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Evolution of photoperiod sensing in plants and algae

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Measuring day length confers a strong fitness improvement to photosynthetic organisms as it allows them to anticipate light phases and take the best decisions preceding diurnal transitions. In close association with signals from the circadian clock and the photoreceptors, photoperiodic sensing constitutes also a precise way to determine the passing of the seasons and to take annual decisions such as the best time to flower or the beginning of dormancy. Photoperiodic sensing in photosynthetic organisms is ancient and two major stages in its evolution could be identified, the cyanobacterial time sensing and the evolutionary tool kit that arose in green algae and developed into the photoperiodic system of modern plants. The most recent discoveries about the evolution of the perception of light, measurement of day length and relationship with the circadian clock along the evolution of the eukaryotic green lineage will be discussed in this review.

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Introduction

Earth rotation around its axis and around the sun produces predictable day length (photoperiod) changes through the seasons that plants use, via sophisticated mechanisms, to measure time and take crucial physiological decisions [1]. Photoperiodism, or the ability to detect day length, is present in early photosynthetic eukaryotes so that algae can produce several photoperiod responses [2]. This way, during the green lineage evolution, photoperiodism pervaded into the major physiological systems, allowing them to predict the passing of the seasons and prepare plants for year-round predictable changing conditions.

The photoperiod sensing system involves a way to detect light (photoreceptors) and an internal system to measure time (circadian clock). In time they became so important for unicellular free living algae that for some marine picoeukaryotes 90% of its transcriptome is controlled by the clock [3]. However, more evolved and flexible species like modern plants, which developed the capacity to adapt to different environments, have reduced this number to less than 50% [4]. Paradoxically, more intertwined, complex systems allowed for a more independent response to external cues, thus permitting the colonization of ever demanding new niches and the acquisition of novel and complex physiological functions [5].

Photoreceptors evolution

Living organisms use a cluster of photoreceptors to measure the quality, quantity and direction of light to modulate physiological responses to changing lights [6]. This is particularly important for photosynthetic organisms that require light energy for photosynthesis and consequently to grow and develop. Photoreceptors can be divided into three groups according to the light quality they detect. Red and far-red lights are absorbed by phytochromes (PHYs) while three types of photoreceptors perceive the blue/UV-A: Cryptochromes (CRYs), Phototropins (PHOTs) and three plant-specific LOV/F-box/Kelch-repeat proteins ZEITLUPE (ZTL), FLAVIN-BINDING KELCH REPEAT F-BOX (FKF), and LOV KELCH REPEAT PROTEIN 2 (LKP2). Finally, UV RESISTANCE LOCUS 8 (UVR8) was recently shown to be a UV-B photoreceptor [7]. Excellent reviews on plant and algae photoreceptor structure and function have recently been published [8–13].

The specific photoreceptor set has evolved across photosynthetic eukaryotes (Figure 1). In the chlorophyte model alga *Chlamydomonas reinhardtii*, UV-B light is detected by UVR8 while blue/UV-A is detected by one PHOT (pho1), two DASH (*Drosophila*, *Arabidopsis*, *Synechocystis* and Human) CRYs, one plant-like CRY (pCRY) and one animal-like CRY (aCRY). The latter can respond both to blue and red light [12,14••,15]. In the fern *Adiantum capillus-veneris* four canonical plant PHYs have been

