70°C for one hour, a common duration for the most extreme temperatures in the field. Such a high temperature appears to be lethal to other vascular plants that have been studied.

The underlying basis of acclimation to high temperatures is not well understood, but there is evidence that binding of the variant histone H2A.Z to nucleosomes acts as a thermosensor with occupancy by H2A.Z decreasing as temperature increases over a wide range of ambient temperature (Kumar & Wigge, 2010). These changes mediate genome-wide transcriptional changes (for a review see Iba, 2002) in response to temperature. There appear to be some parallels between thermal adaptation and light responses with the phytochrome signalling pathway and PIF4 being involved in both responses. As the temperature rises above a critical value (often around 38 to 40°C in plants) normal protein synthesis stops and is replaced by the rapid and coordinated synthesis of a characteristic set of heat shock proteins (HSPs). Many of these HSPs show a very high degree of homology in all organisms that have been studied (e.g. HSP70), though higher plants also synthesise a unique group of small (15 to 18 kDa) proteins. The rapid synthesis of HSPs is related to increased transcription and the appropriate mRNAs can increase within 3 to 5 min of high-temperature stress. Heat shock protein levels tend to decline fairly rapidly, even if the high temperatures continue.

Although the detailed functions of the many HSPs are not well known, they tend to bind to structurally unstable proteins and act as molecular chaperones both helping the correct folding of proteins after synthesis, and preventing aggregation of denatured proteins and on occasions promoting renaturation. The synthesis of HSPs tends to be associated with the development of thermotolerance caused by exposure to even brief periods at high temperature. A common HSP, ubiqitin, is thought to be involved in tagging thermally denatured proteins for subsequent proteolysis by a special protease. Interestingly, some of the plant HSPs can be induced by other factors such as abscisic acid, heavy metals, osmotic stress, arsenite or anaerobiosis, though the physiological significance is not clear. In addition, many of these stresses and other stresses such as pathogenesis also give rise to specific stress proteins (Sachs & Ho, 1986). Other changes during acclimation to high temperatures include alterations in membrane lipids and changes in the complement of compatible solutes.

9.4.2 Low temperatures

There are two main types of low-temperature injury (Levitt, 1980). The first, which is common in plants of tropical or subtropical origins (such as beans, maize, rice and tomatoes) is called *chilling injury*. It is usually manifest as wilting or as inhibited growth, germination or reproduction, or even complete tissue death, and occurs in sensitive species when tissue temperatures are lowered below about 8 to 10°C (though this varies with species and degree of acclimation and may occur at temperatures as high as 15°C). As long as exposure to chilling temperatures is of short duration, the damage is usually reversible. The other major type of low-temperature injury is *freezing injury*, which occurs when some of the tissue water freezes. All growing tissues are sensitive in some degree to frost though sensitivity varies. In many plants that have not been given a chance to acclimate, tissues are killed by freezing to only −1 to −3°C. After acclimation the range of temperatures that can be survived is very wide, depending on species and tissue. Many seeds, for example, can withstand liquid nitrogen temperatures (−196°C), while many tissues from acclimated frost-tolerant species can survive −40°C or below (Table 9.3).

Chilling injury

An early event in the signalling cascade involved in cold sensing by plants is the transient influx of calcium into the cytosol (Knight *et al.*, 1991). It is also clear that an important early, if not primary, effect of chilling involves damage to the cell membranes with an early symptom in whole plants often being wilting, which is characteristic of inhibited water uptake. For example, within minutes of lowering the temperature of the roots of chilling-sensitive species such as cucumber to 8°C, root water uptake decreases and any root pressure decreases. Many associated changes in root-cell ultrastructure rapidly become visible; these include alterations to cell walls, nuclei, endoplasmic reticulum, plastids and mitochondria (Lee *et al.*, 2002). There is also evidence that chilling injury can be related to the breakdown of cytoplasmic microtubules; this is supported by evidence that microtubule-disrupting agents enhance chilling injury, while abscisic acid tends to increase chill resistance and also retards disruption of microtubules (Rikin *et al.*, 1983). Chilling-damaged tissues tend to lose electrolytes rapidly because of increased permeability of the plasma membrane, while there is also particular evidence for damage to chloroplast and mitochondrial membranes.

