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Review

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Light and temperature cues: multitasking receptors and transcriptional integrators

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Summary

The combined information provided by light and temperature cues helps to optimise plant body architecture and physiology. Plants possess elaborate systems to sense and respond to these stimuli. Simultaneous perception of light and temperature by dual receptors such as phytochrome B and phototropin leads to immediate signalling convergence. Conversely, cue asynchronies initiate separate pathways and the information of the earliest cue is stored, awaiting the arrival of the later cue to control transcription. Storage mechanisms can involve changes in the activity of selected clock components or epigenetic modifications, depending on the time delay between cues (hours, days or several months). We propose a conceptual framework in which the mechanisms of integration relate to the timing of cue sensing.

I. Introduction

Plants use the dynamic fluctuations in light and temperature conditions as major sources of information to adjust their growth patterns and developmental transitions to the conditions that they experience (Lorenzo *et al.*, 2016; Quint *et al.*, 2016; Legris *et al.*, 2017). Many processes respond to both light and temperature, and therefore these cues have to converge at some point of the signalling process. For instance, compared to plants grown under light at moderate temperatures, stem growth is enhanced by darkness to facilitate soil penetration of buried seedlings (skotomorphogenesis), by shade to compete with neighbours (shade avoidance) and by warm conditions to reduce the risk of heat stress (thermomorphogenesis). The precise timing of flowering to the most favourable season may require three pathways, which respond to the length of the daily light period (photoperiodic pathway), prolonged low temperatures (vernalization) and high temperatures (ambient-temperature pathway; Andrés & Coupland, 2012).

Multisensory integration can help to optimise plant architecture to the multifaceted environment and to achieve perceptual disambiguation, which takes place when a single cue does not provide enough information to univocally specify the environment (e.g. the same photoperiod can take place in late summer and spring) and a second cue resolves the ambiguity (e.g. the memory of

winter temperatures complements photoperiodic information to define the season). Light and temperature are not fully independent (Legris *et al.*, 2017). Beyond global trends in climate change, there is a fine scale of local variation in which increased solar radiation amplifies warming, reducing the chances of generating 'microrefugia' (Maclean *et al.*, 2017). Light–temperature integration could be crucial to exploit these pockets of suitable microclimate.

Sensation can be defined as a process in which a sensory receptor changes its activity as a result of a stimulus. It is the first step in the perception of stimuli-related information. Plants have a sophisticated array of photo-sensory receptors: phytochromes (phy), cryptochromes (cry), zeitlupes, phototropins (phot) and UV-B RESISTANCE 8 (UVR8; Galvão & Fankhauser, 2015; Fig. 1). Temperature affects molecular (proteins, nucleic acids) and supramolecular (cellular membranes, cytoskeleton, chromatin) structures through simple thermodynamic effects, making it difficult to identify the entry point of temperature cues (Zhu, 2016; Liu *et al.*, 2017; Markovskaya & Shibaeva, 2017; Fig. 1). Temperature can differentially affect the components of a network and modify its output; in which case the sensor is the network system, not a dedicated receptor. Nevertheless, the photo-receptors phyB (Jung *et al.*, 2016; Legris *et al.*, 2016) and phot (Fujii *et al.*, 2017) have recently been identified as temperature sensors.

II. Convergence at the receptor

How can phyB sense both light and temperature? phyB is synthesised in its inactive form, called Pr because its maximum absorbance is in red light. Upon excitation, and due to the interactions between the chromophore and its apoprotein, Pr relaxes to the active form rather than going back to Pr in its ground state. The active form is called Pfr because its maximum absorbance is in far-red light and, for instance, inhibits stem growth. In turn, light-excited Pfr relaxes to Pr. In this simple model, the amount of Pfr depends only on light (Fig. 2a, rates k1, k2). The photo-transformation can be saturated by a rather low fluence of light, which establishes a photo-equilibrium dependent on the spectral composition. For instance, photosynthetic organs of neighbour plants absorb strongly in the 400–700 nm range including blue and red wavebands, but transmit and reflect most of the far-red waveband modifying the red : far-red ratio, the relative strength of k1 and k2, and hence the level of Pfr (Fig. 2a). In this simple model, temperature has no effect within the physiological range.

