

eXtra Botany

Special Issue Editorial

High and low temperature signalling and response

Plants must deal with (sometimes extreme) temperatures ranging from intense cold (freezing) to severe heat. This necessitates adequate responses to tolerate temperature stress and/or maintain optimal performance. This special issue provides an update on the current knowledge of signalling and response mechanisms associated with both low and high temperatures in model species and relevant crops. A picture emerges that, although different temperature regimes are likely to involve dedicated signalling mechanisms, there is a degree of commonality and overlap in the responses and molecular networks involved.

From a physical perspective, cold and heat are part of the same temperature continuum. This is, however, very different on the biological level, where different temperature regimes trigger utterly distinct responses in organisms to safeguard their survival and reproductive success. Being sessile, plants need to deal with fluctuations in temperature on a daily/diurnal, seasonal, and climate change-induced level without having the opportunity to take refuge. Hence, temperature cues provide critical input for life history decisions such as the timing of flowering or germination and the duration of seed dormancy (Penfield, 2008). At any stage in plant development, temperature cues can, however, also trigger tolerance or escape mechanisms (Vu *et al.*, 2019; Zhu *et al.*, 2021a). Plants are able to induce tolerance mechanisms if exposed to (close to) lethal temperatures at the extreme ends of the temperature spectrum, namely freezing tolerance and heat stress tolerance (Hincha and Zuther, 2020; Ritonga and Chen, 2020; Haider *et al.*, 2021).

On the other hand, mild changes within the physiological temperature range typically trigger (growth) acclimation responses that allow for optimal performance under suboptimal temperature conditions (reviewed in Quint *et al.*, 2016; Casal and Balasubramanian, 2019).

Temperature acclimation can be roughly divided into cold acclimation and thermomorphogenesis (Fig. 1). Acclimation to

the cold side of the spectrum is characterized by compact (insulated) growth and processes such as membrane rigidification and cytoskeletal rearrangements. Cold stress perception involves activation of Ca²⁺ channels and the plasma membrane protein calmodulin (CaM)-regulated receptor-like kinase (CRLK)1/2 (Guo *et al.*, 2008).

Thermomorphogenesis describes morphological and physiological acclimation responses to warm temperatures to stimulate evaporative cooling (Crawford *et al.*, 2012; Park *et al.*, 2019). Research on mild elevated temperature signalling and thermomorphogenesis regulation was sparked by two founding papers showing that auxin triggers temperature-induced hypocotyl elongation (Gray *et al.*, 1998) and demonstrating a central role for PHYTOCHROME INTERACTING FACTOR 4 (PIF4) (Koini *et al.*, 2009). The field of ambient temperature signalling sky-rocketed from there in the last decade, fuelled by increased awareness of the detrimental effects global warming will have on plants in their natural environment, on crop production, and on food security.

Arguably the most notable milestones from the last decade are the discovery of long sought after specific thermosensory mechanisms. First, phytochrome B was demonstrated to be a thermosensor via its temperature-sensitive dark-reversion reaction (Jung *et al.*, 2016; Legris *et al.*, 2016), followed by the discoveries that temperature provides direct input to the PIFs by affecting translation efficiency of PIF7 through warm temperature relaxation of its mRNA hairpin structure (Chung *et al.*, 2020). In addition, it was shown that temperature-dependent phase separation of EARLY FLOWERING 3 (ELF3), a negative regulator of PIF4, into inactive condensates at warm temperatures likewise provides thermosensory input to the plant (Jung *et al.*, 2020). Notably, all three sensory mechanisms modulate the activity of the PIF family of major temperature signalling components.

Recent advances in plant temperature research were discussed during the *Ambient Temperature Signalling and Response* session at the 2021 online conference of the Society of Experimental Biology, which formed the basis of the current *JXB* special issue.

