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Abstract

Microalgae can be cultivated in closed or open photobioreactors (PBR). In these systems, light rapidly decreases as it passes through the culture due to the turbidity of the medium. Thus, microalgae experiment different light intensities depending on their position in the medium. In this paper, we study theoretically how the growth rate of microalgae is affected by different factors; incident light intensity, form of the PBR, microalgae population density, turbidity of non-microalgae components, and light path-length of the reactor. We show that for different types of PBR the average growth rate is completely determined by the incident light intensity and the optical depth. In the case of vertical cylindrical PBRs illuminated from above (e.g. race-way or panel-type reactors), we described (and we prove under general assumptions) in details the dependence of the AGR on the aforementioned factors. Finally, we discuss some implications of our analysis; the occurrence of the Allee effect, if light ostensibly limits or inhibits the growth rate in outdoor cultures, and how the geometry of the PBR affects microalgae growth rate and productivity.

Keywords: `Photobioreactor; Optical depth; Photoinhibition; Light limitation; Turbidity; Modelling`

1. Introduction

Microalgae are photosynthetic microorganisms whose biotechnological potential has been highlighted in the last decade. They grow naturally in all the aquatic environments, and can also be cultivated industrially, for production of compounds such as food complements, colorants, antioxydants, pharmaceuticals, or molecules for green chemistry, including biofuels [1]. They can be mass cultivated in closed or open reactors named photobioreactors (PBR). Depending on the applications, they are grown with artificial or natural light.

Light penetrating a PBR rapidly decreases as it passes through the microalgae culture due to absorption and scattering by algal cells. Thus, phytoplankton cells perceive a different light intensity depending on their position in the PBR. In the case of wastewater treatment or aquatic systems, the light extinction is exacerbated by the high content of highly diffusive particulate matter and the presence of colored substances [2, 3]. Experimental evidence in perfectly mixed PBRs shows that photosynthetic efficiency increases with depth [4], consequently phytoplankton cells respond almost intantaneously to all light intensities within the culture medium and not to an average light intensity. Thus, an appropriate way to model the growth rate in phytoplankton population models, consists in accounting for the differences in local growth rates to obtain the average growth rate (AGR). This way of computing the average growth rate is a trade-off between simple models and complicate models accounting for photosynthesis dynamics [5] which are more difficult to handle and to analyse. Huisman et al.(1994) [6] used the

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AGR for constructing the theory of light-limited chemostats. Gerla et al.(2011) [7] and Hsu et al. (2011)[8] extended the work of Huisman by including photoinhibition i.e. a decrease in the photosynthetic rate due to high light intensities. Some other works are devoted to optimization of the microalgae productivity [9, 10, 11]. The main objective of this paper is to understand how the AGR is affected by different factors; incident light intensity, form of the PBR, microalgae concentration, background turbidity, and light path-length of the reactor (or distance between the illuminated surface and the darkest point).

Most of the mathematical models describing the microalgae growth in PBRs assume that the system is perfectly mixed. Even if real systems are not always perfectly mixed, these models have shown good performances [12, 13, 14, 15]. An important property in perfectly mixed phototrophic cultures in vertical cylindrical PBRs illuminated from above (e.g. race-way photobioreactors or panel-type reactors), is that the AGR is completely determined by the incident light intensity and the light intensity at the bottom of the culture. This property has been used by the works cited above. It allows to study the dynamics of microalgae populations, to scale-up theoretical results, and to set-up experiments for measuring the growth rate. In the first part of this work, we extend this result to PBRs with a flat light-exposed surface and to cylindrical PBRs radially enlightened.

An important variable in our study is the optical depth. This dimensionless variable describes how much absorption occurs when light travels through the PBR. It includes the effects of the light path-length, the background turbidity, and the microalgae population density. In the second part of this work, we study how the AGR varies with the incident light and the optical depth in flat-plate reactors (or in general vertical cylindrical PBRs illuminated from above). We assume that phytoplankton can suffer from photoinhibition. Theoretical works [7, 8] show that photoinhibition can lead algae cultures to the washout, while experimental results show that photoinhibition may cause a loss in biomass productivity even in high dense outdoor cultures [16, 17]. How much microalgae are affected by photoinhibition strongly depends on temperature [18] and photoacclimation [19, 20].

