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Photoreceptor-dependent regulation of photoprotection

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In photosynthetic organisms, proteins in the light-harvesting complex (LHC) harvest light energy to fuel photosynthesis, whereas photoreceptor proteins are activated by the different wavelengths of the light spectrum to regulate cellular functions. Under conditions of excess light, blue-light photoreceptors activate chloroplast avoidance movements in sessile plants, and blue- and green-light photoreceptors cause motile algae to swim away from intense light. Simultaneously, LHCs switch from light-harvesting mode to energy-dissipation mode, which was thought to be independent of photoreceptor-signaling up until recently. Recent advances, however, indicate that energy dissipation in green algae is controlled by photoreceptors activated by blue and UV-B light, and new molecular links have been established between photoreception and photoprotection.

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Introduction

In photosynthetic organisms, light collected by pigments present in the light-harvesting complexes (LHCs), such as chlorophylls and carotenoids, is transferred to the reaction centers of photosystems (PS) I and II, triggering electron flow, leading to ATP and NADPH generation for use in CO_2-fixation. The protein superfamily making up the LHC includes the chlorophyll-a/b-binding proteins (CAB), the early light-induced proteins (ELIP) and the high-light-induced proteins (HLIP), as well as the PSBS protein [1,2].

Mostly blue and red light are collected by LHCs to fuel photosynthesis, but plants also express photoreceptor proteins collectively sensitive to almost every light wavelength. These photoreceptors convert light, sensed by chromophore molecules, into biological signals controlling gene expression, photo-orientation, developmental processes, entrainment of the circadian clock, and many other processes. Thus, in higher plants, light signals are perceived through five distinct families of photoreceptors: phytochromes, which respond to red and far-red illumination; blue-light-activated phototropins; cryptochromes; Zeitlupe family proteins; and the ultraviolet B (UVB) photoreceptor UV Resistance locus 8 (UVR8) [3] (Box 1).

Regardless of the color of the light, if its intensity exceeds the photosynthetic capacity of the cells, plants activate efficient photoprotective mechanisms to avoid light-induced damage. These mechanisms involve regulation of the absorption of light and dissipation of excess absorbed light. To regulate light absorption sessile plants can move their chloroplasts away from the light, whereas motile algae can swim away from the light (photophobic response). To dissipate excess light energy both plants and algae induce a photoprotective mode known as non-photochemical quenching (NPQ). The fastest component of NPQ is the energy quenching (qE); under excess light conditions the photosynthetic electron transfer acidifies the lumen modifying the pigments composition via the xanthophyll cycle and activating the switch of LHCs from harvesting mode to energy-dissipation mode. The qE process relies on pH-sensing proteins from the LHC-Stress Related family (LHCSR) and/or PSBS [4–6] that convert excess light energy into heat, but the exact mechanism of energy dissipation remains unresolved [7,8].

It has been long believed that qE is triggered by photosynthetic stress perception in the chloroplast and up until recently, the photoprotective mechanism qE and photoreception were considered to be unrelated in photosynthetic organisms. However, a recently-acquired body of evidence suggests that they are in fact interlinked. In this review, we will focus on the interconnections that have been identified between photoperception and photoprotection, summarized in Figure 1.

Chloroplast photorelocation and phototaxis: responses to blue and green light

In *Arabidopsis thaliana*, chloroplasts accumulate at the cell surface under low-light conditions (accumulation response); in response to strong light, they move away from the irradiated area (avoidance response). The two

Box 1 Glossary of photoreceptor-related, photoprotection-related and other key terms

Chromophore: light-sensing molecule of photoreceptors.

UVR8: UV-B specific photoreceptor. Seven-bladed β-propeller protein in which UV-B is sensed by specific tryptophan residues. UVR8 interacts with the E3 ubiquitin ligase COP1 to modulate gene expression.

PHOT: phototropin. Blue-light photoreceptor composed of two similar flavin mononucleotide chromophores (Light–Oxygen–Voltage LOV domains) and a Ser/Thr kinase domain regulating the downstream signaling.

CRY: cryptochromes. Flavoprotein receptors activated by UV-A and blue light.

Zeitlupe: additional UV-A and blue light photoreceptor found in land plants.

ChR: channelrhodopsin: light-gated ion channels involved in phototaxis in *Chlamydomonas reinhardtii*.

