THE PHYSIOLOGICAL EFFECTS OF TEMPERATURE ON PLANT GROWTH

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ABSTRACT

The overall response of plants to temperature, although possibly determined by a major change in a single process, may represent a summation of responses either within or between the different parts of the system. Photosynthesis, translocation and growth show their own individual pattern of response to variations in temperature, yet all three processes discriminate to some extent between chilling sensitive and chilling resistant species. A distinction must be made between "sub-optimal" conditions for growth and "critical" temperatures, above or below which a plant will either die, or become dormant. Temperatures which only slow down vegetative growth may become "critical" for certain organs at a sensitive stage, while in contrast, temperatures low enough to limit growth severely may be essential for development to proceed.

If an understanding of the physiological responses to temperature is to be of use to the agronomist, forester or plant breeder, a careful assessment is needed of the precise conditions under which each part of the plant operates in the field, as well as a knowledge of genetic variation.

INTRODUCTION

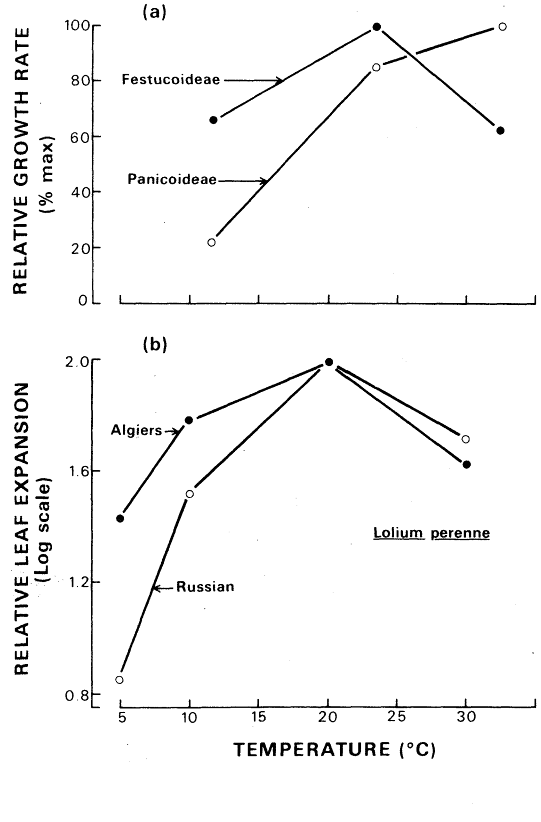
Air temperatures as low as -70°C have been recorded in the antarctic, and as high as +57°C in North Africa, but the temperature range for active growth in higher plants is generally considered to be from 0°C to about 40°C. Plant tissues can survive and to some extent function outside this range, but it is necessary to remember that the time factor becomes particularly important when analysing plant responses to extreme temperatures (Parker, 1963; Levitt, 1972).

From the extensive literature relating to the effect of temperature on the growth and development of plants certain patterns have emerged, patterns that are governed not only by the genetic make up of the plants, but also by their previous environmental history.

When considering temperature responses it is possible to divide the higher plants very broadly into four overlapping groups. One division is based on differences in the pathway of CO_2 fixation during photosynthesis - the "C_3-species" where the initial fixation occurs via the Calvin cycle, and the "C_4-species" where fixation occurs via the C_4-dicarboxylic acid pathway (Hatch and Slack, 1970). A second division is provided by sensitivity to low temperature, with ‘,chilling sensitive" species unable to grow and often suffering visible damage below 10 to 15°C and "chilling insensitive" species able to grow down to 0°C and to survive below this temperature.

The C_4-species, which include maize and sorghum, always appear to have a high optimum temperature for growth ($\geqslant$30°C) and many, but not all, are chilling sensitive. The 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 (Mark, 1975), and they also include a wide range of both chilling sensitive and chilling insensitive plants (van Dobben, 1962; Friend and Helson, 1976; Monteith, 1977).

Figure 1. The relation between temperature and growth. (a) The effect of temperature on the Relative Growth Rates of festucoid (●) and panicoid (0) grasses. Combined data for 7 species in each group, from Kawanabe (1968). (b) The relative effect of temperature on leaf expansion in two contrasting lines of perennial ryegrass; Algiers 1(●) and Russian (0). Redrawn from Cooper (1963).



