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Review

Tansley insight

New insights into the mechanisms of phytochrome–cryptochrome coaction

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Contents

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Summary

Plants perceive and respond to light signals by multiple sensory photoreceptors, including phytochromes and cryptochromes, which absorb different wavelengths of light to regulate genome expression and plant development. Photophysiological analyses have long revealed the coordinated actions of different photoreceptors, a phenomenon referred to as the photoreceptor coaction. The mechanistic explanations of photoreceptor coactions are not fully understood. The function of direct protein–protein interaction of phytochromes and cryptochromes and common signaling molecules of these photoreceptors, such as SPA1/COP1 E3 ubiquitin ligase complex and bHLH transcription factors PIFs, would partially explain phytochrome–cryptochrome coactions. In addition, newly discovered proteins that block cryptochrome photodimerization or catalyze cryptochrome phosphorylation may also participate in the phytochrome and cryptochrome coaction. This Tansley insight, which is not intended to make a comprehensive review of the studies of photoreceptor coactions, attempts to highlight those recent findings and their possible roles in the photoreceptor coaction.

I. Introduction

The red/far-red light receptors phytochromes and the blue light receptors cryptochromes are among the most extensively studied sensory photoreceptors in plants (Quail, 2002; Cashmore, 2003). These structurally distinct photoreceptors become photochemically active only in response to the specific wavelengths of light to affect overlapping developmental processes in plants. The coaction of phytochromes and cryptochromes have been recognized for decades (Mohr, 1994; Sellaro *et al.*, 2009; Su *et al.*, 2017a), but the mechanistic explanation of this complex phenomenon has not been fully understood. At least two previously discovered mechanisms may partially explain the photoreceptor coaction. First, phytochromes may interact directly with cryptochromes to coordinate red/far-red light and blue light responses. Light-responsive physical interactions between phyA and CRY1, phyB and CRY2, or phyB and CRY1 have been reported (Ahmad *et al.*, 1998; Devlin & Kay, 2000; Mas *et al.*, 2000; Hughes *et al.*, 2012). Second, phytochromes and cryptochromes may interact with the common

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signaling partners to coordinate their actions. It is known that both phytochromes and cryptochromes physically interact with the bHLH transcription factors PHYTOCHROME INTERACTING FACTORS (PIFs) or the CONSTITUTIVE PHOTOMORPHOGENIC 1/SUPPRESSOR OF PHYA-105 (SPA1/COP1) E3 ubiquitin ligase complex to directly or indirectly (respectively) regulate transcription (Martinez-Garcia *et al.*, 2000; Hoecker & Quail, 2001; Wang *et al.*, 2001; Yang *et al.*, 2001; Huq *et al.*, 2004; Liu *et al.*, 2008, 2011; Saijo *et al.*, 2008; Sellaro *et al.*, 2009; Leivar & Quail, 2011; Lian *et al.*, 2011; Zuo *et al.*, 2011; Weidler *et al.*, 2012; Zheng *et al.*, 2013; Lu *et al.*, 2015; Sheerin *et al.*, 2015; Ma *et al.*, 2016; Pedmale *et al.*, 2016). Therefore, the wavelength-specific photochemical reactions of phytochromes and cryptochromes appear to define not only signal transduction of individual photoreceptors, but also their coactions under natural light conditions. In addition to these previously discovered mechanisms, it has been found recently that the Blue-light Inhibitors of Cryptochromes (BICs; Wang *et al.*, 2016) and Photoregulatory Protein Kinases (PPKs; Casas-Mollano *et al.*, 2008; Wang *et al.*, 2015b; Huang *et al.*, 2016; Liu *et al.*, 2017; Ni *et al.*, 2017; Su *et al.*, 2017b) may also play roles in the phytochrome–cryptochrome coaction.