There have been many studies that suggest that membrane properties in chilling-sensitive plants undergo a sudden change at about the temperature where chilling injury occurs, while chilling-resistant plants show no such abrupt change. It has been suggested, on the basis of changes in the slopes of *Arrhenius plots* (ln(rate) against $1/T$) at this critical temperature, that this results from a phase change in the membranes from a relatively fluid form to a more solid gel structure, so that normal physiological activity can only occur above the critical temperature. It appears that this phase change does not occur in the bulk membrane though it may be localised in small 'domains' within the membrane. There is some evidence that the temperature of any phase change is correlated with the fatty acid composition of the lipids, with a high proportion of saturated fatty acids occurring in the membranes of chilling-sensitive species, but the correlations are not always very good. Fructose-based polymers called fructans appear to play a major role in stabilising membranes in stress conditions including low-temperature stress where they can stabilise membranes by direct hydrogen-bonding to membrane lipids (Valluru & Van den Ende, 2008). Other factors, such as changes in membrane protein composition, may also be involved.

9.4.3 Mechanisms of damage: freezing

With freezing injury the damage results not from the low temperatures directly but from the formation of ice crystals within the tissue. These ice crystals disrupt the protoplasmic structures and cell membranes (Levitt, 1980). Although freezing-tolerant species can apparently withstand some extracellular ice formation, intracellular ice formation is commonly fatal to cells. A precise value for frost sensitivity in different plants is difficult to determine because the actual damage depends on the rate of thawing (though not generally on the time frozen), as well as on the lowest temperature reached. Membrane damage is a universal result of freezing damage, though it is still not certain whether it is the primary effect. As temperatures are lowered, ice starts to form in the extracellular water (e.g. in the cell walls). Because ice has a lower vapour pressure (and chemical potential) than liquid water at the same temperature, extracellular freezing causes water to be removed from within the cells to the sites of extracellular freezing. This leads to rapid dehydration of the cell (see Levitt, 1980) so that at least some of the effects of ice formation result from this dehydration.

The amount of water that must be lost from a cell before equilibrium is reached between intracellular water and extracellular ice depends on the temperature and on the osmotic properties of the cell. Water continues to be lost until the reduction in cell volume causes the cell water potential to balance the extracellular water potential.

The cell water potential that is in equilibrium with pure extracellular ice at the same temperature can be obtained, using Eq. (5.14), from:

$$\psi = \frac{\mathscr{R}T}{\overline{V}_W}\ln(e_{ice}/e_{s(T)}) \qquad (9.31)$$

where e_{ice} is the vapour pressure over pure ice and $e_{s(T)}$ is the vapour pressure over pure water at the temperature T (see Appendix 4). The value of ψ given by Eq. (9.30) decreases by approximately 1.2 MPa $°C^{-1}$ below 0°C. The equivalent increase in solute concentration is given by the van't Hoff relation (Eq. (4.8)) as approximately 530 osmol $m^{-3}\ °C^{-1}$ lowering of temperature (i.e. $-\psi/\mathscr{R}T = 1.2 \times 10^6/2270$).

Since solute concentration, c_s, is proportional to $1/V$ it follows that relatively large absolute changes in cell volume are required to maintain equilibrium for a 1°C drop in temperature near the freezing point compared with lower temperatures. That is, the relationship between cell volume and temperature at equilibrium should be hyperbolic. As expected from this it is found that the amount of liquid water present in tissue at any temperature (minus the 'bound' water), expressed as a fraction (f) of the liquid water in unfrozen tissue (minus the bound water), decreases hyperbolically as temperature falls below that at which freezing first occurs (adjusted from Gusta *et al.*, 1975) according to:

$$f = (\Delta T_f/T) \qquad (9.32)$$

where ΔT_f is the temperature at which freezing first occurs, known as the freezing point depression, and T is the temperature (°C).

A difficulty with simple dehydration hypotheses of freezing damage is that most water freezes at relatively high temperatures (above about −10°C), so that differences in tolerance of lower temperatures would require sensitivity to relatively small changes in hydration. For example, for a typical cell sap concentration, ΔT_f is −1.5°C so it follows from Eq. (9.32) that less than 20% of the original water would remain in the cell at −10°C.

9.4.4 Hardening and mechanisms of frost tolerance

Many plants show some degree of acclimation to chilling or freezing temperatures such that the damage temperature is lowered after exposure to a period of low temperatures. Figure 9.18 shows the changes in minimum survival temperatures that occur in two winter cereals over the winter period. Some degree of winter hardiness can also be induced by exposure to drought or salinity, while conversely, frost hardening can induce a degree of drought or salinity tolerance. At least in insects cold hardening can be rapid, occurring within two hours, where it has been associated with glycerol accumulation (Lee *et al.*, 1987).

