Chapter 14 - Temperature: a driving variable for plant growth and development



Fighting ice with ice! Alleviating frost damage in a New Zealand orchard with overhead sprinklers. Plant tissues encased in ice that is continuing to form will remain at 0°C, that is, just above the threshold for injury (see Colour Plate 52) (Photograph courtesy E.W. Hewett)

Habit is hereditary with plants, ... and this leads me to say a few words on acclimatisation. As it is extremely common for distinct species belonging to the same genus to inabit hot and cold countries, if it be true that all the species of the same genus are descended from a single parent-form, acclimatisation must be readily affected during a long course of descent. It is notorious that each species is adapted to the climate of its own home: species from an arctic or even from a temperate region cannot endure a tropical climate or conversely ... But whether or not this adaptation is in most cases very close, we have evidence with few plants, of their becoming, to a certain extent, naturally habituated to different temperatures; that is they become acclimatised: ...

(*Charles Darwin,* The Origin of Species, *1910 edition)*

Introduction

Life on earth is restricted to a narrow thermal band (Figure 14.1). Within that range, global conditions can still be extreme with air temperatures as low as −70°C in Antarctica and as high as +57°C in North Africa. Remarkably, life can endure those circumstances, and worse. Thermophilic bacteria exist in hot volcanic springs at +94°C and seeds, lichens and mosses may survive down to −260°C as forms of latent life. However, the temperature range for active growth in higher plants is much more modest and generally con-strained between about 5°C and 45°C (Figure 14.1).

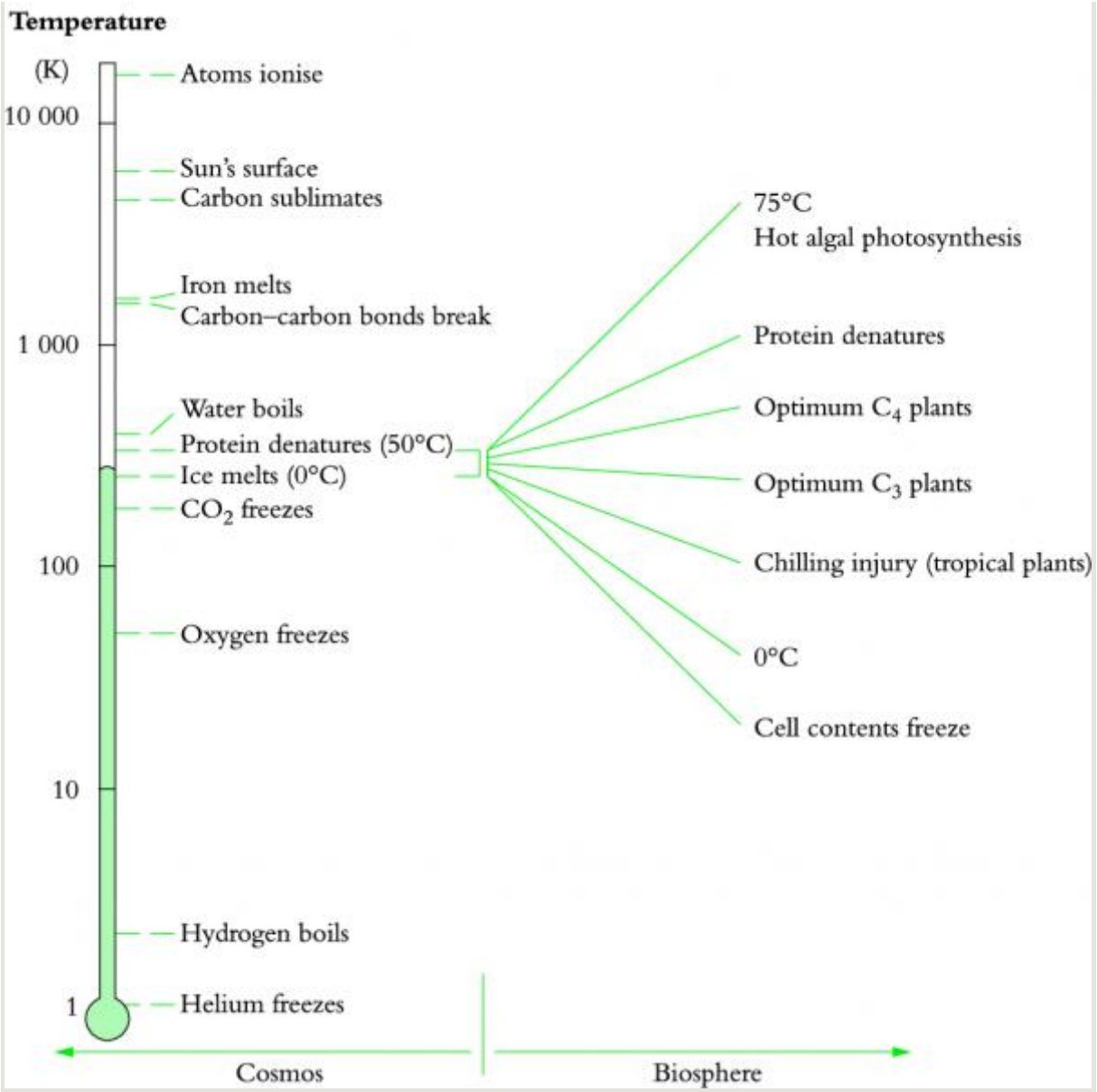


Figure 14.1 Plant growth within the earth's biosphere is limited to a narrow range of temperatures compared with the overall cosmic span from absolute zero, where molecular motion ceases, to 10 000 K where atoms are ionised. Taking the life zone as spanning -5 °C to 45 °C vascular plants show remarkable thermal resilience within this range which enables them to colonise a great diversity of habitats. (Notional values, generalised from various sources)

Compared to temperate species, the minimum temperature for active growth in tropical and subtropical plants that are chilling sensitive is from 10°C to 15°C (Section 14.4). Survival outside the active growth range of all plants is nevertheless dependent on developmental stage, duration of temperature stress and degree of acclimation (Section 14.6). Terrestrial plants have evolved with life cycles that match seasonal necessity, especially winter dormancy and vernalisation. Temperature relations feature prominently as an environmental selection pressure in those adaptations (Section 14.5). Moreover, genetic variation in plant capacity for acclimation to chilling or freezing conditions is widely expressed, and given the highly heritable nature of such traits, a knowledge of processes responsible can be put to good effect for genetic improvement.

Within the dynamic range of plant–temperature relations, that is, where short-term responses are readily reversible, phenology and productivity have been successfully linked with various measures of accumulated heat (thermal time), and predictive models validated. Again, genetic variation between species, and even between cultivars within a species, becomes evident in those heat dose:growth response curves. The basic physiology underlying such differences is discussed in Section 14.1.

On a global scale (Figure 14.2) vegetation types have broad mean annual temperature ranges, from the arctic and alpine tundra at the low end of the temperature scale to tropical forests at the high end. Within this classification Australia and New Zealand cover a wide range of temperature conditions with mean annual temperatures varying from 4°C in the alpine areas of Australia and New Zealand to 28°C along the tropical northern coast of Western Australia. Natural and managed ecosystems will be discussed within that framework.

