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# Impacts of chilling temperatures on photosynthesis in warm-climate plants

**Damian J. Allen and Donald R. Ort**

**Photosynthesis in warm-climate plants is substantially reduced after chilling. Tropical and subtropical species offer the opportunity to study the effects of low temperature on photosynthetic processes undisguised by the myriad of protective responses observed in temperate species. In this article, we highlight the primary components of photosynthesis that are affected by a short chill, in both the dark and the light, and discuss what is known of the mechanisms involved. Recent work implicates impaired redox and circadian regulation among other processes.**

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Low temperature is a major factor limiting the productivity and geographical distribution of many species, including important agricultural crops. The formation of ice inside plant cells is devastating. Freeze-tolerant plants have several strategies to reduce the probability of this occurring, even when air temperature drops below zero, including maintaining high intracellular solute concentrations and encouraging ice nucleation outside the cells. These plants also commonly exhibit xerophytic adaptations to survive the reduced water availability within the plant and the soil. Temperatures of –5°C can kill an unhardened winter wheat plant even though it has the genetic capacity to acclimatize, harden and acquire tolerance of freezing down to –20°C (Ref. 1). The cold-hardening mechanisms conferring freeze tolerance have been described elsewhere[2–5] and include changes in lipid composition, increases in active-oxygen-scavenging enzymes, anthocyanin accumulation and altered growth morphology. There is also a recent comprehensive update on freezing stress and acclimation[1].

Here, our focus is on chilling, referring to non-freezing temperatures (0–12°C) that are common during the growing season in temperate regions and can substantially compromise plant productivity. Many crops cultivated in temperate climates (e.g. maize, tomato, cucumber and mango) come from tropical and subtropical evolutionary backgrounds. These species apparently lack the genetic information to be or become freeze or even chill tolerant. These thermophilic crops thus offer the opportunity to study the effects of chilling on photosynthesis relatively undisguised by the gamut of protective and other acclimatory responses observed in chilling tolerant species.

Occasional short chilling episodes within a generally clement temperature environment are typical in many temperate regions where thermophilic crops are grown (e.g. maize in the Midwest USA). This is different to the suboptimum temperatures (e.g.

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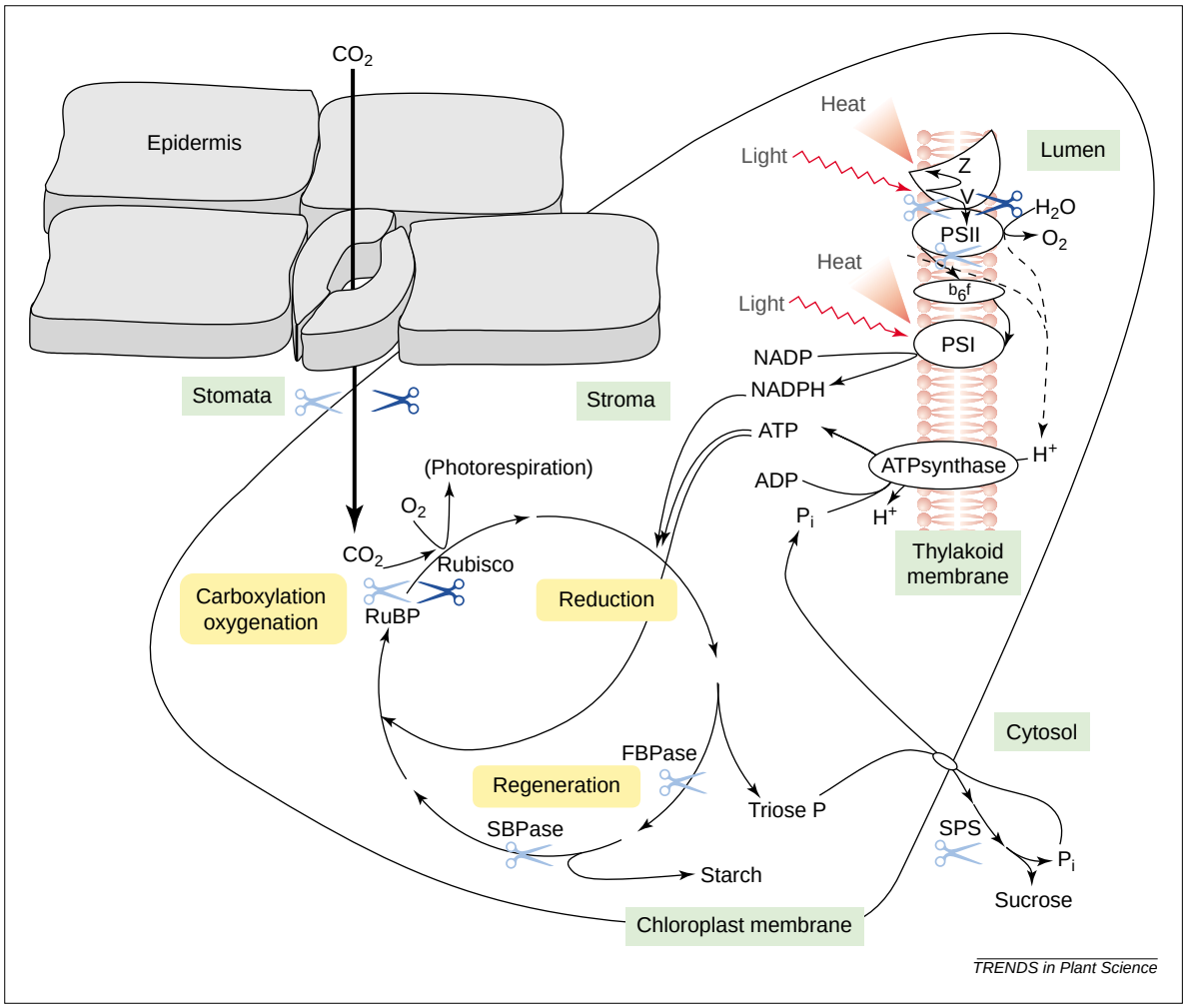


