

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 identi?ed.

14.2.1?Photosynthesis

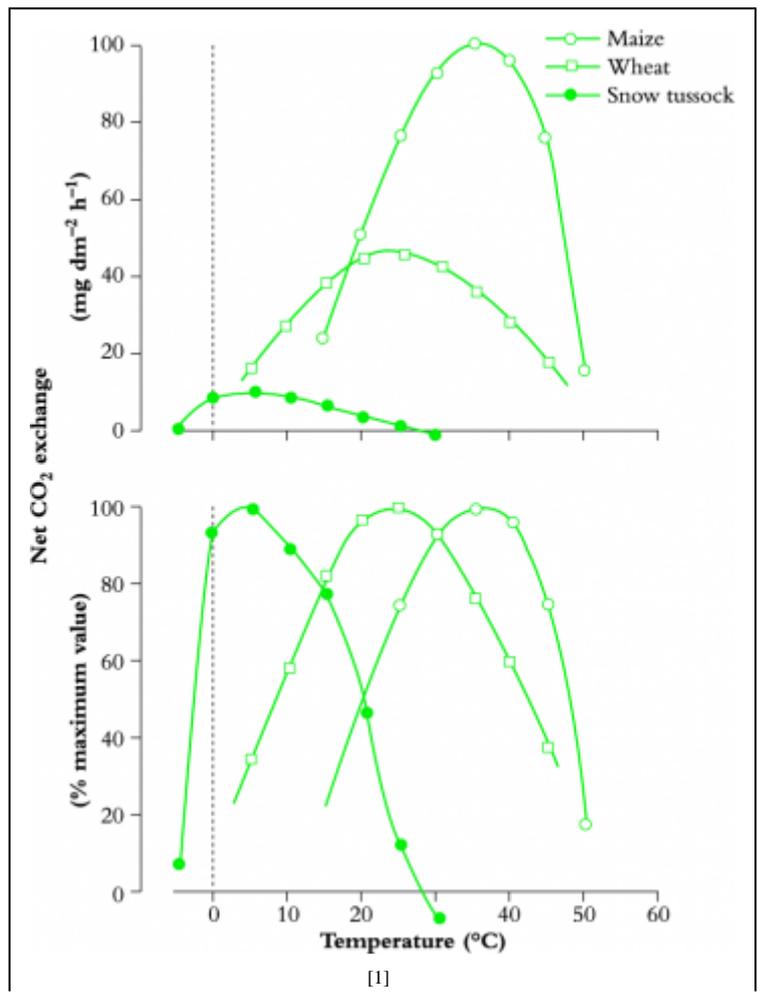


Figure 14.8 Plant species show characteristic variation in the way photosynthetic tissue responds to temperature. Maize (a subtropical C₄ species) has a high maximum rate of CO₂ assimilation with a high optimum temperature, while wheat (a temperate C₃ species) has a lower maximum rate and a lower optimum temperature. (a) Absolute values; (b) shows those same data normalised to 100% at optimum temperature.

Alpine plants (C₃ species) have an even lower optimum temperature and may show CO₂ assimilation below 0 °C, but their maximum rates of photosynthesis are often low compared with warmer climate species. (Based on Wardlaw 1979)

CO₂ 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 C₃ species such as snow tussocks have an optimum temperature for CO₂ 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 C₃ species show only small changes in CO₂ uptake. In contrast to temperate C₃ species, CO₂ assimilation by C₄ 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 C₃ species, has a higher temperature optimum for CO₂ assimilation than temperate C₃ species. Under high light, C₄ species have a characteristically greater photosynthetic rate than the C₃ 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 C₃ species to respond more favourably to high temperature in terms of CO₂ assimilation. One is the limit placed on photosynthesis by ambient CO₂ (Figure 14.9), and a second is the concurrent rise with increasing temperature of light-stimulated photorespiration, which is effectively absent from C₄ species. Increased atmospheric CO₂ inhibits photo-respiration and results in a much greater uptake of CO₂ in response to increased temperature in C₃ species.