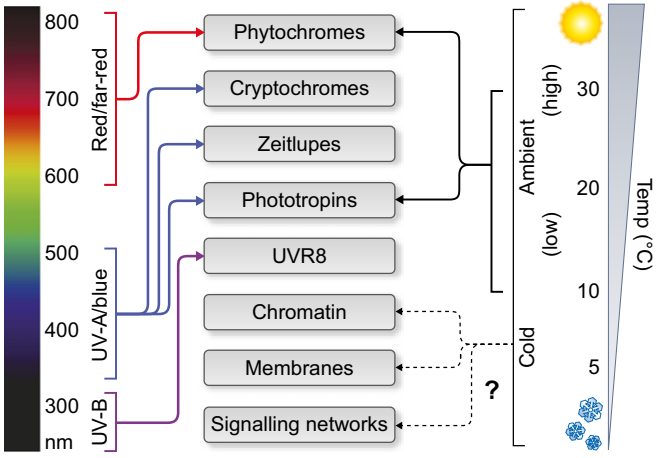

Fig. 1 Light and temperature sensors. Light cues are sensed by different families of photo-receptors and at least phyB and phot can also sense temperature (solid arrows). Putative temperature sensors (dashed arrows, the list is not exhaustive) include multi-molecular systems that are not dedicated receptors.

However, Pfr can spontaneously revert back to Pr in a reaction called dark reversion because it does not require light, although it also occurs in the light. In plants exposed to light (to establish Pfr) followed by darkness, dark reversion is evidenced by a gradual decrease in the abundance of Pfr, while the amount of total phytochrome (Pfr + Pr) remains stable. In the presence of light, the occurrence of dark reversion can be inferred because eventually the photo-equilibrium is not reached; rather, a steady-state level of Pfr is established, which is lower than that expected at photo-equilibrium because Pfr reverts to Pr. phyB is a dimer *in vivo* and there are two different rates of dark reversion: a slower rate from Pfr-Pfr to Pfr-Pr (kr2) and a faster rate between Pfr-Pr and Pr-Pr (kr1) (Klose *et al.*, 2015; Fig. 2b). This implies that making a dimer with Pr reduces Pfr stability. Due to Pfr-to-Pr dark reversion, more light is needed to establish a given level of Pfr and phyB expands its range of sensitivity to irradiance (Fig. 2b). Because dark reversion is a thermal reaction, the level of phyB Pfr, measured by *in vivo* or *in vitro* spectroscopy, becomes sensitive to temperature (Jung *et al.*, 2016; Legris *et al.*, 2016). In other words, phyB can be activated by red light and de-activated by far-red light and high temperatures. The association of phyB to its DNA target sites and the size of phyB nuclear bodies, two features linked to phyB activity, decrease with higher temperatures, in line with a decrease in phyB activity with temperature (Jung *et al.*, 2016; Legris *et al.*, 2016). Shared responses to darkness, shade and high temperatures, such as the enhanced growth of the hypocotyl (Fig. 2), can partially be accounted for by the reduced phyB activity in the three scenarios. The control of hypocotyl growth by phyB in seedlings exposed to different light and temperature conditions is more accurately captured by models in which the temperature effects on phyB activity are taken into account (Legris *et al.*, 2016). The magnitude of dark reversion can be affected by phytochrome phosphorylation (Medzihradszky *et al.*, 2013), which could help to modulate the relative input of light and temperature in a context-dependent manner.

There are many downstream signalling components shared by thermo- and photomorphogenesis, including the E3-ligase CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) and the stem-growth promoting transcription factor PHYTOCHROME INTERACTING FACTOR 4 (PIF4) (reviewed by Franklin *et al.*, 2014; Quint *et al.*, 2016; Legris *et al.*, 2017; see also Park *et al.*, 2017). This indicates that light and temperature cues can control growth via a common pathway downstream of phyB. However, light and temperature are likely to converge at multiple points in the control of growth and, for instance, UV-B radiation perceived by UVR8 (Hayes *et al.*, 2017) and blue light perceived by cry1 (Ma *et al.*, 2016) counteract the induction of PIF4 activity by high temperatures.