Fig. 1. Primary effects of a short chill in the light and the dark on photosynthesis in thermophilic plants. Chilling effects are apparent within the processes of photophosphorylation in the thylakoid membrane, the carbon reduction cycle in the stroma, carbohydrate use in the cytosol and the $CO_2$ supply to the chloroplast through the stomata. Abbreviations: ATPsynthase, chloroplast ATP synthase; $b_6f$, cytochrome $b_6f$ complex; FBPase, chloroplast fructose 1,6-bisphosphatase; $P_i$, inorganic phosphate; PSI, photosystem-I complex; PSII, photosystem-II complex; RuBP, ribulose 1,5-bisphosphate; SBPase, sedoheptulose 1,7-bisphosphatase; V, violaxanthin; Z, zeaxanthin and antheraxanthin; light-blue scissors represent the primary impact of a light chill; dark-blue scissors represent the primary impact of a dark chill.

<18°C) that persist for much of the growing season when warm-climate crops are planted at the low-temperature margins of their geographical range (e.g. maize in northern Europe). The underlying effects of these two chilling circumstances differ substantially. Here, our focus is on short low-temperature excursions from a normally permissive temperature range.

There are reports that chilling can disrupt essentially all major components of photosynthesis including thylakoid electron transport, the carbon reduction cycle and control of stomatal conductance. One of the important challenges to research in this field is identifying the primary effects within this highly interactive and regulated system that actually underlie the *in vivo* dysfunction. For example, stomatal closure following a chill could be a direct low temperature effect on guard cell function or an indirect response to a rising internal leaf $CO_2$ concentration ($c_i$) caused by a chill-induced loss of Rubisco activity.

Studying the effects of chilling in the dark on subsequent photosynthesis is important partly because plants in natural and agricultural habitats generally experience the lowest temperatures at night. At a specific low temperature, the effects of concurrent light are typically greater and therefore are likely to mask those induced by chilling alone. Consequently, at a particular low temperature, there are substantial differences between plants chilled in the light and in the dark in both the scale of the inhibition of photosynthesis and the primary mechanisms involved.

## Thylakoid electron transport

### *Photodamage (chronic photoinhibition) and repair*

Its ease of measurement means that the ratio of variable to maximal chlorophyll fluorescence ($F_v/F_m$) in dark-adapted leaves is often used to identify photosystem II (PSII) photodamage, an inhibition of PSII photochemistry that is not rapidly reversible. The amount of $^{14}$C-atrazine that can bind to the plastoquinone-reductase site of PSII in isolated thylakoids, produces a more direct and quantitative assessment[6]. There are some excellent reviews of the proposed mechanisms involved in photodamage[7,8].

