REVIEW PAPER

Exploring the molecular basis of responses to light in marine diatoms

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Received 5 December 2011; Revised 5 December 2011; Accepted 3 January 2012

Abstract

Light is an essential source of energy for life on Earth and is one of the most important signals that organisms use to obtain information from the surrounding environment, on land and in the oceans. Prominent marine microalgae, such as diatoms, display a suite of sophisticated responses (physiological, biochemical, and behavioural) to optimize their photosynthesis and growth under changing light conditions. However, the molecular mechanisms controlling diatom responses to light are still largely unknown. Recent progress in marine diatom genomics and genetics, combined with well-established (eco) physiological and biophysical approaches, now offers novel opportunities to address these issues. This review provides a description of the molecular components identified in diatom genomes that are involved in light perception and acclimation mechanisms. How the initial functional characterizations of specific light regulators provide the basis to investigate the conservation or diversification of light-mediated processes in diatoms is also discussed. Hypotheses on the role of the identified factors in determining the growth, distribution, and adaptation of diatoms in different marine environments are reported.

Key words: Diatoms, functional genomics, light acclimation and adaptation, photoreceptors.

Introduction

The oceans cover ~70% of the Earth’s surface, and photosynthetic organisms living in the photic zone are responsible for half of the global primary productivity (Falkowski and Raven, 2007). Marine photosynthesis is dominated by eukaryotic microalgae, which together with cyanobacteria are collectively called phytoplankton. These organisms drive most of the major oceanic processes; for >3 billion years, they have actively influenced the composition of the Earth’s atmosphere, ultimately creating conditions that have allowed multicellular organisms to evolve (Knoll, 2003; Katz et al., 2004; Falkowski and Knoll, 2007).

Contributing at least 20% of the global CO₂ assimilation and to the biogeochemical cycling of important nutrients, such as carbon, nitrogen, and silicon (Smetacek, 1999), diatoms are key ecological players in the contemporary ocean. These enormously diverse microalgae (Guillard and Kilham, 1977; Vanormelingen et al., 2008) possess unique biological features (e.g. silicon frustules) (Kooistra et al., 2007) and complex metabolic pathways (Bowler et al., 2008; Allen et al., 2011), probably obtained from their ancestors via secondary endosymbiosis (Tirichine and Bowler, 2011). Since their radiation 180 million years ago, diatoms have shown high plasticity in adapting to different environmental conditions (Kooistra et al., 2007). Diatoms proliferate in ice (Thomas and Dieckmann, 2002), generally dominate in upwelling systems (Margalef, 1978), thrive in subsurface layers (Crombet et al., 2011), and are considered the best-fit group in turbulent environments (Margalef, 1978). The basis of their ecological success is still poorly understood, although recent results suggest that diatoms utilize sophisticated mechanisms to respond to environmental changes (Falciatore et al., 2000; Ianora et al., 2004; Vardi et al.,...
2006; Matsuda et al., 2007; Bowler et al., 2008). In particular, as will be summarized in a following section, several species can cope with highly variable light conditions, suggesting that diatoms are capable of perceiving, responding to, and, probably, anticipating light variations and that they possess suitable molecular systems for mediating light responses. Notwithstanding, our understanding of light-driven processes in marine diatoms is still in its infancy, and present knowledge of their photobiology is largely based on physiological and in situ studies, with less information available at the molecular level, in contrast to other aquatic model systems, such as cyanobacteria (Grossman et al., 2001) or Chlamydomonas (Rochaix, 2002).

The recent progress in marine diatom genomics and genome-enabled resources, combined with the well-established (eco) physiological and biophysical approaches, offers novel opportunities to explore the molecular basis of the response to light in marine diatoms. Here some of the recent advances in the diatom photobiology field with regard to two specific aspects, photoprotection and photoperception, are described. These processes do not cover the entire complexity of light responses, but, to date, they have been better investigated in terms of their functional aspects. The analysis of these processes facilitates an understanding of a possible diversification of diatom light sensors and light regulators. It also allows the design of novel hypotheses about their role in controlling diatom growth and adaptive responses in the oceans. Because the differences between the marine and terrestrial environments have probably contributed to the evolution of specific light adaptation and light acclimation mechanisms in diatoms, the features of the underwater light field are first summarized.

The underwater light field

Aquatic environments differ from the terrestrial environment in many aspects and impose different constraints on photosynthetic organisms. Light intensity and nutrient concentrations are lower in aquatic than in terrestrial environments. In contrast, terrestrial photosynthetic organisms can suffer from water limitation and can be exposed to stronger temperature variations (Margalef, 1974). The intensity of direct light is at least one or two orders of magnitude higher on land and can decrease to levels comparable with marine conditions only beneath dense canopies (Fig. 1). The spectral properties of light and their spatial and temporal variations are also different. The light spectrum on land is modified by atmospheric attenuation and by the absorption or reflectance of other plants, the

![Fig. 1.](https://academic.oup.com/jxb/article-abstract/63/4/1575/449618/Exploring-the-molecular-basis-of-responses-to by guest on 15 September 2017)
latter resulting in a general bias towards longer wavelengths (Björn, 2008). In aquatic environments, light varies not only because of the incident solar radiation and time of the day but also because of the absorptive and scattering processes of the water, the depth of the water column, and the presence of coloured dissolved organic matter and suspended particles, to which photosynthetic organisms themselves contribute (Kirk, 1994). Water strongly absorbs light in the red and infrared wavebands, and the absorption slightly increases towards UV wavelengths, which causes a progressive dominance of the blue-green (400–500 nm) spectral components with depth (Fig. 1). Nonetheless, despite the strong attenuation of the red and infrared light from the sun, these components are still present in the sea, although at low intensities. Their presence is due to transspectral processes that are responsible for the emission of the absorbed light at longer wavelengths, such as in the case of chlorophyll a fluorescence (Mobley, 1994). All of the aforementioned processes combine differently in different regions of the hydrosphere (e.g. lacustrine versus marine, eutrophic versus oligotrophic) and make the variability of underwater light fields very distinct from the terrestrial variability.

