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Light-induced changes in the photosynthetic physiology and biochemistry in the diatom *Skeletonema marinoi*

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ABSTRACT

Light is a driving force behind the synthesis of biomass in photoautotrophs. In pelagic ecosystems, highly variable light strongly affects microalgae at an ecological (success and succession), molecular (acclimation, carbon allocation), photosynthetic and growth levels. Therefore, manipulation of light appears to be an attractive tool for enhancing growth of microalgae in order to extend the use of these organisms in biotechnological field. In this study, we investigate the responses of the diatom alga *Skeletenoma marinoi* to different growth light regimes, that induced composite acclimative patterns manifesting in strong alterations in the cell biology. Although the growth rate is dependent upon the integrated daily light dose received by the algae, we demonstrate that physiological and biochemical acclimation responds to additional light stimuli. The application of fluctuating red light on a sinusoidal blue light spectral distribution induces an increase in non-photochemical quenching and the de-epoxidation state of the xanthophyll cycle along with modifications of the metabolic state of the cells, e.g. an increase in carbohydrates, glycolipids and saturated fatty acids. Providing an unnatural square-wave light course induces drastic changes in photosynthesis, pigment and macromolecular composition of the cells.

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1. Introduction

Pelagic microalgae often experience drastic fluctuations in the environmental factors such as very high or very low light intensity, and low nutrient concentrations, that affect their growth and productivity. Light is one of the most vitally important variable parameters in both amplitude and frequency over daily and annual cycles [1,2,3]. Light directly affects the photosynthetic rate of cells. If limited it inhibits the growth rate and in excess can lead to the photooxidative damage also affecting the growth. In addition, light influences the metabolic state of cells by altering the costs of carbon production and its allocation [4,5]. To cope with dynamic light environment, microalgae have evolved various adaptive processes consisting of acclimation and regulation (e.g., [6]). The optimization of photosynthesis and growth is a dynamic process, which results from physiological switching between (photo) protective and low light photoacclimative states of algae [7]. As was mentioned above, in excess, light is one of the primary natural factors that strongly induces formation of reactive oxygen species (ROS) as well as antioxidant activity [8,9]. The defense mechanisms against high light damage and oxidative stress strongly affect microalgal growth [10,11,12,13] since the part of the biochemical energy from photosynthetic reactions is diverted in repairing and maintenance, membrane protection, defense against ROS and respiration [13]. Photoprotective mechanisms minimize photo-oxidative damage caused by the formation of ROS in the photosystems [2,14,15]. Among the responses developed in chloroplasts against ROS formation the synthesis of antioxidant carotenoids was demonstrated [13]. The xanthophyll cycle (XC) and non-photochemical quenching (NPQ) are crucial photoprotective processes that are rapidly activated (seconds to minutes) to dissipate excess absorbed light energy and ensure efficient light harvesting in the photosynthetic membrane [16,17].

It is possible to optimize the physiological state of cells through the manipulation of light conditions by providing a better balance between light capture and the photochemical processes [18,19,20] and to

Abbreviations: AP, ascorbate peroxidase; β-Car, β-carotene; CAT, catalase; Chl.*a*, chlorophyll *a*; Chl.*c*, chlorophyll *c*; Con, control; Dd, Diadinoxanthin; DES, de-epoxydation state; Dt, Diatoxanthin; DU, degree of unsaturation; E, Irradiance; ETR, electron transport rate; FA, fatty acid; Fuco, fucoxanthin; GPX, glutathione peroxidase; GR, glutathione reductase; His, histidine; LCYB, lycopene beta cyclase; LUT, lutein deficient protein; NPQ, non-photochemical quenching; PAR, photosynthetically available radiations; PDS, phytoene desaturase; PFD, photon flux density; Phe, phenylalanine; PS, photosystem; PUFA, polyunsaturated fatty acid; PUR, photosynthetically usable radiations; Quad, square-wave light course; ROS, reactive oxygen species; SOD, superoxide dismutase; Thr, threonine; VDE, violaxanthin de-epoxidase; Viox, violaxanthin; XC, xanthophyll cycle; Zeax, zeaxanthin; ZEP, zeaxanthin epoxidase.