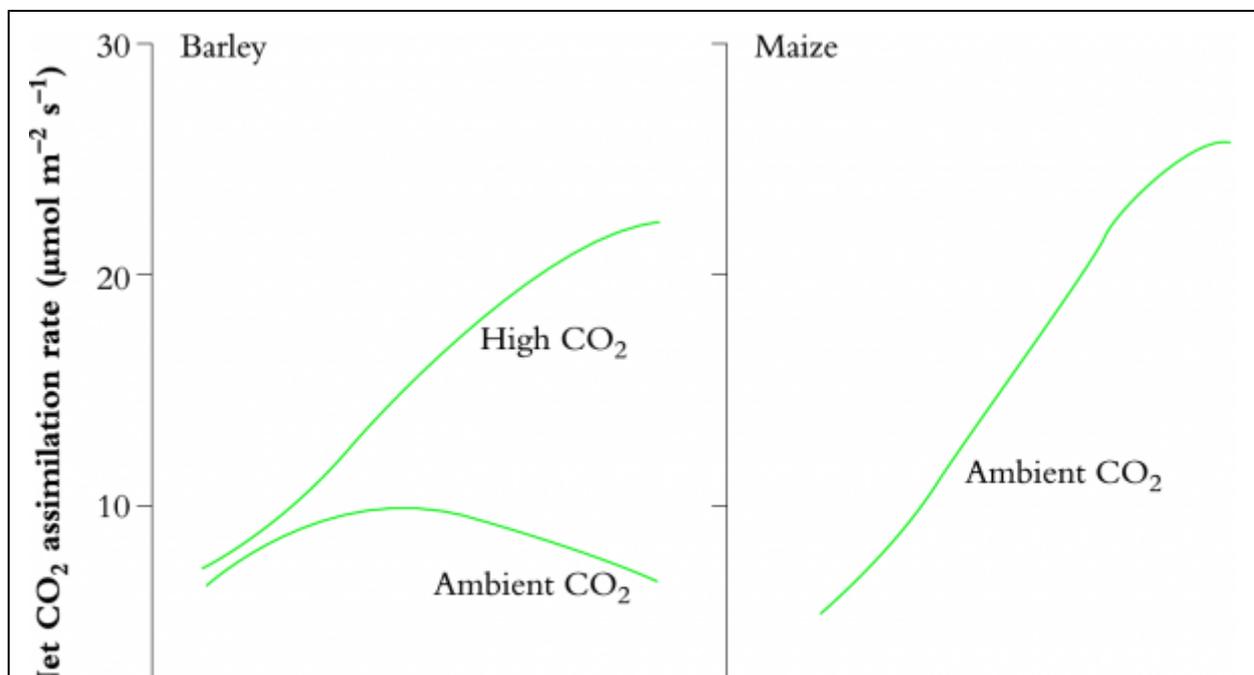


Figure 14.9 Maize (a subtropical C₄ species) has a high optimum temperature (~30 °C) for CO₂ assimilation, while barley (a temperate C₃ species) has a lower, but less distinct optimum (~15 °C). Doubling CO₂ has little effect on CO₂ assimilation rate by maize (not shown here), but greatly increases the absolute rate and optimum temperature for barley by suppressing photorespiration. This O₂-dependent loss of carbon increases with temperature and is largely responsible for the low optimum temperature of photosynthesis in many C₃ 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 CO₂ 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 CO₂, 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 CO₂. 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 CO₂ by rice at high temperature, in comparison with the more temperate C₃ species, is associated with a greater response of ribulose-1,5-bisphosphate carboxylase in rice to increasing temperature.

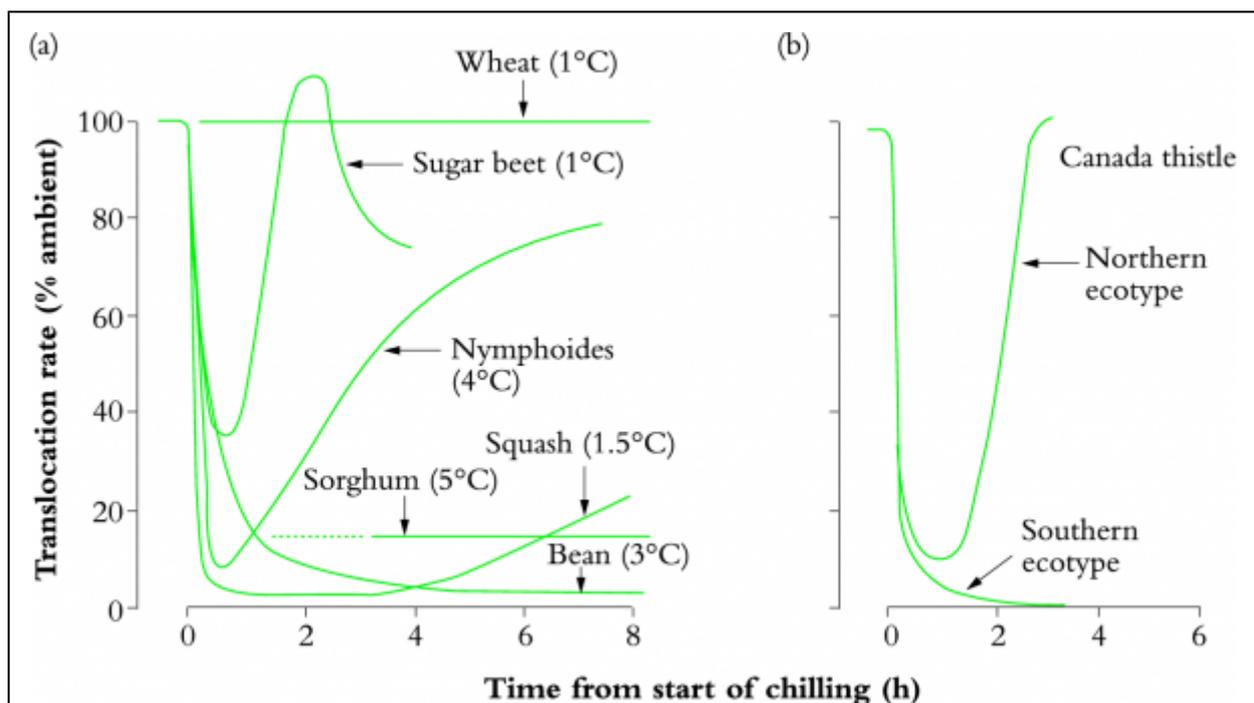
In chilling-sensitive species such as maize, sorghum and mung bean, chlorophyll formation and chlorophyll destruction both occur in light at low temperatures. However, once greening has occurred quite low temperatures (but not usually freezing) can be tolerated as long as these occur during darkness. 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 apoplast (space external to cell membranes) and the symplast (space contained by cell membranes); (2) cell to cell transfer (within the symplast) 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 adjustments 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.



