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PLANT BIOLOGY

Light-sensing phytochromes feel the heat

Plant phytochrome activity is governed not just by light, but also by prevailing temperature

By Karen J. Halliday¹ and Seth J. Davis²

Plants expect light and warmth during the day and darkness and coolness at night. But dim, overcast days and unusually warm nights also occur. How is the perception of this variability integrated into more regular daily cycles? A major photoreceptor class in plants, called the phytochromes, respond to brightness and color ratio. In so doing, the phytochrome family of receptors coordinate growth and development. The phytochromes are therefore a vital surveillance system that enables plants to adapt to a changing environment. Two papers in this issue, by Legris *et al.* (1) on page XXX and Jung *et al.* (2) on page YYY, now implicate phytochrome B (phyB) in thermal regulation of the light-activated pathways.

The phytochrome receptors are chromic proteins that must operate under both predictable and unpredictable conditions, which can span, for example, a ~30°C range in temperature (3). Responding to the sometimes massive, daily fluctuations in temperature under a mostly predictable light environment is a major challenge. Phytochromes have intriguing properties that allow them to sense changes in light quality and quantity. Like other phytochrome receptors, phyB exists as dimers in inactive Pr and active Pfr forms. Red light drives the photoconversion of Pr to Pfr, whereas far-red light switches it back (see the figure). In this way, changes in light quality lead to different proportions of active Pfr to inactive Pr. The amount of active Pfr also depends upon light-independent thermal (or dark) reversion back to Pr. Mathematical modeling of phytochrome-receptor kinetics indicates that dark reversion is essential for accurate detection of light quantity (4). A simple and quantitative readout of phytochrome action is hypocotyl (seedling stem) length, which inversely correlates with Pfr. Phytochrome signaling operates in part by negatively regulating transcription factors, such as those in the PHYTOCHROME INTERACTING FACTOR (PIF) family. This is achieved by triggering PIF proteolysis and through direct binding to PIFs at target promoters (5, 6). As such, phytochrome binding to PIFs is thought to be important in transcriptional regulation. Indeed, Jung *et al.* could de-

tect phyB at DNA sites where PIFs target genes that control an array of responses, including hypocotyl growth.

Active phytochrome-Pfr accumulates in nuclear bodies. Small nuclear bodies form at fluence rates that generate low levels of Pfr, whereas large nuclear bodies form when Pfr levels exceed a higher threshold (7). Pfr-Pfr constitutes the main dimeric form in nuclear bodies and most likely represents the “active” form (8). By using nuclear body size as a proxy for active Pfr levels, Legris *et al.* conducted multivariate analysis with wild-type and dark-reversion-defective phytochrome variants, grown under varying light quality, quantity, and temperature to examine the relationship of dark reversion to thermal inputs and nuclear body dimensions. A consistent feature, not observed in dark reversion variants, was the reduction in number of large nuclear bodies at high temperatures. By mathematically modeling nuclear body size as a function of Pfr amount, warmth was shown to deplete Pfr levels in a dark-reversion-dependent manner. Although this analysis delineates a key role for dark reversion in nuclear body thermal stability, as nuclear body constituents have not been fully determined, other factors could contribute to this response.

Both Legris *et al.* and Jung *et al.* establish that phytochrome signaling is thermally controlled. The importance of phyB thermal reversion was demonstrated in regulating phytochrome activity during the early night (2) and in dim daylight conditions (1). Jung *et al.* showed that temperature effects on post-dusk Pfr result in a phyB enrichment at PIF-associated target promoters when plants experience cooler temperatures. These data imply that at permissive temperatures, phyB inhibits PIF activity through direct binding at target promoters. In this way, phyB conveys temperature information to PIFs. These results indicate that the phytochrome active state, Pfr, determines the receptor’s signaling life-time and this is dependent on the ambient temperatures during the first hours of darkness.

Further, Legris *et al.* that show temperature profoundly affects the abundance of active Pfr under low-light conditions. This study considers that phytochrome exists as a dimer and that dark reversion is a two-part process comprising a slow step from Pfr-Pfr to Pfr-Pr (3), and a fast step: Pfr-Pr to Pr-Pr (1, (8) (see the figure).

Legris *et al.* demonstrate how these dark-reversion-rate kinetics underlie thermal regulation. At very low light levels, there is a higher proportion of the Pfr-Pr heterodimer, but the balance tips toward Pfr-Pfr as light intensity increases (8). Critically, the authors showed that temperature was particularly effective in reducing Pfr at very low light levels, which suggests that Pfr-Pr to Pr-Pr dark reversion kinetics are more temperature sensitive than Pfr-Pfr to Pfr-Pr. This illustrates that active phytochrome is particularly sensitive to temperature at very low levels of light typical under a dense canopy. Nonetheless, using hypocotyl growth as an indicator of phyB action, temperature effects on phyB were also observed at higher intensities. The active phytochrome pool is therefore highly dynamic as determined by both light-activated Pr-to-Pfr photoconversion and thermal reversion.

