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REVIEW

Light and temperature receptors and their convergence in plants

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Abstract

Light and temperature are two essential environmental cues for plants, helping to optimize plant body architecture and physiology. To sense a broad spectrum of sun radiation spanning from UV-B to far-red wavelength, plants are equipped with a sophisticated array of photoreceptors, including phytochromes, cryptochromes, phototropins, Zeitlupes, and UV-B photoreceptor UVR8. On the contrary, since the thermodynamic effects extensively affect the molecular and supramolecular structures, it is difficult to identify the entry point or initial receptor of temperature. Even so, several putative temperature sensors have been proposed, such as calcium ion channels, H2A.Z, and the thermodynamic change of plasma membrane fluidity. Considering that many processes in plant respond to irradiance and temperature, scientists devote to finding out the converge point of these environmental cues. As a typical example, circadian rhythm is such an integration point, which receives the signal input of both irradiance and temperature. The updating evidence shows, as an important photoreceptor, phytochrome B acts as temperature sensors *via* a thermodynamic active state revision. These findings suggest that the studies on light and temperature receptors in plants should not be separated. Their extensive convergence during signalling provides a new direction for understanding the stimuli perception mechanisms.

Additional key words: calcium channels, circadian rhythm, cryptochromes, phototropins, phytochromes, Zeitlupes.

Introduction

As the compensation to their relatively poor mobility (Nakashima *et al.* 2014), plants adjust their physiological and metabolic processes according to the ever-changing environment (Stavang *et al.* 2009). Recently, the global climate alterations make the situation worse for plants (Toledo-Ortiz *et al.* 2014). It is urgent to understand the biological mechanism involved in environmental stimuli perception and subsequent signalling cascades.

Irradiance (Kami *et al.* 2010) and temperature (Hu *et al.* 2012, Mittler *et al.* 2012, Xin *et al.* 2016) synergistically influence plant physiology, growth, and development, providing plants with valuable locational and seasonal information. Radiation quality is determined by its fluence, wavelength, and duration (Jiao *et al.* 2007). The temperature information is coded into intensity, duration, and rate (Hasanuzzaman *et al.* 2013).

Seeds germination, elongation growth, and flowering are three typical processes under the cooperative regulation of irradiance and temperature (Seaton *et al.* 2015, Kigel 2017). As the initial and crucial stage in plants life cycles (Penfield 2017), seed germination, unpredictable over time and space (Gorai *et al.* 2011), is affected by biotic and abiotic factors such as temperature (Guan *et al.* 2009, Tozzi *et al*. 2014) and irradiance (Motsa *et al.* 2015, Simlat *et al.* 2016). After germination, hypocotyl elongation is another plastic physiological exhibition, repressed by low temperature (Miyazaki *et al.* 2015, Ma *et al.* 2016) and high irradiance (Kurepin *et al.* 2010). Conversely, it can be promoted by high temperature and low red:far-red (R/FR) conditions (Proveniers and Van Zanten 2013). Afterwards, the optimal combination of radiation and temperature determines the flowering time for plants (Capovilla *et al.*

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Abbreviations: APB - active phyB binding; CCA1 - circadian clock associated 1; CRY - cryptochromes; FMN - flavin mononucleotide; H2A.Z - histone variant; LHY - late elongated hypocotyl; LOV - light oxygen voltage; PHOT - phototropins; PHY - phytochromes; PIF - phytochrome-interacting factor; PRR - peripheral loops; R/FR - red:far-red; TOC1 - timing of cab expression 1; UVR8 - UV-B photoreceptor.

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2014, Fernández *et al.* 2016). To shift from vegetative stage to reproductive stage with optimal time, information about the temperature (Romera-Branchat *et al.* 2014, Lee *et al.* 2010) and day-length (Song *et al.* 2013, Higuchi *et al.* 2012) is essential.

For biological processes discussed above, environmental stimuli perception is the first step and the key step. During this initial stage, the structural and functional switch of sensory receptors is critical (Casal and Questa 2018). Therefore, the identification of these biological sensors, as well as their working mechanisms, is fundamental.

