



## Research paper

## Overyielding potential of microalgal polyculture with complementary light absorption spectra: A model-based analysis

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## ABSTRACT

Several recent experiments of microalgal polyculture have observed an increased yield compared to monocultures, leading to the suggestion that improved use of the available light resource due to complementary light absorption spectra may be among the underlying reasons. Using numerical simulation, this work explores the impact of conditions (including both operation settings and species traits) on the possibility of biomass overyielding by a co-culture of two algal species. From the study of a system with simplified light absorption spectra, it was found that both operation settings such as incident light intensity and loss rate of algal biomass and species traits such as light use efficiency and maximum specific growth rate can affect the possibility and degree of overyielding. Co-culture of two actual species with light absorption spectra that exhibit complementarity was also simulated, which further confirmed the importance of some of these factors in a realistic case. This work thus suggests that complementary light absorption alone may lead to overyielding in a polyculture of microalgae, only when a number of biological and operational conditions are met.

## 1. Introduction

In the last few decades, microalgae have been considered to possess great potential for a variety of industrial applications. A lot of existing work has focused on developing practical algal biotechnology for bio-fuel production [1–3]. Microalgae-based systems have also frequently been considered for biological wastewater treatment [4] [5] and CO<sub>2</sub> sequestration [6,7]. Microalgae can be cultured by either a mono-culture system, or a poly-culture system that grows multiple micro-algal species. Some of poly-culture systems aim at overyielding, which means the collective yield of multiple microalgae species, in terms of either whole biomass or a specific biomass component such as lipids, exceeds that of any single species when cultivated under the same condition [8–13]. A key mechanism that has been used to explain overyielding in a poly-culture system is the complementarity effect [8] [9]. Complementarity refers to resource partitioning or facilitation among different species causing a more complete consumption of the involved resources, which may lead to an increase in the overall yield. In particular, the complementary use of light at different wavelengths by different algal species has been speculated by several authors as a possible explanation of experimentally observed overyielding in polyculture systems (e.g. Refs. [8] [9], [14] [15]) which, if confirmed, can be taken as a guiding principle for designing productive co-culture

systems. However, this hypothesis is yet to be evaluated.

This work attempts to evaluate the above hypothesis, by means of modelling. In the past, several model-based analyses have been made on the co-growth of multiple phytoplankton species in connection of light utilisation. The rather early work in Ref. [16] confirmed that a growth rate model that takes into account the effect of the spectral qualities of light could predict the co-existence of multiple photosynthetic microorganisms in a well-mixed environment. The more recent work in Refs. [17] and [18] showed that red and green picocyanobacteria, using the pigments phycoerythrin and phycocyanin to absorb green and red light respectively, could co-exist due to the complementarity in light use, as confirmed by experimental observations. Theoretical analysis was also carried out on multiple species competing over light (as a homogeneous resource) and nutrients, which revealed conditions for co-existence in such circumstances [19] [20]. It should be noted that the above model-based or theoretical work has all focused on co-existence of multiple algal species, but not on overyielding which is a key objective of the engineering systems based on algal co-cultures.

Focusing on overyielding, this work aims to theoretically examine the hypothesis that complementary light utilisation leads to overyielding in microalgal poly-culture, as proposed in some previous work. A mathematical model is formulated to predict the potential of

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overyielding as a function of several influencing factors. The model is then used in the numerical simulation of a two-species system, with hypothetical (simplified) and actual light absorption spectra, to explore the conditions for overyielding to occur in a poly-culture system. To our knowledge, this is the first attempt to study the relationship between (i) complementary light absorption between different algal species to be co-cultured and (ii) the overyielding potential of such systems. The findings from this study have the potential to provide insight to the design of algal co-culture systems.

## 2. Methodology

### 2.1. The modelling approach

This work considers light supply as the only limiting factor to the growth of microalgae; nutrients such as nitrogen and phosphorus are assumed sufficient for cultivation. Mass balance of microalgae species  $i$  in a well-mixed bioreactor follows equation (1):

$$\frac{dN_i}{dt} = \frac{N_i p_{i\max}}{z_m} \int_0^{z_m} f_{i_l}(z) dz - L_i N_i \quad (1)$$

where  $N_i$  represents the cell density (i.e. number of cells per unit reactor volume),  $p_{i\max}$  is the maximum specific growth rate,  $z$  is the vertical position in the bioreactor between the top ( $z = 0$ ) and the bottom ( $z = z_m$ ) surface,  $L_i$  is the rate of biomass loss, assumed to be dominated by the dilution rate in a continuous bioreactor, a parameter that can easily be manipulated. In this work, the loss rate is an important parameter, as it directly affects the steady-state concentration of cells which in turn influences the extent of light utilisation by the algal culture. The light factor  $f_{i_l}$  indicates the extent to which the algal growth is affected by light.