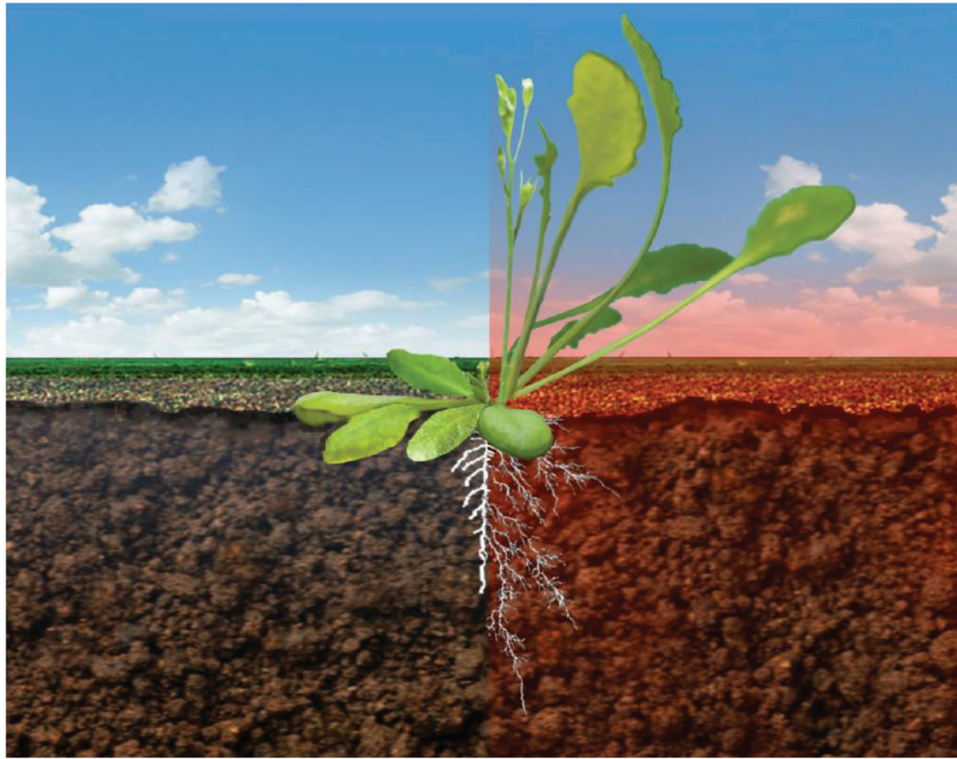


Fig. 1. Artist's impression of thermomorphogenesis phenotypes in *Arabidopsis thaliana*. On the left side, a typical *Arabidopsis* plant grown in control temperature conditions is shown, having a compact appearance and vertical main root. Under mild warm temperature conditions, indicated on the right, above ground the leaves become hyponastic (thermonasty), both hypocotyl and petioles elongate, leaves become smaller and thinner, and early flowering is induced. Below ground, roots elongate and exhibit enhanced branching. Thermotropism occurs in some species, although this is not observed in *Arabidopsis*. Image courtesy of Julia Bellstädt (Martin-Luther-Universität Halle-Wittenberg).

Temperature acclimation and tolerance responses

Plant responses to temperature are as diverse as the temperature signal itself. In this issue, [Penfield *et al.* \(2021\)](#) summarize molecular aspects of plant responses to winter chill and how variation in the intensity of winter chilling or devernalization can lead to effects on post-chilling plant development, including that of structures necessary for crop yields.

While PIF4-dependent temperature signalling ultimately results in transcriptional regulation of target genes, the above-mentioned regulation of *PIF7* translation occurs on a post-transcriptional level ([Chung *et al.*, 2020](#)). Similarly, alternative splicing, another post- or co-transcriptional process, is known to respond to ambient temperature with different splice products for numerous transcripts. Insights into the role of alternative splicing in plant temperature responses are provided in a review by [Dikaya *et al.* \(2021\)](#). Although current knowledge is still fragmentary, the authors demonstrate the diversity of biological processes that are regulated by temperature-sensitive splicing, indicating its general importance in plant acclimation to a changing environment.