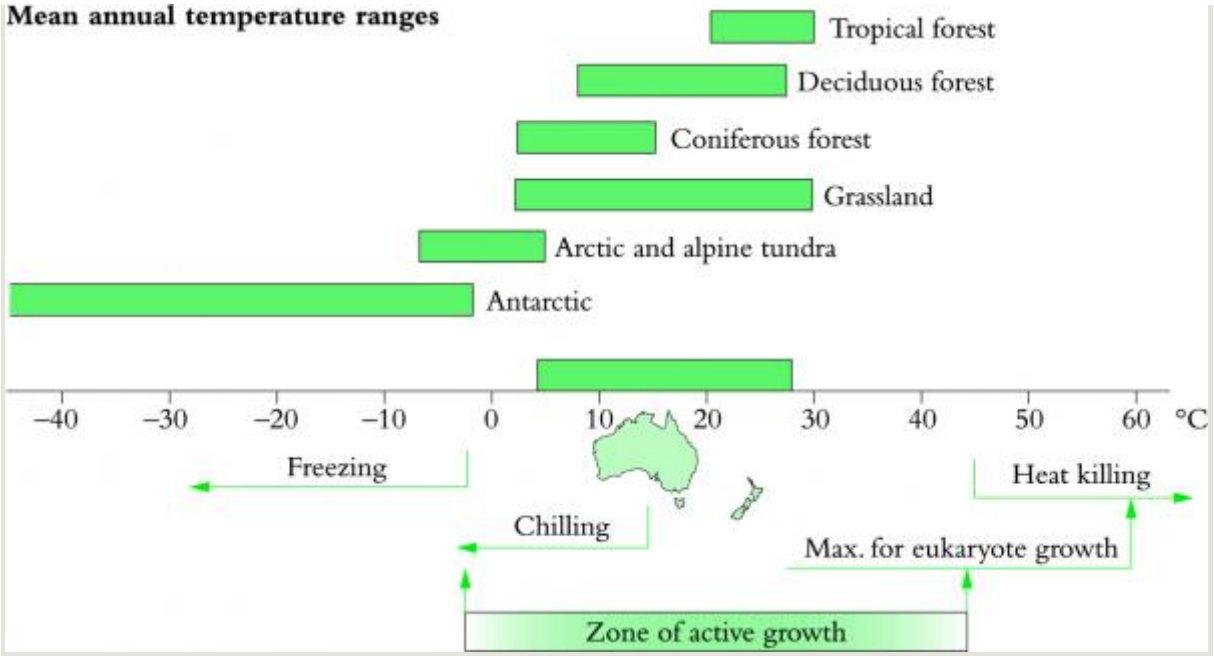


Figure 14.2 Mean annual temperatures in Australia and New Zealand range from 28°C in the north (tropical forest zone) to 4°C at higher elevations in the south (arctic and alpine tundra zone). Temperature extremes are an important factor in regulating survival and growth of many species, with periods of heat stress (>45°C) and freezing temperatures (<-2°C) common to some areas. Active growth of higher plants is normally limited to temperatures ranging from 0°C to 40°C, but many subtropical species will be chill damaged by temperatures lower than 10—15°C and many temperate species will not survive long periods of temperatures higher than 30°C. (Generalised from various sources)

14.1 Thermal environment and growth responses

Temperatures vary with latitude, altitude, size of land mass (and position within that land mass), atmospheric conditions (cloud cover and air movement) and local topography. As a rough guide atmospheric temperatures decrease by about 1°C for each 2° increase in latitude, or for each 100 m increase in altitude, but there is considerable variation in this relationship. A crop such as potato, which has its origin in tropical high altitudes, is now grown widely in temperate low-altitude

regions of the world where temperature conditions are similar. How-ever, temperature is not the only concern in this expansion of a crop plant to new growing regions, as a change in latitude and altitude may require some adaptation to changing photoperiod and radiation levels. Seasonal variation in temperature is greatest near the poles, while at high altitudes the increased solar radiation which can result in rapid local heating is balanced by greater night radiation losses. The most stable temperatures occur under oceanic conditions in the tropics.

Average monthly air temperatures, which take account of seasonal changes, are much more relevant to plant growth than mean annual values. Some idea of the temperature range in Australia can be seen by comparing the alpine areas, where the average monthly maximum for July (midwinter) is 5°C and the average monthly minimum is −5°C, with the north coast of Western Australia where the average monthly maxi-mum for January (midsummer) is 40°C and the average monthly minimum is 27°C. While average temperatures may provide a useful base for studying plant development, extreme conditions must also be taken into account, particularly in relation to sensitive stages of development.

Air temperatures greater than 50°C have been exceeded in all states of Australia except Tasmania and the ACT. The frequency of heatwave temperatures in Australia is generally greater to the north and away from the coast. At Marble Bar (in the northwest) summer temperatures may exceed 40°C for several weeks at a time and on one occasion lasted from November through to February.

Frosts are widespread in the winter and spring months in southern Australia and extend northwards along the Eastern Highlands of New South Wales to the Darling Downs in Southern Queensland and into central Australia. In the south-eastern highlands of Australia there is a median frost period of 200 days and the lowest temperature recorded in this area was −23°C at Charlottes Pass.

Temperature extremes are not so great in the agricultural regions of New Zealand, which has a more maritime climate, although in some regions (Otago) the frost season lasts 250 days and there is permanent snow in more mountainous regions above 2000 m.

Unseasonal weather and temperature extremes will of course influence distribution of native plant species, as well as limiting growth of crop plants.

14.1.1 Temperature means and extremes

Timing cardinal stages in plant development (phenology) can often be predicted from temperature measurements taken during the growing season. This integration of time and temperature is expressed in terms of degree-days (see later comments). However, when considering the effect of temperature on yield it is necessary to take extreme conditions into account, particularly at sensitive stages of growth.

Although unseasonally warm growing conditions late in winter are not necessarily harmful to fruit trees, this will often result in early bud break and flower development, increasing the possibility that these more sensitive stages of development will be damaged by a late frost (see the Frontispiece to Chapter 14).

For annual crops some degree of adjustment is possible to avoid a particular environmental stress by varying the cultivar or time of planting. However, even this increased flexibility may not be adequate to cope with the irregular nature of many stresses. In the wheat-growing areas of Australia temperatures increase from the time of heading through to crop maturity and grain filling often occurs at above-optimum temperatures. Added to this is the possibility of extreme high temperatures (heat shock) or drought. In warmer growing regions these temperature extremes may be avoided in part by earlier planting, but this approach will depend on suitable temperature con-ditions and the availability of water for germination and seedling establishment early in the year. In cooler wheat-growing regions earlier planting may expose the developing infloresence to possible frost damage resulting in reduced fertility and grain set (Figure 14.3).

