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# Maximizing microalgae productivity in a light-limited chemostat <sup>★</sup>

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**Abstract:** Light supply is one of the most important parameters to be considered for enhancing microalgae growth in photobioreactors (PBR) with artificial light. However, most of the mathematical works do not consider incident light as a parameter to be optimized. In this work based on a simple model of light-limited growth, we determine optimal values for the dilution rate and the incident light intensity in order to maximize the steady-state microalgal surface productivity in a continuous culture. We also show that in optimal conditions there is a minimal initial microalgal concentration (and we give a simple expression to determine it) to guarantee the persistence of the population. Finally, in the context of enhancing microalgae productivity by reducing light absorption by microalgae, we conclude our work by studying the influence of the chlorophyll-carbon quota on the maximal productivity.

*Keywords:* Dynamics and control; Industrial biotechnology; Photoinhibition; Biomass productivity; Microalgae; Photoacclimation; Chlorophyll

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## 1. INTRODUCTION

Microalgae can be grown in photobioreactors (PBR) illuminated by artificial light. Carvalho et al. (2011) discusses the importance of providing light at the appropriate intensity to enhance growth. Low light intensities will become growth-limiting, notably in dense cultures due to self-shading. On the other hand, too high levels may lead to photoinhibition i.e. a decrease in the rate of photosynthesis due to high light intensities (Long et al. (1994)). Despite the importance of the incident light, most of the mathematical works concerned with the optimization of PBRs focus only on the control of the dilution rate. See for example the works of Mairet et al. (2013), Masci et al. (2010), or Grognard et al. (2014).

Here, we determine optimal values for the dilution rate and the incident light intensity in order to maximize the biomass productivity in a continuous culture. In our approach, we follow the works of Gerla et al. (2011) and Hsu et al. (2013) for describing the dynamics of a microalgae culture. Then, we determine the optimal operational parameters at the steady state of the system.

Another route for enhancing microalgae productivity in PBRs can be to minimize light absorption by individual cells so that cells deeper inside the culture will receive enough light (Carvalho et al. (2011)). Light absorption is related to the chlorophyll content of microalgae. In this context, along the paper, we indicate how the chlorophyll content is related to some parameters. This allows us, in the last section, to show the existence of an optimal chlorophyll-carbon quota for maximizing productivity.

This article is organized as follows. In section 2, we describe a model for light-limited cultures. In section 3, we analyze the dynamics of this model. Finally, in section 4, we present the criterion for maximizing productivity and discuss the influence of chlorophyll content on productivity.

## 2. MODELLING LIGHT-LIMITED GROWTH OF MICROALGAE.

Let us consider a perfectly mixed PBR of depth  $L$  where microalgae grow (see Figure 1). Let us assume that light is attenuated exponentially with depth according to the Lambert-Beer law i.e. at a distance  $z \in [0, L]$  from the illuminated surface, the corresponding light intensity  $I(x, I_{in}, z)$  satisfies

$$I(x, I_{in}, z) = I_{in}e^{-axz}, \quad (1)$$

where  $x$  denotes the microalgae concentration,  $I_{in}$  is the incident light intensity, and  $a > 0$  is the specific light attenuation coefficient. According to Bernard et al. (2016), the extinction coefficient  $a$  is correlated to the chlorophyll quota  $\theta$  by means of

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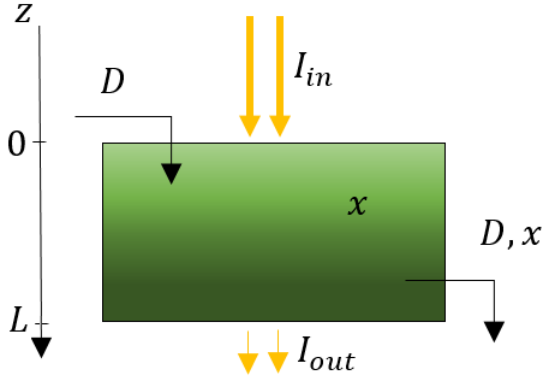


Fig. 1. Scheme of the light-limited chemostat.