II. Phytochromes mediate light-induced transcription of *BICs* to inactivate cryptochromes

BICs are novel proteins recently identified in a gain-of-function genetic screen (Wang *et al.*, 2016). In this screen, several lines that exhibit the long-hypocotyl phenotype when grown in continuous blue light, but not in red light or far-red light or darkness, were isolated from a transgenic Arabidopsis library that overexpresses arbitrary cDNAs (Ichikawa *et al.*, 2006; Wang *et al.*, 2016). The Arabidopsis genome has two *BIC* genes, *BIC1* and *BIC2*. BICs are novel proteins with no previously identified sequence motif, except a highly conserved carboxyl terminus that turns out to be the cryptochrome-interacting domain. Although cryptochromes are found in all major evolutionary lineages, BICs appear to exist only in land plants, including bryophytes and vascular plants, but not in bacteria, fungi, algae or animals. Transgenic plants overexpressing BIC1 or BIC2 and the loss-of-function *bic1bic2* double mutant exhibited blue light-specific hyposensitive (longer hypocotyl) and hypersensitive (shorter hypocotyl) photoresponses, respectively. *BICs* are the only genes reported so far, other than cryptochromes, that show a blue light-specific phenotype when they are mutated or overexpressed, suggesting that the BIC proteins play roles in the early steps of the cryptochrome signal transduction. Indeed, BICs interact with photoexcited cryptochromes to suppress all presently known photochemical reactions of Arabidopsis cryptochromes tested, including phosphorylation, photobody formation, proteolysis, de-etiolation, floral promotion and alteration of genome expression changes in response to blue light. Importantly, it was further demonstrated that plant cryptochromes undergo blue light-induced homodimerization (Wang *et al.*, 2016), which had been shown previously to be necessary for cryptochrome activation (Sang *et al.*, 2005; Rosenfeldt *et al.*, 2008), whereas BICs bind to cryptochromes to inhibit their dimerization and oligomerization (Wang *et al.*, 2016). These results established BICs as the negative regulators that function by interacting with the photoexcited cryptochromes to block cryptochrome photodimerization and photoactivation.

Although BICs appear to function only in blue light, but not in red light or far-red light, the mRNA expression of both *BIC1* and *BIC2* genes are induced by light in a wavelength-independent manner (Wang *et al.*, 2017). It was shown that the *BIC* mRNAs are almost undetectable in etiolated seedlings, but their abundance increased 10^2–10^3-fold in etiolated seedlings exposed to either blue light, red light or far-red light (Wang *et al.*, 2017). Mutations of cryptochromes or phytochromes impair light induction of *BIC* mRNA accumulation in response to blue light or red/far-red light, respectively. Light induction of BIC expression increased or decreased dramatically in the *cop1* or *hy5* mutant, respectively. The HY5 transcription factor binds to the promoters of *BIC* genes in a light-independent manner. These results argue that the CRY–BIC negative feedback circuitry is controlled not only by cryptochromes, but also by phytochromes. According to this hypothesis, phytochromes and cryptochromes mediate light induction of expression of not only genes required for photomorphogenesis but also the *BIC* genes that inhibit cryptochromes and photomorphogenesis (Fig. 1). The phytochrome and cryptochrome co-activation of the CRY–BIC negative-feedback circuitry may serve as a safety valve to prevent germinating seedlings from over-reacting to light.

III. PPKs phosphorylate light-signaling proteins and histones to affect plant development

PPKs (previously referred to as MUT9-like kinases or MLKs) are a four-member family of plant-specific protein kinases that are related to the ubiquitous Casein kinase I. PPKs diverge from CKI significantly. PPKs have the N-terminal extension (of *c.*100 residues) that is absent in CKI, whereas the C-terminal domain

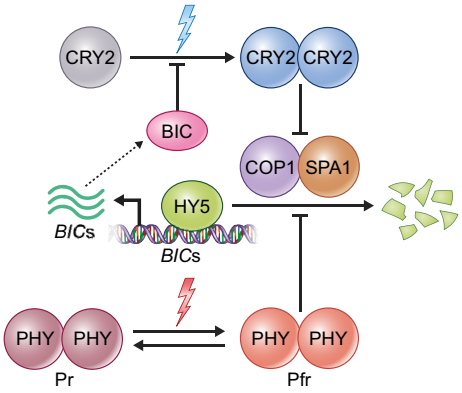

Fig. 1 Phytochromes (PHY) mediate light-induced transcription of *Blue-light Inhibitors of Cryptochromes* (*BICs*) to inactivate cryptochromes. This model depicts that CRY2 undergoes photodimerization to become active. The active CRY2 inhibits SPA/COP1 ubiquitin ligase activity, leading to increased activity of the HY5 transcription factor, and accumulation of BIC proteins that inhibits CRY2 photodimerization. Phytochromes also activate *BIC* expression to suppress CRY2 photodimerization and photoactivation. Solid arrows or T-bar indicate positive or negative actions, respectively, dotted arrow indicates translation. Pr, Pr form of PHY; Pfr, Pfr form of PHY.