This paper is focused on the summarization of light and putative temperature sensors in plants, and introduces the stimuli-response mechanism of these sensors. Subsequent signalling cascades have been well-described in previous reviews (Chamovitz *et al.* 2008, Franklin 2009, Mittler *et al.* 2012, Wigge 2013), thus they will not be included here. Afterwards, plant circadian clock is discussed, as a typical example of simultaneous light and temperature signals, and how these two signalling pathways are related. At last, a concise description of thermal reversion of red/far-red light receptor phyB is given, which shows an updating opinion that light and temperature perception in plants not only converge with each other during information transduction, but also associated with each other in the stimuli perception stage by sharing the common biological sensors.

Photoreceptors in plants

Highly conserved in plants species, photoreceptors are critical for light signal perception and transduction. Wideband of sun radiation is monitored by light-active molecules, including R/FR light photoreceptors phytochromes, UV-A/blue light absorbing cryptochromes, phototropins, Zeitlupe family, and a UV-B photoreceptor UVR8 (Kong and Okajima 2016, Yin and Ulm 2017).

The R/FR light receptors phytochromes (PHYs; PHYA~E in *Arabidopsis*) had two distinct and interconvertible forms: the red light (R ~660 nm) absorbing inactive form (Pr), and the far-red light (FR ~730 nm) absorbing active form (Pfr) (Lorenzo *et al.* 2016). After the absorption of a photon, inactive Pr form is photo-converted into biological active Pfr form, which will be transformed back into the Pr form upon FR stimulus (Ballaré and Pierik 2017) (Fig. 1*A*). During this photo-induced transformation, one of the double bonds in the chromophore is *cis*-trans isomerized, resulting in the reorientation between chromophore and polypeptide, as well as the conformational change in the protein three-dimensional structure (Chamovitz *et al.* 2008). Subsequently, the active Pfr translocates towards nuclei and combines with the phytochrome-interacting factor (PIF**)** transcriptional regulators family. The translocation of Pfr and its interaction with PIFs then lead to a set of downstream reactions (Franklin 2009) and physiological processes (Hornitschek *et al.* 2009, Chen and Chory 2011).

Being capable of absorbing 400 - 500 nm wavebands, the flavin-containing blue light detectors cryptochromes (CRY1-3) (Higuchi *et al.* 2012, Xu *et al.* 2018) and two phototropins (PHOT1-2) regulate series of plant processes, such as the seedling de-etiolation, stomatal opening (Webb 2003), and phototropism (Goyal *et al.* 2013). Before blue-light irradiation, a flavin adenine dinucleotide (FAD) chromophore in cryptochrome stays in an oxidized ground state. Upon blue-light activation, an electron transfer reaction turns the FAD chromophore into a reduction state or a "signaling state" (Fig. 1*B*), causing light-regulated interactions between photoreceptor and signalling intermediates (Galvao and Fankhauser 2015).

Phototropins are flavoproteins responsible for blue-light perception, carrying two flavin mononucleotide (FMN) chromophore-binding light oxygen voltage (LOV1 and LOV2) domains (Gyula *et al.* 2003, Okajima *et al.* 2014). A light-driven covalent binding of FMN to the LOV1/2 domains (Kennis *et al.* 2003) initiates the conformational changes and auto-phosphorylation of phototropins (Kasahara 2002) (Fig. 1*C*), which regulates subsequent signalling steps. Besides, there is a blue-light induced re-localization of phototropins (Kong *et al.* 2006): In the opposite direction to nuclear-localization of photo-activated Pfr, phot1 targets the cytoplasm and phot2 anchors to Golgi apparatus from their original position in nucleus (Gyula *et al.* 2003).

Another group of blue light receptors, Zeitlupe family, are also equipped with LOV domain. Similar with phototropins LOV domains, Zeitlupe LOV domains bind to flavins and sense light, affecting the activation of downstream components (Kim *et al.* 2013).