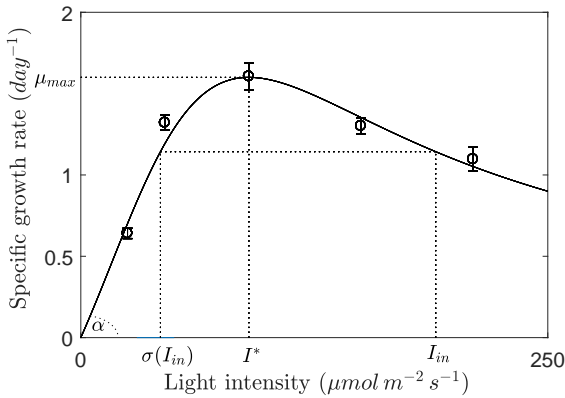


Fig. 2. Growth rate function  $\mu$  for *Chlorella vulgaris* calibrated with experimental data obtained by Yeh et al. (2010) and graphical description of the function  $\sigma$ .

$$a = a_1\theta + a_2, \quad (2)$$

with  $a_1$  and  $a_2$  non-negative parameters. The chlorophyll quota represents the cellular chlorophyll-to-carbon ratio.

Let us denote by  $\mu$  the specific growth rate function of the microalgae. We assume that nutrients and carbon dioxide are so that light is the single factor that limits growth i.e.  $\mu : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  is a function of the light intensity  $I$  perceived by the microalgae. Following Huisman and Weissing (1994), we compute the average growth rate function (AGR) in the reactor, denoted  $\bar{\mu}$ , by integrating the local growth rate over all the reactor

$$\bar{\mu}(\cdot) := \frac{1}{L} \int_0^L \mu(I(x, I_{in}, z)) dz. \quad (3)$$

Following Gerla et al. (2011), we do the change of variables  $I = I(x, I_{in}, z)$ . From Eq. (1)  $dI/dz = -axI$ . So if  $x > 0$ , we can rewrite the AGR

$$\bar{\mu}(\cdot) = \frac{1}{axL} \int_{I_{out}(x, I_{in})}^{I_{in}} \frac{\mu(I)}{I} dI, \quad (4)$$

where  $I_{out}(x, I_{in})$  is used for indicating the light intensity at the bottom of the reactor i.e.  $I_{out}(x, I_{in}) = I_{in}e^{-axL}$ . If  $I_{in} > 0$ , note from (1) that

$$axL = \ln(I_{in}) - \ln(I_{out}(x, I_{in})). \quad (5)$$

By substituting (5) in (4) we have

$$\bar{\mu}(\cdot) = g(I_{in}, I_{out}(x, I_{in})), \quad (6)$$

with

$$g(I_{in}, I_{out}) = \frac{1}{\ln(I_{in}) - \ln(I_{out})} \int_{I_{out}}^{I_{in}} \frac{\mu(I)}{I} dI. \quad (7)$$

Eq. (6) shows that the AGR is determined by the incident light intensity and the light intensity at the bottom. The function  $g$  was first defined by Gerla et al. (2011).

In the literature we find different models for  $\mu$ , for example the model of Eilers and Peeters (1988) and the following reparametrization presented by Bernard and Rémond (2012);

$$\mu(I) = \mu_{max} \frac{I}{I + \frac{\mu_{max}}{\alpha} \left(\frac{I}{I^*} - 1\right)^2}, \quad (8)$$

with  $\alpha$  the initial slope of the light response curve,  $\mu_{max}$  the specific maximum growth rate, and  $I^*$  the light intensity at which  $\mu$  reaches  $\mu_{max}$ . Figure 2 shows the function  $\mu$  given in (8) with kinetic parameters from Table 1. From now on, we assume that  $\mu$  is given by Eq. (8).

According to Bernard et al. (2016), the parameter  $\alpha$  can be written as

$$\alpha = \alpha_1\theta, \quad (9)$$

with  $\alpha_1$  the initial slope of the chlorophyll-specific growth rate  $\mu^{chl} := \mu/\theta$  which is independent of  $\theta$ . Expression (9) shows that  $\alpha$  is directly proportional to the pigment content, therefore lower values of  $\alpha$  are related to more transparent microalgae.

Table 1. Kinetic parameters of  $\mu$  in (8).

Parameter	Value
$\mu_{max}$	$1.63 \text{ d}^{-1}$
$I^*$	$87.2 \mu\text{mol m}^{-2} \text{ s}^{-1}$
$\alpha$	$0.027 \mu\text{mol}^{-1} \text{ m}^2 \text{ s d}^{-1}$

Let us remark that  $\mu$  (and any Haldane-type model<sup>3</sup>) satisfies:

$$\mu(I_1) = \mu(I_2) \text{ if, and only if } I_1 = I_2 \text{ or } I_1 I_2 = I^{*2}. \quad (10)$$

We will write  $\sigma(I) = I^{*2}/I$  for any  $I > 0$ . Thus, according to (10), microalgae grow at same rate when they perceive the light intensity  $I$  or  $\sigma(I)$  (see Figure 2). Property (10) is reflected in the function  $g$  by the following property;

$$g(I_{in}, \sigma(I_{in})) = g(I_{in}, I^*), \quad I_{in} > I^*. \quad (11)$$

<sup>3</sup> By a Haldane-type model, we mean  $\mu(I) = \frac{I}{aI^2 + bI + c}$  with  $a, c > 0$ .