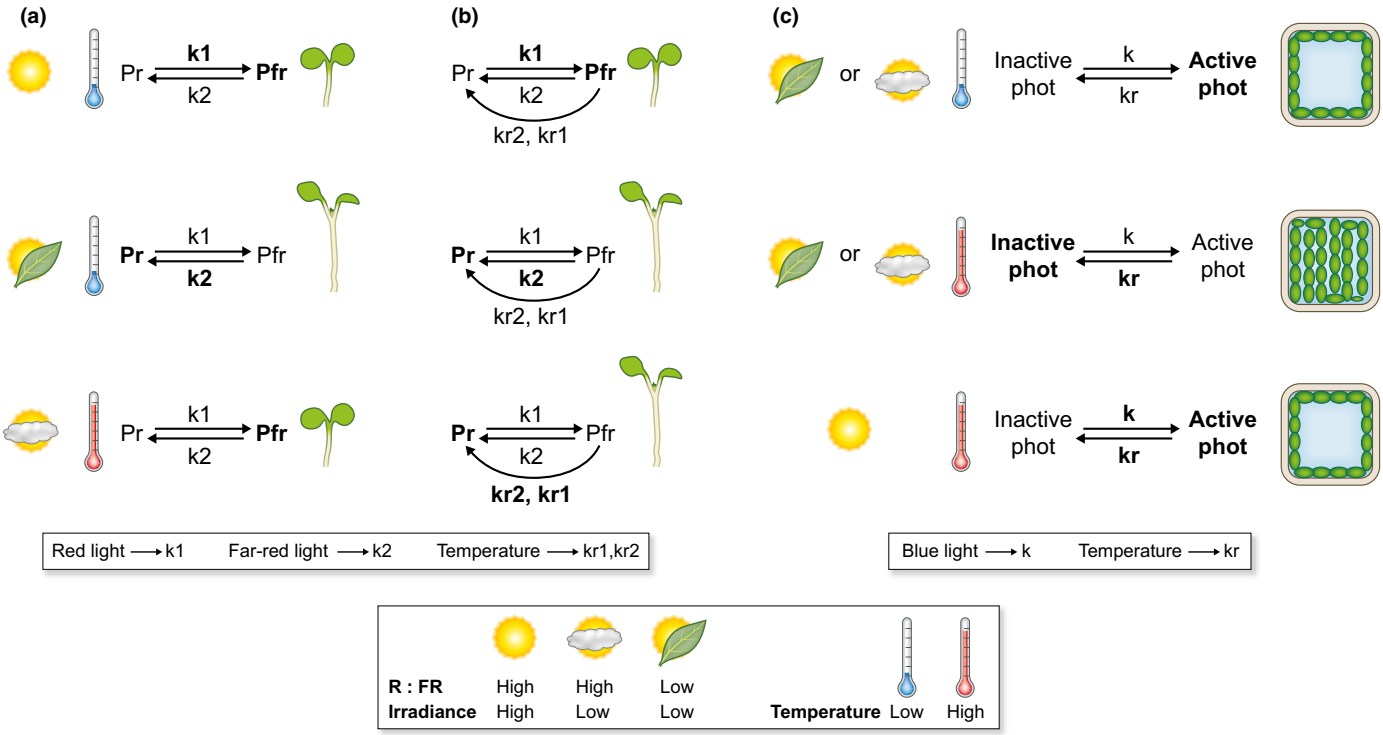

Fig. 2 Perception of light and temperature by phyB and phot. (a, b) Changes in abundance of the active (Pfr) and inactive (Pr) forms of phyB and its physiological output (inhibition of hypocotyl growth) as a function of the light reactions (k1, k2) and thermal reactions (kr1, kr2) under different conditions of light and temperature. (a) Model based only on light reactions; phyB reaches a photo-equilibrium where the level of Pfr depends on the red : far-red ratio (R : FR), not on irradiance (above a minimum level) or temperature. (b) Model including light and thermal reactions; phyB reaches a steady state where the level of Pfr depends on the R : FR, irradiance and temperature. (c) Changes in abundance of active phot and its physiological output (chloroplast position) as a function of the light reactions (k) and thermal reactions (kr) under different conditions of light and temperature.

phot is activated by blue light on a microsecond scale and returns to the inactive form with a half-life of 30 s at 22°C and 120 s at 5°C (Fujii *et al.*, 2017). Therefore, there are two ways to increase phot activity: to increase blue light or to reduce temperature to extend the lifetime of active phot (Fujii *et al.*, 2017; Fig. 2c). Both high blue light and low temperature at low blue light induce the movement of phot-mediated chloroplasts towards the cell walls parallel to the direction of incident light to avoid photo-oxidative damage in the liverwort *Marchantia polymorpha.*