Regarding high temperatures, although it is now clear that thermomorphogenesis traits ([Fig. 1](#)) such as hypocotyl elongation,

petiole elongation, and hyponastic growth (thermonasty) of above-ground tissues are induced to promote the plant's cooling capacity ([Crawford *et al.*, 2012](#); [Park *et al.*, 2019](#)), below-ground effects of mild elevated temperatures are far less well understood. A consensus has been reached that, generally speaking, mild temperatures lead to enhanced root elongation, whereas heat stress inhibits root (and shoot) growth, as reviewed in this issue by [Fonseca de Lima *et al.* \(2021\)](#). Although not specific to roots, one particular type of root response is thermotropism, being a directional response of the root towards—or away from—a temperature cue. Although root thermotropism is a long-known concept and well described by botanists, the response is poorly understood. In a review paper, thermotropism is proposed as an adaptive strategy that is induced to explore 'virgin' soil that is not covered by above-ground vegetation ([van Zanten *et al.*, \(2021\)](#)). It will be of interest to study whether and how root elongation ([Fonseca de Lima *et al.* \(2021\)](#)) contributes to thermotropism.

While thermomorphogenesis signalling and physiology, at least of shoot tissues, are rather well understood (reviewed in [Quint *et al.*, 2016](#); [Casal and Balasubramanian, 2019](#)), the vast majority of experimental data are based on the model eudicot *Arabidopsis thaliana*. As such, it is unclear how well conserved—if at all—physiological responses and signalling

pathways are in distantly related plant lineages and crops alike. To shed some light on this, the Darwin review of this issue speculates about the evolution of thermomorphogenesis (Ludwig *et al.*, 2021). It seems that at least some physiological responses such as evaporative cooling of photosynthetic tissues are conserved across land plants, and a model of distinct evolutionary origins of shoot and root thermomorphogenesis is proposed. Transduction of warm temperature cues in shoot tissues may have been co-opted from existing light signalling pathways. In roots, which obviously grow in dark soil, major shoot thermomorphogenesis mutants that are also known to be disturbed in diverse light signalling responses, such as *pif4*, indeed have either no or only weak phenotypes (Martins *et al.*, 2017). This suggests a signalling mechanism independent of light. Possibly, the origins of root thermomorphogenesis may be associated with drought responses, which tend to be needed especially in warm temperatures when evaporation demands are high. However, clearly more research in phylogenetically diverse plant species is needed to understand the evolution of acclimation responses to elevated ambient temperatures.

When temperatures rise further, and a threshold level is reached where (long-term) survival is at stake, heat stress tolerance mechanisms are induced. Park *et al.* (2021) provide an overview on the effects of heat on protein homeostasis, and macromolecular and cellular integrity, and discuss how genome integrity is safeguarded, and DNA damage is effectively repaired.

One intriguing feature of heat stress is that it can prime the plant to tolerate and survive a recurrent heat stress episode (Nishad and Nandi, 2021). A key player in maintaining heat stress memory is the plastid-localized small heat shock protein 21 (HSP21). In this issue, it is shown that degradation of HSP21 protein diminishes heat stress memory, so protein recycling of HSP21 through autophagy exerts control of heat stress recovery and memory (Sedaghatmehr *et al.*, 2021). In line with this finding, the autophagy cargo receptor ATG8-INTERACTING PROTEIN1 (ATI1) mediates heat stress memory (Sedaghatmehr *et al.*, 2021). The authors propose that autophagy is important for balancing between maintenance of heat stress memory and recovery. On the one hand, memory can prepare for possible upcoming heat stress episodes by maintaining stress proteins such as HSP21, while on the other hand recovery to normal temperatures and resuming growth and life cycle completion benefits from re-usage of amino acids as building blocks for new molecules (by degradation of stress proteins such as HSP21). In line with this proposition, van Hoogdalem *et al.* (2021) demonstrate that resource limitation indeed has an influence on growth in a temperature-dependent manner. They found that circadian clock functioning is disturbed in a growth regime of warm nights and cold days (called -DIF), which results in compact growth (reduced leaf elongation) due to altered circadian clock-controlled starch metabolism. As a result, a temporary

carbon starvation at the end of a warm night restricts growth, which is proposed to be in a PIF4-dependent manner (van Hoogdalem *et al.* (2021).