To prove (11), by using Eq. (10), we can easily show that is enough to prove the following identity

$$\int_{I^{*2}/I_{in}}^{I^*} \frac{\mu(I)}{I} dI = \int_{I^*}^{I_{in}} \frac{\mu(I)}{I} dI. \quad (12)$$

This follows directly from doing the change of variables  $J = I^{*2}/I$  on the right side.

To end this section, we give an explicit expression for  $g$ . Indeed, let

$$\Delta := 4 \frac{\mu_{max}}{\alpha I^*} - 1 > 0 \quad (13)$$

then

$$g(I_{in}, I_{out}) = \frac{2\mu_{max}/\sqrt{\Delta}}{\ln(I_{in}/I_{out})} [\tan^{-1}(\kappa(I_{in})) - \tan^{-1}(\kappa(I_{out}))], \quad (14)$$

$$\text{with } \kappa(I) = \frac{2\mu_{max}}{\alpha I^* \sqrt{\Delta}} \left( \frac{I}{I^*} - 1 \right) + \frac{1}{\sqrt{\Delta}}.$$

### 3. DYNAMICS OF A LIGHT-LIMITED CHEMOSTAT.

Considering a dilution rate  $D$  and a loss rate  $m$  (sum of respiration and mortality rates), the dynamic evolution of the microalgae concentration  $x$  is given by

$$\dot{x} = [g(I_{in}, I_{out}(x, I_{in})) - D - m]x. \quad (15)$$

By standard arguments (i.e.  $\partial(xg(I_{in}, I_{out}(x, I_{in}))/\partial x$  and  $g(I_{in}, I_{out}(x, I_{in}))$  are both bounded by  $\mu_{max}$  for all  $x \geq 0$ ) it can be shown that Eq.(15) admits a unique global solution for any non-negative initial condition.

It is clear that  $\mu$  (see Eq.(8)) is differentiable,  $\mu'(I) > 0$  for all  $I \in [0, I^*]$ ,  $\mu'(I) < 0$  for all  $I \in (I^*, \infty)$ ,  $\mu(0) = 0$  and  $\lim_{I \rightarrow \infty} \mu(I) = 0$ . Let us assume that  $I_{in} > I^*$ . Following the work of Hsu et al. (2013), we know that  $g(I_{in}, 0) = 0$ ,  $g(I_{in}, I_{in}) = \mu(I_{in})$  and that there exists  $\gamma(I_{in}) < I^*$  such that the function  $g(I_{in}, \cdot)$  is strictly increasing on  $[0, \gamma(I_{in})]$  and strictly decreasing on  $[\gamma(I_{in}), I_{in}]$  (see Figure 3 a)). Thus, if  $m + D > g(I_{in}, \gamma(I_{in}))$ , then the equation  $m + D = g(I_{in}, I_{out}(x, I_{in}))$  for  $x$  has no solution (see Figure 3 a)) and  $x_s = 0$  is the unique equilibrium of Eq. (15) which is globally stable. Let us assume that

$$0 < m + D \leq g(I_{in}, \gamma(I_{in})). \quad (16)$$

Then, there exists a unique  $I_s$  such that

$$g(I_{in}, I_s) = D + m, \text{ and } I_s \leq \gamma(I_{in}). \quad (17)$$

Thus, we have the positive equilibrium  $x_s$  of Eq.(15)

$$x_s := \frac{1}{aL} \ln \left( \frac{I_{in}}{I_s} \right), \quad (18)$$

If  $D + m \leq \mu(I_{in})$ , then  $x_s$  is the unique positive equilibrium of Eq. (15) and is globally stable. If