of PPKs bears no similarity to that of CKI. However, PPK and CKI share very high sequence similarity in their kinase domains (Casas-Mollano *et al.*, 2008), and they appear to act by a similar catalytic mechanism (Liu *et al.*, 2017). This group of kinases was originally identified in green algae *Chlaymydomonas* from a genetic screen for mutations that reactivate transcriptionally silenced genes (Casas-Mollano *et al.*, 2008). The gene corresponding to one of the MUT mutants, MUT9, was identified and its protein product referred to as MUT9 kinase (Casas-Mollano *et al.*, 2008). The related kinases were later studied in Arabidopsis and referred to as the MUT9-LIKE KINASES or MLKs (Wang *et al.*, 2015b). MLKs phosphorylate histone H3 and H2A in algae and plants; mutations of MLK resulted in altered chromosome organization, hypersensitivity to DNA-damaging reagents and hypersensitivity to osmotic stresses (Casas-Mollano *et al.*, 2008; Wang *et al.*, 2015b; Su *et al.*, 2017a, b). The name of plant MUT9-like kinases (MLKs) was later changed to Photoregulatory Protein kinases (PPKs; Liu *et al.*, 2017; Ni *et al.*, 2017), because all four members of this type of protein kinase interact and phosphorylate cryptochrome (Liu *et al.*, 2017), phytochrome-interacting factor (Wang *et al.*, 2015b; Ni *et al.*, 2017) and the circadian clock components (Huang *et al.*, 2016; Su *et al.*, 2017b).

The first hint that PPKs are likely regulators of photoreceptor signal transduction derives from an affinity purification mass spectrometry (AP-MS) study of the Arabidopsis proteins EARLY FLOWERING 3 and 4 (ELF3 and ELF4; Huang *et al.*, 2016). ELF3 and ELF4 are part of the evening complex that peaks in dusk and carries out important functions in the circadian clock and light regulation of transcription (Nusinow *et al.*, 2011). This study identified all four PPKs, in addition to phytochromes, phytochrome signaling proteins and the circadian clock components, as the evening complex-associated proteins. The association of PPKs with the evening complex is dependent on phyB, because PPK is no longer associated with the ELF3 and ELF4 proteins expressed in the *phyB* mutant. The *ppk* single, double, or triple mutants exhibited long-period circadian rhythms of transcription, indicating that PPKs may play direct roles in the circadian clock. It remains unclear whether PPK phosphorylate components of the evening complex or the circadian clock.

Direct roles of PPKs in the photoreceptor signal transduction were demonstrated in two more recent studies (Liu *et al.*, 2017; Ni *et al.*, 2017). These studies showed that PPKs interact with photoexcited CRY2 in response to blue light, via the C-terminal nonkinase domain of PPKs. In addition, PPKs interact with the phytochrome-signaling protein PIF3 in response to red light, through the N-terminal kinase domain of PPKs. Results of protein phosphorylation analyses demonstrate that PPKs catalyze blue light-dependent phosphorylation of CRY2 and red light-dependent phosphorylation of PIF3. Mass spectrometry analyses confirmed that all four PPKs are catalytically active to collectively phosphorylate multiple serine and threonine residues of CRY2 and PIF3. PPK-dependent phosphorylation of CRY2 enhances the activity, ubiquitination and degradation of CRY2 (Shalitin *et al.*, 2003; Wang *et al.*, 2015a; Liu *et al.*, 2017; Fig. 2). PPK-dependent phosphorylation of PIF3 stimulates ubiquitination and degradation of PIF3, leading to degradation of phyB through the 'mutually assured destruction' mechanism (Ni *et al.*, 2013, 2014, 2017; Fig. 2).

