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## Review

## Light acclimation in diatoms: From phenomenology to mechanisms

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## ABSTRACT

This review summarizes the current knowledge about light acclimation processes in diatoms. Against the background of the phenomenological description of the process in the 70s–80s, the recent progress in diatom genetics has generated new information about the underlying mechanisms. Although the general responses of diatoms to changes in the light climate are comparable to the green algal lineage, many differences in the underlying mechanisms have been observed in the last ten years, yielding clear evidence that the regulatory network in diatoms has unique traits that might explain their ecological success.

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Abbreviations: A, antheraxanthin;  $a^*_{phy}$ , Chl-specific absorption coefficient; Chl *a*, Chlorophyll *a*; DGDG, Digalactosyldiacylglycerol; MGDG, Monogalactosyldiacylglycerol; SQDG, Sulfoquinovosyldiacylglycerol; Dd, Diadinoxanthin; Dt, Diatoxanthin; DW, Dry weight; FTIR, Fourier transform-infrared; PAR, photosynthetically available radiation; P<sub>max</sub>, Maximal photosynthesis rate; Q<sub>phar</sub>, Photosynthetically absorbed quantum irradiance; PQ, plastoquinone pool; NPQ, non-photochemical quenching; V, violaxanthin; XC, xanthophyll cycle; Z, zeaxanthin.

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## 1. Introduction

**Q3** Engelmann (1902) described a quantitative relationship between absorptivity and carbon assimilation based on experiments with a homemade “microspectralphotometer”. Since that time, the molecular components that harvest the photons and funnel the photosynthetic electrons to the final macromolecules in the biomass producing cell have been identified in detail. These basic components have been found to be phylogenetically well conserved in the different taxa of photoautotrophic cells, with only the exception of the light collecting antenna complexes. Historically, the three major lines of light harvesting complexes have been attributed with three phylogenetic developments: the phycobilin-containing red algae, the green algae and the “chromophytes” which appear as green-brownish cells due to their major carotenoid fucoxanthin (Anderson et al., 1981). The basic assumption to explain the different pigmentation of the photoautotrophs was that a plant-like host organism has taken up different photosynthesizing bacteria. Engulfing a cyanobacterium would lead to the red algal line, whereas the uptake of a Prochloron-like organism would have led to the green line. The brownish symbiont was still a missing link. However, this view has been changed in the last 20 years, as molecular phylogenetic analysis provided new evidence that the “chromophyte” algae derived from a second endosymbiosis with a red alga as host organism, which had lost its primary endosymbiont (Adl et al., 2005). This new understanding has strong impacts when comparing green and chromophyte algae. It is now clear that such a comparison does not only consider a different chloroplast, but also a different host nucleus. This became even more complex after the publication of the whole genomes of two different diatoms. Their genomes are composed of genes of “green” and “red” origin and, as a surprise, of many bacterial genes. Therefore, in the comparison of processes that include complex alterations in gene expression, it can be expected that diatoms use different molecular targets, switches and regulators than green algae.

It has been shown that the process of light acclimation can be observed in all major taxa of photoautotrophic organisms. Although a clear experiment is still lacking to show that the ability of light acclimation improves primary productivity or is advantageous in ecological competition, the fact that it is omnipresent has been interpreted in such a way that the ability of photoacclimation is essential for survival. The phenomenology of photoacclimation becomes obvious in shift experiments from high light (HL) to low light (LL) or vice versa or when shifting the cells from blue light (BL) to red light (RL) or green light. Changing the light climate leads to characteristic alterations in the (1) pigmentation, (2) the stoichiometry of thylakoid protein complexes, (3) the resistance against photoinhibition and (4) the carboxylation capacity (Prezelin, 1981; Richardson et al., 1983). Recently, Deblois et al. (2012) compared the photoacclimation reaction of different cell types (flagellates, filamentous) from different taxa and showed that, independent of the thallus organization and the taxonomic position, all cells, when shifted from low to high light, reduced their chlorophyll (Chl) content per cell volume, increased the ratio carotenoid/Chl and enhanced their maximum photosynthetic capacity. However, the extent of change was different in large versus small cells.