Additionally, natural water movements (such as tides, streams, and mixing in the upper layer) cause relevant spatial displacements of marine microorganisms, which have no equivalent in the terrestrial environment (Mann and Lazier, 2006). Consequently, the variation of the underwater light field sketched above, in combination with vertical displacements, produces light variations that may significantly impact cell physiological responses (Esposito et al., 2009). Vertical displacement is always coupled with a parallel variation of the light spectrum, which may allow for organisms to distinguish the variation in intensity due to clouds or time of the day from the variation produced by the displacement itself. Whether and how marine unicellular phototrophs discriminate among the different origins of light variations (e.g. diurnal, seasonal, and global changes, both in irradiance and in spectral distribution) is still an open and intriguing question.

In recent years, exciting discoveries derived from recent progress in genomics and metagenomics have revealed that differences in the marine light field can lead to previously unsuspected types of phototrophy in aquatic microorganisms (Béjá et al., 2000; DeLong and Béjá, 2010; Slamovits et al., 2011) and to a variety of evolutionary adaptations (e.g. the depth-dependent niche separation of picophytoplankton ecotypes with different light adaptation properties) (Stomp et al., 2004; Cardol et al., 2008; Partensky and Garczarek, 2010; Demir-Hilton et al., 2011). These discoveries also highlight the fact that light-driven processes are still largely unknown in marine organisms, and it is expected that many mechanisms remain to be discovered.

**Diatom responses to light**

All photosynthetic organisms must reconcile two requirements: capturing a sufficient number of photons to run the photosynthetic machinery and avoiding the photons’ damaging effects. This general strategy is pursued in different ways by different organisms and with multiple responses spanning various time scales (Rochaix, 2004; Eberhard et al., 2008). Generally, under high irradiance, when the main need is photoprotection, the responses are rapid (seconds or less) and do not require changes in gene expression. Excess energy is rapidly dissipated as heat or by changing the distribution of the excitation energy between photosystems. To face the effects of excess energy, the systems for repairing damage to photosystem II (PSII) or for scavenging reactive oxygen species (ROS) are activated. If the exposure to high light continues, gene expression is activated to modify the photosynthetic apparatus and the photochemistry (Eberhard et al., 2008). Reciprocally, under low light, when the primary need is to sustain photocapture, the responses are generally slower and generate changes in the light-harvesting pigment content via a change in the size or number of the photosynthetic units (Falkowski and Owens, 1980; Eberhard et al., 2008).

Different studies indicate that diatoms are no exception to this general scheme, and it may also be assumed that for these successful photoautotrophs, photosynthesis is one of the main targets of regulation (Falkowski and Raven, 2007; Nymark et al., 2009; Finazzi et al., 2010; Lepetit et al., 2011). However, a direct extrapolation of the well-established knowledge of the regulation of photosynthesis, acquired from the study of green algae and plants, is not always applicable to diatoms. The diatom chloroplast is significantly different from those of chlorophytes (an envelope with four membranes instead of two, the thylakoids are arranged in stacks of three, there is no spatial segregation of the photosystems, and there is a peculiar protein and pigment organization) (Wilhelm et al., 2006; Lepetit et al., 2011). Furthermore, ecophysiological studies have also indicated that different species possess different capabilities to cope with light variations. Fundamental differences in photosynthetic architecture between coastal and oceanic diatoms have been reported (Strzepek and Harrison, 2004), and different photoprotection capacities among species living in different habitats, for example with different patterns of light variability and intensity, have been demonstrated (Dimier et al., 2007; Lavaud et al., 2007; Brunet and Lavaud, 2010). All of these observations imply a possible diversification of the diatom light-regulatory mechanisms and adaptive responses, compared not only with other photoautotrophs but also among different diatom species.

In addition to managing the light variations for effective photosynthesis, it is very likely that diatoms monitor the quality, periodicity, and direction of light to gain information about their external world. For example, the upward and downward migration of benthic diatoms in sediments following the daily cycle of illumination (Harper, 1977) or the light-mediated plastid displacement in *Pleurosigma laevis* (Furukawa et al., 1998) hints at the presence of photoreceptors. Moreover, different gene expression analyses have revealed that diatoms respond to low fluences of blue,
red, and far-red light, suggesting a photoreceptor regulation of the relevant cellular processes (Table 1 and below). Finally, the circadian variation in photosynthetic and photoprotective pigments in the model species *Phaeodactylum tricornutum* hints that these rhythmical variations are not only dependent on light availability (Post et al., 1984) but may also respond to internal regulation through a putative endogenous circadian clock (Raghi and Ribera d’Alcala, 2007).

Genomic tools and knowledge from the genomes of representative species now permit a deeper exploration of the molecular components regulating diatom responses to light, making these organisms attractive models for photobiology research.

### A suite of new resources

#### Genomic information

The sequencing of *Thalassiosira pseudonana* (Armbrust et al., 2004), *P. tricornutum* (Bowler et al., 2008), and several other diatom genome sequences [e.g. the polar species *Fragilariopsis cylindrus* (http://genome.jgi-psf.org/Fracy1/Fracy1.home.html)] has been completed or is near to completion (e.g. the toxic species *Pseudo-nitzschia multiseries*) (Tirichine and Bowler, 2011). Comparative genomic analyses now facilitate the discovery of their peculiar metabolic pathways and the presence of novel genes that might help to explain diatoms’ remarkable physiological flexibility. The genomic data offer the opportunity to investigate the conservation or the diversification of the diatom regulators of light responses and are enriched by novel information from the chloroplast genomes of *Odontella sinensis*, *T. pseudonana*, and *P. tricornutum* (Kowallik et al., 1995; Oudot-Le Secq et al., 2007). Following the endosymbiotic events, plastid genomes have retained a limited number of genes related to the chloroplast function, and other genes have been either lost or transferred to the nuclear genome. The fact that some genes have both a chloroplast- and a nucleus-encoded copy might indicate that gene transfer to the nucleus could still be ongoing (Green, 2011). As for other photosynthetic eukaryotes, diatom chloroplast biogenesis and functioning may require a tight coordination between the nucleus and chloroplast genome activities.