Various plant factors have been associated with freezing tolerance in different species, with the main aspect of cold acclimation being the increased stabilisation of the membranes against freezing

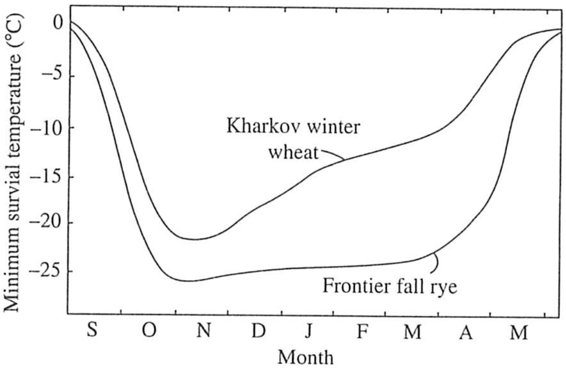

Figure 9.18 Minimum survival temperatures (LD_{50}) for a winter wheat and a winter rye, showing development of cold tolerance during the winter. (After Gusta & Fowler, 1979.)

damage. Many mechanisms are involved in this stabilisation including lowered osmotic potentials, increased concentrations of soluble carbohydrates (especially the so-called 'compatible solutes' such as glycine-betaine), changes in lipid composition, synthesis of membrane stabilising proteins and small cell size (Levitt, 1980; Thomashow, 1999). Cold hardening and cold tolerance involve the expression of a large suite of specific genes that contribute to cold tolerance, these include both those that lead to the production of proteins and other molecules that act to stabilise membranes against freeze-induced injury and the production of a series of transcription factors (especially in the DREB/CBF family) that regulate expression of such genes (for details see Thomashow, 1999). The plant growth regulator abscisic acid (ABA) has also been implicated in the development of freezing resistance. It may be that there are several alternative mechanisms that can increase freezing tolerance. It is interesting to note that although agaves and cacti also show the ability to increase their frost hardiness when grown at low temperatures, the alteration in damage temperature is much smaller than the degree of hardening observed at high temperatures.

Another mechanism that may be important in the frost tolerance of some species is supercooling. The equilibrium state is for ice to form when the temperature falls below the freezing point depression (ΔT_f) appropriate for the solute concentration. As the absolute value of ΔT_f increases approximately 1°C for every 1.2 MPa, typical cell osmotic potentials of down to −3 MPa would lower the freezing point by less than 3°C. In fact the cell contents rarely freeze. This is partly because of the absence of suitable ice nucleation sites within the cells, allowing the water to remain in the unstable supercooled condition. Similarly, the cell-wall water may remain liquid far below the theoretical freezing point, though in most plant tissues only a few degrees of supercooling can be achieved. Ice nucleation usually starts in the extracellular water, either because of the lower solute concentration there or because of the presence of ice-nucleating bacteria. Some hardwoods, including various oak, elm, maple and dogwood species, however, can supercool to the homogeneous nucleation temperature (Burke & Stushnoff, 1979). This is the temperature at which ice forms spontaneously without a requirement for nucleation sites, being between about −41 and −47°C for plant tissues.

Certain tissues and cells in these hardwood species, such as ray parenchyma cells and flower buds, show supercooling. This mechanism for avoiding freezing damage cannot work below the deep supercooling temperature of about −41°C, so that species that rely on deep supercooling cannot survive in areas where lower temperatures occur. Those species that occur in regions where lower temperatures are likely (e.g. pines, willows, etc.) survive by tolerating extracellular freezing.

A wide range of avoidance mechanisms can also contribute to the ability of plants to survive freezing temperatures. For example, the biophysical effect of dense canopies that can shield the sensitive tissues from direct radiative cooling, or bulky organs with a high heat capacity and long thermal time constants may also help avoid damaging tissue temperatures. Both these mechanisms contribute to the frost survival of the giant rosette forms of *Lobelia* and *Senecio* and other genera that are typical of tropical alpine regions with their characteristic dense covering of closely arranged hairy insulating leaves and massive stems.

9.4.5 Frost protection

Because of the economic importance of frost damage in temperate climates, much work has been done to develop techniques for protecting high-value crops from the damaging effects of frost (Snyder & de Melo-Abreu, 2005a,b). Plant and air temperatures may fall below freezing, either by advection of a cold air mass (e.g. from polar regions), or as a result of the net heat loss by longwave radiation that can occur on calm clear nights. Such a *radiation frost* causes the build up of a stable inversion layer where the air near the ground is cooler than that at higher levels.

The various methods of frost protection may be separated into (i) passive protection approaches and (ii) active methods.