Photodamage is rarely observed immediately after chilling of even the most extreme thermophilic species if low temperatures are experienced in the dark[9–11]. By contrast, the combination of low temperature with high light has the potential to induce chronic photoinhibition of PSII (Fig. 1). This is partly because lowering the temperature generally reduces reaction rates and can therefore limit the sinks for the absorbed excitation energy (light), particularly $CO_2$ fixation and photorespiration[5]. Smaller sinks for absorbed excitation energy increases the potential for

oxidative damage to PSII, notably the D1 component of the D1–D2 heterodimer at the core of the PSII functional center. In addition, photodamage becomes apparent as low temperatures interfere with the normal replacement rate of D1 in the turnover–repair cycle. This has been attributed to changes in the expression of *psbA*, the plastid gene that encodes D1, and direct temperature effects on membranes[7]. Low temperature reduces membrane fluidity and thus is believed to reduce the rate of D1 turnover by slowing the diffusion of photodamaged D1 proteins marked for degradation to non-appressed regions of the thylakoid. Genetic manipulation of thylakoid lipids to decrease the saturation of fatty acids can partially mitigate high-light–low-temperature photoinhibition[12], presumably by enhancing diffusion and thereby facilitating repair. Nevertheless, photodamage of PSII is frequently not primarily responsible for light-chill-induced inhibition of photosynthesis in thermophilic plants[13–15].

There are a limited number of reports that photosystem I (PSI) has a greater chilling sensitivity than PSII. This is frequently assessed in isolated thylakoid membranes using artificial electron donors or acceptors[16]. The use of absorption measurements at 820 nm facilitates assessment of the redox state of the PSI reaction center chlorophyll, P700, and hence the quantum efficiency of PSI electron transport in intact leaves[17]. The effects of growth under chilling conditions on PSI, PSII and $CO_2$ assimilation have been investigated[17,18]. Evidence that PSI activity declines to a greater extent than PSII[19,20] is not sufficient to identify PSI as a primary target of chilling. This is because it does not exclude the possibility that the downstream chill-susceptible processes (carbon metabolism and stomatal conductance, as described below), which were not studied, are the primary target, with the observed changes in PSI and/or PSII activities a secondary response. Consequently, there is insufficient evidence from intact leaves to classify PSI as a primary target of a chilling episode.

### *Photoprotection and downregulation (dynamic photoinhibition)*

The rapidly reversible downregulation of PSII quantum efficiency plays an indispensable photoprotective role in leaves. This process involves the interconversion of xanthophyll pigments and the development of a transthylakoid proton electrochemical potential difference, and is clearly a crucial protective measure against the more pernicious impact of photodamage[21]. Changes in the quenching of excitation energy in the antennae of PSII can easily be estimated using modulated chlorophyll fluorescence. Both $F_v'/F_m'$ (the efficiency of excitation energy transfer to open PSII reaction centers) and non-photochemical quenching are parameters widely used to quantify this downregulation of PSII electron transport.

When chilling limits photosynthetic sinks for electrons in the light (simultaneously with or subsequent to the chill), valuable photoprotection is afforded by a reduction in the efficiency of energy transfer from the light harvesting complex to the reaction center, thereby allowing additional absorbed light energy to be dissipated as heat (Fig. 1). This can be observed when thermophilic crops such as maize and tomato are chilled in the light[14,15,22]. However, in warm-climate plants such as tomato and mango, dynamic photoinhibition is clearly not the primary cause of the reduction in photosynthesis following a chill[9,11].

### *Alternative electron sinks and oxidative stress*

Analyses of the relative rates of PSII electron transport with those of $CO_2$ assimilation frequently, but not always[15], imply that chilling leads to an increase in alternative (i.e. non-$CO_2$) electron sinks[10,11,22]. It has been argued[23] that exploiting oxygen as a terminal electron acceptor, in both Rubisco oxygenase photorespiration (see below) and the Mehler–ascorbate-peroxidase reaction, protects plants from photodamage in bright light.

Thylakoid electron transport is intrinsically liable to produce active oxygen species. To prevent calamitous damage to component proteins and lipids, plants have numerous antioxidant systems. It is becoming increasingly clear that the regeneration of these antioxidants, such as ascorbate (vitamin C), can be an important and variable electron sink. The Mehler–ascorbate-peroxidase (water–water) cycle has been recently reviewed[24]. The absence of a method to quantify the size of this sink means that it is currently unclear whether ascorbate regeneration is a major additional sink for electrons observed following a chill.