#### Nuclear transformation and reverse genetics

The establishment of nuclear transformation has represented a major resource for the initial study of gene functions in several diatom species (Dunahay et al., 1995; Apt et al., 1996; Falcicatore et al., 1999; Poulsen et al., 2006; Miyagawa-Yamaguchi et al., 2011). In particular, the modulation of gene expression, either by overexpression (Siaut et al., 2007) or by knock-down through RNA interference (RNAi)-based gene silencing methodology (De Riso et al., 2009), has recently been exploited for the characterization of light sensors and light regulators (see below). Genetic transformation has also been an important tool for the functional characterization of specific transit

### Table 1. Available gene expression data obtained from different diatom species grown under various light conditions

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peptides that drive plastid protein import (Gruber et al., 2007).

Plastid mutation

The first targeted plastid mutagenesis has been achieved by homologous recombination in the \textit{psbA} gene, which encodes the D1 protein (Materna et al., 2009). Although the mechanisms leading to the mutation have not been completely established, this work provided the first evidence that diatom plastid transformation is feasible and that the engineering of chloroplast genes could become a common tool.

Expression profiling

In photosynthetic organisms, responses to light can involve massive changes in gene expression, and the analysis of light-regulated genes provides important information for the identification of light signalling pathways and their regulatory components (Gill et al., 2002; Jiao et al., 2007; Peschke and Kretsch, 2011). In recent years, several gene expression analyses have been performed with diatom cells exposed to different light conditions (Table 1). Transcriptional profiling, following a shift from low light to high light, provided the first picture of the molecular processes implicated in the acclimation to high light stress of several diatom species. Integrated studies described the molecular, metabolic, and physiological responses of diatoms during distinct light acclimation phases (initial, intermediate, and late acclimation phases) (Nymark et al., 2009), unveiling possible novel molecular factors implicated in the light stress responses (e.g. the LHCX gene family, which will be described in more detail below) (Nymark et al., 2009; Bailleul et al., 2010; Park et al., 2010; Zhu and Green, 2010). Similar analyses performed using cells exposed to light of different wavelengths indicated that light quality, potentially perceived by blue and red light photoreceptors, may regulate important processes, such as nutrient metabolism, the synthesis of pigments and light-harvesting components, and even cell cycle progression, a process that is known to require a light–dark periodicity (Leblanc et al., 1999; Coesel et al., 2008, 2009; Bowler et al., 2010). Notably, recent genome-wide analyses unveiled a new class of light-modulated specific cyclins in diatoms (Huysman et al., 2010), and the work of Gillard et al. (2008) highlighted the close coupling between light regulation, chloroplast ontogeny, and cell cycle progression.

Biochemical approaches

The diatom chloroplast still contains many secrets. However, significant progress has been made in recent years in understanding the components of the diatom photosystems and the molecular organization of the light-harvesting complexes (LHCs; Buchel, 2003; Beer et al., 2006), due to the use of novel biochemical and biophysical approaches (see, for example, Nagy et al., 2011; Wu et al., 2011). Proteomics is also an important instrument for identifying differentially expressed or compartmentalized proteins and the biochemical pathways implicated in light responses. A recent study reported a detailed proteome map of the thylakoid protein complexes of \textit{T. pseudonana} and \textit{P. tricornutum}, and revealed the existence of novel diatom-specific photosystem I (PSI)-associated proteins, providing a novel basis for the understanding of the assembly and dynamics of the diatom photosynthetic complexes (Grouneva et al., 2011).

Regulators of the diatom NPQ process

The discovery of novel regulators of diatom light responses came from the characterization of the non-photochemical quenching (NPQ) process. The NPQ consists of the enhanced thermal dissipation of absorbed energy that occurs in PSII whenever the light absorption exceeds the maximum CO$_2$ assimilation rate (Eberhard et al., 2008). Diatoms display an extremely high NPQ capacity, up to five times higher than that of green algae and higher plants (Ruban et al., 2004). Moreover, diatoms are able to apply the photoprotective mechanism to maintain high growth rates and a high photosynthetic efficiency over a wide range of light intensities (Falkowski and Laroche, 1991; Lavaud et al., 2003).

In several model organisms, the NPQ capacity is linked to three main traits: the energy-dependent quenching (qE), state transitions (qT), and photoinhibition (qI) (Li et al., 2009). The qE is the major photoprotective strategy in higher plants, green algae, and diatoms. The qE operates on a time scale of seconds to minutes and serves to avoid photoinhibition. The qT, which involve a redistribution of excitation energy between PSII and PSI through a reversible migration of the LHCs, have not been found in diatoms (Owens, 1986).

In plants, NPQ is triggered by a change of the thylakoid luminal pH under high light, activating the xanthophyll cycle (see below) and the PSII protein PsbS. The latter triggers the onset of NPQ by sensing luminal pH changes and amplifies fluorescence quenching in a concentration-dependent manner (Li et al., 2000). In the green alga \textit{Chlamydomonas reinhardtii}, PsbS is not expressed. Instead, recent studies have shown that the LHC stress-related (LHCSR) proteins play a similar role (Peers et al., 2009). LHCSR protein levels are induced by high light in \textit{Chlamydomonas} and also correlate with the qE capacity in \textit{O. tauri}. Therefore, NPQ in green algae shows the same pH modulation as in plants but relies on LHCSR proteins. Interestingly, the \textit{Physcomitrella patens} moss genome encodes both PsbS and LHCSR proteins (Alboresi et al., 2010), which are both active in NPQ. Thus, it is has been proposed that upon land colonization, photosynthetic organisms evolved a unique mechanism for excess energy dissipation based on PsbS, before losing the ancestral system, found in algae and mosses, that is based on LHCSR proteins (Fig. 2).
Recently, the first regulators of the diatom NPQ have been identified. The process seems to depend on at least two factors: a specific xanthophyll cycle and the activity of LHCSR-like effectors, with different efficiencies and pH requirements from those of terrestrial plants and green algae.