Passive approaches

1. *Site and plant selection.* Perhaps the most important principle is to avoid frost-prone sites for the planting of sensitive crops. Because radiation frosts are associated with calm or very light winds, cold air drainage occurs down slopes, with the cold air accumulating in 'frost pockets' at the bottom of slopes. For an orchard situated on a slope it is feasible to divert cold air draining down the slope away from the crop by installing impermeable fences around the uphill side of the crop. It is also worth noting that other aspects of site selection can be important, with, for example, the presence of large water bodies upwind of the site also tending to reduce frost frequency. The chance of frost damage can also be reduced by the selection of cultivars that flower later, or even, somewhat counter-intuitively, to plant crops on north-facing rather than south-facing slopes because the lower daytime temperatures there can also delay bud burst. Management of the soil to maximise diurnal heat storage also acts to maintain higher minimum soil temperatures; this is achieved by maximising soil thermal conductivity and heat capacity, noting that sandy soils tend to have higher thermal conductivity than clay or peat soils, while there is usually an optimum soil moisture content.
2. *Use of covers.* Plant covers can usefully protect against frost as they may reduce radiative heat loss from the leaves, especially if they are impermeable to longwave radiation, because they increase the net downward radiation to the leaves as the temperature of the covers would normally be substantially higher than the clear sky temperature ($<-40°$C). Where condensation forms on the plastic this would also help as the latent heat released would also warm the plastic. Covers may also inhibit convective heat loss to the bulk air. Covering the soil with plastic can also usefully raise the soil temperature, though it should be noted that the use of soil mulches can actually decrease the diurnal minimum soil temperature (and hence the chance of damage) because of its effect on reducing the thermal conductivity.

Active methods

1. *Water sprinkling.* As water freezes it liberates a large amount of heat (the latent heat of fusion is 334 J g^{-1}). Water sprayed onto sensitive tissues liberates heat as it freezes, preventing tissue temperatures falling below zero, as long as enough water is supplied to maintain liquid on the surface of the tissue. The effect can potentially be enhanced by the inclusion of ice-nucleating bacteria, which ensures that nucleation and frost formation occurs above the critical damage temperature. Since sprinkler irrigation systems are commonly available in fruit orchards, such systems can be relatively cheap to operate in comparison with other active approaches, though it should be noted that the cooling effect of droplet evaporation can counter the thermal benefits from the initial water temperature and the latent heat of fusion.
2. *Direct heating.* Various types of orchard heater have been used to keep air temperatures above freezing, though their main effect is to help break up the inversion layer and to replace the cold air near the surface by warmer air from higher levels. A secondary effect of some heaters results from smoke or soot released, which may act as a screen minimising net longwave radiation losses.

3. *Air mixing.* With radiation frosts a particularly useful approach is to break up the inversion layer near the ground by using fans or propellers. These machines work, not by producing heat, but by redistributing sensible heat that is already available in the air. Clearly this approach only works in conditions where there is a strong temperature inversion.

9.5 Comments on some ecological aspects of temperature adaptation

Different plants exhibit a wide range of adaptations that enable them to live in different thermal climates (Table 9.3). These include biochemical tolerance mechanisms as well as seasonality and morphological or physiological adaptations that lead to avoidance of temperature extremes. Not only is the success of any species dependent on its tolerance or avoidance of extreme temperatures, but also it depends on its capacity to grow and compete at more normal temperatures. An ability to tolerate the short-term extreme temperatures that occur during bush fires is also an important factor in environments where fires are common.

Some species are widely adaptable, being able to grow over a wide temperature range, while others are more specialised. Examples of these two types of plant are found in the flora of Death Valley, California, USA, where the mean maximum temperature ranges from less than 20°C in January to more than 45°C in July (Figure 9.19). Some species, such as the evergreen perennials *Larrea divaricata* and *Atriplex hymenelytra* grow all the year, acclimating to the changing temperatures. Others, for example the perennial *Tidestromia oblongifolia*, are summer active and cannot grow at normal winter temperatures, while winter annuals such as *Camissonia claviformis* grow only at low temperatures. These species differences are reflected in seasonal changes of maximum photosynthetic capacity (e.g. Figure 9.9) and in their ability to grow in, and acclimate to, different temperatures in terms of dry matter yields (Table 9.4). Table 9.4 also illustrates the general point that the more widely adaptable species (e.g. *L. divaricata*) tend not to have as high growth rates in any environment as the appropriate 'specialists'.

Table 9.4 Total dry matter yields (final dry mass/ initial dry mass) for four species over a 22-day growth period in two contrasting thermal regimes.