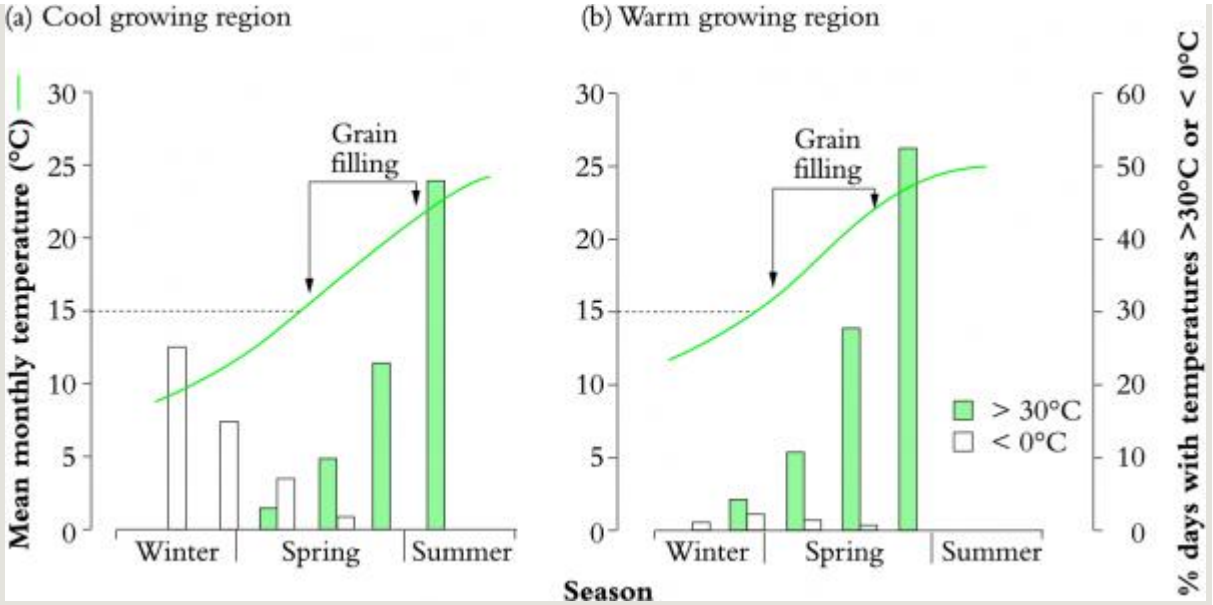


Figure 14.3 Wheat-growing areas of Australia have been classified according to the temperature conditions normally prevailing during crop growing seasons (Nix 1975).Temperature increase following heading is common in all regions and plants frequently suffer periods of heat and drought stress during grain filling. Avoiding these late stresses by earlier planting can be difficult, particularly in those regions subject to spring frosts which may damage the developing florets of the inflorescence (ear) (Based on Nix l975 plus other unpublished sources)

14.1.2 Plant temperatures

Most field studies on the relation between growth (and yield) and temperature are based on meteorological data collected in the vicinity of the crop or ecological area under examination. Although these data have proved to be of considerable value in assessing the response of plants to temperature, actual plant temperatures can differ considerably from air temperature and temperatures can also vary from organ to organ within a plant.

Plant temperatures will be influenced by plant form (erect or prostrate), leaf area, aspect (e.g. north- or south-facing slope), irradiance (sun angle, cloud cover and altitude) and air flow (wind). There are also plant characteristics such as reflection from the surface of the leaf, leaf angle and leaf cooling by transpiration which will reduce plant temperature and may minimise the damage associated with above-optimal air temperatures. At the other end of the scale, where there is moisture on leaves, the latent heat produced during external ice formation (a white frost) may provide some initial protection of tissues against frost damage.

The main temperature gradient within a plant is from leaves to roots. At sunrise with a clear sky there is a rapid rise in air temperature and leaf temperature, with a slower and lower rise in root and surface soil temperature. This relationship is altered considerably by cloud cover and at night root temperatures will be higher than leaf temperatures. Unfortunately a lack of direct measurement of tissue temperatures in field situations can make it difficult to extrapolate from laboratory to field (Figure 14.4). For example, organ volume (thickness) can also have a marked influence on temperature and this can be seen, for example, in the apple-growing regions around Auckland in New Zealand. On a windless sunny day with an air temperature of 26°C, while leaf temperature in an apple orchard may reach 29°C, the peripheral flesh of the fruit on the sunny side of a tree can reach 45°C.

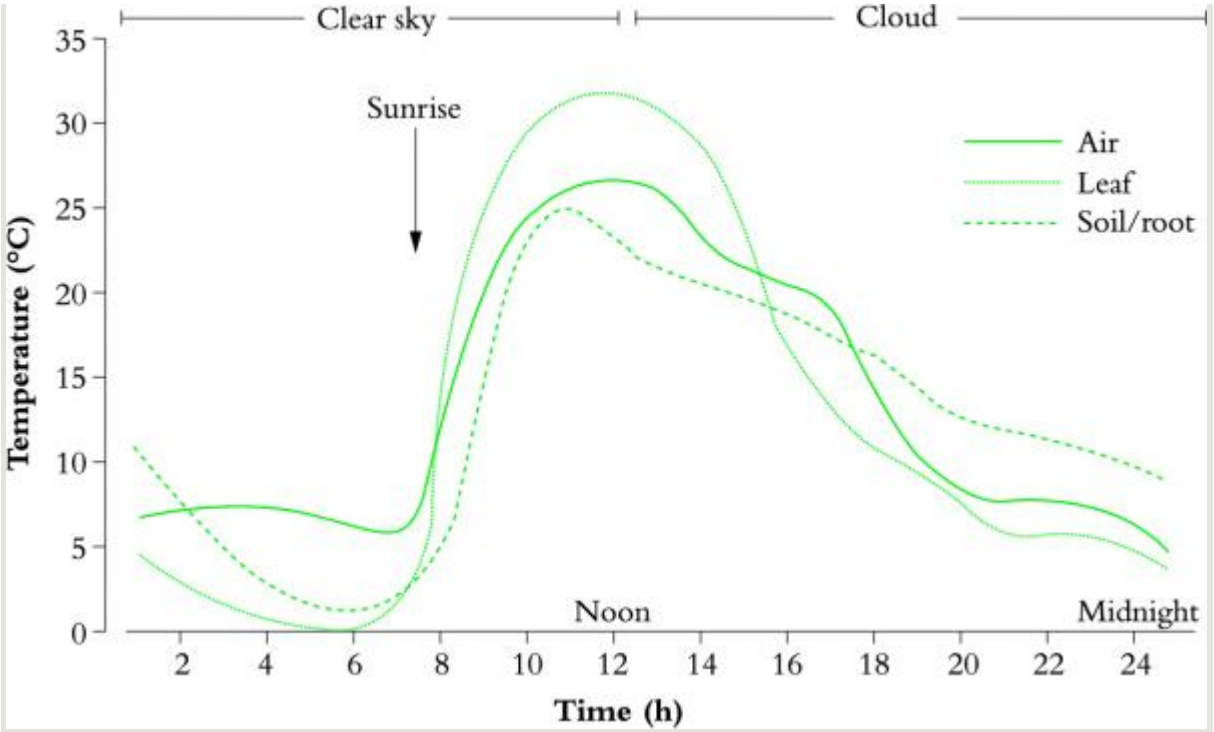


Figure 14.4 Plant temperatures generally follow the diurnal pattern of air temperatures, but may be higher (sometimes 10°C or more) due to strong irradiance from full sunlight, or cooler (often by 2-3°C) due to transpirational cooling. Tissues and organs of a plant are not necessarily at a uniform temperature. Root temperatures are generally lower than those of leaves during daytime and higher at night-time, reflecting the differences between air and soil temperatures (Based on Davidson 1969a)

14.1.3 Variation in sensitivity

At any given stage of development, where other growth conditions are known, it is possible to define the minimum temperature below which a plant will not grow, suboptimal temperatures where a further increase in temperature will result in increased growth, optimal temperatures when growth is at its maximum, supraoptimal temperatures where a decrease in temperature will result in increased growth and the maximum temperature above which a plant will stop growing. Sustained temperatures beyond this range will be lethal.