Aureochrome: blue-light activated transcription factor that regulates blue-light responses in stramenopiles (a major line of eukaryotes that includes diatoms and brown algae).

Phytochromes: red and far-red light specific photoreceptors that usually have phytochromobilin as chromophore.

Neochromes: chimeric phytochrome-phototropin protein found in some green algae and ferns.

NPQ: non-photochemical quenching of chlorophyll fluorescence. Mechanisms associated with PSII leading to the dissipation of excess light energy in the chloroplast.

qE: most prominent and fastest component of the NPQ response. qE corresponds to a thermal dissipation of excess energy that is released as heat. This process is mediated through the activity of PSBS and/or LHCSR proteins and is dependent on the generation of a proton gradient across the thylakoid membrane and on specific carotenoid pigments.

PSBS: This protein enhances the thermal dissipation of NPQ (qE) in plants, mosses and *Chlamydomonas reinhardtii*.

LHCSR/LHCX: Light Harvesting Complex Stress Related proteins. LHC proteins involved in the qE response in green algae, diatoms and mosses.

OCP: Orange carotenoid protein. Protein involved in the qE response in cyanobacteria. This protein is activated by strong blue-green light and dissipates excess energy after its binding to phycobilisomes.

PBS: phycobilisomes. Light harvesting proteins in cyanobacteria, where LHC proteins are absent.

movements are related as chloroplast accumulation is controlled by the overlapping functions of the blue-light-activated kinases PHOT1 and PHOT2 [9], whereas chloroplast avoidance is specifically controlled by PHOT2 [10,11] working in combination with the downstream effector Chloroplast Unusual Positioning 1 (CHUP1), an actin-binding protein [12]. Chamydomonas performs phototaxis in low light and initiates a photophobic response under sudden strong illumination. Phototaxis signaling is mediated by the photoreceptors Channelrhodopsin (ChR) 1 and 2, light-gated proton and calcium channels [13,14]. ChR1 is thought to be the dominant receptor for photophobic responses [15,16]. Its function is partly controlled by PHOT, as when cells are transferred from darkness to light, PHOT is required to reduce both the eyespot's size and the abundance of ChR1. Thus, PHOT – via its kinase function – is considered to be a regulator of phototaxis that desensitizes the eyespot when blue light intensities increase [17].

Whereas no direct link between photoprotection and the photophobic response has been demonstrated in *Chlamydomonas*, Arabidopsis *phot2* and *chup1* mutants, defective in chloroplast avoidance response, suffered from photoinhibition and resulted in severe leaf photo-bleaching and necrosis after exposure to strong illumination [18]. Interestingly, the Arabidopsis *phot2* mutant displayed wild-type levels qE [19•] highlighting the importance of the regulation of light absorption via the chloroplast photorelocation in photoprotection. Due to the chloroplast movement, fewer photon are absorbed and consequently less Chl fluorescence is emitted per leaf area during the NPQ measurements, leading to an overestimation of the amplitude of NPQ, that has been named qM [19•].

Blue light as a key player in regulating LHCSR and NPQ

Action spectrum (light color-dependency) experiments in *Chlamydomonas* recently indicated that blue light induces the qE response and LHCSR3 accumulation much more effectively than red light, even though the cells absorbed both blue and red light almost equally [20••]. This observation led to the discovery that the blue-light photoreceptor, PHOT, controls the induction of LHCSR3 and qE in response to high light (HL) via integration of a signal from the blue-light-activated PHOT kinase with a chloroplastic signal, controlled by photosynthetic activity (Figure 2). The combined signals control transcription of *LHCSR3.1* and *LHCSR3.2*, both encoding LHCSR3. The chloroplastic signal is unrelated with the redox state of the plastoquinol pool [21] but its precise nature remains elusive. The *phot* mutant and the *phot* mutant complemented to express only the LOV domains of the *PHOT* gene – photosensory regions controlling kinase activity – are photosensitive under HL. Taken together, these observations indicate that the combined action of photoreception, photosynthesis and photoprotection is vital for acclimation of the microalgae to changing light conditions. In contrast, a *phot* mutant complemented with a PHOT gene lacking the LOV domains, and thus displaying constitutively active kinase activity, was not photosensitive and induced LHCSR3 and qE in a color-independent but photosynthesis-dependent manner [20••].

The links between photoprotection and blue light are not limited to green algae, but seem to be shared by many other photosynthetic organisms. These interactions may

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