In maize, the activities of the enzymes involved have been reported to rise when grown under cool conditions in the field[22] but to decline following a short chill under controlled conditions[25]. Interference with this process of antioxidant regeneration in response to a light chill might be a major cause of the observed inhibition of photosynthesis. In addition to the direct effects of this oxidative potential, light-chill-induced oxidative stress can lead to a change in the redox state of the stroma. This can interfere with the normal light activation of several enzymes involved in $CO_2$ assimilation including fructose 1,6-bisphosphatase (FBPase) and sedoheptulose 1,7-bisphosphatase (SBPase)[26].

A further possible candidate for a chill-induced alternative electron sink is cyclic electron transport. It has been argued that such a cycle operates around PSI and the cytochrome $b_6f$ complex using a ferredoxin–plastoquinone oxidoreductase to regenerate reduced plastoquinone (plastoquinol) from ferredoxin[27], and contributes to the $\Delta$pH required to engage photoprotection[28]. A chill-induced increase in non-linear electron transport should be visible as a relative stimulation of the quantum efficiency of PSI versus PSII electron transport. The absence of a

**Box 1. Disruption of circadian regulation by a chill**

Rhythms in many cellular processes are maintained with a period of ~24 h, even when plants are held under constant (free running) conditions. These circadian rhythms, by definition, have temperature compensation to maintain the same cycle period over a range of temperatures[a]. However, circadian rhythms in chlorophyll *a*/*b* binding protein and Rubisco activase mRNA expression in tomato are stalled by chilling in the dark[b]. Both of these proteins are so abundant that transient changes in transcription do not have a significant impact on photosynthesis.

However, this work raised the intriguing idea that some of the depression of photosynthesis in thermophilic plants following a chill is the result of the mistiming of multiple circadian processes. This hypothesis was supported by the observation that a low-light chill of tomato disrupts the endogenous rhythm in activity of two key enzymes of the carbohydrate and nitrogen metabolism pathways: sucrose phosphate synthase and nitrate reductase[c]. Incongruity between sucrose phosphate synthase and carbon reduction cycle activities could lead to a transient inorganic phosphate limitation of photosynthesis. However, chilling does not delay all circadian rhythms in all chill-sensitive species, because the endogenous oscillation in mango leaf stomatal conductance was unaffected by a chill that substantially compromised photosynthesis[d].

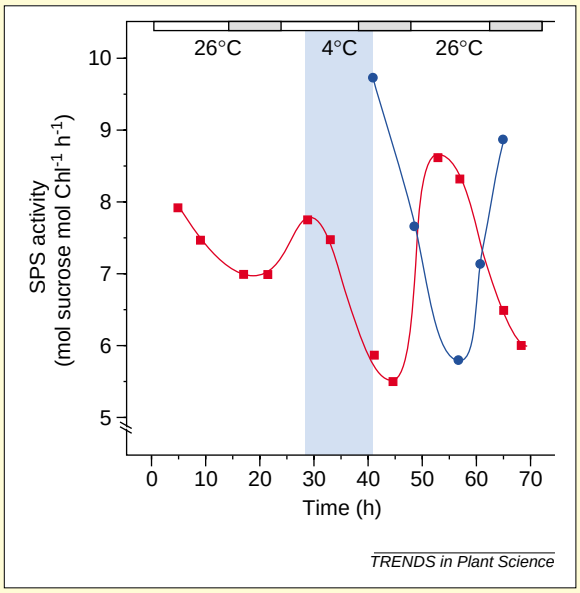


Fig. I. Chilling delays the circadian rhythm in sucrose phosphate synthase (SPS) activity. Control (red square) tomato plants were maintained under constant conditions of low-light [50 μmol photons $m^{-2}$ $s^{-1}$] at 26°C for 3 days, and exhibit a robust endogenous rhythm in SPS activity. This rhythm was held in abeyance during a 4°C (blue circle) treatment under the same low-light conditions for 12 h (pale-blue shaded area). When returned to permissive temperatures, the circadian rhythm resumed but with a ~12 h phase shift. The light and dark bars at the top of the figure reflect the subjective day and night during this constant illumination. *Reproduced, with permission, from Ref. c.*

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substantial shift in this relationship at low temperatures[17] suggests that chilling does not induce a significant increase in cyclic electron transport.