Temperature signalling networks

As indicated above, temperature is sensed by PhyB, PIF7, and ELF3 (Jung *et al.*, 2016, 2020; Legris *et al.*, 2016; Chung *et al.*, 2020), and many additional sensors probably remain to be discovered. Downstream of these sensing events, an extensive molecular network relays temperature cues and integrates the signal with other environmental cues, to induce the most appropriate tolerance or acclimation response given the specific circumstances. In particular, phytohormone biosynthesis, homeostasis, crosstalk, and signalling events govern downstream temperature responses, as summarized in this issue by Castroverde and Dina, (2021). As nicely illustrated in this study, all described plant hormones have roles in high temperature and low temperature signalling in diverse species and, recently, a role for jasmonate in thermomorphogenesis was put forward in both *Arabidopsis* and wheat (Zhu *et al.*, 2021b). Thus, hormone crosstalk is expected to remain a focus point in the temperature research field and will be especially relevant once the community will hopefully start to include different temperature regimes in their studies, rather than study temperature treatments in isolation as is often the current research practice.

Hormone signalling is intrinsically connected to transcriptional control and to diverse cellular signalling pathways, including regulation of post-translational modifications. For instance, kinases and phosphatases that add or remove, respectively, phospho groups to regulate target gene activity or protein stability, have an important role in temperature responsiveness (Praat *et al.*, 2021; Vu *et al.*, 2021). Similar to several plant hormones, some kinases such as MITOGEN-ACTIVATED PROTEIN KINASE KINASE 6 (MPK6) strikingly function in both cold and warm temperature signalling. How one kinase can contribute to diverse responses across the temperature spectrum is currently not well understood. It is proposed that target substrate promiscuity may contribute; that is, the kinase can control different biological processes by (differential) phosphorylation of various protein substrates and sites, depending on the prevailing temperature condition and presence of substrate proteins (Praat *et al.*, 2021). In addition, a more intricate phospho code might also drive specific outputs, similar to specific phosphorylation of BRI1-associated receptor kinase 1 driving immune versus brassinosteroid signalling (Perraki *et al.*, 2018).

Another post-translational modification that is important in temperature signalling is SUMOylation. While SUMOylation is required for thermomorphogenesis and thermotolerance, SUMO-dependent thermoresilience is potentially controlled in a different way compared with the protein damage pathway that underpins thermotolerance (Hammoudi *et al.*, 2021).

Although it is shown that SUMO is critical for plant longevity when *Arabidopsis* experiences a prolonged non-damaging period of only 28 °C, it remains to be investigated what the specific targets for SUMOylation are in this context.

In autoimmune mutants, temperature may lead to constitutive immune responses that can severely damage the plant or even have lethal consequences. Hessler *et al.* (2021) show that, although not causal, the formation of cell wall depositions generally occurs in *Arabidopsis* autoimmunity and depends on reduced temperature. In *saul1-1* autoimmunity mutants, low temperature stimuli are elegantly used as a switch to induce first callose deposition and then immune response phenotypes. As such, temperature treatments are being used as a tool for the mechanistic understanding of, in this case, autoimmunity.

Effect of high and low temperatures on crops and food security

While most of our mechanistic insight in temperature perception and signalling has come from the model plant *Arabidopsis*, there is—when consulting the recent IPCC report (IPCC, 2021)—an urgent need to translate this knowledge to crops or to explore the molecular mechanisms associated with low and high temperature responses directly in relevant crops. In view of climate change, elevated CO₂ levels in the atmosphere will cause and affect heat and drought stress (Zhu *et al.*, 2021a), so developing climate-tolerant varieties that can cope with climate change is essential.