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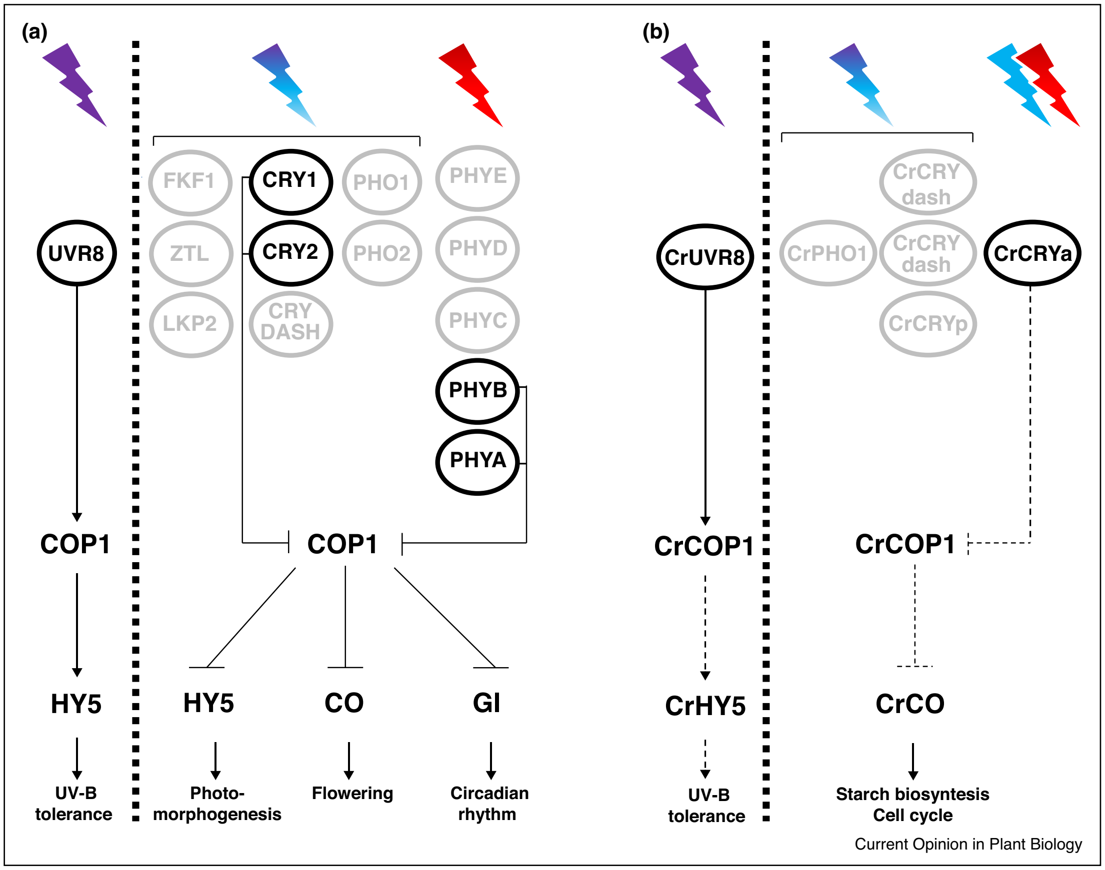
Figure 1



Light signal transduction and photoperiodic regulation by COP1 in *A. thaliana* **(a)** and *C. reinhardtii* **(b)**.
In *A. thaliana*, photoactivated CRY1, CRY2, PHYA and PHYB inhibit COP1 allowing accumulation of effectors and resulting in the specific light responses. Under UV-B, COP1 acts as positive regulator activating, among others, UVR8, HY5 and consequently upregulating UV-B tolerance genes. UV-B signal transduction is conserved in *C. reinhardtii*, although CrHY5 implication has not been investigated (dash lines). Arrows indicate positive regulation, while bars represent negative regulation. Low levels of *CrCO* expression observed in *crcrya* mutant suggest a conserved CRY-COP1-CO pathway, although CrCOP1 implication has not been described (dash lines). Photoreceptors not involved in COP1 regulation are shown in grey.

identified, two PHOTs and five CRYs [16]. Ferns include a specific neochrome, a chimeric photoreceptor consisting of an N-terminus PHY domain and several C-terminus PHOT domains that can sense both blue and red/far-red light to regulate chloroplast movement and phototropism [6]. However, UV-B photoreceptors have not been described in ferns, their absence justified by their growth habits under low-light angiosperm canopies. In the model plant *Arabidopsis thaliana*, red/far-red lights are detected by five PHYs (A-E), blue/UV-A by two PHOTs, three CRYs, and ZTL/FKF1/LKP2 proteins [6,11,13], while UV-B by a canonical UVR8 (Figure 1a). Increase in photoreceptors number and function during plant evolution has been related to fitness improvement [9].

In plants and algae, photoperiod regulates a number of processes including photomorphogenesis, growth, flowering, stress tolerance and circadian rhythms [16,17,18•]. In darkness, some of these pathways are inhibited by CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1), a RING-finger E3 ubiquitin ligase. During the day, COP1 is inhibited by the photoreceptors allowing the activation of photoperiodic-dependent processes (Figure 1a). At night, COP1 interaction with SUPPRESSOR OF PHYTOCHROME A (SPA1) targets the transcription factors ELONGATED HYPOCOTYL 5 (HY5) and CONSTANS (CO) for ubiquitination and degradation, suppressing photomorphogenesis and flowering respectively [20,21]. Photoactivated CRY1, CRY2 and PHYA directly bind SPA1 and inhibit the formation of COP1-SPA1 complex [19]. PHYB also promotes COP1-SPA1 dissociation and photomorphogenic development [22]. COP1 interaction with EARLY FLOWERING 3 (ELF3) induces degradation of GIGANTEA (GI), a circadian clock associated protein, process inhibited by CRY1/CRY2 in blue light [23]. Upon UV-B irradiation, UVR8