



Light signaling in photosynthetic eukaryotes with ‘green’ and ‘red’ chloroplasts



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ABSTRACT

Light drives one of the most important processes on earth—photosynthesis. Besides providing the energy for carbon reduction, it is also an important signaling source, which largely influences the acclimation and adaptation behavior of algae and plants. Two different ways of light perception can be differentiated: direct and indirect light signaling. Direct light signaling is based on the action of photoreceptors. Indirect light signaling originates from the photosynthetic light reaction and is either based on the redox state of the photosynthetic electron transport chain or on reactive oxygen species. Especially the indirect signaling raises a specific challenge for plants and algae: while the signal perception occurs in the chloroplast, the largest part of the target genes is located in the nucleus, i.e. the triggering signal needs to cross several membranes. Green algae and plants (the ‘greens’) achieved to establish mechanisms which transfer the so called ‘retrograde’ signal from the chloroplast into the nucleus. Besides identifying the primary light triggers and regulated target genes, researchers discovered a bunch of secondary messengers, which may connect the light trigger with the target genes in a signaling network. Still, the exact signaling cascades are basically unknown so far.

The knowledge about direct light signaling in organisms with ‘red’ plastids (red algae and those with secondary red plastids, such as stramenopiles, hacrobian and dinoflagellates) is comparatively little compared to the ‘greens’. However, it is clearly advancing and interesting novelties were found in recent years, e.g. the discovery of the aureochrome photoreceptor class. In contrast, the knowledge about indirect light signaling in these organisms is still in its infancy. Given their ecological importance in the aquatic environment and for global net primary production, this lack of information needs to be removed in future research. This review aims at providing a comparatively short summary about light signaling in the ‘greens’, while gathering most of the information available for the ‘reds’, which may attract researchers to start studying light signaling in this largely neglected group.

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Abbreviations: APX, ascorbate peroxidase; β -CC, beta-cyclocitral; CRY, cryptochrome; LOV, light, oxygen and voltage; MECPP, methylerythrol cyclodiphosphate; PAP3⁻, phosphoadenosine 5'-phosphate; PEP, plastid encoded RNA-polymerase; PET, photosynthetic electron transport chain; Phangs, photosynthesis associated nuclear genes; PHOT, phototropin; PHY, phytochrome; PQ, plastoquinone; ROS, reactive oxygen species; SOD, superoxide dismutase; TRX, thioredoxin.

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1. Background

During evolution of eukaryotic photosynthesis, three different eukaryotic organism groups developed after engulfment of a cyanobacterium by a heterotrophic eukaryotic host cell and the subsequent establishment of the bacterium as a stable, primary plastid (primary endosymbiosis): the glaucophytes, the green algae and the red algae (Gould et al., 2008). While the land plants evolved from green algae (both are called the ‘green’ line in the following), red algae gave rise to a variety of photosynthetic supergroups by becoming their plastid due to secondary endosymbiosis. These algae primarily inhabit aquatic habitats and include the hacrobian (cryptophytes and haptophytes), the alveolates (dinoflagellates as the most important photosynthetic lineage) and the stramenopiles (diatoms, brown algae, eustigmatophytes, chrysophytes, raphidophytes, xanthophytes) (Keeling, 2013). Among these ‘red’ plastid

containing organisms are the most important eukaryotic primary producers of the oceans, i.e. diatoms, haptophytes and dinoflagellates (Uitz et al., 2010; Taylor et al., 2008).

For all these photosynthetic lineages, light is not only the energy source which drives photosynthesis, it also carries information about its quantity, quality and temporal availability. Hence, much information is encoded in the light which is perceived by photosynthetic organisms and helps to determine environmental factors such as day length, light quantity and spectral composition. This information can be intercepted by plants, algae and cyanobacteria, is then deconvoluted and analyzed by a highly sophisticated sensory system and finally becomes integrated into the cellular signal transduction network which triggers the circadian and annual rhythms, photoprotective mechanisms, quantitative balancing of the photosynthetic apparatus, phototile movements in unicellular algae, developmental processes such as germination, shade avoidance and flowering, and metabolic light acclimation responses. Light even provides information about the position in a plant community or quorum sensing, as it is the case for some algal communities. In sum, there is a lot of information in the light which helps to acclimate, adapt and survive in the environment as a photosynthetic organism. Therefore, in every photosynthetic organism ranging from 'ancient' cyanobacteria over the green algae and land plants to red algae and species with plastids evolved by secondary endosymbiosis, a huge arsenal (tool box) of light sensing and signaling mechanisms have evolved. Many of them, especially in the 'green line', have been dissected in molecular detail and a lot of excellent work has been done and published in order to clarify the role of photoreceptors and other light signaling pathways (Casal, 2013; Hegemann, 2008; Rockwell et al., 2006; Falciatore and Bowler, 2005; Rüdiger and López-Figueroa, 1992). In this review we want to compare direct and indirect light sensing and signaling mechanisms between photosynthetic organisms from the 'green' line with those of the 'red' line. While we only provide a relatively short summary about light signaling in the 'greens' and refer to the respective excellent works which treat the issue exhaustively, we will try to present everything known so far in organisms with 'red' plastids. By doing so, we want to show up the commonalities and differences in light signaling of eukaryotic photosynthetic organisms in order to pave the way for future research questions which will close the immense knowledge gap between 'greens' and 'reds'. As even in 'greens' the exact mechanisms behind the respective light signaling process are only revealed to a minor extent so far, the comparison of organisms with 'red' and 'green', with primary and secondary plastids as well as of eukaryotic photosynthetic organisms living in aquatic or terrestrial habitats may help to identify universal and specific traits of light signaling characteristics.