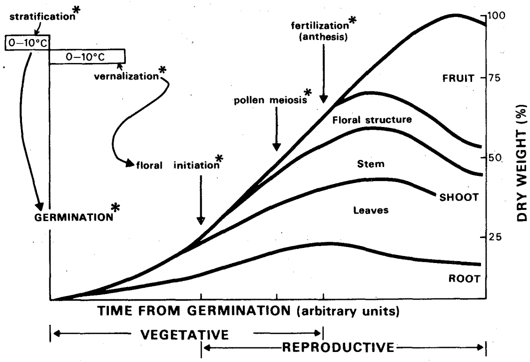
A comparison made by Kawanabe (1968) of the effect of temperature on the growth of the Festucoid (C_3) and Panicoid (C_4) grasses serves to illustrate some of the difference between C_3- and C_4-species (Fig. 1a). The Panicoid grasses showed a high optimum temperature for growth, but a much greater drop in growth as temperatures were lowered. Differences in response to temperature are also evident within a species and these differences are illustrated for climatic races of perennial rye grass in Fig. 1b (Cooper 1963). Here leaf expansion in a Russian race was shown to be relatively more sensitive to low temperature than a race from Algiers.

The following presentation examines some of the physiological changes that are associated with these plant responses to temperature. However in view of the aims of the present symposium and the impossible task of adequately covering a very extensive literature, greater emphasis has in this instance been placed on the response of plants and plant processes to low rather than high temperatures.

TEMPERATURE AND DEVELOPMENT

Figure 2 illustrates the sequence of growth and development that occurs in a hypothetical annual plant from germination to harvest. It is important to realize the extensive overlap in growth that occurs both between different parts of the plant and also between the different phases of development.

Figure 2. Phases of plant growth and development, illustrating the partitioning of dry matter between the parts of an annual plant with time from germination to seed maturity.
* Indicates special temperature requirements and critical stages of development.



A comparision is frequently made between the growth of roots and shoots (stems and leaves), and the root/shoot ratio often decreases with an increase in temperature up to the optimum for dry matter production (Beevers and Cooper, 1964). This change in the pattern of partitioning with temperature however may not necessarily be associated with differences in the optimum temperature for growth between organs, but can express a difference in the ability of each part to compete for substrate; a difference that becomes more acute as maximum growth rates are achieved (Wardlaw, 1968).

There is considerable overlap in the development of the vegetative and reproductive organs - an overlap that is even more complex in woody perennials (Padwick, 1979). The reproductive structures are therefore in some ways both dependent upon and competitive with, the vegetative organs. Seed and fruit numbers are in turn dependent both upon the development of the reproductive structure and upon a continued supply of photosynthate and nutrients from the vegetative tissue.

In addition to the more general effects of temperature on growth there are often specific temperature requirements that must be met if development is to continue. Many seeds, such as those of apple, will not germinate without being subject to temperatures in the range from 1°C to 10°C (stratification), although the optimum for subsequent germination and seedling establishment is much higher than this (Bierhuizen, 1973). Many winter annuals, including the temperate cereals, may require a prolonged period (4 to 6 weeks) of low temperature (0° to 10°C) before flowering can occur (vernalization) (see Evans, 1969). These temperatures are also well below the optimum for growth. Donald (1960) pointed out that limitations to the growth of subterranean clover at high temperature can result from the failure to meet the low temperature requirement for flowering. Some more specific aspects of the effect of temperature on development are examined in a later paper in this symposium by R. G. Thomas.

In addition to the more general responses of growth to temperature there are certain stages of development that are particularly sensitive to variation in temperature. These cannot be dealt with in detail here, but include floral induction (see Evans, 1969), pollen meiosis (Hayase *et al.,* 1969; Downes and Marshall, 1971; Brooking, 1976) and fertilization (see Evans, 1975).

TEMPERATURE AND PHYSIOLOGICAL PROCESSES

Unlike the single celled algae, higher plants are characterized by the development of specialized cells and tissues that are spacially separated, but whose functions are closely integrated. Root activity is, for example, closely tied to that of the leaves, even though these may be separated by distances of more than 50m.

Carbon dioxide entry into a leaf is governed both by stomatal aperture and chloroplast function. Once the carbon has been fixed in photosynthesis and incorporated into various metabolites it can be used in normal cell maintenance, put aside as storage material for later use, or be transferred directly to the vascular system for distribution to other parts of the plant. During this distribution, which occurs through the sieve elements of the phloem, there can be further lateral exchange and storage, particularly if the current demand for carbon in growth is low. Many of the nutrients entering the leaf in the transpiration stream are also redistributed to other parts of the plant through the phloem (Pate, 1975). In the growing organ, photosynthate and nutrients are actively transferred out of the phloem, metabolized and used in a range of activities from cell division and expansion in roots to starch and protein storage in developing seeds.

