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Dynamic response of *Synechocystis* sp. PCC 6803 to changes in light intensity

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ABSTRACT

With changing light intensities, microalgae exhibit the inter-connected phenomena of photoacclimation, photodamage, and photodamage repair. Together they result in unique growth responses to changes in light intensity. In this work, we experimentally evaluated the growth responses using *Synechocystis* sp. PCC 6803 subjected to a series of light-step experiments. In these experiments, the biomass density and average light intensity were held constant (after the step in light intensity), and the dynamic response of the specific growth rate was measured. The over-arching trend is that an increasing-light step gave a rapid spike in growth rate, followed by a depression and ultimately restabilization of the growth rate for the new light condition. A decreasing-light step led to a small depression in growth rate before a gradual restabilization for the new light condition. Photoacclimation was faster after an increasing-light step than a decreasing-light step. Using a model accounting for photoacclimation, photodamage, and photodamage repair (presented in a companion paper), we captured the dynamic growth response and explained how the responses were the result of the combined effects of light absorption, photoacclimation, and photodamage.

1. Introduction

Following a change in light intensity (LI), microalgae (collectively referring to single-celled algae and cyanobacteria) undergo a series of physiological changes that can be grouped into photoacclimation and photodamage to photosystems I and II (PSI and PSII). Photoacclimation occurs as microalgae optimize their photosynthetic machinery for the LI they are experiencing [1]. For many species, this includes increasing their light-absorbing pigmentation at lower LI and decreasing it at higher LI. Microalgae experience PSII photodamage under all LI conditions, but it is balanced by PSII photodamage repair with constant LI [2]. When microalgae are photoacclimated to low LI and the LI increases more rapidly than the cells can photoacclimate to the new condition, their ability to repair the PSII photodamage declines, causing a temporary excess of PSII photodamage [3]. When the light-step increase is extreme, microalgae experience PSI photodamage, which is a semi-permanent decrease in their ability for photosynthetic growth [4]. In a companion paper, we more thoroughly review the mechanisms underlying these phenomena [5].

Here, we explore the dynamics of microalgal growth for shifts in light using the representative cyanobacteria *Synechocystis* sp. PCC 6803 (simply *Synechocystis* from here). The primary absorption pigments in *Synechocystis* are phycobilisome pigment-protein complexes and Chlorophyll a, and *Synechocystis* also contains orange carotenoid proteins to perform non-photochemical quenching of excess light energy [6–8]. It is well documented that *Synechocystis* cells change the quantity and composition of these pigments in response to incident light intensity as a means to optimize light utilization and minimize photodamage [9,10]. Additionally, cyanobacteria change the ratio of PSI to PSII in response to light [4,11].

As we demonstrate with extensive experimental results and has been noticed in other cyanobacteria [12,13], for an increasing-light step, *Synechocystis* shows an immediate spike in photosynthetic growth rate, followed by a depression and then a gradual increase to stabilize at the new steady-state condition. The spike in growth is due to an initially low level of PSII photodamage and over-absorption of light energy, consistent with the cells photoacclimation to a lower light intensity. PSII photodamage occurs proportional to light intensity, and is balanced by repair under stable light [14]. However, following the spike in growth after an increasing-step change in light intensity, the excess of absorbed light quickly leads to an excess of PSII photodamage and depression of the growth rate before *Synechocystis* can restabilize to the new steady-state growth rate. In contrast, during a decreasing-light step, we observe a sharp depression in growth rate that rebounds quickly near the new steady-state and finally slowly restabilizes to the new steady-state.