The occurrence of receptors involved in the perception of very different cues (in particular, light and temperature) is not exclusive of plant systems. The transient receptor potential (TRP) superfamily of cation channels contribute to vision (light), taste, olfaction, hearing, touch, and thermo- and osmosensation in a great variety of multicellular organisms, including worms, fruit flies, zebrafish, mice and humans (Venkatachalam & Montell, 2007). Rhodopsin, one of the best known photo-sensory receptors, is also involved in temperature sensation in the larvae of *Drosophila*, an unconventional role fully independent of light (Shen *et al.*, 2011). Blue light sensing using FAD (BLUF) domain-containing receptors present in bacteria and some algae has also been implicated in temperature sensing (Nakasone *et al.*, 2010). Bacterial phytochromes have been proposed to sense light and temperature (Lamparter *et al.*, 2017).

In plants, high temperatures increase dimerisation of UVR8 and reduce the proportion of its active monomer (Findlay & Jenkins, 2016), but this reaction depends on REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1 (RUP1) and RUP2, suggesting that temperature sensation could occur upstream of UVR8. A comparable scenario might be the case for cry2, where light absorption leads to the formation of physiologically active homodimers and BLUE-LIGHT INHIBITOR OF CRYPTOCHROME 1 (BIC1) and BIC2 counteract the reaction (Wang *et al.*, 2016). By contrast, temperature dependence of phyB dark reversion (Legris *et al.*, 2016) and of the photocycle of the light/oxygen/voltage domain of phot (Fujii *et al.*, 2017) has been observed in the absence of accessory proteins, indicating that phyB and phot themselves are the sensors.

III. Convergence at transcriptional hubs

Light (daylength) and temperature cues that provide seasonal information do not converge at the sensor level. Rather, they initiate distinct signalling pathways that converge on the control of transcriptional regulators such as the C-repeat binding factors (CBFs), which mediate cold acclimation and freezing tolerance in anticipation to winter (Lee & Thomashow, 2012), and *FLOWERING LOCUS T* (*FT*, Fig. 3), which encodes a systemic signalling molecule that directly activates floral genes in the favourable season (Andrés & Coupland, 2012). The following paragraphs briefly describe the pathways connected to *FT*.

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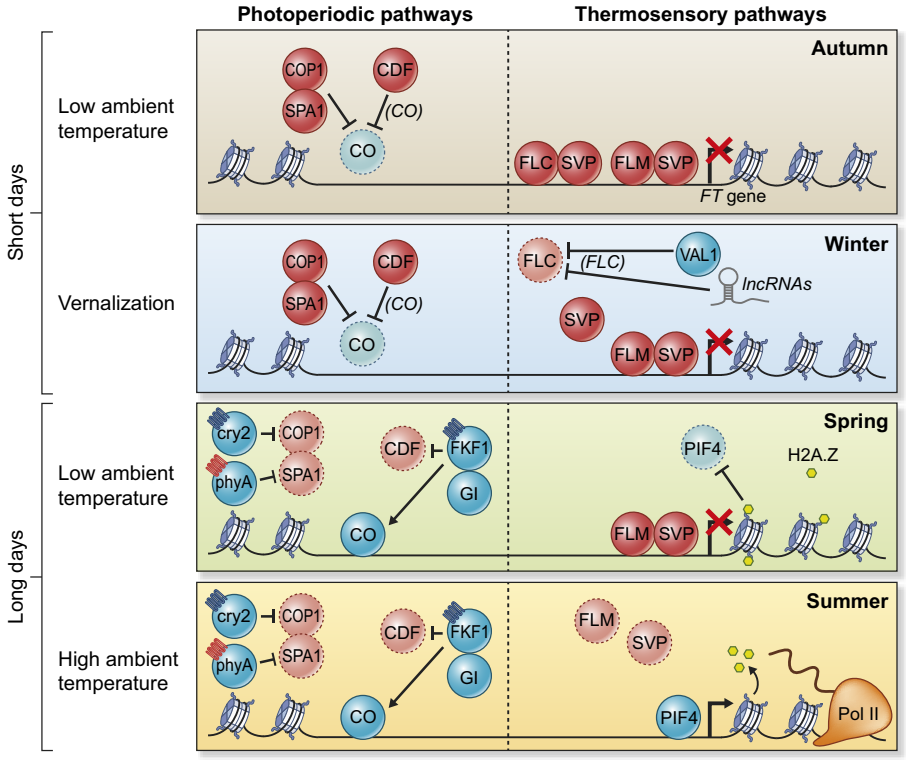