Even in this simplified system it should be apparent that the effect of temperature on the function of a whole plant can be exceedingly complex.

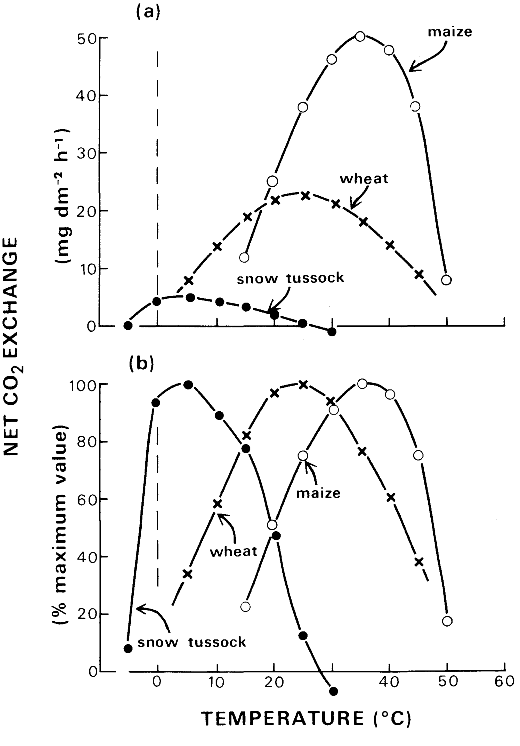
Photosynthesis

The photosynthetic system forms the basis of almost all plants productivity and is therefore central to any analysis of the response of plants to a change in temperature.

When considering photosynthesis, or more conveniently, the Net CO_2 Exchange (NCE) of leaves, plants can be divided broadly into the groups discussed earlier in relation to growth - that is chilling sensitive and insensitive C_3- and C_4-species.

Some C_3-species such as the snow tussocks have an optimum temperature for net CO_2 exchange as low as 5°C. This is illustrated in Figure 3 (Mark, 1975), note however that the absolute rates are very low. Most temperate grasses and cereals have optima in the range from 15° to 25°C, and within this range net CO_2 exchange rates for many C_3-species are comparatively stable (Stoy, 1965; Woledge and Jewiss, 1969; Downes, 1970). In contrast to the C_3-species, net CO_2 exchange in the C_4-species increases rapidly with a rise in temperature from 15° to 30°C, and optimum temperatures are generally greater than this. These differences are shown in Figure 3 in a comparison between wheat and maize. Characteristically, under high light conditions, the C_4 species have greater maximum rates of net CO_2 exchange than the C_3-species, but these differences disappear and may be reversed at low temperatures (see Hofstra and Hesketh, 1969a).

Figure 3. Net CO_2 exchange by the leaves of three Gramineae - maize, a sub-tropical C_4-species (0), wheat, a temperate C_3- species (+); and *Chionochloa* an alpine C_3- species (●)
(a) Absolute rates
(b) Rates expressed as a percent of the maximum.
Drawn from data obtained by Hofstra and Nelson (1969) Wardlaw (1974); Mark (1975).



If the response of NCE to temperature is expressed as a percent of the maximum rate (Figure 3b) it can be seen that the response patterns for all three species are very similar, except for the abrupt fall-off in NCE by the snow tussock below 0°C - the main difference between the species is a shift in the optimum temperature.

A combination of at least two factors could be involved in the failure of C_3-species to respond more favourably to high temperatures. One is the limitation placed on photosynthesis by low ambient CO_2 concentrations (Wardlaw, 1974a) and the second a concurrent rise with temperature of light stimulated (photo-) respiration (Hofstra and Hesketh, 1969a; Keys *et al.,* 1977). The absence of photo-respiration from C_4-species also explains in part why these show higher maximum rates of NCE than the C_3-species (Long and Woolhouse, 1978).

