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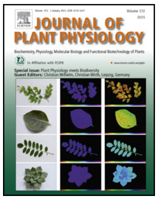

Review

Dealing with light: The widespread and multitasking cryptochrome/photolyase family in photosynthetic organisms☆

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SUMMARY

Light is essential for the life of photosynthetic organisms as it is a source of energy and information from the environment. Light excess or limitation can be a cause of stress however. Photosynthetic organisms exhibit sophisticated mechanisms to adjust their physiology and growth to the local environmental light conditions. The cryptochrome/photolyase family (CPF) is composed of flavoproteins with similar structures that display a variety of light-dependent functions. This family encompasses photolyases, blue-light activated enzymes that repair ultraviolet-light induced DNA damage, and cryptochromes, known for their photoreceptor functions in terrestrial plants. For this review, we searched extensively for CPFs in the available genome databases to trace the distribution and evolution of this protein family in photosynthetic organisms. By merging molecular data with current knowledge from the functional characterization of CPFs from terrestrial and aquatic organisms, we discuss their roles in (i) photoperception, (ii) biological rhythm regulation and (iii) light-induced stress responses. We also explore their possible implication in light-related physiological acclimation and their distribution in phototrophs living in different environments. The outcome of this structure-function analysis reconstructs the complex scenarios in which CPFs have evolved, as highlighted by the novel functions and biochemical properties of the most recently described family members in algae.

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Introduction

Sunlight is composed of different wavelengths of light from ultraviolet (UV) to infrared (IR), all playing important roles in how organisms perceive their environment and alter their physiology accordingly. Light perception is particularly important as the spectra and intensity of solar radiation changes depending on factors

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like the geographical location, the time of the day or season, the weather conditions and the presence of phototrophs. Photosynthetic organisms, which rely on light as source of energy, have evolved a variety of photoreceptors and sophisticated mechanisms to perceive variation in light intensity and quality that tightly regulate growth, development and acclimation in different environments (Kami et al., 2010; Rockwell et al., 2014).

Characteristics of particular ecosystems may determine variations in light distribution and quality. Prominent examples of light alteration are the wavelength-selective irradiance attenuation that occurs under leaf canopies in terrestrial environments and along the water column in the oceans. Leaves strongly absorb ultraviolet (UV) wavelengths and the blue and red parts of the photosynthetically active radiation (PAR, 400–700 nm), whilst far-red (700–800 nm) and green light (550 nm) are mostly transmitted or reflected (Casal, 2013). These leaf-specific light absorption properties lead to enrichment in the ratios of far-red to red and, to some extents, of green to blue wavelengths. Light quality under the tree canopy or under the shade of higher plants is a result of a plant's position in the environment and the presence of neighbors. In the oceans, light penetration is affected by the absorption and scattering processes of water itself and of dissolved and particulate substances in seawater. The result is a strong decrease and uneven distribution of light irradiance in oceans. Since light absorption by water is wavelength dependent – stronger in the UV, red and far-red ranges than in the blue and green wavelengths – the blue and green components of sunlight penetrate farther into the seawater, so deep ocean waters are enriched in blue light (Depauw et al., 2012; Kirk, 2011). In the ocean, these variations in the light spectrum and intensity with depth may influence the distribution and performance of photosynthetic organisms (Scanlan et al., 2009).

Periodic light variations, a way to measure the time of day or in the year (seasons), are often an important cue for organisms. The light/dark cycle is one of the most regular periodic signals for all the organisms and governs rhythmic changes in the metabolism, physiology and behavior of most species. The rhythmic responses are essentially controlled by an endogenous cellular mechanism, the circadian clock, which is daily synchronized to the diurnal light variations, allowing organisms to anticipate environmental changes (Hotta et al., 2007; Song et al., 2010).

Besides its beneficial effects, light can also be toxic. In particular, the UV components of sunlight can damage DNA, mainly by inducing the formation of pyrimidine dimers. Living organisms have evolved a variety of repair mechanisms to counteract UV-induced damage, some of which are light-dependent themselves like the photolyase photoreactivation mechanism (Sancar, 2008). Excessive amounts of light can also produce other types of biological damage like the formation of cytotoxic reactive oxygen species (ROS) through the blue light-dependent excitation of natural photosensitizers such as flavins or porphyrins (Losi and Gartner, 2012). In addition, when the rate of photosynthesis reaches saturation, excess light causes an increase in ROS production with consequent photoxidative stress and cellular damage (Li et al., 2009; Ziegelhoffer and Donohue, 2009). This is normally prevented by controlled heat dissipation via the photosynthetic pigments (Büchel, 2015) and by complex regulation of pigment-protein interactions (Goss and Lepetit, 2015). Photosynthetic bacteria, plants and algae have diverse strategies and complex acclimation processes to survive under intense light stress (Bray and West, 2005; Eberhard et al., 2008; Li et al., 2009).