The study of the AGR can lead to some interesting discussions as shown in the last part of the paper. We study the AGR as a function of the microalgae population density, which gives conditions for the occurrence of an Allee effect. Then, we discuss conditions such that the incident light intensity (sunlight) ostensibly limits or inhibits the AGR in outdoor cultures. Then, based on the results of section 2, we compare the AGR of flat plate PBRs with that of other PBRs. Finally, in order to compare the performance of the different PBRs, we evaluate numerically the productivity that can be reached by each PBR.

This paper is organized as follows. In section 2, we define the average growth rate and we determine which factors determine its value of the AGR. In section 3, we describe in details the properties of the average growth rate in the case of a vertical cylindrical PBR illuminated from above. Then, in section 4, we discuss some implications of the analysis of the growth rate in PBRs and compare productivities depending on PBR design.

2. Average growth rate (AGR)

This section begins with the study of PBRs with a flat light-exposed surface. These PBRs serve to introduce the law of Lambert-Beer, the concept of optical depth, and the definition of AGR. Then, we briefly describe the cylindrical PBR radially enlightened. These PBRs are described by simple models which allow to obtain theoretical results. The main results of this section are given by Theorems 2 and 3. They state that the AGR is completely described by two factors; the incident light intensity and the optical depth.

Geometry of PBRs with a flat light-exposed surface. Let us consider a perfectly mixed PBR having a flat surface illuminated perpendicularly with an unidirectional light field. We can described the region Ω occupied by the PBR (more precisely the volume of the culture) by

$$\Omega = \{(x, y, z)\,;\, (x, y) \in \Omega_0, z \in [0, h(x, y)]\},$$

with $\Omega_0 \subset \mathbb{R}^2$ (compact set [1]) the illuminated flat-surface of the PBR that receives the same light

[1] This is necessary to ensure the existence of the maximum of h on Ω_0 and define L at the end of this paragraph.

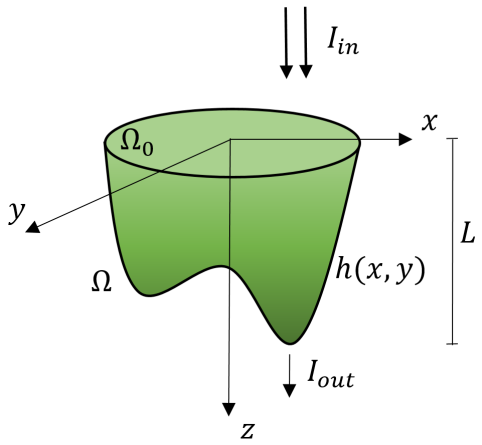

Figure 1: Region Ω occupied by the culture in a Cartesian coordinate system. I_{in} is the incident light intensity, $\Omega_0 \subset \mathbb{R}^2$ is the illuminated flat-surface, Ω is the volume occupied by the culture, $h(x, y)$ is the height of the culture at different positions $(x, y) \in \Omega_0$, L is the maximum depth of the culture, and I_{out} is the light intensity through the lowest part of the culture.

intensity at any point denoted I_{in} (incident light intensity) moving in the positive direction of axis z (see Fig. 1), and $h(x, y)$ a continuous function that represents the depth of the PBR at different points $(x, y) \in \Omega_0$. In this way we can describe different PBRs [21]; a flat plate, a vertical-column (illuminated in one base), or an open pond PBR. A flat-plate PBR is described by a constant function h. By choosing adequately Ω_0 and h we can describe other kind of PBRs like a (horizontal cylindrical) triangular PBR (see Fig. 2A) or a (horizontal cylindrical) semicircular PBR (see Fig. 2B). In the following we will denote by L the maximum depth of the PBR that corresponds to the distance from the light-exposed surface to the lowest point of the reactor (i.e. $L := \max_{(x,y)\in\Omega_0} h(x, y)$).