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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 proteinaceous 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.

14.2.3 Water and nutrient uptake by roots

Temperature can influence water movement through plants in a number of ways. Major control relates to stomatal conductance and transpirational demand for water, but temperature can also modify hydraulic conductance in the soil–plant–atmosphere continuum. Changes to root cortical tissue, endodermis and xylem elements of the central stele all contribute. Low temperature can reduce root permeability to water, effectively droughting shoots and causing leaves to wilt. Over time, water movement through roots may recover enough to restore shoot water relations even though the low temperature is maintained.

Although the initial movement of nutrients from the soil to the cortical tissue of the root involves water flow and diffusion the uptake and transfer of nutrients through the stele into the xylem is an active process and therefore temperature sensitive. Increasing root temperature favours nutrient uptake and shoot growth in a wide range of species.

14.2.4 Growth and development

The response of both vegetative and reproductive growth to a temperature change is often associated directly with the response of a growing organ to that change. This conclusion is reached by comparing whole-plant responses to temperature with the response obtained when temperature changes are restricted to just part of the plant, or by measuring the growth response of isolated parts to temperature change. The optimum temperature for leaf growth in intact maize plants is about 33°C and this is also true when the variation in temperature is restricted to the meristematic regions of the leaf. However, detached growing organs do not always show an identical response to temperature as the same organs still attached to the plant.

Growth response to temperature may be controlled by enzyme activity and there are examples where

specific enzymes associated with sugar metabolism or starch synthesis have been linked directly with growth of both vegetative and reproductive tissues. Temperature effects on expansion growth may also be regulated by cell wall properties and any control mechanism is likely to involve a number of interacting factors.

Temperature effects on growth can be viewed in terms of rate *times* duration of growth where individual components have different temperature optima (Figure 14.11). As temperature increases within a plant's dynamic range, duration of growth decreases but rate of growth increases. As a consequence, organ size at maturity may change very little in response to temperature despite variation in growth rate. As temperatures are raised further, an increased rate of growth is no longer able to compensate for a reduction in duration, and the final mass (or volume) of a given organ at maturity is reduced. This response can be seen in a range of tissues including leaves, stems and fruits (and seeds). A smaller organ size at maturity due to high temperature is associated with smaller cells rather than a change in cell number. This implies that cell enlargement is more sensitive to temperature than is cell division (Section 6.2.2).