Species	16°C day/ 11°C night	45°C day/ 31°C night
Atriplex glabriuscula (coastal C_3)	24.4	0.1 (died)
Atriplex sabulosa (coastal C_4)	18.2	0.3 (died)
Larrea divaricata (desert C_3)	5.4	3.2
Tidestromia oblongifolia (desert C_4)	<2.5	88.6

9.5.1 Experimental manipulation of temperature

As was pointed out in Chapter 1, it is difficult to manipulate temperature in a natural way to study, for example, the potential effects on plant growth of small temperature differences as may occur with climate change. The use of *common garden* experiments where plants are grown at different sites where temperatures are naturally different (e.g. at different altitudes) can be a useful approach, though results may be confounded by other climatic factors that may vary in parallel. Although it is straightforward to manipulate temperature in controlled environments and glasshouses, other aspects of the microenvironment, including aspects such as atmospheric coupling and the temperature gradients between shoots and roots tend to be very unnatural. Even the use of covers, polyethylene

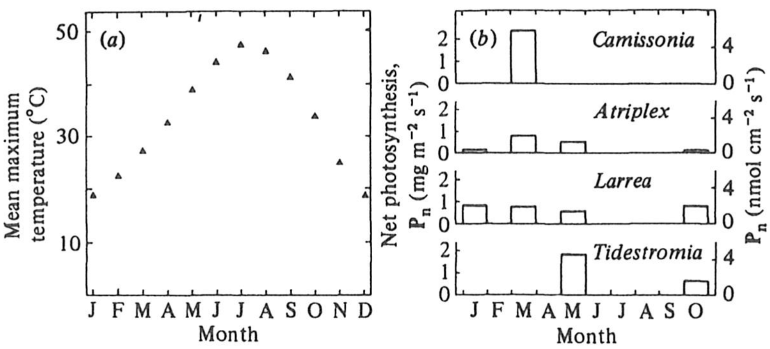

Figure 9.19 Seasonal changes of (*a*) monthly mean maximum daily temperatures for Furnace Creek, Death Valley, California and (*b*) maximum photosynthetic capacity of native species: *Camissonia claviformis*, *Atriplex hymenelytra*, *Larrea divaricata* and *Tidestromia oblongifolia* (after Mooney *et al.*, 1976).

tunnels and open-top chambers in the field (with or without supplementary heating or cooling) seriously affect the aerial environment and energy balance of the plants and can lead to misleading results, even where a paired design is used with similar covers being used for the different temperature regimes. While soil warming may conveniently be used to manipulate soil temperatures (Siebold & von Tiedemann, 2012) this approach does not substantially enhance aerial temperatures and leads to unnatural temperature gradients and differences between root and shoot temperatures. Some workers have recommended the use of infrared heating as an experimental tool (Aronson & McNulty, 2009), but again this approach does not well mimic natural temperature gradients within the system. In all cases it is important to consider implications of raised temperatures on evaporative demand, with the vapour pressure deficit and potential evaporation increasing with temperature if the temperature increase is applied only locally because the water vapour content of the air is determined by the airstream flowing over the crop.

9.5.2 Avoidance mechanisms

There are many possible avoidance mechanisms that can result in particular species not being subject to unfavourable tissue temperatures. (The terms 'avoidance' and 'strategy' used below, are used in a strictly non-teleological sense in that they do not imply that the plant can be rational or have a sense of purpose. Rather, they provide simple descriptions of particular physical or biological responses.)

Perhaps the most important avoidance mechanism is seasonality (see e.g. Figure 9.19). Annual species may avoid periods of potentially damaging temperatures by completing their life cycle entirely within the period of favourable temperatures. Perennial species, on the other hand, often have the capability of going into a dormant state where the tissues are less sensitive to temperature extremes. In other plants the sensitive tissues may avoid being subject to the extremes of daily temperature range as a result of the damping (long thermal time constant) that results from a high thermal capacity of the tissues or of their immediate surroundings or from a high degree of insulation. This is particularly important in the grasses, where the meristematic tissues (at least in the vegetative phase) are at or below ground level and thus not subject to the temperature fluctuations found in the aerial environment. Similarly, the long time constants for large stems or fruits (Table 9.1) can lead to a significant reduction in the amplitude of daily temperature fluctuations.

Because the thermal time constants for most other aerial plant tissues are relatively short (Table 9.1), the steady-state energy balance can be used to obtain a good indication of their temperature control mechanisms. These may be discussed in relation to the different components of the steady-state energy balance ($\mathbf{R}_n$, $\mathbf{C}$ and $\lambda\mathbf{E}$), with radiation absorption, and leaf and boundary layer resistance being of prime importance. The principles described above (Eq. (9.6), and Figures 9.1 and 9.2) will now be discussed in relation to some examples.