Light gradient. Light decreases progressively in moving deeper into the culture medium due to light absorption and scattering by light-absorbing substances [22, 2, 3]. As a first approximation, the law of Lambert-Beer can be used to determine the light intensity I at any position in the PBR. This means that multi-diffusion effects are not explicitly represented. Thus

$$\frac{\partial I}{\partial z} = -\xi I, \tag{1}$$

with $\xi \geq 0$ an extinction coefficient that depends on the medium. Since the culture is perfectly mixed, ξ does not depend on z. Thus, we can easily integrate Eq.(1) to obtain

$$I(\xi, I_{in}, z) = I_{in} e^{-\xi z}, \text{ for all } (x, y, z) \in \Omega. \tag{2}$$

Here, z corresponds to the distance from the illuminated surface of the PBR to the position (x, y, z). A key variable in our study is the light intensity in the lowest (or the darkest) part of the culture, that is

$$I_{out}(I_{in}, \xi L) := I_{in} e^{-\xi L}. \tag{3}$$

We emphasize the fact that I_{out} depends only on the product ξL, and not on L and ξ separately.

In microalgae cultures illuminated with natural light, the incident light is in general not perpendicular to the surface. The incident flux must be computed accounting for loss due to reflection. The transmitted light fraction is then refracted into the medium. Due to the very diffusive character of the microalgae culture, we assume that it is rapidly anisotropic and therefore, we keep the Lambert-Beer approximation, assuming now an incident flux ηI_{in} with $\eta \in [0, 1]$.

Extinction coefficient. In the case of a monoculture, ξ is mainly correlated to the microalgae population density X [3];

$$\xi(X) = kX + K_{bg}, \tag{4}$$

with $k > 0$ the specific light extinction coefficient of the microalgae specie and $K_{bg} \geq 0$ the background turbidity that summarizes the light absorption and difussion due to all non-microalgae components i.e. suspended solids and dissolved colored material. Typical values of the coefficient k for several microalgae species are given in Table 1. To use expression (4), the density of the culture must be low enough so that most of the photons are diffused at most once. For multi diffusion regimes, which characterize industrial reactors, the latter condition is generally not satisfied [23]. Various empirical expressions have therefore been developed to macroscopically account for multi scattering (see table 6 in [24]). For example, in [25] the following expression is proposed

$$\xi(X) = \frac{k_1 X}{k_2 + X},$$

with k_1 and k_2 empirical parameters.

Extinction coefficient ($m^2\,gC^{-1}$)	Algae
0.214	*Monodus subterraneu*
0.175	*Spirulina platensis*
0.150	*Porphyridium cruentum*
0.200	*Chlorella pyrenoidosa*

Table 1: Values of the specific light attenuation coefficient for different microalgae species [24]

AGR definition. The specific growth rate of microalgae, denoted by μ, represents the net growth potential of the population. If biomass is defined in terms of cell density, μ is the cell division rate, minus the mortality rate. If X is a mass of algal carbon, then μ is the rate of CO_2 fixation, minus the respiration rate. In section 3 (paragraph *Assumptions over* μ) some explicit expressions of μ as a function of the light intensity I perceived by microalgae are presented. In this section, we only assume that I is the single factor that limits algae growth i.e $\mu : \mathbb{R}_+ \longrightarrow \mathbb{R}$ is a function of I. Let $V(\Omega)$ be the volume of the culture. Following [6], we compute the average growth rate (AGR) in the PBR, denoted by $\bar{\mu}$, by integrating the local specific growth rates over all the culture

$$\bar{\mu}(\cdot) := \frac{1}{V(\Omega)} \int_\Omega \mu(I(\xi, I_{in}, z))dxdydz. \quad (5)$$

We note that for $\xi = 0$ (transparent culture), expression (5) is reduced to

$$\bar{\mu}(\cdot) = \mu(I_{in}). \quad (6)$$

This is consistent with the fact that all microalgae will perceive the same light intensity. To study the case $\xi > 0$, let us define $A_\Omega(z)$ as the area of the cross section of Ω at depth $z \in [0, L]$. The following lemma gives a useful expression for determining the AGR in different PBRs.