When considering temperature responses it is possible to divide higher plants into broad, overlapping groups. One division is based on differences in the pathway of CO_2 fixation during photosynthesis, where species in which initial fixation occurs via Rubisco and the photosynthetic carbon reduction cycle are designated C_3species and species in which initial fixation occurs via phosphoenolpyruvate (PEP) carboxylase and the four-carbon dicarboxylic acid pathway are designated C_4 species (Section 2.1). A second division is provided by sensitivity to low temperature: 'chilling-sensitive' species are unable to grow, and often suffer visible damage, below 10–15°C and 'chilling-tolerant' species are able to grow down to 0°C and able to survive below this temperature.

C_4 species include maize and sorghum and such species have high optimum temperatures (≥30°C) for growth. Most C_4 plants are also chilling sensitive (Section 14.4). C_3 species, on the other hand, show considerable variation in their optimum growth temperature, which can range from close to 30°C in rice to less than 10°C in some alpine species, and they also include a wide range of both chilling-sensitive and chilling-tolerant plants (Figure 14.5).

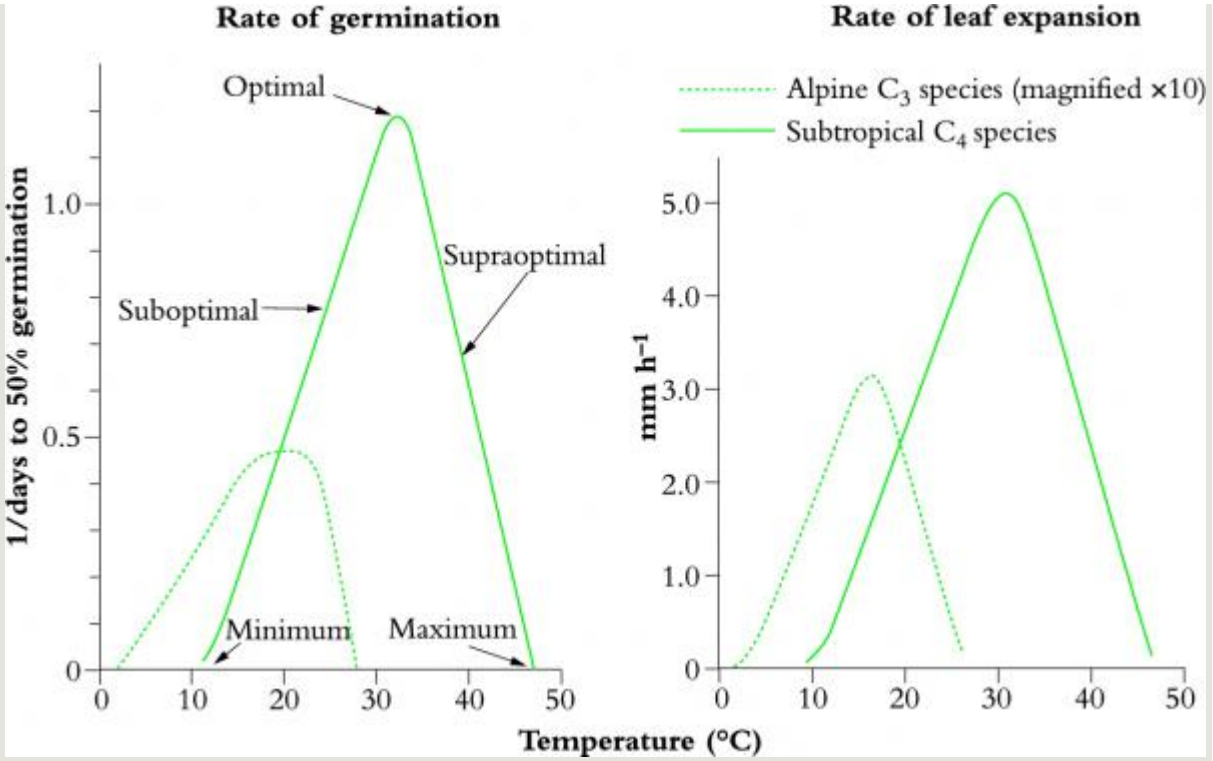


Figure 14.5 Plant species differ widely in their response to temperature, with alpine C_3 species having a low optimum temperature and subtropical C_4 species a high optimum temperature. While the alpine species will survive at temperatures below zero, temperatures of 10°C to 15°C are critically low for many subtropical C_4 species. Maximum temperatures for active growth are generally higher in subtropical than in alpine species (Based on Wardlaw 1979)

Temperature is an important factor in controlling changes in development from germination, through vegetative growth to floral initiation and reproductive growth (Section 7.1). Not all stages of development, or different physiological processes, are equally sensitive to temperature. For example, the stage of pollen meiosis during anther development in the major cereals is particularly sensitive to temperature extremes (low temperature is an issue for rice culture in the Murrumbidgee Irrigation Area, and high temperature a common problem in wheat).

Variation in temperature tolerance is also evident within single plants as well as between genotypes. Young actively growing tissues are generally more sensitive to temperature variation than mature tissues and dormant tissues such as buds and seeds can often survive quite extreme temperatures. Frost tolerance in apple is greatest in the stem and then follows a sequence of decreasing tolerance from the mature leaf to the young leaf and floral parts, with the ovary, style and stigma of flowers being least tolerant of frost.

Variation in temperature sensitivity between tissues and physiological processes is also seen in sorghum, a subtropical C_4 species. Frost damage occurs to green tissue below –1°C, there is poor seed germination below 6°C, chlorophyll destruction occurs in mature green tissue under high light at 10°C, there is poor pollen development below 13°C and chlorophyll formation in young developing leaves is inhibited at temperatures below 16.5°C (Bagnall 1982).

14.1.4 Biochemistry and basic concepts

Enzymes play a major role in regulating the way in which plants respond to temperature. The effect of temperature on enzyme activity is expressed through the maximum rate (V_{max}) and the enzyme–

substrate affinity (K_m) and this in turn is related to the effect of temperature on enzyme synthesis, activation and stability.