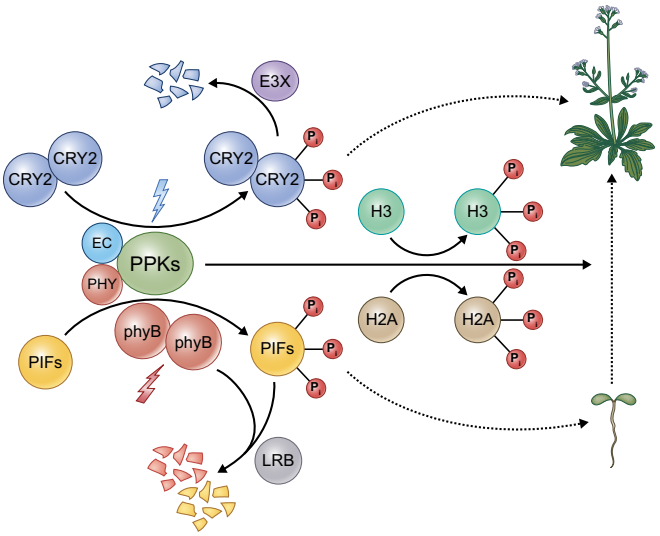

Fig. 2 Potential roles of photoregulatory protein kinases (PPKs) in phytochrome–cryptochrome coactions. This model depicts that PPKs phosphorylate CRY2 and PIF3, resulting in degradation of CRY2, PIF3 and phyB. PPKs also phosphorylate histones H3 and H2A, which may affect phytochrome- and cryptochrome-dependent chromatin remodeling and plant development. Pi, phosphorylation; EC, evening complex; PHY, phyA, B, C, D, E, E3X, COP1 and unknown E3 ubiquitin ligases; LRB, Light Response Bric-a-Brack/Tramtrack/Broad (BTB) E3 ubiquitin ligase. Solid or dotted arrows indicate positive actions possibly by multiple steps.

Given that PPKs directly affect modification, activity and abundance of CRY2, PIF3 and phyB, these protein kinases must be involved in the phytochrome and cryptochrome coactions (Fig. 2), yet it is not clear exactly how they play this role. One possibility is that PPK-catalyzed phosphorylation of CRY2 and PIF3 may affect the function of phytochromes and cryptochromes in some more complex processes, such as light regulation of the circadian clock or histone modifications (Wang *et al.*, 2015b; Su *et al.*, 2017b; Fig. 2). It has been reported that CRY2 mediates blue light stimulation of chromatin decondensation in rosette leaves during floral transition of Arabidopsis plants (Tessadori *et al.*, 2007). In contrast, in cotyledons of young seedlings, cryptochromes mediate blue light-induced nuclear expansion, chromatin condensation and formation of chromocenters enriched in heterochromatin (Bourbousse *et al.*, 2015). It has been shown that PPK2 (MLK1) and PPK3 (MLK2) are required for phosphorylation of histone H3 at threonine 3 in pericentromeric regions (Wang *et al.*, 2015b), whereas PPK1 (MLK4) phosphorylates histone H2A at serine 95 (Su *et al.*, 2017b). It is conceivable that cryptochromes, which are the substrates of PPKs, may mediate light regulation of the activity of PPKs to affect histone phosphorylation and chromatin reorganization. Given that phytochromes also mediate various histone modification and chromatin structural changes in response to light (Guo *et al.*, 2008; Tessadori *et al.*, 2009; Jang *et al.*, 2011; Bourbousse *et al.*, 2012), it would be interesting to investigate whether the PPK-dependent histone phosphorylation may convey concerted light signals to the chromosome remodeling process to affect genome transcription (Fig. 2).

IV. Prospect

Phytochromes and cryptochromes are evolutionarily adapted to coact in plants naturally exposed to light of mixed wavelengths. Given that almost all extensively studied phytochrome and cryptochrome signaling molecules are associated with both types of photoreceptors by one mechanism or another, phytochromes and cryptochromes may never act alone in nature. Recent studies have added two previously unrecognized mechanisms for the photoreceptor coaction. Phytochromes activate transcription of the *BIC* genes to negatively regulate the activity of cryptochromes, which may serve as a safe valve to prevent cryptochromes from over-reacting in germinating seedlings. PPKs interact with and phosphorylate cryptochromes and phytochrome-interacting factors, suggesting that these protein kinases may act as both the signaling molecules and the negative feedback regulators for both phytochromes and cryptochromes. It remains to be investigated whether or how phytochromes and cryptochromes may coact via PPK-dependent phosphorylation of histones to affect chromatin structure and transcription in response to light.

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