Lemma 1. *If $\xi > 0$, then*

$$\bar{\mu}(\cdot) = \frac{1}{\xi V(\Omega)} \int_{I_{out}(\xi L, I_{in})}^{I_{in}} \frac{\mu(I)}{I} A_\Omega\left(\frac{1}{\xi}\ln\left(\frac{I_{in}}{I}\right)\right) dI. \quad (7)$$

Proof. By doing the change of variables $I = I(\xi, I_{in}, z)$ we rewrite expression (5);

$$\bar{\mu}(\cdot) = \frac{1}{\xi V(\Omega)} \int_{(x,y)\in\Omega_0} \int_{I(\xi, I_{in}, h(x,y))}^{I_{in}} \frac{\mu(I)}{I} dIdxdy.$$

After changing the order of integration in the latter expression we obtain

$$\bar{\mu}(\cdot) = \frac{1}{\xi V(\Omega)} \int_{I_{out}(\xi L, I_{in})}^{I_{in}} \int_{(x,y)\in\Omega_0(I)} \frac{\mu(I)}{I} dxdydI. \quad (8)$$

$\Omega_0(I)$ corresponds to the projection onto the plane $x - y$ of the set formed by all the points of Ω at which the light intensity equals I. From Lambert-Beer law, the latter is the intersection of Ω and the plane parallel to Ω_0 that intersects $z = \frac{1}{\xi}\ln\left(\frac{I_{in}}{I}\right)$. Thus $\int_{(x,y)\in\Omega_0(I)} dxdy = A_\Omega\left(\frac{1}{\xi}\ln\left(\frac{I_{in}}{I}\right)\right)$ and we conclude the proof. □

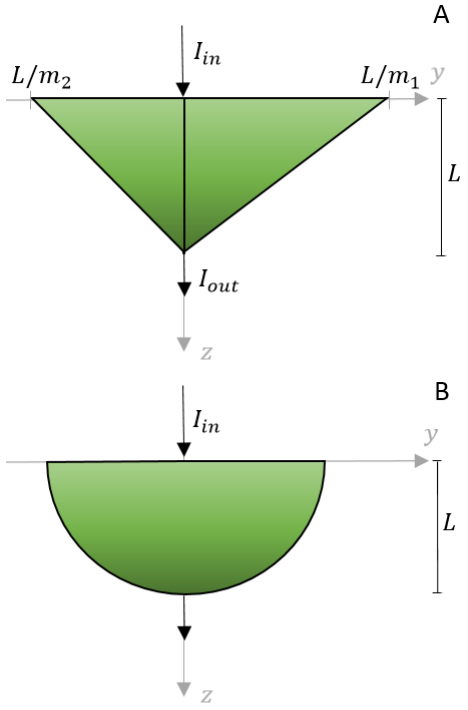

Figure 2: Schematic representation of a cross section through a cylindrical horizontal PBR. A. Triangular cylinder. The base measures $L(1/m_1 + 1/m_2)$ and the height L. B. Semicircular cylinder of radius L.

Flat-plate PBR. In the case of a flat-plate PBR (i.e. $h(x, y) = L > 0$ for all $(x, y) \in \Omega_0$), $A_\Omega(z)$ is constant and $V(\Omega) = LA_\Omega(z)$. By using Eq.(7), it is straightforward to verify that

$$\bar{\mu}(\cdot) = \frac{1}{\xi L} \int_{I_{out}(\xi L, I_{in})}^{I_{in}} \frac{\mu(I)}{I} dI. \quad (9)$$

This shows that in flat-plate PBRs, the AGR is completely determined by ξL and I_{in}.