Although stomatal resistance could be another factor associated with the effect of temperature on net CO_2 exchange, the available data are inadequate to establish any consistent patterns (Hofstra and Hesketh, 1969b; Raschke, 1970; Dowton and Slatyer, 1972; Long and Woolhouse, 1978). Also, the stability of the photosynthetic enzymes, or their rate of formation, may be important at extreme temperatures (Phillips and McWilliam, 1971; McWilliam and Ferrar, 1974; Taylor *et al.,* 1974), but it is less clear what regulatory role these may play in the normal growth range.

In chilling sensitive species such as maize, sorghum and mung bean, chlorophyll formation is inhibited and photodestruction of chlorophyll occurs at critically low, although not necessarily identical, temperatures. However in established plants, healthy leaves can be formed without any signs of temperature damage, if the temperatures are only low during the period of darkness (McWilliam and Naylor, 1967; Alberda 1969; Brooking 1979; Bagnall 1979). In several C_3-species it appears that low temperatures may regulate leaf function by reducing root permeability to water and inducing water stress (Jones, 1938; Kramer, 1942; Wright, 1974; Wilson, 1976; Dalton and Gardner, 1978), an effect that is less noticeable in C_4-species (Taylor and Rowley, 1971; Bagnall, 1979).

Consideration must also be given to other 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 substances to the shoot. If there is an interaction between temperature and nutrition it should be particularly noticeable in the legumes where root nodulation and nitrogen fixation are known to be temperature sensitive (Gibson, 1963; 1967), and aspects of this problem are discussed more fully in a later presentation by Hoagland. Unfortunately time and space will not allow a fuller discussion of the interaction between temperature and nutirition, although nutrient uptake and exchange is generally considered to be a metabolically active process (Pitman, 1976).

A predictable response to low temperature in many plants is the accumulation of carbohydrates in stems, leaves and roots (Went, 1953; Dobben, 1962; Clarkson *et al.,* 1974), an effect indicating that growth is perhaps more sensitive to temperature than photosynthesis. Feedback inhibition of photosynthesis due to this carbohydrate accumulation in the leaves is a distinct possibility (Hartt, 1963; Waldron *et al.*, 1967; King, *et al.*, 1967; Habeshaw, 1973). However when maize, a chilling sensitive species, is held at temperatures that will severely limit photosynthesis (2° to 14°C), it has been shown that root growth can be stimulated by the application of exogenous sugars (Crawford and Huxter, 1977). This response suggests that the supply of photosynthate was limiting the growth of maize at these low temperatures and not the reverse.

It is important to take account of the possibility of indirect effects of temperature on the photosynthetic tissue when looking for genetic differences in the response of the photosynthetic system to temperature.

Translocation

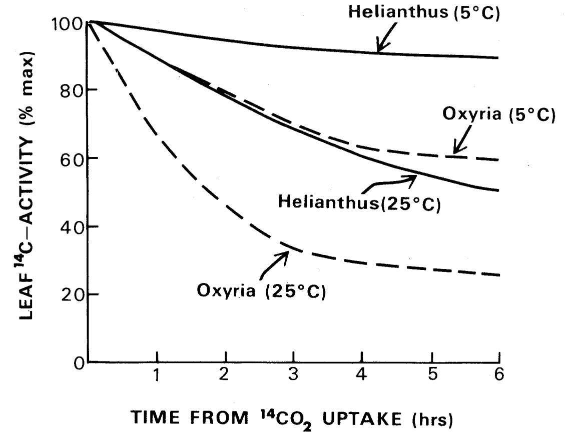
There are two facets of the transport system in plants that may respond to temperature changes in different ways. One is the cell to cell transfer of metabolites that occurs between the vascular system and adjacent tissue, whether this is at the "source" of photosynthate in the leaf, into and out of storage tissue along the path of transport, or into the actively growing "sink" tissues. The second facet is the movement of metabolites over long distances, through the sieve elements of the phloem.

The transfer of metabolites across a membrane is an energy requiring process, involving respiratory activity and membrane bound ATP-ase. This active process is probably associated with the movement of metabolites both into and out of the vascular system, a step that is both pH and substrate concentration dependent and also selective of the metabolites transferred (Geiger, 1975; Ziegler, 1975; Hutchings, 1978). Thus temperature may affect this transfer directly, or more indirectly by regulating the nature of the metabolites available for transfer.

It has been demonstrated, both through dry weight measurements and the use of carbon-14, that the export of carbohydrates from a leaf is temperature dependent (Hofstra and Nelson, 1969; Webb, 1970; Wallace and Harrison, 1978). The effect of temperature on "vein loading" also varies between species, and this is illustrated in Figure 4, where a comparison is made between the movement of ^{14}C-labelled photosynthate out of the leaf of sunflower and a cold adapted species *Oxyria* (Wallace and Harrison, 1978).