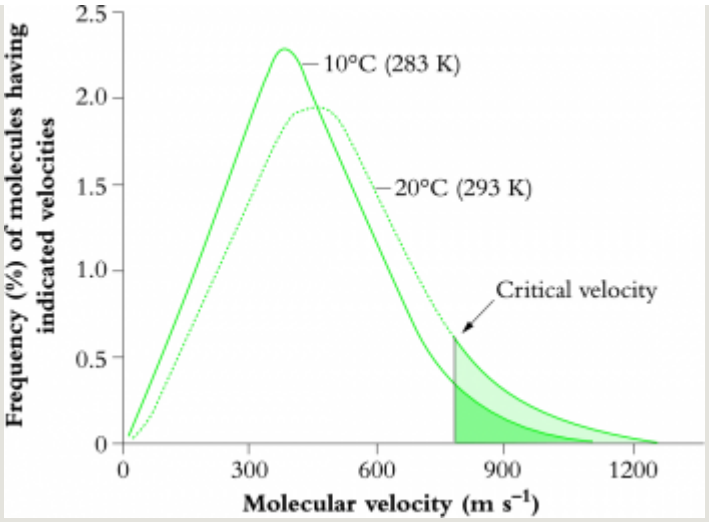


Figure 14.6 Molecules must collide for a chemical reaction to occur, but from the expected number of collisions in a given solution it is clear that only a small number of these collisions actually result in a reaction. For a reaction to occur not only must molecules collide but they must do so above a critical velocity or minimum energy (activation energy).This explains an apparent anomoly where kinetic theory predicts that a 10 K (Kelvin) increase in absolute temperature (K = °C + 273) would be expected to increase the number of collisions by about 2%. However, above a critical value the rate of a reaction can increase two- to three-fold (200-300%) per 10°C rise because the number of collisions increases considerably more than average behaviour would predict. This change in the rate of a reaction with a rise in temperature of 10°C is known as the Q10 value and is around 2 to 3 for many chemical (enzyme) reactions which are operating within their dynamic range (Based on various sources, courtesy I.F. Wardlaw)

Basic metabolic rates tend to increase exponentially within their dynamic range (10–30°C) so that a rise in temperature of 10°C will at least double reaction rate, that is, 'Q_{10}' = 2 (Figure 14.6). Q_{10} represents the net outcome of increased activity of an enzyme system with increased temperature, offset by any deactivation of the enzyme associated with this increase. Q_{10} values for metabolic processes are generally in the range of 2–3 and values below this imply that the reaction is at least partly governed by physical rather than metabolic processes. Q_{10} values for physical processes are commonly around 1.3. Physical limitation occurs when there are barriers to the transfer of substrate to reaction sites in a cell. Reaction rates of whole organisms or even organs often increase approximately linearly with temperature. Respiration is a case in point. This departure from an exponential increase results from a progressive shift in the reaction rates of component processes which first increase exponentially with temperature but then become modified by physical constraints such as substrate availability.

Enzymes can adjust to changes in the temperature environment, such that rates in acclimated plants are not as divergent as would be anticipated from the immediate response to temperature change. Acclimation can take a number of forms which may involve changes in isozymes or enzyme concentration, modification of an enzyme by substrate and effectors, or changes in metabolic regulation.

The concept of Q_{10} values has been extended to complex cellular and even whole-plant functions and has been used to provide some insight into the nature of the factors limiting the response of plants to temperature.

The ‘thermal kinetic window’ is a concept that relates enzyme activity and optimal plant metabolism to the temperature characteristics of the Michaelis–Menten constant (K_m) of substrates and cofactors. Thermal kinetic windows define the temperature range outside which plants experience thermal stress. Many enzymes operate under non-saturating substrate concentrations and substrate binding (K_m) may at times be of greater importance than maximum velocity (V_{max}) for the characterisation of enzyme function under physiological conditions. The thermal kinetic window for a specific enzyme in a particular species (often spanning 8–15°C) is generally narrower than the plant temperatures experienced on a seasonal or daily basis, and temperature extremes that induce heat shock and chilling injury are not required for plants to experience some degree of thermal stress.

In the event of a sustained change in temperature conditions of plant growth, temperature:K_m relationships for key enzyme reactions can adjust towards a temperature optimisation for metabolism and hence growth under those conditions, an out-come referred to above as acclimation and amenable to analysis via an Arrhenius plot to reveal underlying bioenergetics.

By analogy with graphs used to illustrate Michaelis–Menten kinetics, the natural logarithm of a physiological reaction rate (k) plotted against the reciprocal of absolute temperature ($1/T$) yields a straight line (Figure 14.7). This procedure in effect linearises an exponential response of reaction rate to temperature, and can be summarised in general terms as:

$$k = Ae^{-Ea/RT} \quad (14.1)$$

where k is the rate constant of the reaction;

A is a constant (exponential or frequency factor);

Ea is the activation energy;

R is the universal gas constant;

T is absolute temperature in degrees Kelvin (K).

This equation can be rearranged to facilitate comparisons of reaction rate at two temperatures, T_1 and T_2:

$$((\ln k_2) / (\ln k_2)) = A ((T_2 - T_1) / (T_1/T_2)) \quad (14.2)$$

This relates enzyme activity to temperature where k_1 and k_2 are the reaction rates at absolute temperatures $T_1$and T_2.

Plotting log k as a function of $1/T$ yields a linear relationship in the dynamic temperature range where the organism shows readily reversible responses to temperature, and can live indefinitely. Slope indicates the ‘energy of activation’ (Ea) which is the minimal energy required for the reaction to occur. A change in slope of this line indicates a change in sensitivity. A steeper slope at low temperature indicates that the energy of activation has increased and has therefore become more limiting to maximum velocity (V_{max}) of the overall reaction (Figure 14.7).