As the only identified UV-B receptors so far, UVR8

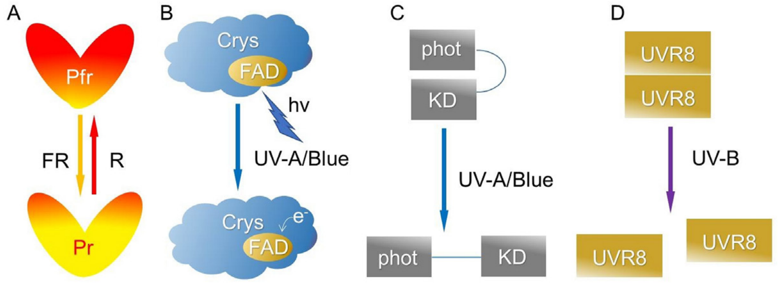

Fig. 1. Light-driven responses of photoreceptors: *A* - Photoconversation of phytochromes (Pfr:Pr), *B* - blue light activated electron transfer reaction in crys (FAD chromophore), *C* - conformational changes of phototropin upon light activation (KD - Ser/Thr kinase domain in the C-terminal region), *D* - monomerization of UVR8 homodimer upon UV-B stimulus.

perceives light stimulus with a specific triad of closely packed tryptophan residues (W233, W285, and W337) (Yin and Ulm 2017). In its ground and inactive state, two UVR8 molecules constitute a homodimer, with the force provided by the electrostatic interactions between charged amino acids. In response to UV-B, salt bridges flanking tryptophan triad at the dimer interface are disrupted (Christie *et al.* 2012), which leads to an instant monomerization of UVR8 homodimer (Rizzini *et al.* 2011) (Fig. 1*D*) and signalling initiation (Yin and Ulm 2017).

Temperature perception sensors in plants

Exposed to high temperature, almost all macromolecules such as protein complexes, membranes, and nucleic acid polymers instantly perceive the heat. In this case, all these macromolecules can be termed as thermosensors, as they respond to temperature alteration by changing their own structure and active forms, or delivering information to associated biological components (Mittler *et al.* 2012). The heat-induced responses are more complex (Kosova *et al.* 2015, Legris *et al.* 2017) than responses to radiation, making it harder to identify thermosensors (Penfield 2008, Miura and Furumoto 2013).

Even so, we are still eager to identify the very initial sensors. They should acquire temperature fluctuation directly from the environment, and regulate large-scale downstream reactions. So far, there are three candidates: temperature-dependent membrane fluidity alterations, calcium channels in the plasma membrane, the histone variant H2A.Z-nucleosome in the nucleus.

An alteration of temperature has direct effect on membrane fluidity. A decrease in temperature causes “rigidification” and lows membrane fluidity, whereas its increase causes “fluidization” and enhances membrane fluidity (Fig. 2*A*). Subsequently, this physical state change of membrane lipids affects the activity of membrane-bound proteins, making temperature information delivered (Ruelland and Zachowski 2010). From this dimension, plasma membrane has the potential to be the primary thermal sensor, which perceives and transfers ambient temperature signals (Mittler *et al.* 2012).

Then, it is speculated that Ca^{2+} channels act as relayed stations (Murata and Los 1997), which receive messages from dynamic changes of membrane physical states, and adjusts following biological processes (Saidi *et al.* 2009). They function as fundamental versatile second messengers (Steinhorst and Kudla 2014), relating environmental stimuli with inner cellular machinery. The Ca^{2+} signal is characterized by transient translocation of Ca^{2+} from high content compartments (such as vacuole and apoplast) to low content compartment cytosol. This process is elicited by abiotic and biotic factors, including irradiance, temperature, salinity, and osmotic stress. Then the stimulus-associated Ca^{2+} signature (duration, amplitude, and frequency) is recognized and delivered to the subsequent sensing and responding system