One general factor in the avoidance of extreme tissue temperatures is a consequence of the temperature dependence of s and D. At high air temperatures (above about 30 to 35°C), T_ℓ tends to be below T_a, but the converse occurs at low temperatures (Figure 9.2). The exact changeover temperature is a function of plant and environmental factors.

Hot environments

Leaf temperature may be kept low either by decreasing net radiation absorbed or by increasing latent heat loss. Whether or not sensible heat transfer needs to be minimised or maximised depends on whether the leaf is below or above air temperature.

For the case where water is freely available, the most productive strategy is to maximise latent heat loss ($\lambda \mathbf{E}$) by having a low leaf resistance, but to minimise any sensible heat gain from the air by having large leaves with a large boundary layer resistance. This combination is common in drought-evading desert annuals and in some perennials with access to ample water. As an example, *Phragmites communis*, although a temperate species, can grow in summer in a wet part of Death Valley. It survives the high temperatures there because leaf temperature is maintained as much as 10°C below air temperature by a large latent heat loss (Pearcy *et al.*, 1972). A similar mechanism probably explains why *Caliotropis procera*, a shrub with leaves 10 cm or more wide, is common in areas of the Thar Desert of northwest India. It is worth noting that transpirational cooling to below air temperature is most effective for large leaves, as sensible heat transfer (which tends to negate the effect) is then minimal.

Where water is limited, however, as it often is in hot environments, large leaves are likely to be disadvantageous. In this case, small leaves with their low boundary resistance and efficient sensible heat exchange can avoid heating up much above air temperature, but equally they cannot cool much below air temperature even when transpiring rapidly. For example, *Tidestromia oblongifolia* has small leaves that closely track air temperature (e.g. Pearcy *et al.*, 1971). Many summer-active desert perennials have small leaves.

Either strategy for latent and sensible heat exchange can be combined with minimising radiation absorption by means of vertical leaf orientation (as in the Eucalypts of Australia), wilting, leaf rolling, para-heliotropic movements keeping leaves edge-on to the solar beam, or high leaf reflection coefficient. In a rather different fashion, shading by other tissues (as, for example, by the spines on cacti (Nobel, 1988)) can also protect sensitive tissues from an excessive heat load. The effects of leaf angle and reflectivity are additive and can be evaluated by means of Eq. (9.6). As an example, it has been calculated (Mooney *et al.*, 1977) that an alteration of leaf angle from horizontal to 70° could be expected to lower leaf temperature of *Atriplex hymenelytra* in Death Valley by 2 to 3°C, while halving the total absorptance for shortwave radiation can lower leaf temperature by a further 4 to 5°C. A factor in determining the low leaf temperatures in *Phragmites* is that the leaves are normally fairly erect.

Leaf reflectance depends on a variety of characters (see Chapter 2) including leaf water content and the presence of crystalline surface salts, pubescence, and the amount and structure of surface waxes. Of particular ecological interest is the observation that the spectral properties of leaves tend to alter with environmental aridity. The environmental and seasonal changes in reflectivity with variation in leaf water content in *Atriplex* (Mooney *et al.*, 1977) and with pubescence in *Encelia* (Figure 2.18) both help to minimise leaf temperatures in summer. The increased radiation absorption in winter may help to increase leaf photosynthesis both by raising leaf temperature when air temperatures are suboptimal and by increasing total absorbed PAR.

It is questionable whether the primary effect of many of the radiative high-temperature avoidance mechanisms described above is to avoid direct thermal damage or to minimise transpirational water loss. Any mechanism lowering T_ℓ lowers the water vapour pressure inside the leaf and tends to reduce water loss and conserve moisture as well as tending to increase the ratio of photosynthesis to water loss (particularly at supraoptimal temperatures). The efficiency of water use is discussed in more detail in Chapter 10. It is worth noting, however, that water conservation often tends to have higher priority than minimising leaf temperature (at least by means of evaporative cooling).

Cold environments

Many arctic and alpine species have 'cushion' or 'rosette' habits where the plant forms a dense canopy within a few centimetres of the ground surface. This gives rise to a high boundary layer resistance as air movement is inhibited within the canopy and the whole plant is within the layer of markedly reduced wind speed. Coupled with efficient radiation absorption, this enables the temperatures of leaves and flowers to be 10°C or more above air temperature (Geiger, 1950). It is even possible that the dense pubescence on the lower surfaces of the leaves of many alpine plants (e.g. *Alchemilla alpina*) may increase radiation absorption by reflecting transmitted light back into the leaf (Eller, 1977). The metabolic component of tissue energy balance can also significantly affect tissue temperature (Section 7.2.2): for example, spadix temperatures of certain Araceae can even be raised as much as 35°C above air temperature by thermogenic respiration in the early spring (Seymour *et al.*, 1983). Thermogenesis is, however, unlikely to be a significant factor in determining leaf temperature in most other plants even though there does appear to be enhanced operation of the potentially thermogenic alternative respiratory pathway in arctic plants.