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modulate the macromolecular composition of the cells [7,21]. This is crucial for enhancing the growth capacity and therefore the sustainable microalgal biomass production [18,22,23]. Many characteristics are contemplated behind the term "light". These are the instantaneous photon flux density (PFD), the daylength over the 24 h cycle, the daily light dose, the spectral composition and the light over the day. Many studies show that modifying either photoperiod or the instantaneous or daily-integrated photon flux density significantly affects the biomass production of phytoplankton, ranging from limitation to inhibition of growth [24,25,26]. The effects of light intensity on microalgal growth, photosynthesis and photoacclimation are well documented (e.g., [6,17,27]). On the contrary, it is not possible to univocally extract the information on the influence of the spectral quality on the biology of microalgae due to a great variability in the results, biological models and experimental approaches [28,29,30,31,32,33,34,35,36,37,38]. Investigations on the diversity and role of photoreceptors have been undertaken during the last few years in order to catch the effects of light of specific wavelengths on key processes in microalgae [36,39,40,41]. Recent studies revealed that spectral composition of light has a key role on the ability of diatoms to finely balance light harvesting and photoprotective capacity [21,37,38,42,43], modulating the efficiency of growth [38] and the photosynthetic carbon allocation in the cell [5]. Another property of illumination concerns the succession of light and dark periods, as it occurs in nature allowing cells to be more efficient at matching their physiological processes to the day–night cycles [44,45,46]. Short term fluctuations in PFD and changes of the frequency of flashing lights are known to modulate growth and physiological state of algae [47,48,49,50,51]. Recently, it has been observed how the rate of light intensity increase from dawn to midday modulates the photophysiological state of diatoms [52]. While in nature the light intensity follows a sinusoidal course with gradual PFD variations from dawn to midday and to twilight, in laboratory, microalgae are generally grown using a fast switch off/on system. The effects of the sinusoidal light course on production efficiency and physiological or metabolic state of cultured algae are almost unknown. This requires a special investigation aiming at optimizing microalgal growth capacity in laboratory to explore feasibility of their biotechnological use. Hence, our study aimed to investigate the photobiological and metabolic states of the coastal diatom *Skeletonema marinoi* grown under different spectral and light courses. This study was based on a previous investigation, which determined the optimal sinusoidal blue light course condition in terms of growth performance and carbon allocation for the same species [21].

2. Material and methods

2.1. Experimental strategy and sampling

Experiments were conducted on the coastal centric diatom *S. marinoi* (CCMP 2092), by cultivating at 20 °C in 4.5-L glass flasks with air bubbling, containing natural sterile seawater amended with f/2 nutrients [53]. All the experiments were performed in triplicate, lasting one day during the exponential growth phase, on cultures pre-acclimated to each experimental light condition for two weeks before the experiments.

Light was provided by a custom-built illumination system [38], that allows to monitor and regulate the light intensity and distribution, composed of blue and red light emitting diodes — peaking at 460 nm (422–496 nm) and 626 nm (590–656 nm range), respectively. Light intensity was measured inside each flask by using a laboratory photosynthetically available radiation (PAR) 4 π sensor (QSL 2101, Biospherical Instruments Inc., San Diego, CA, USA). The spectral composition (PAR(λ)) was measured at light peak by using a radiometer (Hyper OCR I, Satlantic, Halifax, CA).

Four different light conditions were tested, each with a 12:12 h light:dark photoperiod. The control condition corresponds to a sinusoidal blue light course, with midday PFD peak of 150 μmol photons m^{-2} s^{-1} (Table 1; Fig. 1a, Con, daily light dose: 3.66 mol m^{-2} d^{-1}). From a previous study, Chandrasekaran et al. [21] asserted that this culture condition was the optimal one for *S. marinoi* in terms of growth and synthesis of primary metabolites comparing four different sinusoidal blue light intensities. To this condition, fluctuating red light peaks have been superimposed upon blue sinusoidal light with two procedures: 3 Red Peaks (Table 1; Fig. 1b; 3 Red Peaks; daily light dose: 4.10 mol m^{-2} d^{-1}) and 9 Red Peaks (Table 1; Fig. 1c; 9 Red Peaks; daily light dose: 4.65 mol m^{-2} d^{-1}). Each superimposed red peak lasted 40 min and was setup with a red:blue ratio of 1. Red wavelength was selected to (i) investigate the biological effects of red + blue lights compared to pure blue light, and (ii) prevent an access of instantaneous light energy experienced by microalgae (red being less energetic than blue wavelength), in order to avoid potential photoinhibition.