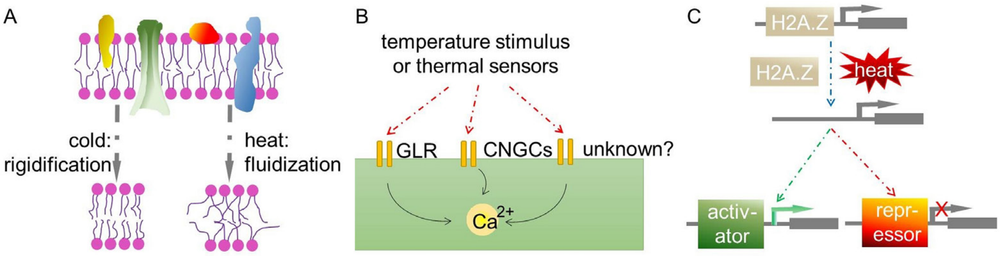

Fig. 2. Putative thermal-sensors and their temperature-driven processes. *A* - Thermodynamic physical state change of lipid membrane fludity. *B* - Potential Ca^{2+} channels on plasma membrane, which “sense” temeprature alteration and send out Ca^{2+} signal. *C* - Binding site release of H2A.Z upon high temperature.

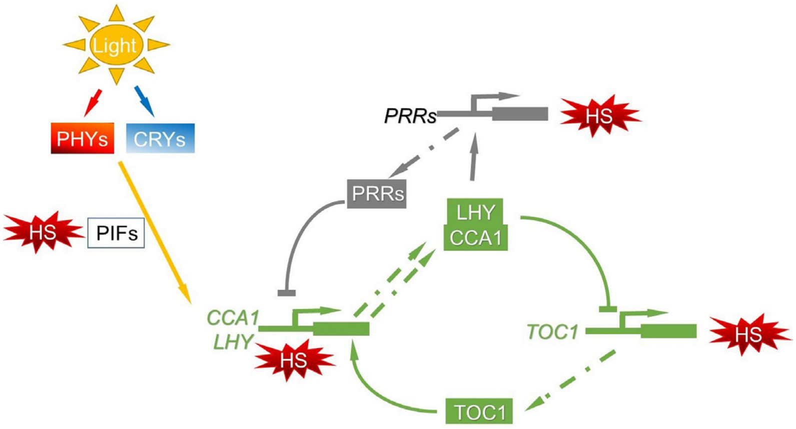

Fig. 3. Central osillator of circadian rhythms in plant. Light signal entries: PHYs and CRYs. Temperature responsive components: PIFs, PRRs, CCA1/LHY, TOC1.

(Ca^{2+}-binding proteins) (Perochon *et al.* 2011).

However, the identification of Ca^{2+} channel is a long-lasting and fundamental conundrum in plant research (Steinhorst and Kudla 2014). Emerging evidence indicates that glutamate receptor-like (GLR) and cyclic nucleotide-gated channels (CNGCs) take crucial roles in Ca^{2+} signals in plants (Steinhorst and Kudla 2014, Lorenzo *et al.* 2016) (Fig. 2*B*). Beyond that, our knowledge about other potential Ca^{2+} channels and associated regulation processes is still limited. Even we get more information about Ca^{2+} channel, there is another question: do these Ca^{2+} channel associated proteins feel the dynamic physical changes of membrane lipid directly by themselves, or obtain messages from upstream sensory receptors (if exist)?

Another potential thermosensor is the histone variant H2A.Z, which mediates genome-wide transcription changes to ambient temperature (Boden *et al.* 2013, Proveniers and Van Zanten 2013). Experimental results demonstrated that H2A.Z-containing nucleosomes occupy the -1 position of numerous genes. This occupancy is inversely correlated with temperature intensity. High temperature tends to release H2A.Z from -1 position, leaving that location available for gene promoters or inhibitors. This results in the gene expression promotion or inhibition (Kumar and Wigge 2010) (Fig. 3*C*). For example, at lower temperatures, H2A.Z nucleosomes have a higher occupancy at PIF4-binding site in the flowering locus T promoters. As temperature raises, H2A.Z nucleosomes occupancy declines, and PIF4 binding enhances, which promotes the lowering locus T expression (Proveniers and Van Zanten, 2013 Wigge 2013, Ma *et al.* 2016).