The xanthophyll cycle

Carotenoids play fundamental roles in light harvesting and photoprotection (Demmig-Adams and Adams, 1996). Exposure to different light conditions induces changes in carotenoid composition via the xanthophyll cycle (XC) (Li et al., 2009). The XC involves the reversible light-dependent conversion of violaxanthin (Vx) to zeaxanthin (Zx) via antheraxanthin (Ax) intermediates. Under excessive light intensity, the violaxanthin de-epoxidase (VDE), activated by the decrease in thylakoid lumen pH, binds the thylakoid membrane and converts Vx to Zx. Zx is involved in the NPQ response through either a direct or an indirect mechanism (see Lepetit et al., 2011). Following dark or low light conditions, the zeaxanthin epoxidase (ZEP) converts the Zx back to Vx in a reverse reaction.

Diatoms and other chromophytes display a simple XC, which comprises the one-step conversion of diadinoxanthin (Ddx) to diatoxanthin (Dtx) (Goss and Jakob, 2010). However, if subjected to prolonged high light, diatoms are also able to perform a conventional XC (Lohr and Wilhelm, 1999). The superior NPQ capacity of diatoms has been partially attributed to this peculiar XC. A correlation between Dtx and NPQ increase has been shown under high light and in different light stress conditions (Brunet and Lavaud, 2010). However, the mechanistic aspects of the Dtx-dependent NPQ in diatoms are much less established, and the binding site of Dtx, either to the FCPs or the lipid phase of the FCPs, has not been elucidated yet (Goss and Jakob, 2010; Lepetit et al., 2011 for discussion).

Again, diatom genome sequences have provided some clues regarding the possible diatom XC actors (Coesel et al., 2008; Frommolt et al., 2008). More copies of the genes encoding the VDE and ZEP enzymes were found in P. tricornutum and T. pseudonana genomes compared with other photosynthetic eukaryotes (Fig. 2). Some of the genes are similar to the VDE and ZEP of higher plants, while others are more distantly related (e.g. the violaxanthin de-epoxidase-like gene, VDL). Interestingly, the diatom-specific VDL and ZEP variants show some differences in protein domains that are critical for the localization of the plant ZEP and VDE into specific chloroplast compartments and for their light-dependent activation and deactivation (Coesel et al., 2008). Overall, the diatom-specific variants might be involved in the chloroplast-specific Ddx cycle, but their functional and biochemical characterization is still missing.

The diatom LHCSR family

Phylogenetic studies revealed multiple members of the LHCSR light-harvesting complex protein family in diatoms, which are related to the green algal LHCSR/LI818 proteins (Fig. 2). Recent gene expression studies showed that several LHCSR proteins are strongly and quickly induced upon exposure to high light in T. pseudonana (LHXC4 and LHXC6), in P. tricornutum (LHXC2 and LHXC3), and in Chaetoceros neogracilis (FCP12, FCP14, and FCP15), in support of their direct role in excess energy dissipation (Table 1 and references). However, interesting novel information has been derived from the functional characterization of P. tricornutum LHXC1, which is not high light responsive, in contrast to the other gene members of the family. A structural role within the PSII–FCP supercomplex was originally proposed for this isoform (Zhu and Green, 2010). However, molecular and biophysical analyses have demonstrated that LHXC1 plays a central role in the regulation of NPQ. Knockdown mutants generated using RNAi had a significantly reduced NPQ capacity, although their XC capacity, PSII efficiency, photosynthetic yield, and pigment composition were unaffected. The mutants also showed a decreased fitness, demonstrating a key role for the protein in mediating light acclimation (Bailleul et al., 2010). Altogether, this work challenges the long-standing dogma that the peculiar NPQ in diatoms is solely due to the presence of a different XC. The results also demonstrate the key role of LHXC1 as a molecular gauge that controls the NPQ level, similarly to the plant PsbS protein. The constitutive presence of LHXC1 proteins in cells acclimated to non-stressful light conditions could provide diatoms with the capacity to anticipate unpredictable changes in light intensity, providing a selective advantage in turbulent waters. Interestingly, the LHXC1 protein significantly contributes to the natural variability of diatom photoprotection. This contribution is exemplified by the analysis of different P. tricornutum ecotypes isolated from different worldwide locations that show different NPQ capacities (Bailleul et al., 2010). In particular, the Pt4 ecotype, from the Baltic Sea, exhibits low NPQ (possibly due to an adaptation to the weak illumination conditions at high latitudes) and also a low LHXC1 expression level, suggesting that this NPQ effector is subjected to adaptive evolution in specific environments.

The function of other LHCSR family members has not been elucidated yet. Their expression under excessive light hints at their involvement in photoprotection, similarly to the Chlamydomonas LHCSR protein. Thus, these proteins may support LHXC1 function under prolonged high light stress, but they could also play additional or specialized roles to improve diatom fitness.

Biochemical information about the diatom LHCSR proteins is still very limited, and therefore, how these proteins act in the NPQ process is not clear. Several studies suggest that these proteins are not essential for sensing the lumenal pH. Data have shown that pH variations modulate fluorescence quenching in P. tricornutum by acting only on the turnover of the XC enzymes (Goss et al., 2006). Moreover, comparative protein sequence analyses confirm that the residues important for sensing pH in algae and plants are absent in the diatom orthologues (Li et al., 2009; Bailleul et al., 2010). An interesting novel scenario has
arisen through the proteomic analysis of the thylakoid membranes of two marine diatom species that identified some LHCX members as part of PSI (Grouneva et al., 2011). These data suggest a possible role for the LHCX proteins in uncharacterized PSI-specific photoprotection mechanisms or in an unknown function. Additional biochemical and structural information regarding LHCX proteins in the protein–pigment complexes and functional studies of different diatom species will be necessary to clarify these aspects.

**Light sensors**

Light-sensing molecules, such as photoreceptors, allow many organisms to perceive light signals and to initiate a downstream signal pathway. Photosensory proteins are usually modular in their architecture. One or more domains serve as a sensory input domain and may bind the chromophore, an organic, non-protein component that confers specific photochemical properties. Chromophores undergo physicochemical and structural changes upon light absorption, which are essential for the signal propagation (Moglich et al., 2010). Six main classes of photoreceptors have been identified and classified according to the chemical nature and photochemistry of their chromophores (Moglich et al., 2010): the light–oxygen–voltage domain (LOV) with a flavin mononucleotide (FMN) as the chromophore; cryptochrome (cry) and the blue light sensor using FAD (BLUF), both using flavin adenine dinucleotide (FAD); photoactive yellow protein (PYP), with a \( p \)-coumaric acid (\( p \)CA) chromophore; rhodopsin, with retinal; and the...
phytochrome (phy) class, with a tetrapyrrole as the chromophore. Because of the increased number of sequenced genomes, a variety of photoreceptors are being revealed, in which specific sensory domains are found in novel combination with different effectors.

