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A mechanistic model of photosynthesis in microalgae including photoacclimation dynamics

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ABSTRACT

In this study, an extension and actualization of a dynamic model of photosynthesis, previously published (Camacho Rubio et al., 2003), is presented. This model uses the concept of Photosynthetic Unit (PSU). In it, the processes of excited PSU net disappearance rate, photoinhibition and damaged PSU repair have been redefined in the context of photochemical and non-photochemical quenching. The phenomenon of photoacclimation in microalgae has been extensively incorporated into this model, significantly improving its prediction capabilities. A significant number of previously reported experimental results are successfully interpreted by the novel formulation: 1. Photosynthetic response of cells photoacclimated to different constant continuous irradiances (photoacclimated cells); 2. Short-term photosynthetic response of cells non-photoacclimated to different constant continuous irradiances (non-photoacclimated cells); 3. Kinetics of the photoacclimation response; 4. Photosynthetic response under intermittent light. It is expected that this model will contribute notably to the simulation of industrial algal mass cultures.

1. Introduction

Mathematical models of photosynthesis in bioreactors are important for both basic science and the bioprocess industry. Various and highly sophisticated models of this process are found in the literature.

The actual well-known behaviour of photosynthetic cultures is not easily represented by simple kinetic expressions: this is especially true so when the dynamic behaviour of these cultures is considered. Therefore, the mathematical models of photosynthesis that are currently available are based on the lumping of a large number of biochemical reactions into simpler steps or into hypothetical concepts. The selection of a model is, thus, the result of the compromise between the known biochemical steps and the computational burden resulting from complex mathematical formulation.

There is a group of 'physiological' models attempting to represent the dynamic behaviour of photosynthetic cells and to propose approximations for the mechanism operating inside these cells, a mechanism associated with their capacity to adapt to different illumination intensities. These models express the dynamics of a photosynthetic culture taking into account a considerable amount of variables. In addition to the obvious (a carbon source and light), various substrates that algae require for growth, such as nitrate, phosphate and intracellular concentrations of chlorophyll-*a*, the extent of light-damaged protein D1 in Photosystem II (PSII), the nitrogen and carbon content in the cells, etc. are all considered (Pahlow and Oschlies, 2009; Marshall et al., 2000; Geider et al., 1998; Ross and Geider, 2009; Harmon et al., 1997). Usually, those mechanistic models are based on a certain cycle, e.g., the D1 damage and repair cycle (Marshall et al., 2000) or they follow a certain strategy, such as an optimal allocation of energy and nutrients during cell activities: nutrient uptake, light harvesting and growth (Ross and Geider, 2009; Pahlow, 2005; Pahlow et al., 2008; Shuter, 1979). The goal of those advanced models is to represent the physiology of the photosynthetic cells. Furthermore, some of them target the modelling of photosynthesis in the sea and aim at understanding the marine environment and the sustainability of human-originated changes (Ross and Geider, 2009; Pahlow, 2005; Pahlow et al., 2008; Moore et al., 2006; Pahlow and Vézina, 2003).

In addition to those mentioned above, there is another class of models based on the concept of the 'photosynthetic unit' (PSU), also called 'photosynthetic factories' (Camacho Rubio et al., 2003; Zonneveld, 1997; Eilers and Peeters, 1988; Han, 2002; Megard et al., 1984; Prézelin, 1981; Zonneveld, 1998) which are instrumental in representing the dynamics of the photobioreactors.