$$\mu(I_{in}) < D + m. \quad (19)$$

then there exist another equilibrium  $x_u$  given by

$$x_u = \frac{1}{aL} \ln \left( \frac{I_{in}}{I_u} \right), \quad (20)$$

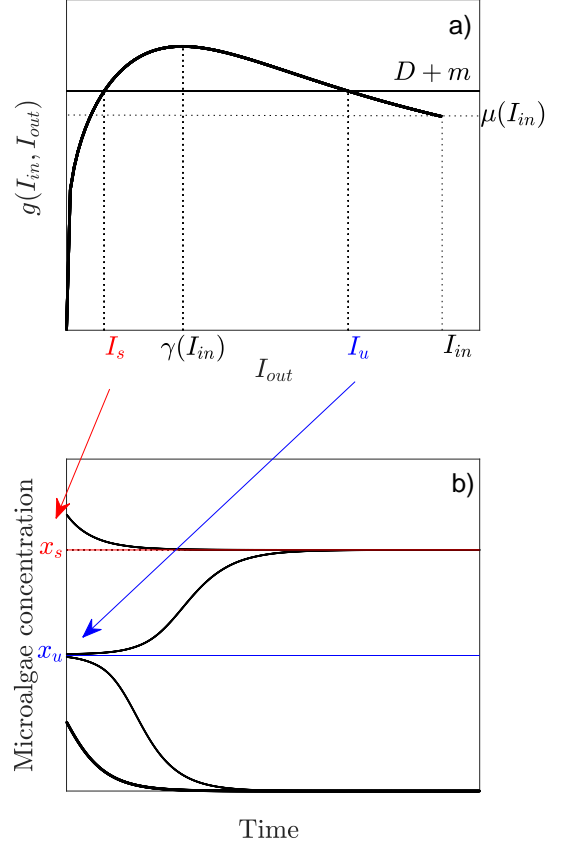


Fig. 3. **a)** Function  $g$  and its intersection with  $D + m$ . **b)** Graphical representation of bi-stability. The black lines represent the solution of Eq. (15) for different initial conditions.

with  $I_u$  satisfying

$$g(I_{in}, I_u) = D + m, \text{ and } \gamma(I_{in}) \leq I_u. \quad (21)$$

In this situation  $x_s$  attracts any solution of (15) with an initial concentration higher than  $x_u$ , and  $x = 0$  attracts any solution with an initial concentration lower than  $x_u$  (see Fig. 3b)). In this case we say that the system faces bi-stability. This behavior is due to photoinhibition. If the initial biomass concentration is high enough, self-shading reduces this effect of inhibition. We note that if  $D + m = g(I_{in}, \gamma(I_{in}))$  then  $x_u = x_s$ .

### 4. MAXIMIZING MICROALGAE PRODUCTIVITY.

Let us assume that condition (16) holds. We define the *steady-state micro-algal biomass surface productivity* as  $P := DLx_s$ , with  $x_s$  defined by Eq. (18). We will simply speak of productivity when referring to  $P$ . The productivity represents the quantity of microalgae that is produced per unit of area and time when the system reaches its steady state. Recalling Eq.(17) we can rewrite the productivity as

$$P = \frac{D}{a} \ln \left( \frac{I_{in}}{I_s} \right). \quad (22)$$

From Eq.(17) we note that  $I_s$  is strictly increasing on  $m$  (see Figure 3 a)), therefore the productivity is decreasing on  $m$ . However, the dependence of  $P$  on  $D$  and  $I_{in}$  is not trivial. By combining equations (17) and (22), we obtain that

$$\begin{aligned} P &= \frac{1}{a}(g(I_{in}, I_s) - m) \ln\left(\frac{I_{in}}{I_s}\right) \\ &= \frac{1}{a} \int_{I_s}^{I_{in}} \frac{\mu(I) - m}{I} dI. \end{aligned} \quad (23)$$

Let  $\hat{I}_{in}$  be such that

$$\mu(\hat{I}_{in}) = m, \quad \hat{I}_{in} > I^* \quad (24)$$

then, the integral in (23) reaches its maximum value when

$$I_s = \sigma(\hat{I}_{in}) \text{ and } I_{in} = \hat{I}_{in}, \quad (25)$$

because in that way the integral is calculated over the maximal interval where the function to be integrated is non-negative. In the following theorem we show that by taking  $D = \hat{D}$  with

$$\hat{D} = g(\hat{I}_{in}, \sigma(\hat{I}_{in})) - m, \quad (26)$$

$I_s$  satisfies Eq.(25).