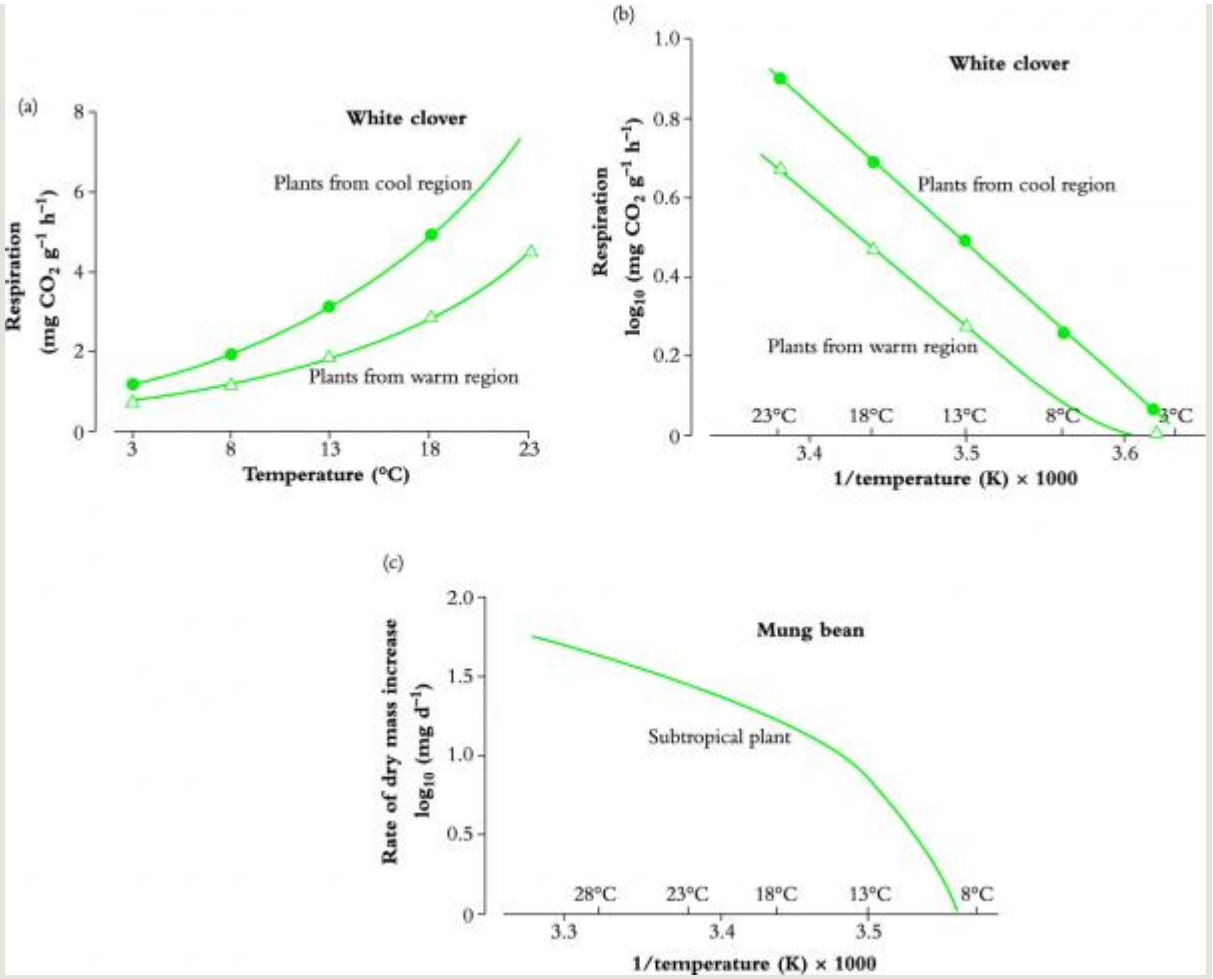


Figure 14.7 (a) Dark respiration of white clover leaves (dry mass basis) increases with temperature. However, respiration rate depends on the conditions under which plants have grown and is greater for leaves grown under cool conditions.

(b) An Arrhenius plot provides a useful basis for comparing the temperature response of two sets of leaves. Respiration (reaction) rate (log transformed) is plotted as a function of the reciprocal of absolute (Kelvin) temperature (1/temperature (K)). An Arrhenius plot (see Equation 14.1) is also used in analysing many chemical transformations and processes in which absolute rates are exponentially related to temperature and thus yield a straight-line relationship as illustrated here. Arrhenius equations have been applied to a whole range of plant functions from photosynthesis to changes in dry mass. Slope is characteristic of a particular reaction and varies between species, but in this example using clover there is little difference between warm and cool region leaves, indicating that the basic activation energies are similar. (c) Many subtropical species, such as mung bean, are chilling sensitive, growing poorly at temperatures well above freezing. An Arrhenius plot of growth (or a more specific biochemical reaction) is no longer linear throughout the whole temperature range. A steeper slope at low temperature implies that the energy of activation has increased and has become more limiting to plant function compared with values above that chilling threshold. At high temperatures the slope of the line is again reversed as enzymes are inactivated. Actual values will vary from one reaction to another and between species ((a) Based on Woledge and Dennis 1982; (c) based on Bagnall and Wolfe 1978)

Considerable use has been made of Arrhenius plots in attempts to determine critical temperatures for key enzymatic reactions in plant cells. Membrane lipids may undergo a phase change from the mobile to the solid state with a fall in temperature and this will vary with the nature of the lipids in the membrane, particularly the degree of unsaturation (double bonds). Any change in lipid properties would be expected to modify the activity of membrane-bound enzymes. Because of the complex nature of membranes, such change will often be a gradual rather than an abrupt change at a precise temperature.

Arrhenius plots have also been used to analyse the response to temperature of individual organs and whole plants in order to determine critical temperatures for growth. In chilling-sensitive species, the slope of the Arrhenius plot becomes steeper at low temperature, indicating a change in enzyme–temperature relationships. Plant taxa which experience broader ranges of temperature during growth in their native habitats can have smaller Arrhenius temperature coefficients.

Membranes and their associated enzymes are likely to provide a key to many temperature responses in plants and this can be extended to frost damage where membrane destabilisation resulting from freeze-induced dehydration is a major factor in freezing injury (Section 14.6).

14.2 Plant coordination

Unlike single-celled organisms, vascular plants develop specialised cells and tissues that are spatially separated, but whose functions are closely integrated. Within such a system the effect of temperature on a particular physiological process will be inextricably connected with other synthetic events, but some major categories of plant function can still be identified.

14.2.1 Photosynthesis

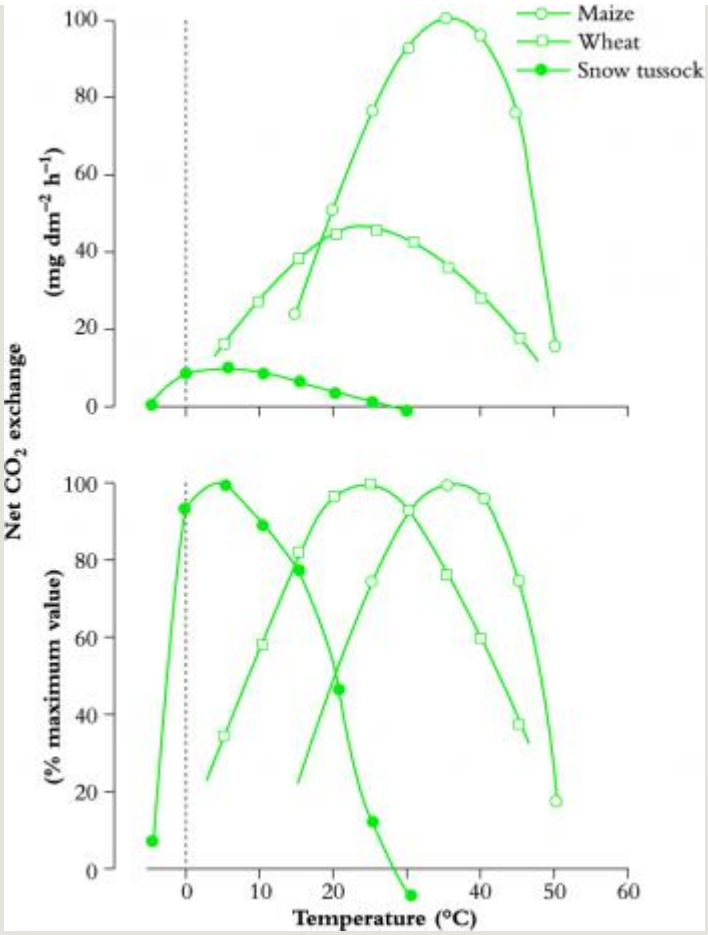


Figure 14.8 Plant species show characteristic variation in the way photosynthetic tissue responds to temperature. Maize (a subtropical C_4 species) has a high maximum rate of CO_2assimilation with a high optimum temperature, while wheat (a temperate C_3 species) has a lower maximum rate and a lower optimum temperature. (a) Absolute values; (b) shows those same data normalised to 100% at optimum temperature.