2 Direct light signaling triggered by photoreceptors

2.1. Direct light signaling in 'greens'

The big leap from water to the land required several adaptations to the new light environment. On the one hand the incident light on the earth's surface is stronger than in the water and almost the full spectrum is found, i.e. photosynthetic organisms are now faced with a stronger red spectrum and stronger UV radiation since waters dampens the incident light in the UV and red to far-red regions (Pope and Fry, 1997; Sogandares and Fry, 1997). This is especially true for photosynthetic organisms which are exposed to direct sunlight at high altitudes. Therefore in plants specialized UV receptors (UVR) for UV-B radiation have evolved.

On the other hand most terrestrial ecosystems are organized in communities with dense population. This leads to rather crowded canopies where photosynthetic active radiation (PAR)

gets absorbed in an exponential manner and most of the surface is rarely exposed to direct sunlight (Fig. 1A). Within the canopies the light gets scattered and especially PAR of blue and red wavelengths is absorbed and drives photosynthesis. The remaining light is primarily of red spectral quality, which cannot be efficiently used to drive oxygenic photosynthesis—the so called red drop effect (Emerson and Rabinowitch, 1960). Consequently, plants possess a comparable high number of red (R)/far red (FR) light receptors in order to sense the R/FR ratio, which is indicative for the position of a plant within a canopy or of a seed above or beneath the surface (Fig. 1B). The group of photoreceptors mediating developmental responses to R/FR light is the phytochromes (see Section 2.1.1). Besides red light also blue light is sensed by plants and green algae: The responsible photoreceptors are cryptochromes, phototropins and the zeitlupe protein. In green algae blue and blue-green light is additional sensed by rhodopsins. In some species even chimeric photoreceptors, e.g. phytochrom-phototropin combinations (called 'neochromes'), have been found like AcNEO in the fern *Adiantum* (Nozue et al., 1998) or MsNEO 1 and 2 in the green alga *Mougeotia scalaris* (Suetsugu et al., 2005). The only waveband not well covered by photoreceptors is yellow light and interestingly, it is besides UV that light quality which causes the most photodamage at high irradiances (Takahashi et al., 2010).

Another specific feature of plants is that they are multicellular organisms with highly specialized tissues, and not all of these tissues are photosynthetically active or possess fully operational light signaling systems. Some light signals have to be transferred within tissues and even through the whole organism, thus in addition to the single cellular response there is a crosstalk between light signaling and hormone responses (Casal, 2013).

2.1.1. Red light photoreceptors—Phytochromes

In the model plant *Arabidopsis* five phytochromes (PHY) have been identified, which can be divided into two subclasses: the photo labile class I where PHY A belongs to, and the relatively stable class II with PHY B-E. All PHYs contain a heme derived bilin (a linear tetrapyrrole) as chromophore. In case of plant PHYs this is phytychromobilin while in cyanobacteria it is phycocyanobilin (for structural details of PHYs, see Ulijasz and Vierstra, 2011; Rockwell et al., 2006; Falciatore and Bowler, 2005). The chromophore is covalently attached via a cysteine side chain to a specific domain at the N-terminus, while the output domain is located at the C-terminus and includes a histidine kinase related domain which resembles the kinase domain in bacterial two-component systems. However, this histidine kinase domain phosphorylates serine and threonine residues (Yeh and Lagarias, 1998). Functional PHYs are organized in dimers. PHYs exist in an inactive (dark) form (Pr), which can be photoconverted into the active form (Pfr) after absorbing visible light with a maximum around 660 nm (Shinomura et al., 1996). The active Pfr form absorbs far red light with wavelengths around 730 nm. The two forms are convertible by absorption of the respective light quality, which leads to structural changes of the chromophore followed by changes of the protein backbone. Usually, the Pr form is localized in the cytosol, while it channels into the nucleus in the Pfr form (Kircher et al., 2002) by exposing a nuclear targeting sequence (NLS). How phosphorylation regulates PHY activity is not fully clear, since the N-terminal dimeric photosensory domain alone is fully functional in the nucleus (Matsushita et al., 2003). The signaling mechanism of PHYs is highly versatile. They may form homodimers (PHY A) or heterodimers (other PHYs, Sharrock and Clack, 2004). After photoconversion by red light they can interact with factors like FAR-RED ELONGATED HYPOCOTYL 1 (FHY1) in the cytosol facilitating nuclear import. In the nucleus PHYs may bind to PHYTOCHROME INTERACTING FACTORS (PIFs), which are bHLH-transcription factors mediating different light responses (Casal, 2013). Genes regulated by PHY typically carry

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