## Carbohydrate metabolism

### *End-product inhibition*

As leaf temperature is reduced, there is a smaller stimulation of $CO_2$ assimilation in response to a switch from ambient to non-photorespiratory conditions (1–2% $O_2$). The temperature at which no stimulation is observed was between 6°C and 22°C for a range of six field-grown species[29]. This lack of response to the removal of photorespiration has been attributed to limitation of thylakoid ATP synthase activity arising from insufficient return of inorganic phosphate ($P_i$) to the chloroplast caused by the accumulation of triose phosphates (Fig. 1).

Carbohydrate metabolism has been reported to have a greater instantaneous low temperature sensitivity than other components of photosynthesis[30]. The low-light chill-induced delay in the circadian rhythm in sucrose phosphate synthase activity[31] (Box I; Fig. I) could affect photosynthesis after the chill through end-product inhibition. Furthermore, soluble carbohydrates can accumulate because of low-temperature inhibition of night-time mobilization of leaf starch[32]. However, when the oxygen sensitivity of $CO_2$ assimilation is examined after return to permissive temperatures, the persistent inhibition of photosynthesis following a dark chill seems not to be directly attributable to end-product inhibition[11].

### *Stromal bisphosphatases*

The widely used models of photosynthesis[33] imply that the activities of the regenerative enzymes of the carbon-reduction cycle do not limit $CO_2$ uptake. Ribulose 1,5-bisphosphate regeneration is described only in terms of the maximum rate of electron transport, which provides the energy (ATP) and reducing power (NADPH) for these reactions (Fig. 1). Over the past decade, it has become increasingly apparent not only that several of these stromal enzymes are regulated in a sophisticated manner but also that, under certain conditions, they can be a primary limitation to photosynthesis.

In particular, the role of the stromal bisphosphatases SBPase and FBPase in moderating photosynthesis under stress needs to be appreciated. Both of these stromal bisphosphatases are activated by the ferredoxin–thioredoxin system and so, under optimum conditions, their activity is tightly coupled to the redox state of the chloroplast. It is clear that, in tomato, the primary restriction on photosynthesis

imposed by a light chill is a decrease in the activity of these two enzymes caused by an impairment in their reductive activation[26,34] (Fig. 1). In maize, chilling at 4°C and 350 µmol photons $m^{-2}$ $s^{-1}$ for 24 h reduces the maximum FBPase activity (measured by incubation with the artificial reductant dithiothreitol) by half after rewarming, indicating an actual loss of the enzyme[15].

### *Rubisco*

Declines in photosynthesis after a chill in both the dark and the light have been attributed in various studies to a loss of Rubisco activity[11,15] (Fig. 1). It has been suggested that chilling damages the Rubisco protein itself[15]. However, recent work with mango shows that the loss of Rubisco activity observed at midday of a warm photoperiod following an overnight chill is not an instantaneous low-temperature effect but rather that Rubisco activity declined throughout the morning[11]. This suggests that it is some aspect of Rubisco activation that is disrupted by the chill. It is tempting to speculate that the recently discovered redox regulation of the larger Rubisco activase isoform[35] can be affected by chilling, as is observed for SBPase and FBPase (Ref. 26).

The argument that Rubisco oxygenase photorespiration is a photoprotective mechanism, acting as an electron sink[23,36,37], does not appear to be plausible for chill-induced photoinhibition. This is because the frequently reported concurrent loss of Rubisco carboxylase activity[11,15] must by necessity be mirrored by a decline in oxygenase activity and therefore a reduction in the photorespiratory sink for electrons. For photorespiration to provide protective energy dissipation, the primary response to a chill has to be a reduction in stomatal conductance. An increase in stomatal limitation of photosynthesis could reduce $c_i$ and hence increase the rate of photorespiration relative to $CO_2$ assimilation (see below). In addition, reducing the oxygen partial pressure from ambient (21%) to 2%, protected the maximum quantum yield of $CO_2$ fixation of bean (*Phaseolus vulgaris*) leaves from a high-light-level low-temperature chill[38], suggesting that photorespiration does not defend photosynthesis under these conditions.

## Stomatal responses

### *Chill-induced water loss*

Reduced air and leaf temperature will usually reduce evaporative demand. However, cool roots reduce hydraulic conductivity and substantially inhibit water uptake from the soil. Owing to the high specific heat capacity of the soil, transient root chills are far less common in the field than low shoot temperatures. As well as not reflecting a natural chill, experiments that chill whole potted plants have to be interpreted with caution because of the ease with which unrealistic drought stress can be induced. This is because the soil warms up after a chill much more slowly than do leaves and the surrounding air, and therefore, unless humidity is maintained close to saturation, the evaporative demand will increase faster than the water supply.