**Theorem 1.** The productivity is maximal when  $D = \hat{D}$  and  $I_{in} = \hat{I}_{in}$  with  $\hat{D}$  and  $\hat{I}_{in}$  satisfying (24) and (26). The maximal productivity is given by

$$P_{max} := \frac{1}{a} \int_{\sigma(\hat{I}_{in})}^{\hat{I}_{in}} \frac{\mu(I) - m}{I} dI. \quad (27)$$

Under these conditions, Eq.(15) faces bi-stability; the solutions of Eq.(15) reach the stable equilibrium if and only if the initial microalgae concentration  $x_0$  satisfies  $x_0 > \hat{x}_u$  with

$$\hat{x}_u = \frac{1}{aL} \ln\left(\frac{I_{in}}{I^*}\right). \quad (28)$$

**Proof.** Let  $\hat{I}_{in} > I^*$  defined by Eq.(24) and  $\hat{D}$  defined by Eq.(26). First, we note that  $\hat{D} > 0$ , indeed

$$\hat{D} = \frac{1}{\ln\left(\frac{\hat{I}_{in}}{\sigma(\hat{I}_{in})}\right)} \int_{\sigma(\hat{I}_{in})}^{\hat{I}_{in}} \frac{\mu(I) - m}{I} dI > 0. \quad (29)$$

From the definition of  $\hat{D}$  and Eq.(11), we have that

$$\hat{D} + m = g(\hat{I}_{in}, \sigma(\hat{I}_{in})) = g(\hat{I}_{in}, I^*).$$

Since  $\sigma(\hat{I}_{in}) < I^*$ , we conclude that  $I_s = \sigma(\hat{I}_{in})$  and that Eq.(15) faces bi-stability with  $I_u = I^*$ . Finally, by using Eq.(20) we conclude that the unstable equilibrium is given by Eq.(28).

Theorem 1 not only gives the maximal productivity but an expression for the minimal initial microalgae concentration  $\hat{x}_u$  to avoid the washout. Eq.(28) shows that  $\hat{x}_u$  increases by reducing the depth of the reactor. Thus, even if the productivity does not depend on the depth of the reactor,

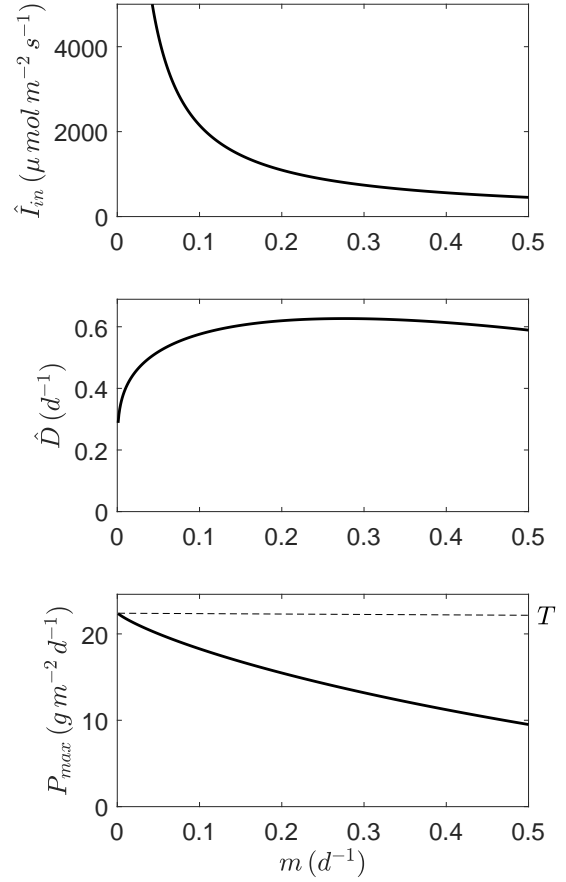


Fig. 4. Plot of the optimal incident light intensity, the optimal dilution rate, and the maximal productivity as functions of the mortality rate. The function  $\mu$  is given by (8) with kinetic parameters of *C. vulgaris* given in Table 1, and  $a = 0.2m^2 g^{-1}$ .

the depth should be chosen such that  $\hat{x}_u$  is not too big. The condition  $x_0 > \hat{x}_u$  can be rewritten as  $I^* > I_{out,0} := I_{in}e^{-ax_0L}$ . Thus, the result related to bi-stability can be stated as follows: the system will washout only if at the beginning the light intensity at the bottom of the reactor is higher than  $I^*$  (i.e. if all microalgae in the PBR are suffering from photoinhibition).

For evaluating the optimal parameters and the maximal productivity we take the kinetic parameters from Table 1. Figure 4 shows that for small values of  $m$  the optimal incident light intensity takes high values; if  $m = 0.1d^{-1}$  then  $\hat{I}_{in} = 2151 \mu mol m^{-2} s^{-1}$ . In fact, as  $m$  approaches to zero, the optimal incident light intensity goes to infinity. To see how  $\hat{I}_{in}$  varies with other parameters, we note that it is the biggest solution of the following equation for  $I$

$$\frac{(I - I^*)^2}{I^{*2}} = \alpha \left( \frac{1}{m} - \frac{1}{\mu_{max}} \right) I. \quad (30)$$