A comprehensive description of photoreceptor functions and evolution is beyond the scope of this review (see Krauss et al., 2009; Moglich et al., 2010; Rodriguez-Romero et al., 2010; Ulijasz et al., 2010; Chaves et al., 2011; Gomelsky and Hoff, 2011, and references therein). Instead the focus will be on the diatom photoreceptors identified in *Phaeodactylum* and *Thalassiosira*, discussing their nature and possible function. Diatoms possess multiple putative photoreceptors belonging to the LOV, cry, and phy families (Fig. 3). The biochemical and functional characterization of these proteins and their chromophores is still very limited, and the signalling cascades and regulatory processes (e.g. transcriptional and post-transcriptional regulation, second messengers, and the role of chromatin remodelling) that they activate are basically unknown. Comparative genomic studies have also revealed that none of the downstream components of plant photoreceptor pathways (Kami et al., 2010) is present in diatoms. Therefore, the elucidation of the light signalling pathways will require novel genetic and biochemical investigations.

**Blue light sensing**

Because of the spectral properties of underwater light (Fig. 1), blue light sensors are expected to be crucial for controlling the life of marine organisms. Interestingly, despite the fact that diatoms are capable of moving plastids within the cell, diatom genomes lack the gene for phototropin that is widely distributed in the green lineage (Christie, 2007). However, two other blue light photoreceptor families, the cry and the aureochrome, are present in multiple copies in these organisms.

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**Fig. 3.** Domain structures of the photosensory molecules found in the *P. tricornutum* (Pt; Phatr2:http://genome.jgi.psf.org/annotator/servlet/jgi.annotation.annotation?pDb=Phatr2) and *T. pseudonana* (Tp; Thaps3: http://genome.jgi-psf.org/Thaps3/Thaps3.home.html) domain architecture according to the PFAM database (http://pfam.sanger.ac.uk/). (A) Cryptochrome/photolyase family. (B) Aureochrome. (C) Phytochrome. In the figure are reported the protein identification (ID) numbers of the *Phaeodactylum* and *Thalassiosira* genomes, the best hit in the NCBI database for *Phaeodactylum* (the BLASTP searches were performed on the NCBI sequence browser on 19 August 2011), the putative chromophores, and a short protein description. The domain abbreviations are as follows: PHR, photolyase-related domain; CCT, cry C-terminal domain; bZIP, basic leucine zipper domain; LOV, light–oxygen–voltage domain; GAF, GAF domain; PHY, phytochrome domain; HK, histidine kinase domain; RR, response regulator; and C, conserved cysteine residue. The chromophore abbreviations are as follows: FAD, flavine adenine dinucleotide; MNTF or pterin, 5,10-methenyltetrahydropteroylpolyglutamate; HDF, deazaflavin; and FMN, flavin mononucleotide. The species abbreviations are as follows: *E. siliculosus*, *Ectocarpus siliculosus*; *O. antarcticus*, *Octadecabacter antarcticus*; *O. tauri*, *Ostreococcus tauri*; *R. baltica*, *Rhodosirellula baltica*; and *D. rerio*, *Danio rerio*. The asterisk in PtDPh corresponds to the conserved cysteine residue for putative chromophore binding.
The cryptochrome/photolyase family

Crys are blue/UV-A light photoreceptors that are widely distributed throughout all of the kingdoms. These receptors mediate various light-induced responses in plants and animals (Chaves et al., 2011), and their function in the generation of circadian rhythms is highly conserved, either as input components in the circadian clock or as transcriptional repressors in the negative feedback loop of the circadian oscillator (Doherty and Kay, 2010).

Crys share sequence similarities with photolyases, flavoproteins that catalyse the repair of cyclobutane pyrimidine dimers (CPDs) and 6–4 photoproducts (6–4PPs) within UV-damaged DNA (Sancar, 2003). It is generally accepted that the functions of photolyases and crys differentiated during evolution, with crys losing the DNA repair activity. However, this assumption has recently been questioned because photolyases exhibiting gene-regulatory activity have been characterized in fungi (Berrocal-Tito et al., 2007; Bayram et al., 2008), in the green alga Ostreococcus (Heijde et al., 2010), and in diatoms (see below). Moreover, the recently identified cry-DASH protein, whose signalling and function remain largely unclear (Brudler et al., 2003; Kleine et al., 2003), has also been shown to have DNA repair activity (Daiyasu et al., 2004; Huang et al., 2006).

In agreement with their common origin, photolyases and crys possess considerable structural similarity in the N-terminal photolyase homology region (PHR) that is responsible for chromophore binding and light absorption. All of the members of the family use FAD and either a pterin (MTHF) or a deazaflavin (HDF) as chromophores. The light activation of these molecules is determined by changes in the flavin redox state and electron transfer. The terminal photolyase homology region (PHR) that is responsible for chromophore binding and light absorption contains a DAS domain with recognizable motifs (Li and Yang, 2007). In contrast, the animal CCT is less conserved, and its role in cry function has been established only in a few organisms (Chaves et al., 2011).

Computational analyses of diatom genome sequences have revealed several members of the cry/photolyase family (Coesel et al., 2009) (Fig. 3). Cry-DASH (CPF2-4) is the most represented, with several members in both Phaeodactylum and Thalassiosira (Fig. 3). In addition, these two species possess another member that is phylogenetically closer to the animal 6–4 photolyases (cryptochrome/photolyase family 1; CPF1) but is nonetheless an independent clade. The presence of an animal-type protein can be explained by the evolutionary history of this group of organisms, and by the fact that many diatom proteins are more similar to their animal rather than to their plant counterparts (Bowler et al., 2008). Surprisingly for photosynthetic algae, diatom genomes do not contain a clear orthologue of plant Cry genes, while several genes encode CPD photolyases. A member of this family (Fig. 3) has a C-terminal extension, which normally is not present in the photolyases. This extension does not contain the plant DAS domain, and it is not known whether the extension has a role in signalling. Besides CPF1, no additional 6–4 photolyases were found in the diatom genomes.