### *Direct effects of chilling on stomata*

In many chilling-sensitive species, such as cucumber, tomato, bean, cotton and soybean, low temperatures can cause stomata to appear locked open and unable to respond normally to leaf water deficit[9,39–41]. Such species will quickly wilt if not warmed under extremely high humidity, especially if their roots are still cool. By contrast, when more realistic, near-saturation conditions with warm roots are used, stomatal closure following a chill can be observed in these and other species.

There are two potential causes of chill-induced stomatal closure. First, a direct inhibition of mesophyll photosynthesis (as discussed above) could lead to a rise in $c_i$, which in turn induces stomatal closure. Alternatively, stomata themselves might be the primary target of the chill and their closure could lead to a reduction in $c_i$, precipitating a decline in photosynthesis. Approaches that distinguish between these two different mechanisms primarily involve the determination of the dependence of $CO_2$ uptake on $c_i$. Such assessments of stomatal limitation of photosynthesis frequently attribute the chill-induced inhibition of $CO_2$ fixation to a combination of stomatal and non-stomatal effects[9–11,42] (Fig. 1). However, because interactions between components of photosynthesis appear to be mediated by $c_i$, identification of the extent to which stomata limit photosynthesis remains problematic.

## Effects on photosynthetic productivity

The effect of the chill-induced inhibition of photosynthesis on plant productivity has been reviewed previously[43] and is in general beyond the scope of this article. However, there are a couple of issues that are useful to keep in mind when considering the effect of chilling on photosynthesis and its effect on plant productivity. When integrated over the whole canopy, day and season, photosynthesis is primarily light limited not light saturated[44]. Therefore, chill effects on the quantum yield of $CO_2$ assimilation are likely to have a much greater deleterious impact on crop productivity than a similar sized decline in light-saturated photosynthesis.

It is also important to recognize that plant growth and productivity are usually correlated with total leaf area and the time of canopy closure rather than with instantaneous photosynthetic rates. However, photosynthesis during early leaf and plant development is crucially important in determining such performance. Therefore, the effects of longer-term low-temperature exposure on the development of photosynthesis, particularly early in the growing season, are crucial[17,22,45–47].

## Conclusions

The major components of photosynthesis that are typically affected by short-term light or dark chills in thermophilic species are shown in Figure 1. Photosynthesis following a dark chill is primarily compromised by interference with carbohydrate metabolism, inhibition of Rubisco activity and stomatal closure, with a concurrent increase in energy dissipation as heat in the thylakoid antennae. The possibility that some of the effects of chilling on photosynthesis are mediated through mistiming of multiple circadian rhythms is intriguing and might underlie the effects of chilling on carbohydrate metabolism. Although these factors can also be observed when chilling concurrently with incident light, the potential for photodamage to PSII is more apparent, as are disruption of the redox control of the stromal bisphosphatases SBPase and FBPase, and possibly Rubisco activase.

Dissection of the relative importance of the seeming multitude of potential chill effects on photosynthesis has frequently relied on a top-down approach. With the development of molecular array and other technologies, it is becoming possible to approach this complex of damage, repair, protection and acclimation processes from a bottom-up perspective. However, chill-induced changes in gene expression could be misinterpreted if, for example, the direct low-temperature effects are not separated from those of cool-root-induced water stress. Therefore, understanding the molecular mechanisms behind the chill-induced effects on photosynthesis by examining the myriad changes in gene expression will be achieved most efficiently by careful reference to the physiological responses outlined here.

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## Book reviews in *Trends in Plant Science*


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If there is a book or CD-ROM that you think should be reviewed then please contact the Assistant Editor (plants@current-trends.co.uk).



## Changes to the Advisory Editorial Board for 2001

As we enter our sixth year of publication, our thanks go to the following Advisory Board Members who have helped to guide the evolution of *Trends in Plant Science* but are now leaving the Editorial Board: Guofan Hong, Russell Jones, Natasha Raikhel and Ko Shimamoto.

At the same time, we are pleased to welcome a further four new members to our Advisory Editorial Board. The new board members will provide expert opinion and advice on such topics as: plant development, plant biotechnology, functional genomics, gene expression and plant hormone signalling.

The new Board Members are:

**Caroline Dean**, Norwich, UK
**Pamela Green**, East Lansing, USA
**Venkatesan Sundaresan**, Singapore, Singapore
**Zhi-hong Xu**, Beijing, China