Fig. 3 Seasonal dynamics of the photoperiodic and thermosensory flowering pathways that converge at the transcriptional control of *FT*. Positive and negative regulators of *FT* are depicted in blue and red, respectively. Dotted lines and pale colours indicate either reduced levels or instability of the different *FT* regulators. From left to right we show CO (with its negative regulators COP1-SPA1 and CDF and positive regulators cry2, phyA, FKF1 and GI) bringing photoperiodic information to *FT*, SVP-FLC (together with VAL1 and lncRNAs that are negative regulators of the latter) bringing vernalization information to *FT* and SVP-FLM and PIF4 (negatively regulated by H2A.Z) bringing ambient temperature information to *FT*.

In *Arabidopsis thaliana*, perception of prolonged winter low temperatures (vernalization), presumably happening at the whole plant level, is decoded into digital silencing of the major floral repressor FLOWERING LOCUS C (FLC) at the cellular level, with increasing proportion of cells silencing *FLC* over time in an all-or-nothing manner (Berry & Dean, 2015). *FLC* reduction is associated with induction of long noncoding RNA (lncRNA) transcripts, both sense and antisense to *FLC* (Kim *et al.*, 2017). Antisense *COOLAIR* is a highly structured molecule (Hawkes *et al.*, 2016) that coats and downregulates the *FLC* locus upon cold exposure (Rosa *et al.*, 2016). Sense lncRNA *COLDWRAP* forms a repressive intragenic chromatin loop, whereas *COLDAIR* facilitates recruitment of Polycomb Repressive Complex 2 (PRC2) to *FLC* (Kim & Sung, 2017; Kim *et al.*, 2017). Another player is the sequence-specific transcriptional repressor VIVIPAROUS1/ABI3-LIKE1 (VAL1), which binds specifically to the PRC2 entry site at *FLC*, most likely to bring to the locus the repressive activity of this complex (Questa *et al.*, 2016). Winter thermo-sensors have yet to be identified and uncovering the mechanisms that trigger VAL1 enrichment at *FLC* will be elucidative. Although challenging to demonstrate *in vivo*, an interesting possibility is that temperature affects the structure of *FLC* lncRNAs, thus modulating sense *FLC* transcriptional status.

The induction of flowering by long days (photoperiodic control) requires the transcriptional activator CONSTANS (CO), which reaches significant levels at the end of the long-days of spring/summer (reviewed by Andrés & Coupland, 2012; Song *et al.*, 2015). When the days are long, the phase of circadian-clock-controlled expression of *CO* coincides with cry2 and phyA activity, which inhibit the COP1-SUPPRESSOR OF PHYA-105 1 (SPA1) complex to stabilise the CO protein. Light activation of FLAVING BINDING, KELCH REPEAT, F-BOX1 (FKF1) (Zeitlpe family) enables the formation of a complex with GIGANTEA (GI) to mediate degradation of the *CO* transcriptional repressors CYCLING DOFS FACTORs (CDFs), enhancing *CO* expression in the evening of long days. FKF1 also binds to and stabilises the CO protein.

Moderately high ambient temperatures can also accelerate *A. thaliana* flowering. The MADS-domain proteins FLOWERING LOCUS M (FLM) and SHORT VEGETATIVE PHASE (SVP) interact to form a complex that represses flowering in low ambient temperatures. Increasing temperatures destabilise SVP protein and induce the formation of a defective spliced variant of FLM (reviewed by Verhage *et al.*, 2014), thus reducing the abundance of the SVP–FLM complex. At high temperatures, H2A.Z histone-containing nucleosomes, which have more tightly wrapped DNA, are removed from the *FT* promoter (Kumar & Wigge, 2010). Plants displaying altered levels of H3K36me3 writers, readers and erasers exhibit impaired temperature-induced flowering (Pajoro *et al.*, 2017). Enhanced expression of *PIF4* at high temperatures may also accelerate flowering (Kumar *et al.*, 2012; Fernández *et al.*, 2016).

