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Review article

An update on aureochromes: Phylogeny – mechanism – function☆

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ABSTRACT

Light is important for algae, as it warrants metabolic independence via photosynthesis. In addition to the absorption of light by the photosystems, algae possess a variety of specific photoreceptors that allow the quantification of the light fluxes as well as the assessment of light qualities. About a decade ago, aureochromes have been described in the xanthophyte alga *Vaucheria frigida*. These proteins represent a new type of blue light photoreceptor as they possess both a light-oxygen-voltage (LOV) domain for light reception as well as a basic region leucine zipper (bZIP) domain for DNA binding, indicating that they represent light-driven transcription factors. Aureochromes so far have been detected only in a single group of algae, photosynthetic stramenopiles, but not in any other prokaryotic or eukaryotic organisms. Recent biophysical work on aureochromes in the absence and the presence of DNA revealed the mechanism of allosteric communication between the sensor and effector domains despite their unusual inversed arrangement. Different molecular models have been proposed to describe the effect of light on DNA binding. Functional characterization of mutants of the diatom *Phaeodactylum tricornutum*, in which the aureochrome genes have been silenced or deleted, indicate that different aureochromes may have different functions, being involved in central processes like light acclimation and regulation of the cell cycle.

1. Introduction

Light for photoautotrophic organisms not only is the driving factor for the energy-providing process of photosynthesis, it also represents an important environmental signal, triggering various physiological responses. Cells and organisms are capable of evaluating the intensity as well as the quality of the light (Kianianmomeni and Hallmann, 2014). For this purpose, they utilize so-called photoreceptors, these are proteins that are able to absorb specific wavelengths in the visible and ultraviolet range of light (Hegemann, 2008). Light absorption by these proteins results in conformational changes that may transduce this information in potentially multi-step signaling processes to the respective cellular regulatory system (Duanmu et al., 2017). While sunlight is composed of a wide spectrum of wavelengths from ultraviolet to infrared, most of the photoreceptors in plants and algae absorb either in the UV/blue or in the red/far-red spectral range of wavelengths (Depauw et al., 2012). Phytochromes, to current knowledge, are the only widely distributed photoreceptors that are absorbing red light. These proteins possess a linear tetrapyrrole as a prosthetic group and can be switched reversibly from an active to an inactive state by red and far-red light, respectively (Chen and Chory, 2011). Recently, spectrally tuned phytochromes have been identified in algae that cover the whole visible spectral region (Rockwell et al., 2014), possibly as adaptation to the light conditions in the ocean. In contrast, a larger number of different blue light photoreceptors are known, most of which are using a flavin as chromophore. Cryptochromes are binding flavin adenine dinucleotides (FAD). They are blue/UV-A light receptors that form a large and diverse family with photolyases that are involved in repair of UV-damaged DNA (Chaves et al., 2011; Mittag et al., 2017; König et al., 2017; Kottke et al., 2017). Another group of blue light receptors contain light-oxygen-and-voltage (LOV) domains (Crosson et al., 2003), which are binding a flavin mononucleotide (FMN). Prominent representatives here are the phototropins and the aureochromes. In euglenophyta, there are also other blue light sensors using FAD (BLUF) (Kennis and Mathes, 2013). Finally, microbial rhodopsins have been identified to be involved in light-induced locomotion of green flagellates (Foster et al., 1984; Ernst et al., 2014). In *Chlamydomonas reinhardtii*, these light-gated ion channels named channelrhodopsins are located in the

Abbreviations: AUREO, aureochrome; BL, blue light; bZIP, basic region leucine zipper; FMN, flavin mononucleotide; FCP, fucoxanthin binding complex; LOV, light-oxygen-voltage; NPQ, non-photochemical quenching; PS, photosystem; RL, red light

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photosensory eyespot (Suzuki et al., 2003).

In algae, a number of physiological responses to blue light are known. One early studied example is phototaxis (Halldal, 1958), the ability of motile algae to move either to or away from light. In the filamentous green alga *Mougeotia scalaris,* photoorientation of the ribbon-shaped chloroplast has been demonstrated to be induced by blue light, probably by phototropins (Gabryś et al., 1984; Suetsugu et al., 2005). For this alga, as well for mosses and ferns (Li et al., 2014), a new type of photoreceptor has been described recently, neochrome, which essentially is a fusion protein of a phytochrome and a phototropin. The role of this chimeric photoreceptor is unknown, especially as the neochrome LOV domains apparently cannot bind flavins (Suetsugu et al., 2005). Also in diatoms, blue light-stimulated chloroplast movement and aggregation has been demonstrated (Shihira-Ishikawa et al., 2007).

In this review, we focus on the distribution, the structural response, as well as the functional characterization of aureochromes, light driven transcription factors that just recently have been discovered (Takahashi et al., 2007) in some stramenopiles, including brown algae (Ishikawa et al., 2009), diatoms (Bowler et al., 2008), raphidophytes (Jia et al., 2017), and eustigmatophytes (Vieler et al., 2012).