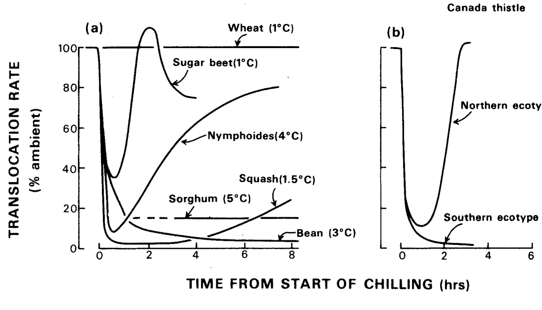
Lowering the temperature of the transport pathway also reduces the lateral transfer of carbon into adjacent tissue, or alternatively the remobilization of stored carbohydrate back into the transport system (Ford and Peel, 1966; Bowling, 1968; Wardlaw, 1972; Die and Tammes, 1975). Directly cooling growing tissue reduces translocation into the organs concerned, an effect that may be related to the transfer of metabolites through membranes, as well as the synthesis of new cell material (Geiger, 1966; Walker and Ho, 1977; Wardlaw, 1974a).

Figure 4. The effect of temperature on the loss of ^{14}C-activity from the leaves of *Helianthus annuus* (——) and *Oxyria digyna* (- - -) following a 30 min pulse labelling with $^{14}CO_2$. Data from Wallace and Harrison (1978).



The effect of temperature on the longitudinal movement of metabolites through the phloem does have implications in relation to the mechanism of translocation (Wardlaw, 1974b), but this is not of direct concern here. The usual way to test the response of the transport system to a change in temperature has been to enclose part of the system in a temperature controlled jacket and observe the effect of an alteration in temperature on the movement of radioactive tracers, such as ^{14}C, ^{32}P, or ^{137}Cs, past the jacket. Some of the effects of temperature on translocation using radioactive tracers are summarized in Figure 5.

Figure 5. The effect of low temperature on the rate of translocation: (a) wheat at 1°C (Wardlaw, 1974a); sugar beet at 1°C (Swanson and Geiger, 1967); squash at 1.5°C (Webb, 1971); sorghum at 5°C (Bagnall, 1979); bean at 3°C (Geiger, 1969); (b) Northern and southern ecotypes of Canada thistle at 0.5°C (Bayer, in Geiger, 1969).



The response of translocation to low temperature varies widely between species. There was no apparent effect on transport of a temperature drop from 21°C to 1°C in a temperate grass such as wheat (Wardlaw, 1974a), but a dramatic effect on chilling sensitive species such as bean at 3°C (Geiger, 1969) and sorghum at 5°C (Bagnall, 1979). In all these cases the effects appeared to hold for long periods, and in sorghum and wheat at least for several days. However, in contrast, it has been shown that in species such as sugar beet (Swanson and Geiger, 1967) and *Nymphoides* (Lang 1974) the initial rapid decline in translocation following a drop in temperature is transient and followed by recovery at low temperature. In sugar beet and *Nymphoides,* which are relatively chilling resistant, the recovery is fairly rapid, but is delayed in squash, a more chilling sensitive species (Webb, 1971). It must be remembered that the data shown here are not derived from identical experimental treatments, having a wide variation in plant growth conditions and differences in the length of the cooling jacket from 2 to 20cm, however it does appear that translocation is more sensitive to temperature in those species that are liable to suffer chilling damage. This is in agreement with an earlier finding by Curtis (1929), that lowering the temperature of the petiole of a bean leaf retarded the loss of starch from the leaf during darkness. An interesting comparison is made in the second part of Figure 6 between northern and southern ecotypes of Canada thistle (Bayer - see Geiger, 1969). The northern, or cooler climate ecotype shows a more rapid recovery of translocation at low temperatures.