Alpine plants (C_3 species) have an even lower optimum temperature and may show CO_2 assimilation below 0 °C, but their maximum rates of photosynthesis are often low compared with warmer climate species. (Based on Wardlaw 1979)

CO_2 assimilation underpins plant productivity and is therefore central to any analysis of the response of plants to a change in temperature. In photosynthetic terms, plants can be divided broadly into the groups discussed earlier.

Some C_3 species such as snow tussocks have an optimum temperature for CO_2 assimilation as low as 5°C, but it is important to note that absolute rates at this temperature may be relatively low (Figure 14.8). Most temperate grasses and cereals as well as many woody species have temperature optima in the range from 15°C to 25°C and within this range many C_3 species show only small changes in CO_2uptake. In contrast to temperate C_3 species, CO_2 assimilation by C_4 species increases considerably with a rise in temperature from 15°C to 30°C and optimum temperatures may be greater than this (Figure 14.8). Rice, a subtropical C_3 species, has a higher temperature optimum for CO_2 assimilation than temperate C_3 species. Under high light, C_4species have a characteristically greater photosynthetic rate than the C_3 species, but these differences disappear and may be reversed at low temperature. Growth temperatures may also influence the optimum temperature for net photosynthesis, which may therefore vary with season or location. However, modifications leading to an improvement in photosynthesis at high temperatures can result in decreased performance at low temperatures and vice versa.

A combination of at least two factors may be associated with the failure of C_3 species to respond more favourably to high temperature in terms of CO_2 assimilation. One is the limit placed on photosynthesis by ambient CO_2 (Figure 14.9), and a second is the concurrent rise with increasing temperature of light-stimulated photorespiration, which is effectively absent from C_4 species. Increased atmospheric CO_2 inhibits photo-respiration and results in a much greater uptake of CO_2 in response to increased temperature in C_3 species.

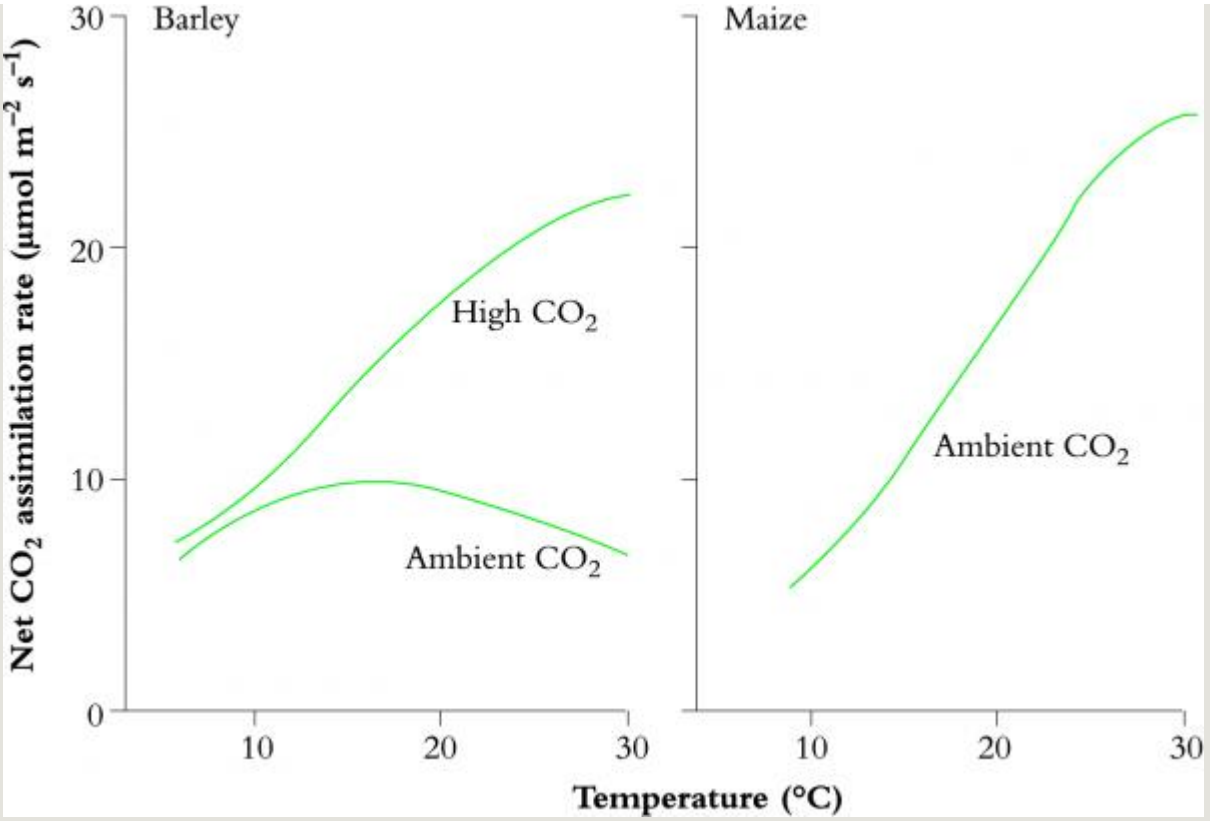


Figure 14.9 Maize (a subtropical C_4 species) has a high optimum temperature (~30 °C) for CO_2assimilation, while barley (a temperate C_3 species) has a lower, but less distinct optimum (~15 °C). Doubling CO_2 has little effect on CO_2 assimilation rate by maize (not shown here), but greatly increases the absolute rate and optimum temperature for barley by suppressing photorespiration. This O_2-dependent loss of carbon increases with temperature and is largely responsible for the low optimum temperature of photosynthesis in many C_3 species (Based on Labate *et al.* 1990)

While net photosynthesis is the resulting balance between gross photosynthesis and respiration, low or even negative net photosynthetic rates can have a significant effect on productivity. An example of this would be photosynthesis by the green pod of many legumes where the net uptake of CO_2 is low because of a high rate of pod and seed respiration. A rise in temperature will result in greater respiratory losses from the pod and a reduction in net uptake of CO_2, but this does not diminish the importance of pod photosynthesis.

Variation in stomatal resistance could be another factor associated with temperature effects on net assimilation of CO_2. Adaptation to high temperature can be related to photosystem II electron transfer, the stability of chloroplast membrane-bound enzyme activities and the stability of the photosynthetic carbon metabolism enzymes that require light for activation. For example, enhanced assimilation of CO_2 by rice at high temperature, in comparison with the more temperate C_3 species, is associated with a greater response of ribulose-1,5-bisphosphate carboxylase in rice to increasing temperature.