Relevant insight on temperature responses may come from studies directly in crops, or from alternative model species. In this special issue, gene function analysis in the cyanobacteria *Synechocystis* 6803, an ancestor of chloroplasts of higher plants, is presented (Migur *et al.*, 2021). It is shown that the low temperature-induced DEAD-box RNA helicase CrhR interacts mainly with photosynthesis-associated and redox-controlled transcripts, and mutants in *CrhR* displayed a cold-sensitive phenotype.

In a totally different approach, Leveau *et al.* (2021) assessed intra- and interspecific diversity of leaf growth and transpiration responses to evaporative demand and temperature, using a diversity panel of wheat-related subspecies consisting of 60 varieties belonging to 12 groups. It is concluded that genome type, ploidy level, and phylogeny together structure the genetic diversity within the panel. Altogether, the work provides parameters that can be used in future studies as tools to unlock the much needed variation to breed for climate-tolerant commercial wheat varieties.

Considering crops directly, the *ISOFLAVONE REDUCTASE-LIKE* (*IRL*) gene could be a promising starting point for developing heat-tolerant wheat (Shokat *et al.*, 2021). In general, some molecular temperature signalling pathways and response mechanisms appear to be conserved. However, given that different crops and different organs have

distinct optimal temperatures (Zhu *et al.*, 2021a), there will probably be (subtle) differences and additional regulatory components, as showcased above in the context of temperature signalling differences between shoot and root. To gain a more detailed understanding of specific responses of specific organs, more precise -omics data derived from different organs and cell types and across a range of temperatures are needed, such as the approach taken in this issue by Xue *et al.* (2021), who present transcriptomic responses in leaves and (crown) roots under differential chilling stresses in maize. With respect to the latter, Zhou *et al.* (2021) review cold response and tolerance in cereal roots, summarizing morphological, physiological, and cellular responses of cereal roots with a focus on how these processes are regulated by plant hormones and the role of cold-responsive genes. Moreover, the roles of beneficial microorganisms and mineral nutrients in ameliorating the effects of cold stress in cereal roots are discussed (Zhou *et al.*, 2021).

Finally, Shanmugam *et al.* (2021) have identified that high temperature stress in *Arabidopsis*, rice, and tomato, while halting the existing pre-rRNA maturation schemes, also transiently triggers an atypical pathway for 35S pre-rRNA processing and produces an aberrant precursor rRNA.

Conclusions

A picture emerges that plant responses to different temperature extremes are to a certain extent regulated by the same signalling components, although they might result in very different responses. For example, the COP1–HY5 module and MPK6 are involved in both low and high temperature signalling (Li *et al.*, 2021; Praat *et al.*, 2021), PIF4 also plays a role in cold tolerance in tomato anthers (Pan *et al.*, 2021), and epigenetic regulation of FLC and FT controls flowering time under different temperature regimes (Pandey *et al.*, 2021).

In the past decade, the temperature field has largely focused on above-ground responses (Crawford *et al.*, 2012; Quint *et al.*, 2016; Casal and Balasubramanian, 2019). However, in recent years, the impact of low and high temperature on root development, growth, and architecture has received more attention (Martins *et al.*, 2017; Fonseca de Lima *et al.*, 2021; van Zanten *et al.*, 2021; Zhou *et al.*, 2021). It will be intriguing to explore to what extent the same players known from the shoot are also playing important roles in the root, if separate perception and signalling cascades exist, and/or how the root–shoot and shoot–root communication is regulated. To this aim, the anticipated increase in the spatiotemporal resolution of future temperature-related analyses will dramatically improve our understanding (Pandey *et al.*, 2021). It will also be important to include temperature ranges instead of fixed temperature settings. Altogether, this will allow us to fully appreciate the wealth of temperature responses and the underlying signalling networks.

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