The solutions of this equation correspond to the intercepts of a parabola (left side of Eq.(30)) and a line (right side of Eq.(30)). Figure 5 shows this situation. Thus, any increase

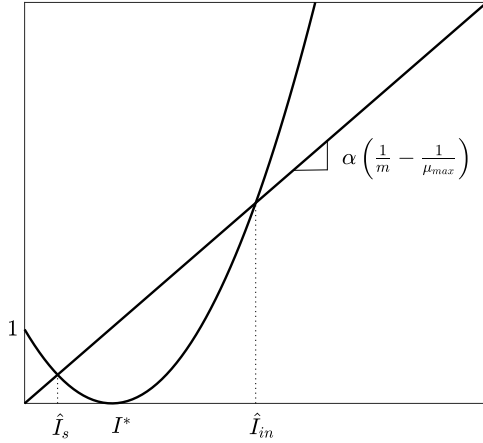


Fig. 5. Plots of the parabola  $y = \frac{(I-I^*)^2}{I^{*2}}$  and the line  $y = \alpha \left( \frac{1}{m} - \frac{1}{\mu_{max}} \right) I$ .

in the slope of the line results in an increase of the value of  $\hat{I}_{in}$ . In particular, this occurs when  $m$  decreases or when  $\alpha$  or  $\mu_{max}$  increases. On the other hand, any increase on  $I^*$  will open wider and translate to the right the parabola. Thus, any increase on  $I^*$  increases the value of  $\hat{I}_{in}$ .

Fig. 4 shows that the maximal productivity approaches a finite value, that we denote  $T$ , when  $m$  approaches to zero. The following proposition gives a simple expression for evaluating  $T$ .

*Proposition 2.* The maximal productivity is bounded from above by

$$T = \frac{2\mu_{max}}{a\sqrt{\Delta}} \left\{ \frac{\pi}{2} - \arctan \left[ \frac{1}{\sqrt{\Delta}} \left( 1 - \frac{2\mu_{max}}{\alpha I^*} \right) \right] \right\}, \quad (31)$$

when  $\Delta > 0$ .

**Proof.** By taking derivative with respect to  $m$  in Eq.(30) we can obtain

$$\frac{\partial \hat{I}_{in}}{\partial m} = \frac{-\alpha \hat{I}_{in}}{m^2 \frac{\hat{I}_{in}-I^*}{\hat{I}_{in}^{*2}} \left[ 1 + \frac{I^*}{\hat{I}_{in}} \right]}. \quad (32)$$

By applying L'Hopital's rule and using Eq.(32) we conclude that

$$\lim_{m \rightarrow 0^+} m \ln \left( \frac{\hat{I}_{in}}{\sigma(\hat{I}_{in})} \right) = 0. \quad (33)$$

Now, by using Eq.(27) and noting that  $\hat{I}_{in} \rightarrow \infty$  and  $\sigma(\hat{I}_{in}) \rightarrow 0$  as  $m \rightarrow 0^+$ , we obtain that

$$T := \lim_{m \rightarrow 0^+} P_{max} = \frac{1}{a} \int_0^{\infty} \frac{\mu(I)}{I} dI. \quad (34)$$

Finally, by using Eq.(14) to evaluate the integral in Eq.(34) we obtain the result of the Proposition.

In the example of Fig. 4, we have that  $T = 22.35g m^{-2} d^{-1}$ . Thus, according to the parameters in this paper,  $C$ ,

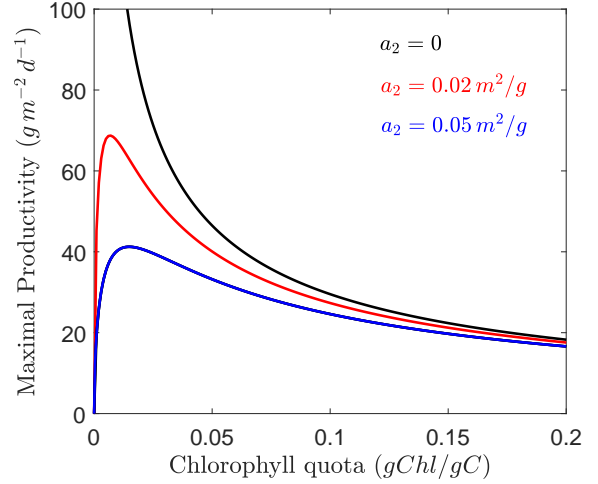


Fig. 6. Maximal productivity as a function of the chlorophyll quota for different values of  $a_2$ . The parameters are taken to be  $\alpha_1 = 1.44d^{-1} \mu mol^{-1} m^2 gC gChl^{-1}$ ,  $a_1 = m^2 gChl^{-1}$ ,  $m = 0.1 d^{-1}$ , and  $I^*$ ,  $\mu_{max}$  from Table 1.