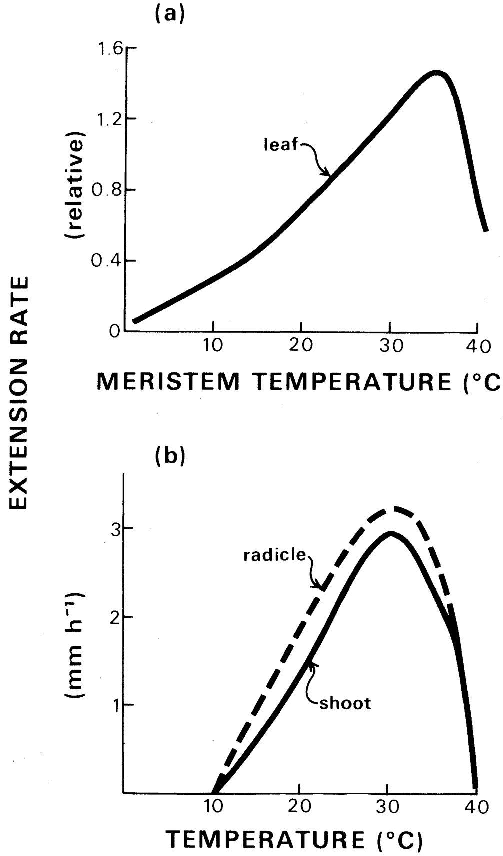
Whether reduced translocation is ever the cause of poor growth at low temperatures is difficult to assess from the available data, partly because of the transient nature of the temperature response in many species and partly because the response of the transport system has been examined in isolation from other processes. At this stage it would perhaps be unwise to completely reject the role of the transport system in regulating plant responses to tempeature.

The nature of the blockage to transport at low temperatures has still to be resolved. Coulson *et al.,* (1972) concluded that the low temperature response in sugar beet petioles was not related to respiration, or the turnover of ATP, and Giaquinta and Geiger (1973) have suggested that the effect in this species may be due to a transient displacement of proteinaceous material and a temporary blockage of the sieve plate pores, translocation returning to normal when this material is dispersed. Although this might also apply to *Nymphoides,* the deposition of callose (a β -1,3 glucan) in the pores (as well as proteinaceous material) suggests that this could also have a role in limiting translocation at low temperatures (Lang, unpublished). Reduced transport at low temperature in bean, a chilling sensitive species (Geiger, 1969), is also associated with a build up of callose (Majunder and Leopold, 1967), and callose deposition occurs in the phloem of many woody species during winter dormancy when translocation ceases (Weatherley and Johnson, 1968). However, the degree of callose blockage does not necessarily correlate with reduced translocation (Eschrich, 1975) and the problem of blockage to transport at low temperatures needs further clarification.

Growth

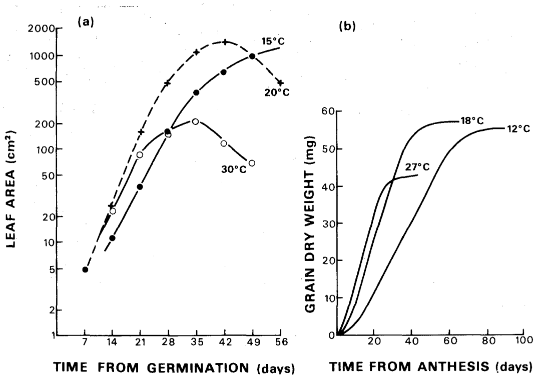
There are some indications that the response of plants to temperature may be directly associated with that of the growing organs, at least above the "critical" temperatures. Duncan and Hesketh (1968) found that the relative leaf growth rate of maize increased with a rise in temperature from 15°C to an optimum at about 33°C, and Watts (1971) was able to show that a similar response could be obtained by restricting the variation in temperature to the meristematic region of the leaf (Figure 6a). In germinating maize, Blacklow (1972) found that the rate of extension of both the radicle and shoot show a similar high optimum, but they did not grow below 10°C, or above 40°C (Figure 6b). Isolated bean cotyledons show the same pattern of response to temperature change as in the attached pod (Egli and Wardlaw, in preparation).

Figure 6. The effect of temperature on the rate of extension growth in maize (a) The relative effect of meristem temperature on leaf extension (Watts, 1971). (b) Radicle (- - -) and shoot (—) extension during dark germination (Blacklow 1972).



In many organs the increased rate of growth with temperature is associated with a characteristic decrease in duration of growth, i.e. a shorter maturation time. Over a moderate temperature range (depending on species) one change balances the other with the end result that there is little alteration in final size. At low temperatures, the increase in duration of growth may however fail to compensate for the reduction in rate, while at high temperatures final size may be limited by a rate that does not increase enough to compensate for the reduced duration (van Dobben 1962). This response to high temperature is illustrated in Figure 7 for both the change in leaf area (Friend *et al.*, 1965) and grain dry weight (Sofield *et al.*, 1974) of wheat with time.