Although the phenomenology of light acclimation is also well described in diatoms (Wilhelm et al., 2006), it is not clear how the cells sense the light and transfer this light signal in a transduction pathway which, in the end, leads to a different phenotypical molecular organization. In green algae and higher plants, three putative regulators have been proposed: first, the redox state of the plastoquinone pool; second, reactive oxygen species; and third, intermediates of the Chl biosynthesis (Li et al., 2009). However, much less is known in diatoms. This review summarizes the progress over the last decade in diatom genetics and improved biochemical methods to understand the molecular processes that underlie structural reorganization during light acclimation.

## 2. Phenomenology

### 2.1. Changes in the absorption properties

Photosynthetic pigments possess the highest absorption coefficients of organic molecules found in nature. Therefore, even low pigment concentrations inside the cell will generate high absorption. A cell with a diameter of 5  $\mu\text{m}$  containing 500 fg Chl has an absorption of about 0.2. This high absorption is essential in the aquatic environment in spring, autumn and winter when the incident light is low, the day length is short and the angle of incidence is lower than 60°. Since the reflectance increases logarithmically with the incidence angle (Austin, 1974), the light in the morning and shortly before sunset is not penetrating the water column. This reduces the day length drastically depending on the geographic position. Since fully autotrophic cells use light as their only energy source, energy availability is not only restricted by the light intensity but also by the day length. The consequence is that cells living under low light conditions should reduce dark respiration and should increase light harvesting capacity and photosynthetic efficiency. Therefore, LL acclimated cells have a high capacity for light harvesting and a low capacity for dark reactions at the level of photosynthetic electron flow and CO<sub>2</sub> assimilation. However, if these cells are exposed to high light, the imbalance of energy absorbed to energy used in the cellular metabolism induces the generation of excited states that can form deleterious singlet oxygen. This can be prevented by short-term activated photoprotective mechanisms, but also by long-term acclimation, which reduces the excitation pressure. The latter can be achieved at best by reducing the photosynthetic pigments in the cell. This can be visualized by electron microscopy showing that the area of thylakoid membranes is much smaller in HL-acclimated cells than in LL ones. In green algae, the number of stacks can be reduced (Berner et al., 1989), whereas in chromophytes, the number of stacks is always fixed to three. These algae regulate the thylakoid area per cell by reducing the numbers of membrane bands (Fisher et al., 1998). This was specifically shown in the diatom *Cyclotella meneghiniana* by Rosen and Löwe (1984).

The reduction in photosynthetic pigments and thylakoid area per cell has strong consequences for the absorption features of the cells, especially on the so-called in vivo Chl *a* absorption coefficient  $a^*_{phy}$ . This coefficient describes the absorption efficiency of the Chl molecules in vivo and can be calculated by dividing the scatter-corrected absorption spectrum of the cell suspension by the concentration of Chl *a*. The dimension of  $a^*_{phy}$  is  $\text{m}^2/\text{mg Chl } a$  and yields the absorption area that is available for a Chl molecule inside the cell. This parameter is highly variable due to the “package effect,” which means that inside the cell the pigment molecules are densely packed because they are bound in a few Å distances to each other in protein complexes embedded in the thylakoid membrane. Therefore, the Chl molecules shade each other, which reduces their chance to be hit by a photon. The consequence of this package effect is that the absorption efficiency decreases with an increase in the pigment content. This is the physical basis for the fact that the cell cannot efficiently improve absorption by accumulating more pigments. The only way to increase light capture is to use pigments with very high absorption coefficients. Under HL, the absorption properties of densely packed pigments would be very disadvantageous. Overexcitation leads to the accumulation of excited states and to the production of singlet oxygen, which is able to destroy the pigments, the proteins and the lipid matrix. Therefore, HL acclimation reduces the pigment packaging, which is, however, counteracted by better absorption efficiency of the pigments. A minor reduction of pigments would thus be overcompensated by the increased absorption efficiency. Therefore, only a drastic pigment decrease has a positive effect on the reduction of the photon capture capacity. Jakob et al. (2007) have shown that a five times lower Chl content per cell reduced the light capture only to a factor of 3. A second factor influencing the absorptivity is the cell size. Kirk (1994) demonstrated that  $a^*_{phy}$  decreases exponentially from small to large cells. The recalculated data of Dubinsky et al.

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