*vulgaris* could never reach a higher productivity than  $22.35g m^{-2} d^{-1}$  in a PBR operated at constant dilution rate and constant incident light.

With respect to the chlorophyll content in microalgae cells, according to Eq.(9),  $\alpha$  decreases with  $\theta$ , and consequently  $\hat{I}_{in}$  becomes closer to  $I^*$  (see Fig. (5)). But how does this affect the productivity? Let us assume that  $\mu_{max}$  and  $I^*$  do not vary with  $\theta$  and that  $a$  and  $\alpha$  vary according to equations (2) and (9) respectively. Fig. 6 shows how the maximal productivity  $P_{max}$  varies with  $\theta$  for different values of  $a_2$ . We can see that if  $a_2 > 0$  (i.e. if light is not only absorbed by chlorophyll), then there exists an optimal value for  $\theta$ . However, if  $a_2 = 0$  (i.e. light is absorbed only by chlorophyll), then the more transparent the microalgae, the higher the maximal productivity.

Experimental results of Anning et al. (2000) and Neidhardt et al. (1998) show that  $\mu_{max}$  and  $I^*$  can also vary with  $\theta$ . Let us assume that all the kinetic parameters ( $\alpha$ ,  $\mu_{max}$ , and  $I^*$ ) and  $m$  depend on  $\theta$  and let us define

$$M(\theta) := \alpha(\theta)I^*(\theta) \left( \frac{1}{m(\theta)} - \frac{1}{\mu_{max}(\theta)} \right). \quad (35)$$

The following theorem gives conditions over  $M$  such that for too high and too low values of  $\theta$  the maximal productivity behaves as in Fig. 6. In particular, it states that for enhancing the maximal productivity when  $a_2 > 0$ , it is not convenient to reduce too much the chlorophyll quota in microalgae cells.

*Theorem 3.* Assume that  $a$  varies according to Eq.(2), that there exists  $N > 0$  such that  $0 < \mu_{max}(\theta) - m(\theta) \leq N$  for all  $\theta > 0$ , and that  $M(\theta)$  (defined in Eq.(35)) is a differentiable function of  $\theta$ . We have that

- (1) If  $\lim_{\theta \rightarrow \infty} M(\theta) = \infty$  and  $\lim_{\theta \rightarrow \infty} M'(\theta) < +\infty$ , then  $\lim_{\theta \rightarrow \infty} P_{max} = 0$ .
- (2) If  $\lim_{\theta \rightarrow 0^+} M(\theta) = 0$  and  $\lim_{\theta \rightarrow 0^+} M'(\theta) < +\infty$ , then

$$\lim_{\theta \rightarrow 0^+} P_{max} = \begin{cases} \infty & \text{if } a_2 = 0, \\ 0 & \text{if } a_2 > 0. \end{cases} \quad (36)$$

**Proof.** Since  $\mu(I) \leq \mu_{max}$  for all  $I \geq 0$ , from Eq.(27) and the definition of  $\sigma(I)$ , we can easily obtain that

$$P_{max} \leq \frac{2}{a_1\theta + a_2} N \ln \left( \frac{\hat{I}_{in}}{I^*} \right). \quad (37)$$

Let  $J := \hat{I}_{in}/I^*$ . Then, from Eq.(30), we have that

$$(J - 1)^2 = M(\theta)J. \quad (38)$$

From where we obtain that

$$\frac{\partial J}{\partial \theta} = \frac{M'(\theta)J}{(J - 1) \left(1 + \frac{1}{J}\right)}. \quad (39)$$

From Eq.(37) and the definition of  $J$ , we obtain that  $\lim_{\theta \rightarrow \infty} P_{max} \leq 2N \lim_{\theta \rightarrow \infty} \ln(J)/(a_1\theta + a_2)$ . After applying L'Hopital's rule and using Eq.(39), we obtain that

$$\lim_{\theta \rightarrow \infty} P_{max} \leq \lim_{\theta \rightarrow \infty} \frac{M'(\theta)}{\alpha_1(J - 1) \left(1 + \frac{1}{J}\right)}. \quad (40)$$

Since  $M(\theta) \rightarrow \infty$  as  $\theta \rightarrow \infty$ , from Eq.(38) we conclude that  $J \rightarrow \infty$  as  $\theta \rightarrow \infty$ . Now, since  $\lim_{\theta \rightarrow \infty} M'(\theta) < +\infty$ , we conclude that the right side of Eq.(40) converges towards 0, and consequently  $\lim_{\theta \rightarrow \infty} P_{max} = 0$ . Thus a) is proved. The part b) follows the same arguments.