Figure 7. The effect of temperature on the pattern (rate and duration) of growth. (a) Wheat leaves (Friend *et al.*, 1965) (b) Wheat grain (Sofield *et al.*, 1974).



The reduction in grain size at maturity in wheat, ripened under high temperatures, appears to be associated with a change in cell size, but not a change in cell number (Hoshikawa, 1962), and a similar conclusion was reached by Auld *et al.*, (1978) when studying the effect of temperature on the leaves of *Vicia faba.*

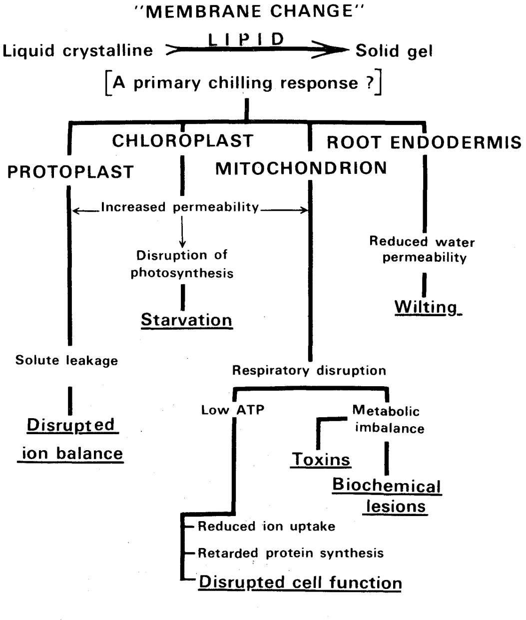
Several basic plant functions, including respiration, show a linear and not an exponential response to temperature and consequently Q_{10} values of much less than 2 occur at the high end of the scale. This suggests that, as temperatures are increased, a physical constraint such as diffusion, rather than a metabolic process, limits many plant reactions (Bierhuizen, 1970; Wassink, 1972; Monteith 1977), although a more sophisticated metabolic control is not impossible. This response is important to the concept of day-degrees, where growth and development are assumed to be proportional to temperature and are related to a summation with time of temperatures above an effective minimum for growth. However this relationship is seriously distrubed if temperatures are low enough to cause tissue damage, or exceed the optimum for growth for a significant part of the time (Bierhuizen, 1970; Monteith, 1977). A near linear response of growth to increasing temperature would explain why fluctuating and steady temperatures, which have the same mean will result in similar yields (Hussey, 1965; Friend and Helson, 1976).

SENSING TEMPERATURE CHANGES

The concept that a simple change in the basic metabolism of a cell may occur in response to critical temperatures and lend itself readily to repair by the addition of specific metabolites, or straight forward genetic selection, has prompted many investigators to examine closely the biochemical changes that accompany plant responses to temperature. Ketellaper (1963) found for example that thiamin promoted the growth of *Cosmos* at temperatures below the optimum and Karbassi *et al.*, (1971) found that the effect of low night temperature (10°C) on the growth of pangola grass was reversed by the application of 10^{-5} M GA_3. However it has been difficult to locate a "primary" chilling-induced metabolic event, as distinct from those which occur as a result of secondary tissue degradation (Christiansen, 1978).

One area that has received considerable attention in recent years is the effect of temperature on cell function in relation to membrane structure. It has been suggested that a change in the condition of membrane lipids from a mobile to a solid state (phase change), could be responsible for a wide range of responses to chilling and freezing temperatures. A basic change of this nature in membrane structure could result in a series of secondary responses, ranging from the reduced permeability to water by the root endodermis (and consequently the wilting of leaves discussed earlier) to metabolic imbalance and the formation of toxins. Some of these associated changes are summarized diagrammatically in Figure 8 (cf. Levitt, 1972; Lyons 1973).

Figure 8. A diagrammatic representation of some of the possible consequences of a low temperature induced membrane phase change, on cell and tissue functions. (Derived from Levitt, 1972; Lyons, 1973).