In other species, particularly the large rosette plants of genera such as *Senecio* and *Lobelia*, that grow at high altitudes in the tropics, the meristematic tissues are protected from frost damage by the formation of 'night buds' where the adult outer leaves fold inwards by a nyctinastic movement (Beck *et al.*, 1982). The insulation provided by the adult outer leaves (that can tolerate freezing) is sufficient, especially when combined with a degree of supercooling and with the large thermal mass of the plants, to prevent the more sensitive tissues from freezing.

9.5.3 Thermal climate and plant response

Different features of the temperature regime are critical at different times of year. In winter, the minimum temperatures may determine what species survive, while the occurrence of blossom-damaging frosts in spring can be crucial for other species. Similarly, the sensitivity of different species to variation in growing-season temperature depends on how close the environment is to their natural optimum. For example, for a hypothetical yield response of the form of that in Figure 9.8 (for $B = 0$), a 5°C rise in temperature would double yield at 9°C, have no effect at 27°C and cause complete failure at 38°C.

Where the complete information required for crop or ecosystem modelling is not available, two simple methods, in addition to mean temperatures, are often used to characterise the temperature regime. The first is to use the concept of thermal time (see Section 9.3.1 above) and to calculate the total number of growing degree-days typically available during the season. Examples of the thermal time required for maturation of different crops range from 1500 °C d above 5°C for spring barley to about 4000 °C d above 10°C for rice. The other approximate approach is to determine the length of the growing season, assuming an appropriate minimum temperature for growth. A minimum of 5 or 6°C is often assumed for temperate crops and about 10°C for crops such as maize. Although these thresholds are not necessarily exact for any species, the length of period during which mean temperatures remain consistently above the appropriate threshold, called the 'length of the growing season', provides a useful simple measure of climate. The potential growing period is particularly important for grain and fruit crops that need a minimum period to complete a reproductive cycle. Growing season duration is most frequently a limiting factor in northern latitudes or at high altitude.

An example of temperature sensitivity

Both growing-season length and growing degree-days are particularly sensitive to small climatic shifts when mean temperatures are close to T_{base}. This is illustrated for Akureyri in Iceland in Figure 9.20. Here a small shift in temperature has a large effect on growing-season length and an even more dramatic effect on growing degree-days. For example, a 2.4°C reduction in temperature from the long-term mean decreases the growing season to 75% of normal and decreases the number of degree-days *D* to only 46% of normal (Table 9.5). Changes of this magnitude would be disastrous if crop yields were affected proportionately. Although it is difficult to quantify the effect of temperature on crop yield using observational data alone, hay yields in Iceland for a period of 25 years are available and can be related to seasonal temperature using multiple regression techniques. As a first approach, Bryson (1974) noted that mean yields averaged 4.33 tonne ha^{-1} in the late 1950s, but only 3.22 tonne ha^{-1}, or 75% of that, in 1966 and 1967. In the same periods, corresponding

Table 9.5 Effects of changes in mean temperature at Akureyri, Iceland, on the growing season and growing degree-days above 5°C, where 'Clino' is the climatic normal temperature. (Data from Bryson, 1974.)

	Mean warm season temperature (°C)	Growing season length (days)		Growing degree-days	
		d	%	°C d	%
Clino	7.47	158	100	597	100
Clino – 1.0°C	6.47	144	91	443	73
Clino – 2.4°C	5.07	118	75	276	46