In the lines requiring vernalization, light and temperature inputs can reach *FT* in a temporally separated and sequential manner (Fig. 3). First, winter low temperatures free the *FT* promoter from the FLC–SVP blockage. Once winter has passed, the epigenetic silencing machinery keeps *FLC* mRNA at low levels (Berry & Dean, 2015). The long days of spring enhance CO activity. However, the photoperiodic induction of flowering is weak under the low ambient temperatures of early spring (*c.* 16°C) and

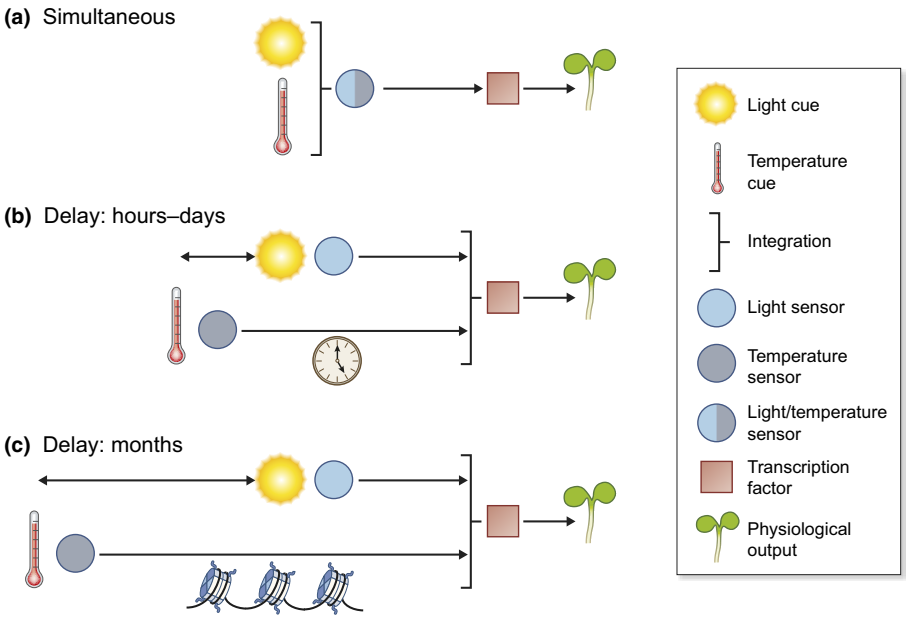

Fig. 4 Mechanisms of integration of light and temperature cues. (a) Simultaneous cues can be integrated immediately by a shared receptor and downstream signalling pathway. (b) Cues delayed by a few hours or days can be perceived by different sensors and integrated downstream via mechanisms that involve clock components. (c) Cues delayed for months can be perceived by different sensors and integrated downstream via mechanisms that involve epigenetic mechanisms.

becomes stronger as temperatures rise above 20°C (Strasser *et al.*, 2009), inactivating SVP–FLM and shaping the chromatin landscape to make the *FT* promoter sensitive to CO (Fernández *et al.*, 2016) and accessible to PIF4 (Kumar *et al.*, 2012).

IV. Convergence involving clock components

Clock components also offer points of integration of light and temperature cues. There is significant co-occurrence of phyB at multiple binding sites of the clock-controlled evening complex that includes EARLY FLOWERING 3 (ELF3), and phyB is known to affect ELF3 activity (Ezer *et al.*, 2017, and references therein). However, ELF3 appears to transmit additional (phyB-independent) temperature information to the control of hypocotyl growth (Ezer *et al.*, 2017), suggesting that it represents a point of convergence of light (phyB) and temperature cues independent of phyB. Similarly, heat shocks can modulate the sensitivity of etiolated (dark-grown) seedlings to subsequent light by inducing rhythmic expression of clock components such as *PSEUDO-RESPONSE REGULATOR7* (*PRR7*), PRR9, *LATE ELONGATED HYPOCOTYL* (*LHY*) and *CIRCADIAN CLOCK ASSOCIATED1* (*CCA1*) (Karayekov *et al.*, 2013).

V. Conclusions

The molecular mechanisms of integration of light and temperature information are diverse and apparently related to the time delay between one cue and the other (Fig. 4). Simultaneous cues can be perceived by the same receptor (e.g. phyB, phot) and become immediately integrated. Alternatively, asynchronous cues initiate separate pathways, where the information provided by the first cue remains stored while awaiting the arrival of the subsequent cue, and the signals finally converge to control the activity of a transcriptional integrator. Long-term (months) and short-term (hours, days) storage mechanisms may respectively involve chromatin modifications and selected clock components. A given process could eventually integrate light and temperature cues via different mechanisms to gather information at different time scales. Stem growth responds dynamically to both simultaneous and shortly delayed stimuli from the microenvironment. Conversely, flowering responds irreversibly to the coming of the seasons by integrating cues over prolonged periods of time.

Acknowledgements

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