Optical depth. The product ξL will be denoted by θ. This variable is usually known as *optical depth*. The optical depth reflects the actual amount of light energy absorbed by the culture medium. Indeed, θ can be determined from

$$\theta = \ln(I_{in}/I_{out}(\theta, I_{in})). \tag{10}$$

Thus, in view of Eq.(9), in a flat-plate PBR, the AGR is determined by the light intensities at the top and at the bottom of the PBR.

Triangular horizontal cylinder. Consider now that the PBR is a triangular horizontal cylinder (see Fig. 2A) i.e. $h(x,y) = -m_1 y + L$ for $y \in [0, L/m_1]$ and $h(x,y) = m_2 y + L$ for $y \in [-L/m_2, 0]$ with $m_1, m_2 > 0$. So we have that $A_\Omega(z) = H\left(\frac{1}{m_1} + \frac{1}{m_2}\right)(z+L)$ and $V(\Omega) = HL^2(1/m_1 + 1/m_2)/2$ with H the length of the cylinder. Thus, Lemma 1 gives

$$\begin{aligned}\bar{\mu}(\cdot) &= -\frac{2}{\theta^2}\int_{I_{out}(\theta,I_{in})}^{I_{in}} \frac{\mu(I)}{I}\ln\left(\frac{I_{in}}{I}\right)dI \\ &\quad + \frac{2}{\theta}\int_{I_{out}(\theta,I_{in})}^{I_{in}} \frac{\mu(I)}{I}dI.\end{aligned} \tag{11}$$

This expression shows that the family of all the triangular PBRs have the same AGR, which is determined by the incident light intensity and the optical depth (or the light intensity at the lowest point according to Eq.(10)). Expression (11) is clearly different from expression (9). This shows that the form of the reactor must be taken into account for determining the AGR.

Shape of a PBR. We say that two PBRs have equivalent shape if one of them can be obtained by scaling the other one. Mathematically, a PBR occupying a region Ω has equivalent shape of a PBR occupying a region Ω' if there exist positive numbers s_x,s_y, and s_z such that

$$\Omega' = \{(s_x x, s_y y, s_z z)\,;\,(x,y,z) \in \Omega\}.$$

If $s_x = s_y = s_z$ we speak of an uniform scaling, otherwise of a non-uniform scaling. The following theorem shows that by fixing the shape of the PBR, we obtain the same AGR and that is determined by the incident light intensity and the optical depth.

Theorem 2. *Two PBRs with equivalent shape lead to the same AGR, which is completely determined by the incident light intensity and the optical depth.*

Proof. First we note that

$$\begin{aligned}V(\Omega) &= \int_0^L A_\Omega(z)dz \\ &= \int_{I_{out}(\theta,I_{in})}^{I_{in}} \tfrac{1}{I} A_\Omega\left(z = \tfrac{1}{\xi}\ln\left(\tfrac{I_{in}}{I}\right)\right)dI.\end{aligned}$$

Then, we can write

$$\bar{\mu}(\cdot) = \int_{I_{out}(\xi L, I_{in})}^{I_{in}} \mu(I) f(I;\xi,I_{in},\Omega)dI, \tag{12}$$

with f defined by

$$f(I;\xi,I_{in},\Omega) := \frac{\frac{1}{I}A_\Omega\left(\frac{1}{\xi}\ln\left(\frac{I_{in}}{I}\right)\right)}{\int_{I_{out}(\xi L,I_{in})}^{I_{in}} \frac{1}{I}A_\Omega\left(\frac{1}{\xi}\ln\left(\frac{I_{in}}{I}\right)\right)dI}. \tag{13}$$