Together, the papers by Legris *et al.* and Jung *et al.* suggest that phytochrome signaling is perturbed by heat. Sensitivity to temperature is particularly acute under conditions that impede conversion to Pfr-Pfr, such as very low-light, far-red-rich canopy shade, or warmth during early night darkness (see the figure). These studies support the idea that cool temperatures boost phyB action, which may be important to restrict elongation growth and adjust metabolism to cope with cold spells or cooler seasons (3). Future work could reveal the different molecular circuit architectures that respond to or protect from temperature changes.

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Sensing light and heat. Plants are susceptible to heat, particularly in low light, far-red (FR)-rich vegetation, or darkness (top panel). Phytochrome exists as a dimer (bottom panel): high red (R) fluence rates drive the production of active Pfr-Pfr, whereas low fluence rate (or

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1 low R:FR ratio) favors Pr-Pr and Pfr-Pr. Lev-
2 els of active Pfr-Pfr are also governed by
3 thermal (or dark) reversion, a two-step pro-
4 cess (kr_2 , kr_1) that converts Pfr-Pfr back to
5 inactive Pr-Pr.
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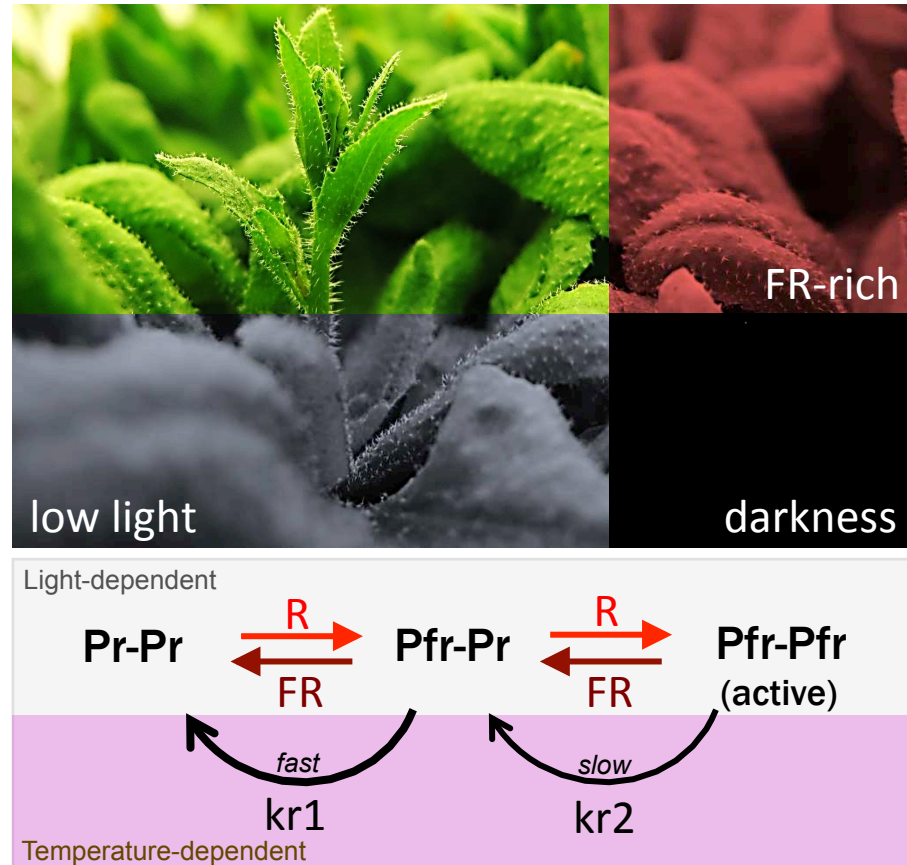


Figure 1. Plants are more susceptible to warmth, particularly in low light, far-red (FR) rich vegetation, or darkness (top panel). Phytochrome exists as a dimer (bottom panel): high red (R) fluence rates drive the production of active Pfr-Pfr, while low fluence rate (or low R:FR ratio) favor Pr-Pr and Pfr-Pr. However, the active Pfr-Pfr pool is also governed by (light independent) thermal (or dark) reversion, a two-step process that converts Pfr-Pfr back to inactive Pr-Pr (kr2, kr1). While temperature affects Pfr-Pfr levels over a range of light conditions, plants are more vulnerable to warmth in darkness, low light or FR rich conditions that prevent or limit photoconversion to Pfr.