The functional and biochemical characterization of the Phaeodactylum CPF1 has provided novel information regarding the diatom cry family. The primary structure of CPF1 exhibits a high similarity with animal crys. It notably displays residues that are important for cellular circadian regulations (Stanewsky et al., 1998). PtCPF1 also contains a 28 amino acid C-terminal extension, which is comparable with the extension described in Drosophila but lacks the plant DAS domain (AF, unpublished results). On the other hand, the Phaeodactylum and the Thalassiosira CPF1s both possess residues that are crucial for the (6–4) photolyase activity (Hitomi et al., 2001). This activity was confirmed through biochemical studies. The Phaeodactylum CPF1 binds and repairs 6–4 PP in vitro (Coesel et al., 2009), and transgenic cpf1 knock-down lines are hypersensitive to UV exposure (De Riso et al., 2009). Additionally, the demonstration that PtCPF1 can act as a circadian clock transcriptional repressor in a heterologous mammalian cell system, similarly to the mouse cry, provided the first indication of an additional regulatory role for this protein. The function was confirmed by blue light-dependent gene expression studies showing that the genes encoding proteins involved in distinct processes (photosynthesis, photoprotection, cell cycle, DNA repair, and others) are misregulated in overexpressing CPF1 lines, suggesting a possible function for CPF1 as a photoreceptor (Coesel et al., 2009; Table 1).

Because crys and photolyases share many residues, it is not possible from the sequence alone to predict if the other diatom CPFs possess DNA repair activity or a role in light signalling (Fig. 3). This limitation also prevents the estimation of the nature of their chromophores. Further biochemical and functional analyses combined with structural studies will be necessary to identify the residues responsible for these different functions and to determine the light properties allowing their specific activity.

The LOV sensors

LOV-containing photoreceptors are widely distributed among prokaryotes and eukaryotes (Krauss et al., 2009; Losi and Gartner, 2011). The receptors contain a LOV domain that binds FMN as a chromophore and acts as a sensor module. Light induces structural changes in the LOV domain, which has a photochemistry distinct from that of other flavin-based sensors. LOVs can be found associated with other different protein domains, in a variety of combinations, and in tandem as in the phototropins. Among the different LOV photoreceptors identified in eukaryotes [the phototrops and ZEITLUPE family in plants, the white-collar (WC-1) in fungi, the LOV-HKs, and the aureochrome; Moglich et al., 2010], only the aureochromes have been found in diatom genomes.
The aureochromes

The recent finding of the aureochromes as specific blue light receptors in the heterokont clade is particularly significant. The discovery suggests the presence of a suite of novel photoreceptors in marine organisms derived from the secondary endosymbiosis event (Takahashi et al., 2007; Krauss et al., 2009) and whose expansion has probably been favoured by the predominance of blue light in marine environments.

Initially discovered in the algae Vaucheria frigida (Xanthophyceae) and Fucus distichus (Phaeophyceae) and the diatom T. pseudonana, the aureochromes are blue light-regulated transcription factors with an N-terminal basic zipper domain (bZIP) and a C-terminal LOV domain. The LOV domain contains a cysteine residue in a highly conserved sequence motif, which is required for flavin-cysteiny1 adduct formation upon light excitation, and blue light increases the affinity of the bZIP domain for DNA (Takahashi et al., 2007). To date, functional studies have only been reported for the V. frigida aureochrome. Gene knock-down experiments revealed the role of the aureochrome in mediating blue light-induced branching and sex organ development, similar to the role of plant photoreceptors for photomorphogenesis (Takahashi et al., 2007).

The biological functions of diatom aureochromes are still unknown. However, by searching for the LOV domain within the genomes, it is possible to observe an expansion of this protein family. Four aureochrome-like proteins have been identified in both P. tricornutum and T. pseudonana (Fig. 3), and a recent in silico study highlighted them as potential blue light-regulated transcription factors (Rayko et al., 2010). Although experimental work is still required, it is likely that these molecules, together with the cry/photolyase family, play major roles in blue light signalling.

Red light sensing

Despite its strong extinction in the water column (Fig. 1), red light constitutes a significant signal underwater. Importantly, a rapidly decreasing, but still detectable, flux of red photons is present throughout the photic zone (Ragni and Ribera d’Alcàlà, 2004). It has been argued that band ratios (e.g. R:FR, B:R, and G:R) may act in marine phytoplankton as complex switches controlling relevant processes, such as pigment synthesis, photoadaptation, phototaxis, swimming velocity, gravitaxis, and chloroplast displacement (Lopez-Figueroa, 1992). Similar reports also exist for some bacteria and green algae (Kraml and Herrmann, 1991; Sineshchekov et al., 2000), with red light phototaxis often being negative (Kondou et al., 2001). Thus, perceiving red light may allow different scopes. Red light perception may allow for the determination of the proximity to the water surface, where excessive light can induce photodamage. A more intriguing hypothesis is that red light deriving from chlorophyll autofluorescence may be perceived (Ragni and Ribera d’Alcàlà, 2004). At a close distance (<100 μm), notably when cells aggregate or form chains, chlorophyll autofluorescence could overcome the background signal, and the red light may then be used for quorum sensing or might affect the process of aggregation.

In fact, several pieces of functional evidence support the presence of red light photoperception in diatoms. As previously described, several genes are induced by both red and far-red light, and red light can accelerate the sinking of diatoms more rapidly than white and blue light (Fisher et al., 1996). Red light can also induce motility responses in some estuarine species (Mclachlan et al., 2009). The biological importance of red light has finally been reported for the sexual reproduction of H. ostrearia, for which exposure to red wavelengths triggered auxosporation (Mouget et al., 2009). Interestingly, for the fungus Aspergillus nidulans, a red/far-red light photoreceptor is also required for sexual sporulation and sexual development (Blumenstein et al., 2005). It will thus be of interest to investigate the role of diatom phys in these and other aspects of their biology.