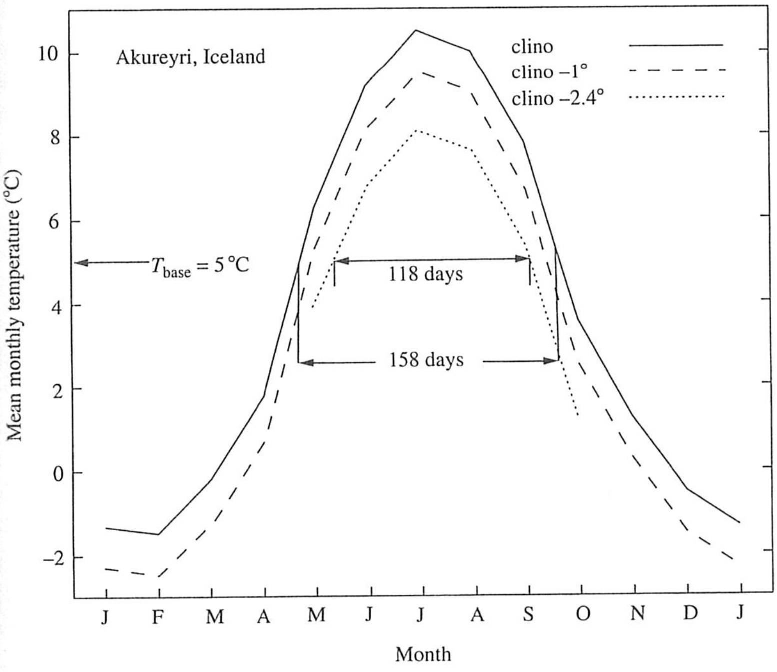

Figure 9.20 The effect of reduction of the annual mean temperature for Akureyri, Iceland, by 1°C or 2.4°C below the climatic 'normal' (clino) on growing season length (measured above 5°C). (After Bryson, 1974.)

mean warm-season temperatures were 7.65°C and 6.83°C. This yield reduction occurred even though more fertiliser was applied in the 1960s, so he attributed the effect to the lower temperature, the actual reduction corresponding approximately to that expected on the basis of the reduction in degree-days. Unfortunately this clear result is an oversimplification as other factors are also important so that the magnitude of the temperature effect is not as great if other combinations of years are selected. In fact more objective regression studies showed that mean cool-season temperature (which averaged −0.08°C, well below the assumed growth threshold) was a better yield predictor (perhaps because it measured winter kill of the grass), while other factors such as nitrogen application also contributed (H. G. Jones, unpublished).

9.5.4 Temperature and plant distribution

Although there are often clear physiological differences in temperature adaptation between species it is not entirely straightforward to explain why specific plants grow in particular thermal climates. One approach to identification of the environmental factors that determine the distribution of any species is to correlate the plant's natural distribution with the climate over the area where it is found; for example Woodward (1988) has demonstrated that a combination of the absolute minimum temperature (T_{min}) and the number of growing degree days (GDD) can provide a very useful predictor of plant distribution for many European species, with some species limited by the length of the growing season and others by the absolute minimum temperature. For example, using GDD defined with a base temperature of 0°C, *Koenigia islandica* in Europe only grows at sites where GDD <1800, but *Bromus* (= *Anisantha*) *sterilis* only grows at sites where GDD >2000, while *Tilia cordata* requires both $T_{min} > -40$°C and GDD > 2000. Although tropical species clearly are not physiologically capable of growing in arctic areas, the question nevertheless arises as to why the more arctic species do not grow in warmer climates where there may be no physiological reason for their absence. Evidence that this exclusion is a result of competitive ability is nicely provided by experiments such as those of Woodward and Pigott (1975) on the alpine species, *Sedum roseum*, and the lowland species, *Sedum telephium*, which showed that when competition was eliminated, both species could grow equally well at the lowland site (though the lowland species could not succeed at the upland site – presumably because of poor cold tolerance). This implies that development of an ability to tolerate low temperatures confers some competitive disadvantage under warmer conditions. More sophisticated climatic correlation studies would use regression against a wider selection of climatic variables, including aspects of the water balance.

9.6 Sample problems

9.1 The net radiation absorbed by a leaf is 400 W m^{-2}. What are (i) the leaf temperature if $T_a = 25$°C, $h = 0.4$, $r_{aH} = 40$ s m^{-1}, $r_{\ell W} = 200$ s m^{-1}; (ii) the thermal time constant for this leaf if $\rho^* c_p^* = 2.7$ MJ m^{-3} and $\ell^* = 1$ mm; (iii) the time constant when the stomata are closed; (iv) the leaf temperature if the whole leaf is wet; (v) the corresponding thermal time constant?

9.2 Respiration rate of a fruit is 0.1 mg CO_2 m^{-2} s^{-1} at 13°C and 0.19 mg CO_2 m^{-2} s^{-1} at 19°C. What are (i) the Q_{10}, (ii) the activation energy?

9.3 The thermal time between flowering and maturity for a certain plant is constant at 600 degree-days above 6°C, while the rate of net photosynthesis (= 50 g m^{-2} day^{-1} for $k = 1$) is given by Eq. (9.16) with $B = -5$ and $T_{max} = 30$°C. Assuming a constant temperature over the period, plot the relationship between the net photosynthesis and temperature. What is the optimum temperature?