## 5. CONCLUSIONS AND FUTURE WORK.

We determined the maximal microalgal productivity that can be reached in a light-limited chemostat operated at constant dilution rate and constant incident light intensity. A simple criterion is obtained: the biomass productivity is maximal when the incident light intensity and the light intensity at the bottom of the culture are such that the growth rates at the top and at the bottom equal the loss rate. Under these optimal conditions the system faces bi-stability i.e. the system washouts when the density is below a certain threshold. We provided a simple expression for determining this threshold. We also studied the effects of the chlorophyll content on the maximal productivity. We showed, that if light is not only absorbed by chlorophyll, then there is an intermediate value of the chlorophyll quota maximizing the productivity.

As a future work, we will deal with the optimization of productivity by considering the background turbidity of the medium (i.e. by adding terms to Eq.(5)) and (or) by including a model of photo-acclimation. By adding turbidity the productivity becomes dependent of the depth of the reactor, which makes more tricky the choice of the depth. By adding photo-acclimation, in long term, the pigment content become dependent of the incident light which could change the compensation condition (25) for maximizing the productivity.

## REFERENCES

Anning, T., MacIntyre, H.L., Pratt, S.M., Sammes, P.J., Gibb, S., and Geider, R.J. (2000). Photoacclimation in

- the marine diatom *skeletonema costatum*. *Limnology and Oceanography*, 45(8), 1807–1817.
- Bernard, O., Mairet, F., and Chachuat, B. (2016). *Modelling of Microalgae Culture Systems with Applications to Control and Optimization*, 59–87. Springer International Publishing, Cham.
- Bernard, O. and Rémond, B. (2012). Validation of a simple model accounting for light and temperature effect on microalgal growth. *Bioresource Technology*, 123, 520 – 527.
- Carvalho, A.P., Silva, S.O., Baptista, J.M., and Malcata, F.X. (2011). Light requirements in microalgal photobioreactors: an overview of biophotonic aspects. *Applied Microbiology and Biotechnology*, 89(5), 1275–1288.
- Eilers, P. and Peeters, J. (1988). A model for the relationship between light intensity and the rate of photosynthesis in phytoplankton. *Ecological Modelling*, 42(3), 199 – 215.
- Gerla, D.J., Mooij, W.M., and Huisman, J. (2011). Photoinhibition and the assembly of light-limited phytoplankton communities. *Oikos*, 120(3), 359–368.
- Grogard, F., Akhmetzhanov, A.R., and Bernard, O. (2014). Optimal strategies for biomass productivity maximization in a photobioreactor using natural light. *Automatica*, 50(2), 359 – 368.
- Hsu, S.B., Lin, C.J., Hsieh, C.H., and Yoshiyama, K. (2013). Dynamics of phytoplankton communities under photoinhibition. *Bulletin of Mathematical Biology*, 75(7), 1207–1232.
- Huisman, J. and Weissing, F.J. (1994). Light-limited growth and competition for light in well-mixed aquatic environments: An elementary model. *Ecology*, 75(2), 507–520.
- Long, S.P., Humphries, S., and Falkowski, P.G. (1994). Photoinhibition of photosynthesis in nature. *Annual Review of Plant Physiology and Plant Molecular Biology*, 45(1), 633–662.
- Mairet, F., Muñoz-Tamayo, R., and Bernard, O. (2013). Driving species competition in a light-limited chemostat. *IFAC Proceedings Volumes*, 46(23), 175 – 180.
- Masci, P., Grogard, F., and Bernard, O. (2010). 11th ifac symposium on computer applications in biotechnology microalgal biomass surface productivity optimization based on a photobioreactor model. *IFAC Proceedings Volumes*, 43(6), 180 – 185.
- Neidhardt, J., Benemann, J.R., Zhang, L., and Melis, A. (1998). Photosystem-ii repair and chloroplast recovery from irradiance stress: relationship between chronic photoinhibition, light-harvesting chlorophyll antenna size and photosynthetic productivity in *dunaliella salina* (green algae). *Photosynthesis Research*, 56(2), 175–184.
- Yeh, K.L., Chang, J.S., and chen, W.m. (2010). Effect of light supply and carbon source on cell growth and cellular composition of a newly isolated microalga *chlorella vulgaris* esp-31. *Engineering in Life Sciences*, 10(3), 201–208.