Now, consider another PBR of depth $L' > L$ occupying a region Ω' obtained by scaling Ω. That is, there are $s_x, s_y > 0$ such that

$$\Omega' := \{(s_x x, s_y y, (L'/L)z);\ (x,y,z) \in \Omega\}.$$

Assume now that the extinction coefficient ξ' in this PBR satisfies $\xi L = \xi' L'$. If we note that $A_{\Omega'}(z) = s_x s_y A_\Omega((L/L')z)$, it is straightforward to verify that

$$f(I;\xi',I_{in},\Omega') = f(I;\xi,I_{in},\Omega). \tag{14}$$

Eq.(14) indicates that the value of f is determined by I_{in}, the product ξL, and shape of the PBR. This holds of course for the AGR, since I_{out} depends only on I_{in} and ξL. □

Horizontal semicircular cylinder. As a last example of a flat light-exposed surface PBR, consider a semicircular horizontal cylinder (see Fig. 2B) i.e. $h(x,y) = \sqrt{L^2 - y^2}$. So we have that $A(z) = 2\sqrt{L^2 - z^2}$ and Lemma 1 gives

$$\bar{\mu}(\cdot) = \frac{4}{\pi\theta}\int_{I_{out}(\theta,I_{in})}^{I_{in}} \frac{\mu(I)}{I}\sqrt{1 - \frac{1}{\theta^2}\ln^2\left(\frac{I_{in}}{I}\right)}dI. \tag{15}$$

This expression for the AGR is clearly different from that of Eq.(9). According to Theorem 2, this expression is also valid for semi-elliptical horizontal cylinders.

Cylindrical PBR radially enlightened. The cylindrical PBR, evenly illuminated around, is also commonly used. The region Ω occupied by the PBR

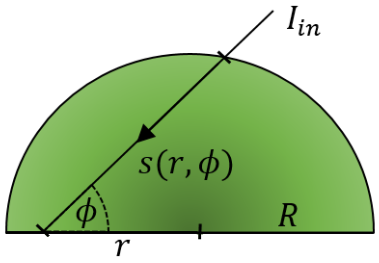

Figure 3: Schematic representation of one-half of a cross section through a cylindrical chemostat vessel (s, light path; R, cylinder radius; r, distance from the center; ϕ, angle of light path with line through the center.

corresponds to a cylinder of radius R, which is radially and evenly illuminated over the sides (not over the bases). From [26], the path length of light to a point at distance r from the center as a function of the angle ϕ (see Fig. 3) equals

$$s(r,\phi) = r\cos\phi + \sqrt{R^2 - r^2\sin^2\phi}. \tag{16}$$

By using the law of Lambert-Beer and accounting for the light flux coming from all the directions (ϕ moving between 0 and 2π), the light intensity at a distance r from the center is given by

$$I(r) = \int_0^{2\pi} I_{in} e^{-\xi s(r,\phi)} d\phi. \tag{17}$$

By using cylindrical coordinates, the AGR can be written as

$$\bar{\mu}(\cdot) := \frac{1}{\pi R^2}\int_0^{2\pi}\int_0^{R} \mu(I(r)) r dr d\phi \tag{18}$$

$I(r)$ is increasing as a function r (see Proof of Theorem 3). Thus, the darkest zone of the PBR is in the center ($r = 0$) and the most illuminated zone is on the sides ($r = R$). Based on the distance between these two zones, we define the optical depth as $\theta := \xi R$. We have the following version of Theorem 2 for the cylindrical PBR.

Theorem 3. *The AGR defined in Eq.(18) is completely determined by the optical depth and the incident light intensity.*

Before proving Theorem 3, note that the optical depth can be obtained explicitly from

$$\theta = \ln\left(2\pi\frac{I_{in}}{I(0)}\right). \tag{19}$$

This shows that Theorem 3 could be stated in terms of I_{in} and $I(0)$.