Membrane bound enzymes such as ATPase will be particularly susceptible to these membrane lipid phase changes, although more direct effects of temperature on enzyme action cannot be excluded. The effect of temperature on soluble enzymes must however be governed by other factors (Mayland and Cary, 1970; Levitt, 1972). In attempts to determine the temperatures that are critical for key enzymatic reactions in cells, considerable use has been made of Arrhenius plots, which compare the log of a reaction rate with the inverse of temperature. Membrane lipid phase changes that occur in response to temperature should influence the activation energies of membrane bound enzymes. However it is likely on theoretical grounds that this will be a gradual rather than an abrupt change as was suggested in earlier work (see Esser and Souza, 1976; Wolfe, 1978), and therefore difficult to interpret in the context of a well defined critical temperature. It appears even less likely that Arrhenius plots will be relevant to the determination of critical temperatures in whole plant studies (Bagnall and Wolfe, 1978).

The nature of the lipids in a membrane, particularly the degree of unsaturation (double bonds) could affect the response to temperature, as this will regulate the change from the mobile to the solid state. However, although this may be a factor in lower organisms (see Heinrich, 1976) it still requires clarification in higher plants (Christiansen, 1978; Quinn and Williams, 1978. Smillie (1979) has used the fluorescence of chlorophyll in leaf discs, held under a range of temperatures, to screen for chilling sensitivity in plants. This technique is dependent on the effect of temperature on the function of chloroplast membranes and does appear to correlate with known plant responses to temperature. Certainly a screening technique of this kind would be invaluable.

Adaptation to chilling temperatures does appear to occur in some crops of tropical origin, but the exact nature of this adaptation and its residual effect is still unclear (Wilson and Crawford, 1974; Christiansen, 1978).

Freezing Injury

This cannot be dealt with in any great detail, but there have been several extensive reviews on this subject in recent years (Tappel, 1966; Mayland and Cary, 1970; Levitt, 1972; Christiansen, 1978; Kacperska-Palacz, 1978; Quinn and Williams, 1978; Steponkus, 1978). Unlike chilling, there is clear evidence for both varietal, or ecotypic variation and adaptation against frost damage.

Although supercooling may occur to some extent in plant tissues, freezing is usually evident a few degrees below zero and almost invariably at -8° to - 10°C. With rapid cooling and the formation of intracellular ice (inside the cell membrane) the resulting damage is almost always fatal, however under most conditions the rate of cooling is comparatively slow and extracellular ice is forced. This extracellular ice places a considerable dehydration stress on the cells, equivalent to -8 MPa (-80 bars) at -8°C. Tolerance to freeze dehydration probably depends largely on membrane properties, particularly their stability and degree of permeability to water. The latter will depend on the nature of the membrane lipids, particularly the unsaturated fatty acids such as linolenic acid, and influence the occurrence of intracellular ice formation, whilst membrane stability may also depend on the presence of cryoprotectants such as sugars and possibly some proteins. The degree of stress precludes osmotic adjustment and thus the retention of bulk cell water as the mode of action of a cryoprotectant. It is possible that the hydroxyl groups of sugars stabilize the water-lipid-protein complex and prevent irreversible denaturation.

Adaptation to freezing is often associated with the accumulation of sugars, a response that can be induced by several days at low temperatures. This also explains why conditions which retard growth, such as mild drought, may induce a degree of frost resistance. In many trees, starch is broken down to sugars at temperatures of +5° to -5°C, i.e. just above freezing, and this may also provide a degree of cryoprotection (Ogolevets, 1964; Sakai, 1966). Alternatively any factor tending to reduce the accumulation of carbohydrate, either by enhancing growth, or by reducing the amount of photosynthetic tissue (see Lambert *et al.*, 1973) should increase the sensitivity to frost.

CONCLUSION

The current surge of interest in the role of membranes and membrane properties as they relate to temperature responses should be exploited to the full, but it is vital that these and other physiological studies be critically examined in relation to the integrated operation of the whole plant system. Unfortunately, the problem of assessing the effect of temperature on plant growth and development has been confounded to some extent by a shortage of field measurements of the actual temperatures experienced by individual plant parts. The temperature of buds on a shoot can for exmaple be 3° to 5°C below air temperature under a clear night sky, whilst the temperature of some leaves, such as coffee, and the bark on the sunny side of a tree can exceed that of ambient air temperatures by as much as 20°C. There are also often big differences between root and shoot temperatures (Levitt, 1972; Monteith, 1977).

Untangling the response of plants to a change in temperature is rather like trying to work backwards through an intricate Maori string game that someone else has woven. As a practical exercise it becomes worthwhile only if the information can be used to develop an improved pattern.

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