Light in the blue part of the spectrum (400–500 nm) triggers or influences many important biological processes such as growth, development and photosynthesis of terrestrial and aquatic primary producers. The ability to perceive and respond to blue light *via* flavin blue light sensors is observed in the majority of living organisms (Losi and Gartner, 2012). In this review, we focus on the cryptochrome/photolyase family, here referred as CPF, a class of structurally related blue light absorbing flavoproteins found in all the kingdoms of life. Although the evolutionary history of this protein family is still not completely resolved, it is well known that CPFs mediate a variety of responses, with prominent roles in blue light-dependent DNA repair, light perception and circadian regulation (Chaves et al., 2011; Thompson and Sancar, 2002).

By taking advantage of the increasing number of sequenced genomes from diverse phototrophs, we searched for novel CPFs in organisms thought to derive from discrete endosymbiotic events that live in a range of environments. We then merged the information on the distribution and evolution of CPFs with data about their characterized functions. We finally discuss how the diversity within the CPF might have contributed to the evolution of a variety of light acclimation physiological processes, promoting the ecological success of photosynthetic organisms in different environments.

Common structural and biochemical properties of the cryptochrome/photolyase family

The CPFs constitute a large group of flavoproteins (from the Latin "flavus" for yellow) including photolyases and cryptochromes (Cry), members of which are found in all organisms. Photolyases are light-activated DNA repair enzymes that can mend two different types of UV-induced DNA damage, either cyclobutane pyrimidine dimer (CPD) or (6–4) pyrimidine–pyrimidone (6–4 PP) photoproducts, and are thus classified either as CPD or as (6-4) photolyases (Sancar, 2008). In contrast, Crys generally do not have catalytic DNA repair activity, but have photoreceptor or transcription regulation functions (Sancar, 2003). Moreover, multifunctional CPFs have been described recently (Beel et al., 2013). Besides the functional diversity, CPF proteins share common structural and biochemical properties (Fig. 1A and B). All members of this family possess the photolyase homology region (PHR), a highly conserved domain to which two non-covalently attached chromophores can bind (Fig. 1A and B) (Muller and Carell, 2009). All CPFs bind a flavin adenine dinucleotide (FAD) chromophore. This FAD undergoes light-dependent reduction through an intramolecular electron transfer involving aromatic residues (Aubert et al., 2000; Chaves et al., 2011; Liu et al., 2013). This reaction could be considered as a common mechanism for the CPF-light activation as it has been observed in all different CPFs tested so far. This reaction generates the active fully reduced form, ($FADH^-$) necessary for the DNA repair activity of the photolyases and has been correlated with light-induction of Cry photoreceptors. In particular, different ground and activation states have been proposed for Cry photoreceptors (Aubert et al., 2000; Iwata et al., 2010; Kottke et al., 2006; Ozturk et al., 2008b; Spexard et al., 2014). In the "oxidized model", it is assumed that blue light absorbing FAD_{ox} is the ground state. Light exposure leads to intramolecular electron transfer allowing the reduction of FAD_{ox} to radical forms (either $FAD^{\bullet -}$ or $FADH^{\bullet}$) which are the signaling forms. Subsequently, the radical form can be completely reduced to the inactive $FADH^-$, which is then rapidly oxidized to the inactive ground state FAD_{ox} (Banerjee et al., 2007; Bouly et al., 2007; Herbel et al., 2013; Muller and Ahmad, 2011). In the "reduced model," it is proposed that the FAD is in the semi-reduced form *in vivo*, either $FAD^{\bullet -}$ (blue light absorbing) or $FADH^{\bullet}$ (blue to red absorbing), and that light induces a cyclic electron transfer initiating the proteolysis of the protein or reduction to the active fully reduced form (Beel et al., 2012; Liu et al., 2010).

In addition to FAD, the PHR domain can also bind a second chromophore that acts as light-harvesting molecule transferring the excitation light energy to the "catalytic" FAD, thus working as antenna (Saxena et al., 2005; Worthington et al., 2003). The binding site for this secondary chromophore is the same in all CPF proteins,