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Nomenclature

a	total concentration of PSUs (PSUs $\cdot$ cell^{-1})
a^*	concentration of activated PSUs (PSUs $\cdot$ cell^{-1})
a_f	concentration of functional PSUs (PSUs $\cdot$ cell^{-1})
$a_{max,min}$	maximum or minimum total concentration of PSUs (PSUs $\cdot$ cell^{-1})
a_{nf}	concentration of non-functional PSUs (PSUs $\cdot$ cell^{-1})
a^0	concentration of non-activated PSUs (PSUs cell^{-1})
ATP	adenosine triphosphate
c	concentration of chlorophyll a per cell (pg Chl$a$ cell^{-1})
C_L	dissolved oxygen concentration (mg O_2 L^{-1})
C_L^*	solubility of oxygen in culture medium (i.e., 8 mg O_2 L^{-1})
C_{Lobs}	measured dissolved oxygen concentration (mg O_2 L^{-1})
$D1$, $D2$	proteins of the PSII
HL	high light or irradiance
I	irradiance (μE m^{-2} s^{-1})
I_c	irradiance constant in Eq. (13) (μE m^{-2} s^{-1})
K_1	rate constant of photoacclimative changes in cellular chlorophyll a in Eq. (14) (s^{-1})
k_a	kinetic coefficient in Eq. (1) (m^2 PSU^{-1})
K_{Chla}	rate constant of photoacclimative changes in cellular chlorophyll a in Eq. (15) (s^{-1})
K^*_{chla}	apparent rate constant of photoacclimative changes in cellular chlorophyll a in Eq. (16) (s^{-1})
K_D	characteristic delay time in Eq. (31) (s^{-1})
k_i	rate constant in Eq. (6) (μE m^{-2} s^{-1})$^{-n}$ cell m^{-2} s^{-1}
K_La	volumetric oxygen transfer coefficient (s^{-1})
k_{nf}	constant in Eq. (8) (PSUs $\cdot$ cell^{-1})
k_p	proportionality constant in Eq. (31) (units dependent on P_m)
K_{PSU}	rate constant of photoacclimative changes in PSU concentration in Eq. (18) (s^{-1})
k_r	maximum rate of the recovery process (PSUs cell^{-1} s^{-1})
K_s^*	constant in Eq. (4) (PSUs $\cdot$ cell^{-1})
LL	low light or irradiance
m	maintenance metabolic rate, $0.1P_m$ (s^{-1})
N	Avogadro's number
NADPH	nicotinamide adenine dinucleotide phosphate
NPQ	non-photochemical quenching
P	gross photosynthesis rate (mg O_2 cell^{-1} s^{-1})
P_{ave}	fractional photosynthetic productivity averaged for an illumination cycle (dimensionless)
P–I	photosynthesis–irradiance curve
P_m	maximum rate of photosynthesis (mg O_2 cell^{-1} s^{-1})
P_{obs}	observed-photosynthesis rate (mg O_2 cell^{-1} s^{-1})
P_q	photochemical quenching
P_R	photorespiration rate (mg O_2 cell^{-1} s^{-1})
PSU	photosynthesis unit
PSU*	activated PSU
PSU_f	functional PSU
PSU_{nf}	damaged or non-functional PSU
PSU^0	resting PSU
q	size of PSU (pg Chl$a$ PSU^{-1})
qE	energy-dependent quenching
qI	photoinhibitory quenching
qT	state-transition quenching
R	respiration rate (mg O_2 cell^{-1} s^{-1})
r_c	disappearance rate of activated PSU due to photochemical quenching (PSU cell^{-1} s^{-1})
r_i	formation rate of non-functional PSU (PSU cell^{-1} s^{-1})
r_m^*	maximum disappearance rate of activated PSU due to photochemical quenching (PSU cell^{-1} s^{-1})
r_p	rate of PSUs activation (PSU cell^{-1} s^{-1})
r_r	reparation rate of non-functional PSU (PSU cell^{-1} s^{-1})
t	time (s)
t_c	duration of light/dark cycle (s)
t_d	length of the dark period within one light/dark cycle (s)
t_f	duration of illumination (s)
x^*	fraction of functional activated PSUs (dimensionless)
X_b	cell concentration (cells L^{-1})
x_{nf}	fraction of non-functional PSUs (dimensionless)
x^0	fraction of resting PSUs (dimensionless)

Greek letters

β	species-dependent characteristic frequency related to the maximum specific rate of photosynthesis (s^{-1})
ϕ	dimensionless time defined by Eq. (43)
ν	frequency of the light/dark cycle (s^{-1})
κ	pseudo-constant defined by Eq. (33) (dimensionless)
τ	response time of oxygen probe (s^{-1})
κ_i	rate pseudo-constant of photodamage defined by Eq. (6) (s^{-1})
κ_{nf}	pseudo-constant defined by Eq. (28) (dimensionless)
κ_r	pseudo-constant defined by Eq. (27) (s^{-1})
η	excitation requirement (μE PSU^{-1})
ξ	cellular absorption cross-section (m^2 cell^{-1})
σ	chlorophyll-specific absorption-cross section (m^2 pg Chla^{-1})
χ	true chlorophyll-specific absorption-cross section (m^2 pg Chla^{-1})
Ω	PSUs or Chl$a$ concentration
ω	rate constant of photorespiration ($0.5P_m$)
α	oseudo-constant defined by Eq. (25) (μE m^{-2} s^{-1})
$\gamma_{L,D}$	Coefficients of respiration rate for light (L) and darkness (D) defined by Eq. (33) (dimensionless)

Subscripts

ad	photoacclimated
f	final or functional
max	maximum
min	minimum
nf	non-functional
0	initial

They do not aim at describing the physiology of the cell, but rather the behaviour of the algal culture. Here, the main variable considered is the light intensity, which is usually the limiting substrate in dense cultures, such as those featuring in industrial production. It is assumed that all the other substrates are provided at such rates that they are in excess and do not need to be taken as variables.

No PSU-based models that contemplate photoacclimation are available. It seems, therefore, that the development of an extended PSU-type model, taking into account the dynamics of photoacclimation, the effect of non-photochemical quenching as a response to high irradiation, as well as other aspects (e.g., dark respiration), is an important contribution to the advancement of the science-based engineering design of photobioreactors.