Light attenuation is modelled by applying the Beer-Lambert law:

$$I(\lambda, z) = I_{in}(\lambda) \exp\left(-\sum_{i=1}^n k_i(\lambda) N_i z\right) \quad (2)$$

$I(\lambda, z)$  represents the light intensity (measured in number of photons per unit area per unit time) of wavelength  $\lambda$  at depth  $z$ ,  $I_{in}(\lambda)$  is the incident light intensity of wavelength  $\lambda$ ,  $k_i(\lambda)$  is the specific light absorption spectrum of species  $i$ . The amount of light absorbed by species  $i$  at depth  $z$  over the photosynthetic active radiation (PAR) wavelength range of 400–700 nm, denoted as  $\gamma_i(z)$ , is

$$\gamma_i(z) = \int_{400}^{700} I(\lambda, z) k_i(\lambda) d\lambda \quad (3)$$

$\gamma_i(z)$  is light absorbed by species  $i$  at depth  $z$ , on a per cell basis.

To quantify the light factor  $f_{i_l}$  introduced in equation (1), the typical relationship between photosynthetic productivity for microalgae

(denoted by ‘ $P$ ’) and light intensity (denoted by ‘ $I$ ’) is considered, as shown on Fig. 1a. Three regimes are distinguished according to the level of light intensity [21]:

- At low light intensity levels, the productivity is proportional to light intensity, the limiting step in this regime is the capture of photons by microalgae.
- As the level of light intensity increases, the rate of photosynthetic reactions becomes slower than the rate of photon absorption by microalgae, and hence approaches saturation.
- If the light intensity increases further and beyond an inhibition threshold, damage of key proteins in the photosynthetic units occurs and consequently the productivity drops [21].

The above  $P$ - $I$  curve is widely adopted when no details of light absorption spectrum are considered. In this work, it is adapted by replacing light intensity ( $I$ ) with light absorption ( $\gamma$ ) to allow the photosynthesis rate to be directly related to the actual amount of absorbed light, which is similar to the modelling approach in a previous work [17]. Therefore, the above  $P$ - $I$  curve essentially becomes a  $P$ - $\gamma$  curve (Fig. 1b). Quantitatively, the light factor in equation (1) is modelled as a nonlinear function of light absorption, reflecting the three regimes mentioned above and adapting a model previously formulated for the  $P$ - $I$  curve [22]:

$$f_{i_l}(z) = \frac{\gamma_i(z)}{a_i \gamma_i(z)^2 + b_i \gamma_i(z) + c_i} \quad (4a)$$

$$P_i(z) \equiv P_{i\max} f_{i_l}(z) = P_{i\max} \frac{\gamma_i(z)}{a_i \gamma_i(z)^2 + b_i \gamma_i(z) + c_i} \quad (4b)$$

The three parameters are calculated by  $a_i = \frac{P_{i\max}}{\gamma_{i\text{opt}}^2 \phi_i}$ ,  $b_i = 1 - \frac{2P_{i\max}}{\phi_i \gamma_{i\text{opt}}}$ ,  $c_i = \frac{P_{i\max}}{\phi_i}$ ,  $\phi_i$  is the light use efficiency, which, as pointed out in Ref. [22], corresponds to the initial slope of the  $P$ - $\gamma$  curve defined by Equation (4b).  $\gamma_{i\text{opt}}$  is the optimum level of light absorption corresponding to the maximum photosynthetic productivity.

### 2.2. Investigating a two-species community with simplified light absorption spectra

To theoretically assess the biomass overyielding potential due to complementary light absorption, it is desirable to obtain easy control over the degree of complementarity between different species. To this end, a hypothetic community of two species with a pair of simplified light absorption spectra was considered. Each spectrum comprises two parts of equivalent size in terms of the PAR wavelength range, i.e. 400–550 nm and 550–700 nm, respectively. In the following, subscripts 1 and 2 refer to the two parts of light, and  $a$  and  $b$  are used to represent

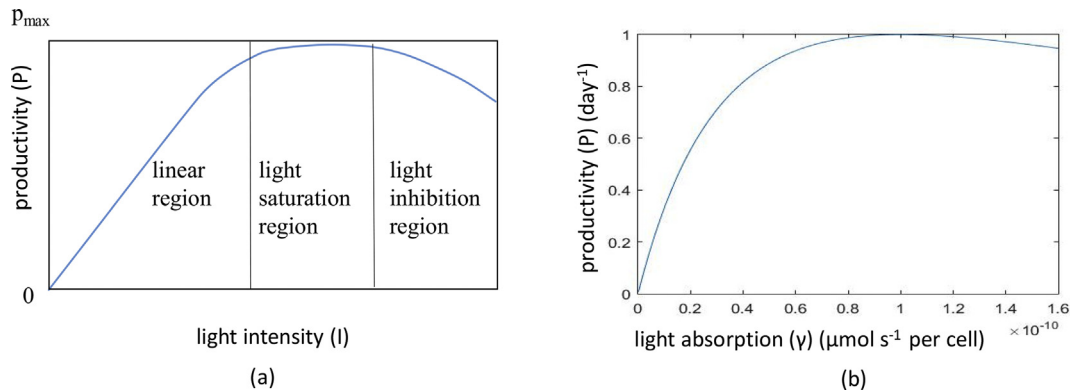


Fig. 1. Relationship between photosynthesis and light supply or absorption. (a) Typical relationship between photosynthetic productivity and light intensity (“ $P$ - $I$  curve”); (b) Predicted photosynthesis rate as a function of light absorption (“ $P$ - $\gamma$  curve”) according to equation (4b) and using parameters in Table 1.

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