Temperature inputs into photoperiod-mediated circadian clock in plants

Jeffrey C. Hall, Michael Rosbash, and Michael W. Young were awarded the Nobel Prize in 2017 for their discoveries of molecular mechanisms controlling the circadian rhythm in *Drosophila melanogaster* (Sehgal *et al.* 1995, Price *et al.* 1998). Their findings fulfill the circadian clock in organisms, and explain how organisms persist diurnal rhythms, even be deprived with exogenous time cues (McClung 2006).

In higher plants, circadian rhythms also work as the bridge between endogenous events with external environmental stimuli (Harmer *et al.* 2000), defining a time cycle of 24 h (McClung 2006). This clock regulates various physiological processes, including photoperiodic induction of flowering, rhythmic hypocotyl elongation (Greenham and McClung 2015), and cotyledon movement (Lou *et al.* 2011). Whereas, the molecular basis underlying plants circadian molecular progresses is different from that in *Drosophila*.

In the beginning, photoreceptors cryptochromes and phytochromes perceive blue and R/FR radiation signals, and transduce these information into the circadian clock (Oakenfull and Davis 2017). These messages regulate the transcription of three central oscillator elements: late elongated hypocotyl (LHY), circadianclock associated 1 (CCA1), and timing of cab expression 1 (TOC1) *via* a negative feedback loop (Hemmes *et al.* 2012, Nohales and Kay 2016). During late evening, *CCA1* and *LHY* transcriptions will be promoted by TOC1, and maximized at dawn. In turn, CCA1 and LHY negatively regulate the expression of *TOC1* by binding to its promoter, which weakens the promotion of TOC1 on *CCA1/LHY* expression during daytime (Niwa *et al.* 2009). Subsequently, as CCA1 and LHY abundance decrease, their inhibitory effect on *TOC1* will be abolished, resulting in the increase of TOC1 at night (Grundy *et al.* 2015). This central oscillator cooperates with another peripheral loops (PRR5, PRR7, and PRR9 as three TOC1 paralogs) and integrates environmental signals with internal cues to coordinate diverse physiological outputs (Hsu and Harmer 2014).

Interestingly, except for light cycles or pulses, abrupt temperature changes, or temperature cycles can act as potent stimuli to shift the phase of this clock (James *et al.* 2012). Circadian clock is both entrained to and compensated with temperature (Franklin *et al.* 2014, Inoue *et al.* 2017). Our previous work figured out the functional elements during this temperature-dependent circadian rhythm response (Song *et al.* 2015): upon the heat stress (37 °C for 30 min), the expression of *CCA1*, *LHY*, and *PRRs* respond to heat stress significantly (Fig. 3). Similar temperature-induced transcription perturbation of circadian rhythm genes has been confirmed (Albihlal *et al.* 2018, Chen *et al.* 2018). This indicates that circadian rhythm in plants works as an information hub, which receives regulation messages from both light and temperature. The integrated signal is then used to modulate the large-scale subsequent biological processes.

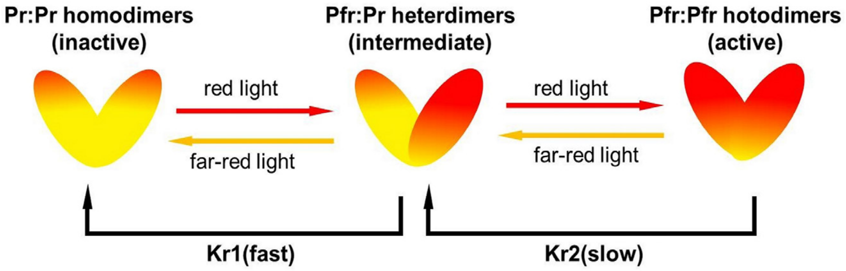

Fig. 4. The phyB active states determined by two aspects: Pr:Pfr reversion upon R/FR light stimulus, and temperature-dependent reversion rate (Kr1/Kr2).