2. Distribution of aureochromes in algae

Aureochromes have been originally identified in the xanthophyte alga *Vaucheria frigida* in 2007 (Takahashi et al., 2007) and have been termed aureochromes referring to “aurum” (latin for gold), because of the golden-yellow color of some stramenopiles. *Vaucheria* is a siphonous alga, which means that it consists of giant coenocytic unicells that are not divided by separating cell walls. There had been very early reports that *Vaucheria* responds to blue light with phototropism (Kataoka, 1979), side branch formation (Takahashi et al., 2001), and plastid movement (Blatt and Briggs, 1980). Takahashi et al. (2007) screened genomic *Vaucheria* sequences for LOV domains, which are common domains involved in different sensory processes in pro- and in eukaryotes (Herrou and Crosson, 2011). The authors then identified so far unknown genes for potential photoreceptors with an unusual domain combination, possessing a LOV domain at the C-terminus, as well as a basic-region leucine zipper (bZIP) domain, indicating that these proteins might also have DNA-binding capacities and may act as transcription factors. In *V. frigida*, two orthologs were identified, *Vf*AUREO1 and *Vf*AUREO2. Using an RNAi approach to silence these two genes individually, Takahashi et al. (2007) could demonstrate that both *Vf*AUREOs are involved in photomorphic responses of *Vaucheria*, and that *Vf*AUREO2 specifically acts as a negative regulator for the differentiation of sex organs. Silencing of both *Vf*AUREO1 and *Vf*AUREO2 simultaneously induced abnormal tube morphology. Interestingly, blue light-induced chloroplast movement was not affected in these mutants, indicating the presence of further blue light receptors. With the upcoming availability of genomic DNA sequences, researchers tried to identify aureochromes in other algae either by sequence similarity (Deng et al., 2014; Schellenberger Costa et al., 2013) or via PCR amplification (Ishikawa et al., 2009). Interestingly, although proteins containing LOV domains are widely distributed in all kinds of organisms (Glantz et al., 2016), aureochromes so far only have been detected in an algal group named stramenopiles (Ishikawa et al., 2009; Schellenberger Costa et al., 2013), with the exception of the related, but generally non-photosynthetic, oomycetes (Fig. 1). Aureochromes apparently are also completely missing in red algae, which are considered to represent the endosymbiotic ancestors of stramenopile plastids (Archibald, 2015), as well as in related algal groups like cryptophytes or haptophytes. Finally, there are also no indications that aureochromes might be present in green algae and in land plants (Fig. 1). This suggests that either the so far unknown host cell of secondary endosymbiosis may have provided the aureochrome gene, or that the aureochromes, possessing this unique combination of LOV and bZIP domains, evolved very early within the stramenopiles, possibly by domain shuffling (Di Roberto and Peisajovich, 2014). A close relative of aureochromes, the blue light receptor phototropin, contains two LOV domains and a Ser/Thr kinase domain for signal transduction (Christie, 2007; Li et al., 2015), but no DNA binding domain. Phototropins have only been detected so far within the Viridiplantae, thus in green algae and land plants (Li et al., 2015), but are missing in red algae. This makes it unlikely that aureochromes might have evolved from phototropins directly via domain shuffling. This notion is supported by phylogenetic studies by Ishikawa et al. (2009), demonstrating that the aureochrome LOV domains are phylogenetically separated from both LOV1 and LOV2 domains of phototropins.

3. Classification of aureochromes

Because of their apparently different functions, the *Vaucheria* aureochromes have been termed *Vf*AUREO1 and *Vf*AUREO2 (Takahashi et al., 2007). After the identification of aureochromes in other organisms, a similar strategy first has been pursued by simply numbering the genes/proteins, even if there were more than two aureochrome genes present in a species. A closer look at the *Vaucheria* aureochromes, however, reveals that the two *Vf*AUREOs are structurally different. *Vf*AUREO2 shows a mutation, which prevents binding of an essential flavin, and which abolishes light absorbance in the blue range. Structural analyses of *Pt*AUREO2 indicate that a steric hindrance by a methionine residue within its binding cavity is responsible here (Banerjee et al., 2016a). Therefore, both *Vf*AUREO2 and *Pt*AUREO2, strictly speaking, are not photoreceptors, but transcriptions factor that may interact with AUREO1 proteins by forming DNA binding heterodimers. Genetic modification of *Pt*AUREO2 from the diatom *Phaeodactylum tricornutum* allowed the restoration of flavin binding (Serif et al., unpublished). Introducing, in a reciprocal experiment, a point mutation at the same site into *Pt*AUREO1a results in a similar loss of flavin binding (Banerjee et al., 2016a). When analyzing the four aureochromes from *P. tricornutum* and from other algae, Schellenberger Costa et al. (2012) observed that all studied groups possessed an AUREO2 protein. The other three *Pt*AUREOs are functionally and phylogenetically more related to *Vf*AUREO1, and thus have been named *Pt*AUREO1a/1b/1c, accordingly. However, phylogenetic analysis indicate three different branches of AUREO1 proteins (Schellenberger Costa et al., 2013). This separation is supported by the gene expression patterns of the four *P. tricornutum* aureochromes. The differential expression of *Pt*AUREO1a/1a/1c/2 was studied in light- and circadian-dependent transcript analyses with cells grown in a day/night cycle or kept in the dark for at least one day (Banerjee et al., 2016b). The results show individual transcription patterns for the different aureochromes. While the non-flavin-binding *Pt*AUREO2 appears to be expressed in a time- and light-independent manner, lacking any significant light/circadian regulation, all other AUREO homologs showed differential expression patterns throughout the day. *Pt*AUREO1a revealed a light-independent circadian regulation, being upregulated during the day both in day/night cycles as well as in continuous darkness. *Pt*AUREO1b transcripts instead were significantly increased in illuminated cultures compared to the cultures grown in darkness, while again *Pt*AUREO1c was strongly expressed during the day in both conditions (Banerjee et al., 2016b). These findings indicate the presence of different amounts of the individual aureochromes in *P. tricornutum* cells in the diel cycle, suggesting either distinctly regulatory, or temporal functions. Considering that aureochromes potentially may form heterodimers, the combination of dominant aureochrome species in a cell at a certain time point may define their regulatory properties by their specific DNA binding affinities.

4. Mechanism of aureochromes

4.1. Differences to other LOV-based photoreceptors

Aureochromes and phototropins share the same light-absorbing unit, the LOV domain. Blue light absorption causes an adduct formation