In chilling-sensitive species such as maize, sorghum and mung bean, chlorophyll formation and chlorophyll destruction both occur in light at low temperatures. However, once greening has occurred quite low temperatures (but not usually freezing) can be tolerated as long as these occur during darkness. Low-temperature tolerance is also associated with a high level of strategic enzymes such as Rubisco, protein stability and membrane lipid composition.

Consideration must also be given to possible indirect effects of temperature on photosynthesis. For example, a change in root growth due to a change in temperature could alter the supply of nutrients or growth regulators, such as cytokinins, to the shoots. It is common to find a build up of non-structural carbohydrates in many parts of a plant under low-temperature conditions, a response indicating that growth is more sensitive to low temperature than photosynthesis. However, feedback inhibition of photosynthesis associated with this excess carbohydrate accumulation under low-temperature conditions occurs in a number of species. In summary, it is important to take into account the possibility of indirect effects of temperature on photosynthetic tissue when looking for genetic differences in photosynthetic responses to temperature.

14.2.2 Assimilate transport

There are three components of nutrient and photosynthate transfer in plants that might respond to temperature in different ways: (1) transfer of metabolites across cell membranes, including the exchange between apoplasm (space external to cell membranes) and the symplasm (space contained by cell membranes); (2) cell to cell transfer (within the symplasm) via plasmodesmal connections, and (3) movement of metabolites over long distances through phloem sieve elements.

Selective transfer of metabolites across a membrane against a concentration gradient is an energy-requiring step involving respiratory activity and membrane-bound ATPase (see Figure 1 in Case study 2.1). This metabolically active process is responsive to temperature. Membrane transfer is associated with many physiological functions including movement of metabolites and photoassimilate loading within source leaves, exchange with storage tissues along the path of transport and photoassimilate loading into sinks. The response of long-distance photoassimilate translocation to low temperature varies widely between species. In many temperate Gramineae (including wheat) a drop in temperature along the path of transport to 1°C has no measurable effect on the translocation of photosynthate, but at this temperature in chilling-sensitive species such as bean and sorghum there is a marked reduction in the translocation of photosynthate. In some chilling-tolerant species such as sugar beet, there is an initial rapid decline in translocation following application of low temperature along the path of transport, but this inhibition is transient in nature, with translocation returning to normal in a number of hours. In species that are more sensitive to chilling such as squash there is some adjustment to low temperature, resulting in partial recovery. Such adjust-ments vary between ecotypes within the one species, for example in Canada thistle where behaviour is related to altitude and thus temperature in natural surroundings (Figure 14.10). Lowering the temperature of the transport pathway also reduces the lateral transfer of carbon into adjacent tissues, or alternatively the remobilisation of stored carbohydrate back into the transport system. By contrast, translocation can be relatively insensitive to temperatures up to 40°C, but will be inhibited by prolonged periods of temperature >40°C. Prolonging a high-temperature treatment, unlike the low end of the scale, does not result in recovery; rather, blockage intensifies.

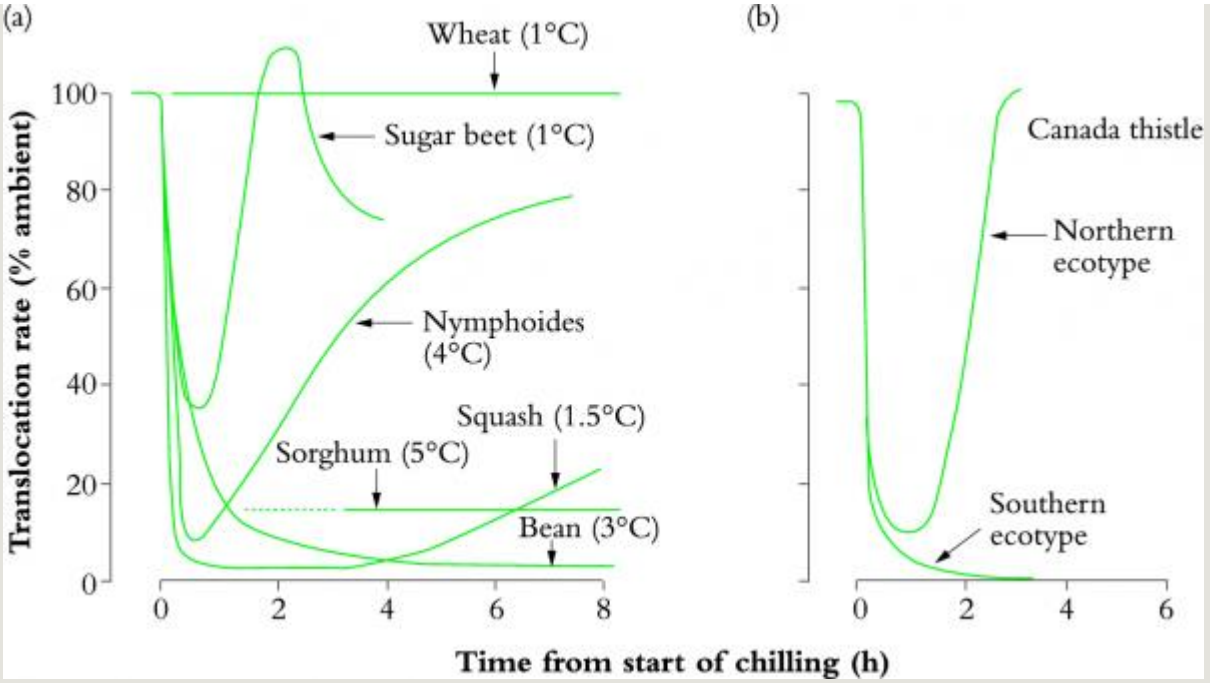


Figure 14.10 Effects of low temperature on translocation of photoassimilate through phloem has frequently been measured by changing pathway temperature between a source and a sink and following variation in the rate of movement of radioactively labelled photosynthate. (a) Translocation in some species such as wheat is especially tolerant of low temperature, but greatly reduced in others such as bean. Again, in other species such as Nymphoides and sugar beet there is an initial retardation of translocation immediately after a low-temperature block is imposed, but translocation subsequently improves even though the low-temperature is retained. (b) Canada thistle has both attributes with the northern (colder) ecotype showing rapid recovery of translocation at low temperature and the southern (warmer) ecotype showing very little recovery over the first 3 h (Based on Wardlaw 1979)

The exact nature of the inhibition of long-distance transport at temperature extremes is still uncertain. Inhibition appears not to be energy related in a metabolic sense, but low-temperature effects may be due to a displacement of proteinacious material. This would lead to transient responses that reverse in time. More sustained responses under either low- or high-temperature treatments are likely to be due to a build up of callose (a β-1,3 glucan) in sieve-plate pores.

Whether reduced translocation is the cause of poor growth at extreme temperatures is often difficult to assess. This is partly because of the transient nature of the temperature response in many species and partly because the response of the transport system to temperature has been examined in isolation from other processes. In sorghum, where temperatures below 20°C effectively reduce translocation, this reduction is minor in comparison with the direct effect of the same temperature on growth. Current findings suggest that long-distance transport in the phloem does not have a direct role in regulating whole-plant responses to temperature.