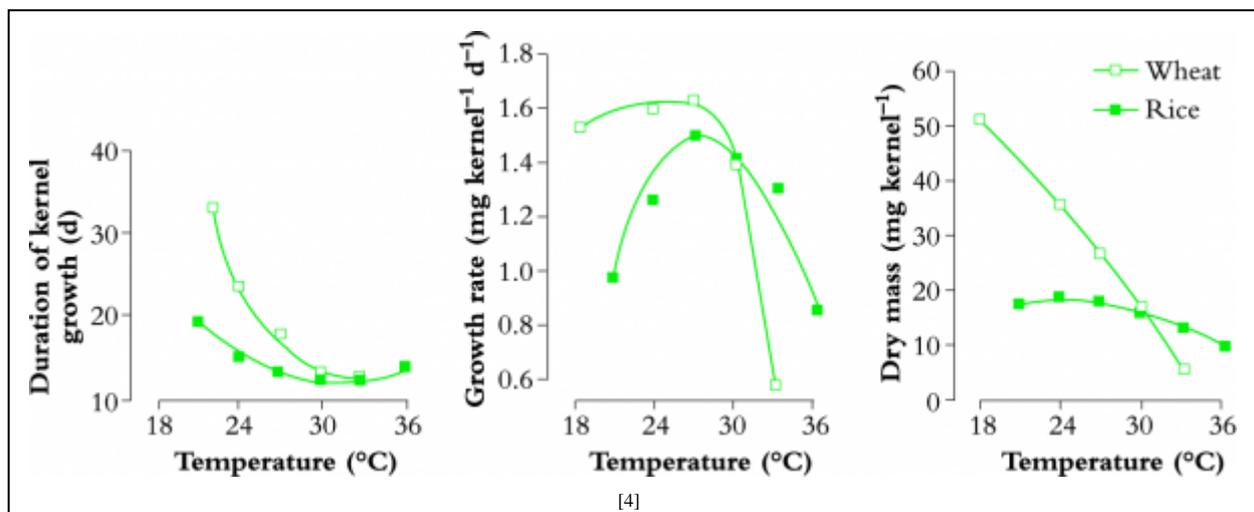


Figure 14.11 Temperature effects on growth can be viewed in relation to either rate of organ production or the final size attained. Size results from both rate and duration of growth, and there are many examples where organ size is reduced at high temperature because rate of growth cannot compensate for a reduced duration of growth. This is illustrated for wheat (a temperate cereal) and rice (a subtropical cereal). At low temperature wheat has a much larger grain than rice, but rice has a much more stable grain size than wheat in relation to temperature and at 30°C grain size in the two species is very similar. (Based on Tashiro and Wardlaw 1989)

14.2.5?Plant form

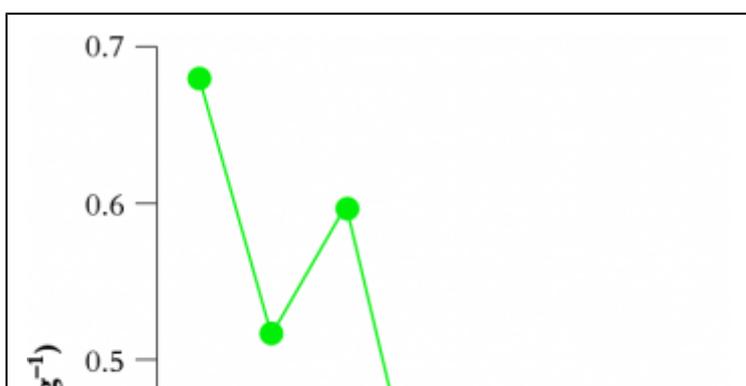


Figure 14.12 The ratio of root mass to shoot mass can change markedly with temperature and this ratio commonly decreases with increasing temperature, illustrated here by an Australian native glycine (*Glycine clandestina*). Cultivated soybean (*G. Max*) on the other hand shows little change in root:shoot ratio with temperature. A high root:shoot ratio at low temperature should not be interpreted to mean that the roots of *G. clandestina* have low optimum temperature for growth without additional sources of evidence. Moreover, root and shoot temperatures are likely to be significantly different under field conditions. (Based on Kokubun and Wardlaw 1988)

A rise or fall in temperature can result in a marked change in plant form. This may be seen as an alteration in plant height, organ shape or branching patterns in either shoots or roots. The leaf area ratio (leaf area/total plant dry mass) of wheat, for example, increases with temperature from 10°C to 25°C because growth in leaf area is promoted more than stem or root growth, and leaves are thinner. In some cases these changes may result from direct temperature effects on the organs concerned, or may reflect changes in either nutrition or the availability of photosynthate (source/sink balance), or possibly changes in the level and location of growth regulators.

Are there different temperature optima for the growth of different plant organs? In an attempt to explain a commonly observed increase in root:shoot ratio at low temperature, carefully structured studies based on split root experiments showed that the optimum temperature for root growth is similar to that for shoot growth. Similarly, in tomato there is no clear differentiation between fruit and vegetative tissue in temperature preference.

A possible explanation for an increase in root:shoot ratio at low temperature (Figure 14.12) relates to an apparent dominance of shoot growth over root growth for a limited supply of photosynthate. Lowering temperature of a whole plant would effectively alter this dominance by decreasing the demand for photosynthate by the shoot and allowing a greater proportion of photosynthate to be partitioned to roots. In grasses and cereals there is a developmental sequence where root growth of tillers follows that of the shoot and the root:shoot ratio will take time to adjust where a change in temperature alters the tillering pattern. Overall, branching and tillering (breaking apical dominance) appear to be favoured by low temperature. This could simply be a response to a greater availability of photoassimilate at low temperature. It is more likely, however, that growth regulators such as cytokinins (of root origin) and auxins (of shoot origin) are involved.

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