We also demonstrate here that an extreme-increasing-light step leads to a semi-permanent (our tests lasted only 4 days) decrease in the

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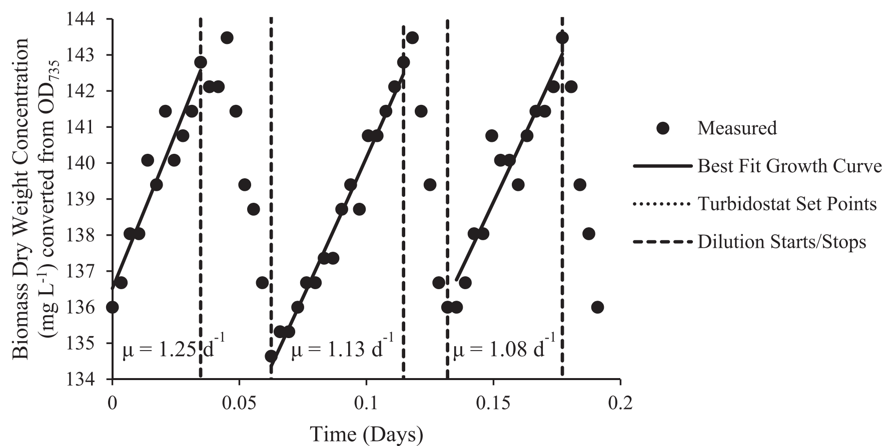

Fig. 1. Specific growth rate (μ) determination for *Synechocystis* grown in an FMT photobioreactor at an average internal light intensity (LI_{ave}) of 84 μmol m^{-2} s^{-1}. The reactor was operated as a sequencing batch reactor that would dilute the culture with BG-11 media when an OD_{735} of 0.21 was reached, and stop when 0.20 was reached. μ was determined using Eq. 1 during the non-diluting periods and is listed beneath each growth curve.

Table 1
Model equations as described in the companion paper [5], with a list of variables and parameters in Table 2 (Correspond to Eqs. (1)–(8) in the companion paper).

$$\frac{dLI_p}{dt} = \left(\varepsilon_{abs} LI - \varepsilon_{nf} LI - \left(\frac{k_{LI} LI_p}{k_{LI} + LI_p} + \frac{LI_p^2}{k_{LI} + LI_p}\right) k_{LIp}\right) \frac{86400s}{d} \quad (3)$$

$$\mu = \frac{\mu_{max} LI_p - \varepsilon_{nf} k_b}{k_{LI} + LI_p} - b \quad (4)$$

$$\varepsilon_{abs,ss} = \frac{(\varepsilon_{max} - \varepsilon_{scat} - \varepsilon_{abs,min}) k_\varepsilon}{k_\varepsilon + LI} + \varepsilon_{abs,min} \quad (5)$$

$$\frac{d\varepsilon_{abs}}{dt} = (\varepsilon_{abs,ss} - \varepsilon_{abs}) k_{ad}{}^{\alpha} \quad (6)$$

$$\frac{d\varepsilon_{nf}}{dt} = LI_p k_{d1} - \frac{(k_{r1}\varepsilon_{nf} - k_{r2} LI_p \zeta)^{\beta}}{k_{LI} + LI_p} \quad (7)$$

$$\frac{d\zeta}{dt} = ((\varepsilon_{abs} - \varepsilon_{abs,ss})^{\beta} - (\zeta - \delta) y^{\gamma}) \frac{k_{r3}}{(k_{r4} + LI_p)^2} + k_{d3}(\delta - \zeta)(1 - y^{\gamma}) \quad (8)$$

$$\frac{d\delta}{dt} = (\varepsilon_{abs} - \varepsilon_{abs,ss} - \delta - (\varepsilon_{max} - \varepsilon_{scat} - \varepsilon_{abs}) k_{d2})^{\beta} k_{d3} \quad (9)$$

$$\varepsilon_{nf,ss} = \frac{k_{d1}}{k_{r1}} (k_{LI} LI_p + LI_p^2) \quad (10)$$

α If $\varepsilon_{abs,ss} > \varepsilon_{abs}$, $k_{ad} = k_{ad,dn}$, else $k_{ad} = k_{ad,up}$
β If term is < 0, the term is 0
γ If $\zeta > \delta$, y = 1, else y = 0

growth rate. It is not clear that cyanobacteria take PSI photodamage in this way [4], although PSI photodamage and a decreased growth rate have been demonstrated in mutants of *Synechocystis* lacking flavodiiron proteins (key protein in preventing oxidative stress) during fluctuating light [15]. Another possibility is that *Synechocystis* is unable to photoacclimate the ratio of PSI to PSII during extreme-light steps. A *Synechocystis* mutant defective in a key gene for photoacclimating the ratio of PSI to PSII showed severe inhibition under high light [6,16]. While we are not able to define the mechanism occurring with extreme-increasing-light steps, we document a semi-permanent decrease in growth rate that we label PSI photodamage.