Diatom phytochromes: putative red light sensors

The phys constitute a superfamily of photoreceptors that usually enable organisms to sense red/far-red light. Initially discovered in plants, in which they play a central role in many developmental processes, phy and phy-like sequences are widely dispersed among bacteria, fungi, and even some non-photosynthetic organisms, in which the phys have diverse functions (e.g. chromatic adaptation, pigment synthesis, phototaxis, sexual development, and probably many other metabolic adaptations) (Karniol et al., 2005; Rockwell et al., 2006; Ulijasz and Vierstra, 2011).

The “prototypic” phys are biliproteins that exist in two photo-interconvertible states, the Pr and the Pfr, which are red (λmax 660 nm) and far-red (λmax 730 nm) light-absorbing forms, respectively (Rockwell et al., 2006). The biliproteins are initially sensitized as Pr (inactive state) and convert into the biologically active Pfr form following red light irradiation. Far-red treatment converts phys back to the Pr form. This peculiar photochemistry is due to conformational changes of the linear tetrapyrrrole chromophore that are followed by changes in the protein conformation. Plant phys have a phytochromobilin (PΦB) as a chromophore, the cyanobacteria a phycocyanobilin (PCB), while the bacterial (BphP) and fungal (Fphs) phytochromes use biliverdin IXa (BV), the precursor of PΦB and PCB.

Structurally, the phys have a modular architecture, consisting of an N-terminal photosensory domain and a less conserved output domain (Ulijasz et al., 2010). In plant phys, Cph, and most BphPs, the N-terminal photosensitive domain comprises Period/ARNT/Single-minded (PAS), cGMP phosphodiesterase/adenylate cyclase/FhLA (GAF), and phytochrome-specific (PHY) domains. The phys and Cph are linked to the chromophore via a conserved cysteine in the GAF domain. In bacteria and fungi, however, the chromophore is bound to a cysteine upstream of the PAS domain. The N-terminal domain of the plant phy is also
involved in the transfer of the light signal by interacting with nuclear-localized transcription factors, such as the phytochrome-interacting transcription factors (PIFs) (Matsushita et al., 2003; Oka et al., 2008). Two additional PAS domains, located in the C-terminal region, are important for the nuclear localization.

The C-terminal regulatory output domain varies among different species but always contains a histidine kinase-related domain (HKRD). In bacteria and fungi, the phys are light-regulated histidine kinases that perform histidine autophosphorylation and transphosphorylation of an aspartate within a response regulator (RR) domain. The RR domain can also be fused to the HKRD. Many plant phys lack the histidine residue required for autophosphorylation. Nevertheless, in vitro Ser/Thr kinase and phosphotransfer activities have been reported (Fankhauser et al., 1999).

New phy-related variants have been discovered, with potential novel functions (Vierstra and Zhang, 2011). Phy-like variants missing the PAS domain or both the PAS and the PHY domains have been found in some cyanobacterial species, along with phy-like proteins with wavelength sensitivities spanning the entire visible spectrum (cyanobacteriochromes; Cycs) (Rockwell et al., 2011). In addition to that, the phy superfamily also includes chromophore-less members, such as the achnomo-Bph found in some Rhodopseudomonas strains that function as redox sensors rather than as light sensors (Vuillet et al., 2007).

The diatom phy genes (DPh) discovered in the P. tricornutum and T. pseudonana genomes most probably represent new phy variants (Fig. 3). Phylogenetic analyses indicate that the DPhs form an independent clade with two brown-algal viruses (Montsant et al., 2007), leading to the hypothesis that a possible ‘brown clade’ of phys may exist, in which virus-mediated lateral transfer would have contributed to spread phy-like genes among the heterokonts. Structurally, the DPhs are similar to the BphPs, with an N-terminal chromophore-binding domain followed by a histidine kinase and an RR module at the C-terminus. The DPhs may therefore act as light-activated kinases (Fig. 3). However, major differences appear in the sensory domain. The T. pseudonana DPh contains an N-terminal PAS domain before the GAF, like the BphP, and presents a conserved cysteine residue upstream from the GAF domain, which in BphP has been shown to bind the BV (Ulijasz et al., 2010). In contrast, the P. tricornutum DPh lacks this PAS domain but contains the conserved cysteine residues for the chromophore attachment at the N-terminal region. Interestingly, the three phy-like sequences found in the genome of the brown algae Ectocarpus siliculosus (Cock et al., 2010) also lack the N-terminal PAS domain, suggesting that the lack of the PAS domain might represent a feature of several heterokont phys. Because this domain has a role in light sensing and in signal transduction in plants and bacteria (Oka et al., 2008; Vierstra and Zhang, 2011), its absence may suggest that the P. tricornutum DPh has different perception properties and a specific light signal cascade, involving uncharacterized downstream elements.

The spectral properties and functions of the diatom phy have not yet been characterized. Nonetheless, the T. pseudonana and P. tricornutum genomes have been thoroughly investigated for genes potentially encoding chromophore biosynthetic enzymes. Both diatom species contain several haem oxygenase genes, suggesting the production of BV from the haem and its use as a chromophore, similarly to the use of BphP and Fph. Interestingly, the genomes also contain putative bilin reductase genes (PebA and PebB), which could mediate the further reduction of BV. However, the proteins encoded by these genes are more closely related to the enzymes involved in phycoerythrobilin synthesis than to the ferredoxin-dependent bilin reductases that mediate the conversion of BV to PΦB and PCB in plants and cyanobacteria, respectively (Rockwell et al., 2006). Because diatoms do not seem to use phycoerythrobilin as a light-harvesting pigment, an interesting alternative hypothesis is that these genes may be used to produce a diatom-specific chromophore. Thus, the functional identification of the diatom chromophores and clarification of DPh spectral properties are necessary to extend the study of the phy superfamily in other secondary endosymbionts, such as diatoms.

**Novel sensors with unknown functions**

Genome-enabled analyses using known sensory domains as probes revealed a long list of uncharacterized proteins that may include some novel photoreceptors (Bowler et al., 2008; AF, unpublished results). Among them, many PAS-domain-containing proteins might be versatile sensors. Some of these proteins appear to be possible members of the LOV-HK, a new class of blue light receptors recently identified in O. tauri (Djouani-Tahri et al., 2011). Additionally, several GAF domain proteins are encoded in the diatom genomes. It remains to be seen if these proteins act as novel sensors increasing the light photosensory potential of diatom photoreceptors, similarly to the cyanobacteriochromes (Rockwell et al., 2011).