Temperature-dependent phyB reversion

The above section describes the synergistic effect of light and temperature on circadian rhythm. As an input parameter, temperature adjusts the performance of circadian clock and associated molecule elements. These compounds, including LHY, CCA1, TOC1, and PRRs, not only work within the circadian clock, but also operate outside the loops and interact with PIFs (Hemmes *et al.* 2012, Leivar and Monte 2014). Will this temperature input eventually be transduced to light signaling pathways *via* PIFs? Will this input even be delivered to phytochromes? Considering the tight interaction of PIFs and PHYs in the effects on protein activity and gene expression (Smith *et al.* 2017), this is highly possible. From this dimension, the light receptor phytochromes can be responsive to temperature stimulus, serving as thermal sensors.

Legris *et al.* (2017) reported a remarkable reduction of biological active Pfr-Pfr dimer abundance and phyB nuclear accumulation under the warmer environment (*e. g.*, 30 °C) in *Arabidopsis*. Interestingly, this phyB pool thermal reversion is light-dependent. At certain irradiance, there is a high proportion of unstable Pfr:Pr heterodimers that can be quickly turned into Pr:Pr homodimers, *via* full name?? (kr1) (Klose *et al.* 2015), while in darkness, the thermal reversion *via* kr2 (Klose *et al.* 2015) is much slower (Legris *et al.* 2016) (Fig. 4).

In the study of Jung *et al.* (2016), the alteration of phyB active states has a significant effect on temperature-induced gene responses. Firstly, the binding-site detection *via* chromatin immunoprecipitation reveal there are more phyB target genes at 17 than at 27 °C. Moreover, most of these genes respond to temperature during night, when phyB stays inactive. This evidence suggests that phyB may act as a repressor of those temperature responsive genes.

Focusing on the dark reversion rate, Jung *et al.* (2016) reported a significant exponential relationship between temperature and $\text{phyB:phyB}_{\text{Pfr}}$ half-life: high temperature shortens $\text{phyB:phyB}_{\text{Pfr}}$ half-life and makes them unstable during nighttime. However, Legris *et al.* (2017) stated that this thermal effect should be more prominent during daytime.

Based on their discoveries, phyB is able to answer temperature changes by altering its own biological states, and regulating its associated genes temperature responses. Therefore, it is fair to define the photo-receptor phyB as a thermal sensor (Delker *et al.* 2017, Song *et al.* 2017).

Conclusions

So far, we have a quite clear picture about light receptors and their signalling pathways in plant. Photoreceptors include R/FR photoreceptors phytochromes, UV-A/blue radiation absorbing cryptochromes, phototropins, and Zeitlupe family members, and a UV-B photoreceptor UVR8. However, the information about upstream thermal sensors is still limited. Although temperature-dependent membrane fluidity, Ca^{2+} channels, and H2A.Z have been suggested as putative candidates, their temperature perception processes and signalling networks are not fully deciphered.

From a biochemistry point, only those molecules containing chromophores can capture photon with specific energy, and perceive radiation of particular wavelength. This light-driven structural transformation affects the subsequent signalling cascades and associated biological components.

On the contrary, temperature effects on molecule elements are not “specific”. Temperature is a basic parameter for biochemical reaction equilibrium, reaction rates, and enzymatic activities. Therefore, the fluctuation of temperature indistinguishably affects the structure and bio-activity of hundred and thousand molecules, regulating the countless biochemical reactions in organisms. In this case, all these macromolecules in plants can be termed as thermosensor, as they are temperature-responsive. Even so, we are still eager to identify those essential biological components, which work as stimuli receiver and signalling pivotal hubs. They should not only obtain temperature information from the environment directly, but also affect large-scale downstream reactions.

Growing in nature and experiencing a considerable complex environment, plants simultaneously receive numerous integrated signals (Wigge 2013). Thus, multisensory systems should work together to deal with these inputs and optimize plant architecture (Casal and Questa 2018). Considering the synergistic effects of light and temperature signals on numerous physiological processes (Bita and Gerats 2013, Hahn *et al.* 2013, Rasmussen *et al.* 2013), the molecular mechanisms of photo- and thermo-perception should not be analyzed separately as before (Loveys *et al.* 2002, Legris *et al.* 2017). Exploring the coordination of the two environmental signalling transduction cascades will offer a new way to understand the plant response to fluctuations in environment, as well as a new avenue to identify new sensory receptors.

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