The fourth condition consisted of a blue square-wave light course (Quad) applied with a PFD of 150 μmol photon m^{-2} s^{-1} (Table 1; Fig. 1d; daily light dose: 6.95 mol m^{-2} d^{-1}), in order to investigate the biological effects of providing square-wave light course compared to sinusoidal.

Sampling was done three times during the day, at dawn (0 h, before the light phase), midday (6 h after the start of the light phase) and in the afternoon (9 h after the start of light phase). Data on lipids and amino acids are missing for the dawn sampling time in the sinusoidal blue light course.

2.2. Cell concentration

An aliquot of 1 mL was used to fill a Sedgewick Rafter counting cell chamber, and cell counts were performed using a Zeiss Axioskop 2 Plus microscope.

2.3. Photochemical efficiency and photosynthetic parameters

Photochemical efficiency of photosystem (PS) II was estimated by a Phyto-PAM fluorometer (Heinz Walz, Effeltrich, Germany). The variable fluorescence analysis was performed on 15-min dark-acclimated samples, to measure the maximum quantum yield of PSII in the dark (Fv/Fm).

Table 1
Photosynthetic properties and growth rate of *Skeletonema marinoi* under the four light conditions. At the exception of light, data represent means ± SD of the three sampling times (dawn, midday and afternoon, $n = 9$). Daily light dose (mol m^{-2} d^{-1}); Mean light intensity (= mean instantaneous irradiance averaged over the 12 h illumination period, mmol m^{-2} s^{-1}); daily red light dose (mol m^{-2} d^{-1}); growth rate (μ, d^{-1}); $a^* \times 10^{-11}$ (cell-specific absorption coefficient, m^2 $cell^{-1}$); PUR × 10^{-6} (photosynthetically usable radiation, μW $cell^{-1}$); $_{rel}ETR_{max} \times 10^{-6}$, (maximal relative rate of linear electron transport, pmol e^{-1} h^{-1} $cell^{-1}$); α (maximum light use efficiency, pmol e^{-1} h^{-1} $cell^{-1}$ (μmol photon m^{-2} s^{-1}) $^{-1}$); Ek (light saturation index for photosynthesis, μmol photon m^{-2} s^{-1}); Fv/Fm (maximum quantum yield of PSII); NPQ (non-photochemical quenching); DES (de-epoxidation state = Dt/(Dd + Dt)).

Light condition	Daily light dose	Mean light intensity	Daily red dose	μ	a*	PUR	$_{rel}ETR_{max}$	α	Ek	Fv/Fm	NPQ	DES
Con	3.66	0.08	0	0.45 ± 0.04	3.52 ± 0.17	1.90 ± 0.18	20.40 ± 3.71	0.046 ± 0.004	254 ± 15	0.64 ± 0.01	0.11 ± 0.03	0.096 ± 0.001
3 Red Peaks	4.10	0.09	0.44	0.47 ± 0.06	2.88 ± 0.07	1.80 ± 0.15	18.77 ± 5.04	0.036 ± 0.003	363 ± 56	0.71 ± 0.02	0.19 ± 0.03	0.210 ± 0.005
9 Red Peaks	4.65	0.11	0.99	0.50 ± 0.05	1.72 ± 0.18	1.85 ± 0.14	13.93 ± 4.71	0.014 ± 0.004	464 ± 17	0.76 ± 0.05	0.51 ± 0.11	0.270 ± 0.005
Quad	6.95	0.16	0	0.65 ± 0.08	2.00 ± 0.60	1.30 ± 0.22	15.03 ± 6.57	0.028 ± 0.006	457 ± 56	0.67 ± 0.06	0.13 ± 0.05	0.360 ± 0.004

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