Using the experimental results obtained in this study, we parameterize a model presented in a companion paper [5] and demonstrate its ability to represent all the phenomena of photoacclimation, PSI and PSII photodamage, and the resulting specific growth rate. The combined experimental and model results provide a complete quantitative interpretation of the dynamic responses of *Synechocystis* to step changes in light intensity. This lays the foundation for understanding how repeated changes in LI, such as caused by mixing in a concentrated culture, affect photoacclimation and photodamage.

2. *Synechocystis* growth-rate experiments

We performed a series of steady-state growth experiments at different LIs ranging from LI_{ave} of 14 to 1750 μmol m^{-2} s^{-1} and carried out dynamic-LI-step-change experiments, tracking the specific growth rate (μ, d^{-1}) over time. We performed a total of 20 light-step experiments. The results of 6 are presented in the Results and Discussion section (LI_{ave} going from 84 to 737, 186 to 53, 272 to 27, 27 to 317, and 85 to 1452 μmol m^{-2} s^{-1}); results from the remaining 14 light-step experiments are presented in Supplemental Information D.

We used the same growth conditions as Straka and Rittmann (2017). Briefly, *Synechocystis* was received from the laboratory of Dr. Willem Vermaas, School of Life Sciences at Arizona State University and inoculated directly from a plate into a Photobioreactor FMT150 (Photon Systems Instruments, Drásov, Czech Republic; simply FMT form here) having an approximate liquid volume of 0.370 L, a fixed temperature of 30 °C, and air sparging at approximately 0.1 L min^{-1}. The FMT was equipped with a cool-white LED panel with adjustable intensity ranging from 0 to 2500 μmol PAR photons m^{-2} s^{-1} (simply μmol m^{-2} s^{-1} from here). It could change its incident light intensity in < 2 μs, which was essential for the light-step experiments. The system was operated with the turbidostat module, which functioned as a sequencing batch reactor diluting the culture when the optical density (OD at 735 nm, or OD_{735}) reached 0.21 and stopped diluting when it reached 0.20. The pH was maintained between 7.5 and 8.5 using carbon dioxide sparging. The growth medium was autoclaved standard BG-11 [17]. OD_{735} and the ratio of OD at 680 nm (OD_{680}) to OD_{735} (OD_{680}/OD_{735}) were tracked over time.

We measured the photosynthetic growth rate based on the change in OD_{735}, which can be directly correlated to biomass dry weight (DW; mg L^{-1}). We also measured dry weight concentration daily by taking a dry 0.7-μm glass microfiber filter (Whatman®, Buckinghamshire, UK), filtering 10 mL of culture, drying the filter at 60 °C overnight, subtracting the final weight from the initial weight, and dividing by 10 mL [10]. Biomass concentrations used for computing μ were the OD_{735} multiplied by the DW/OD_{735} ratio taken the same day. Although we observed some variability in the DW/OD_{735} ratio with steady-state growth (an average and standard deviation of 590 ± 95 DW/OD_{735}), the variation was random and not related to the light intensity (LI). Immediately following an increasing-light step, however, OD_{735} increased rapidly and did not correspond exactly to an increase in DW, which has a slight delay (5–10 min.). A comparison of DW to OD_{735} for a representative experiment with a light-step increase is presented in Supplemental Information A. While the lack of synchrony between OD_{735} and DW was minimal on the time scale of the study, it introduced uncertainly in the experimental estimation of μ immediately following a light step. Therefore, we used a theoretical basis – described in 3. Parameterizing the Model to the Growth Data – to determine μ_{max}.

The experimental values of μ were determined by fitting Eq. (1) for the growth periods (not diluting periods) of turbidostat operation:

$$X = X_0 \exp(\mu t) \quad (1)$$

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