Finally, it is noteworthy that a gene encoding a rhodopsin (Spudich et al., 2000) has been found in the polar diatom Fragilariopsis cylindrus. Related sequences were also found in metatranscriptomic data, indicating the relevance of the gene in an ecological context (T. Mock, personal communication). Diatom rhodopsin photochemistry and physiological function have not been assessed yet. However, the lack of this gene in P. tricornutum and T. pseudonana suggests a selective evolutionary acquisition in some species, possibly associated with specific regulatory roles in particular environments.

**Future prospects**

During recent years, genetic and genomic resources provided novel opportunities to identify and functionally characterize the molecular actors implicated in diatom light responses. These analyses revealed the presence of
photoreceptors that could be used by diatoms to monitor and adapt properly to changing environmental conditions. Those photoreceptors have been shown to display structural or functional differences compared with their analogues in other organisms (e.g. the modular architecture of DPh or the double DNA repair/regulatory role of CPF1), although the adaptive and evolutionary implications of these differences are still not understood.

Among the identified photoreceptors, the blue light sensors in diatoms are the most abundant, showing several cryptochrome/photolyase and aureochrome family members. While the phylogenetic origin of aureochromes is linked to the secondary endosymbiosis event at the base of the hetrokонт clade, the expansion of the blue light sensors was probably favoured by the predominance of blue light in the marine environment. A possible interpretation of such richness could be the diverse range of sensitivity that blue light sensors may possess, being active at different fluence rates and facilitating the fine-tuning of various biological processes. Alternatively, the sensors could activate distinct regulatory pathways or interact with other photoreceptors, thereby increasing the number of light-modulated responses.

In diatoms, the presence of phy superfamily protein members is still puzzling but intriguing. To date, these proteins represent the only putative red light sensors identified in these organisms. However, it is not clear if they display ad hoc light-sensory functions because the identification of an associated chromophore is still missing. It is noteworthy that the recently sequenced genome of *F. cylindrus*, a species that experiences high attenuation for red light in ice (Grenfell and Perovich, 1981), does not encode any DPh (genome.jgi-psf.org/Fracy1/).

As discussed in this review, novel information has also been derived from the study of diatom responses to changing light intensities. These initial studies revealed that diatom-specific proteins of the XC and of the LHCX family are important effectors. These proteins represent an additional example of gene family expansions, whose members probably acquired novel and specific functions, providing a selective growth advantage under light fluctuations.

However, the molecular actors and the regulatory mechanisms controlling the diatom light responses are just beginning to be uncovered, and additional efforts will be required to identify the complex networks linking diatom biology with environmental light conditions.

In *Chlamydomonas* and *Arabidopsis*, the coupling of biochemical, biophysical, and physiological analyses with genetic screening and ‘omics’ approaches has been especially rewarding for the identification of both nuclear- and chloroplast-encoded light regulators. Because the function of a considerable fraction of diatom genes (~40%) (Bowler et al., 2008) cannot be determined by direct comparison with other organisms, similar integrated approaches should be used. For this goal, reverse and forward genetics approaches should be further extended, and, in parallel, novel biochemical tools should also be developed to support gene functional studies in various diatom species. These efforts should notably be directed to unveil the dynamics of the photosynthetic apparatus and to define the structural and functional changes of protein–pigment complexes further under different light conditions. Biochemical studies are also necessary to characterize the diatom photoreceptors and to establish their spectral and fluence properties.

In other phototrophs, light was shown to activate complex signal transduction cascades and regulatory processes, including transcriptional and post-transcriptional networks, second messengers, and chromatin remodelling (Jiao et al., 2007). In addition, light-dependent chloroplast activity and specific plastid signals (e.g. the redox state of the organelles, the tetrapyrrole pathway, and ROS) were also shown to impact nuclear gene expression and protein synthesis (Kleine et al., 2009; Li et al., 2009). Likewise, the endogenous circadian clock may be part of light-driven gene expression regulatory mechanisms, enabling organisms to anticipate daily changes in illumination (Stillman et al., 2007; Doherty and Kay, 2010). As one of the last comers in the marine environment, diatoms have probably embedded many of these regulatory mechanisms. However, their characterization still represents a major requisite to understanding diatom photobiology and, in general, to unveil novel light-dependent regulatory mechanisms in marine organisms.

The conservation and diversification of these processes could be assessed by extending the analysis of diatom regulators to different species. Obviously, considering diatom biodiversity and the versatility of their light responses among different species, this fascinating issue can be addressed by means other than the functional approaches described in this review. Currently, several metagenomic and metatranscriptomic data sets are becoming available for eukaryotic phytoplankton, and novel integrative research merging genomics-enabled analyses and microbial oceanography information can be envisaged (Rusch et al., 2007; Gilbert et al., 2010; Arnaud-Haond et al., 2011; Karsenti et al., 2011). Extending the information derived by molecular and genomics-enabled analyses to experiments in natural environments could facilitate a quantum leap in understanding diatom responses to light changes. For example, a light regulator, previously characterized in a molecular model species, might be identified in a particular environment, shedding light on its role in regulating processes in real-life conditions. When direct experimental approaches are not feasible, such information would also become synergistic with numerical modelling approaches, which, through the simulation of a wide range of processes (from gene regulatory networks to the light variability imposed by hydrodynamics and concurrent photobiological responses), could assess the impact of diatom responses on ecosystem dynamics.

Acknowledgements

The authors are grateful to Giovanni Finazzi, Benjamin Bailleul, and Amy Kirkham for their critical suggestions to
improve the manuscript, and to Antonio E. Fortunato for the genomic photoreceptor analyses. Research at the Laboratoire de Génomique des Microorganismes (UPMC) is supported by the HFSP-Young Investigator Grant (RGY0082/2010), FP7 Marie Curie Initial Training Network (ITN) (COSI; 215174), and the Action Thématicque et Incitative sur Programme (ATIP) award (2009) from the CNRS.

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