Proof. (*of Theorem 3*) Let us denote by f the first derivative of $I(r)$ i.e.

$$f(r;\xi,I_{in},R) = -\xi I_{in}\int_0^{2\pi} e^{-\xi s(r,\phi;R)}\frac{\partial}{\partial r}s(r,\phi;R)d\phi \tag{20}$$

Note that we explicitly indicate the dependence on the radius of the functions f and s . It is straightforward to verify that $I''(r) > 0$ for any $r \in [0,R)$. Thus, f is a strictly increasing function with respect to r. Consequently, $f(r;\xi,I_{in},R) > f(0;\xi,I_{in},R) = 0$. Thus, I is strictly increasing. The latter implies that $I(r) : [0,R] \longrightarrow [I(R),I(0)]$ has an inverse function $\varphi(I;\xi,I_{in},R) : [I(R),I(0)] \longrightarrow [0,R]$.

By integrating Eq.(18) with respect to ϕ and doing the change of variables $I = I(r)$, the AGR can be written as

$$\bar{\mu}(\cdot) = 2\int_{I(R)}^{I(0)} \mu(I)H(I;\xi,I_{in},R)dI, \tag{21}$$

with

$$H(I;\xi,I_{in},R) = \frac{\varphi(I;\xi,I_{in},R)}{R^2 f(\varphi(I;\xi,R);\xi,I_{in},R)}.$$

By evaluating $I(0)$ and $I(R)$, it is easy to verify that they are determined by ξR and I_{in}. It remains to prove the same for H. For this purpose, consider another PBR of radius R' and assume that the extinction coefficient ξ' in this PBR satisfies $\xi R = \xi' R'$. As in Theorem 2 we have to prove that $H(I;\xi,I_{in},R) = H(I;\xi',I_{in},R')$, but this follows rapidly after noting that $\varphi(I;\xi',I_{in},R') = \varphi(I;\xi,I_{in},R)R'/R$. □

3. Properties of the AGR in flat-plate PBRs.

Definition of the function g. In a flat-plate PBR the AGR is given by Eq.(9). If $I_{in} > 0$, by substituting (10) in (9) we have

$$\bar{\mu}(\cdot) = g(I_{in}, I_{out}(\theta, I_{in})), \tag{22}$$

with

$$g(I_{in},I_{out}) = \frac{1}{\ln(I_{in}/I_{out})}\int_{I_{out}}^{I_{in}}\frac{\mu(I)}{I}dI. \tag{23}$$

Eq.(23) gives an explicit expression for the AGR as a function of the light intensities at the top and at the bottom of the PBR. The function g was first

defined in [7] and is useful for studying the properties of the AGR. This function highlights the fundamental link between AGR and the extreme values of light intensity in the PBR.

Assumptions over μ. μ corresponds to the carbon gain rate i.e. $\mu = p - m$, with p the carbon uptake rate and m the specific carbon loss rate that is assumed to be constant. In the literature we find different models for p, for example the classical model of Steele [27]

$$p(I) = p_{max} \frac{I}{I^*} e^{1-\frac{I}{I^*}}, \tag{24}$$

with p_{max} the maximum value of p, or Haldane-type models [2] like the one presented in [28]

$$p(I) = p_{max} \frac{I}{I + \frac{p_{max}}{\alpha}\left(\frac{I}{I^*} - 1\right)^2}, \tag{25}$$

where α is the initial slope of p. Table 2 shows the kinetic parameters of model (25) for three different microalgae species. Fig.4 shows p given in (25) with kinetic parameters from Table 2 for *C.vulgaris*.

Parm.	*C.V.*	*C.P.*	*S.C.*	Unit
p_{max}	1.63	2	1.32	d^{-1}
I^*	87.2	275	119	$\mu mol\, m^{-2}\, s^{-1}$
α	0.027	0.05	0.086	$\mu mol^{-1}\, m^2\, s\, d^{-1}$

Table 2: Kinetic parameters of p in (25) for different microalgae species; *C.V.*: *Chlorella vulgaris* at $25°C$ [29], *C.P.*: *Chlorella pyrenoidosa* at optimal temperature [28], *S.C.*: *Scenedesmus crassus* at $25°C$ [30].

In what follows of this section, we will describe the AGR when p is given by (25) or (24). However, the theory of turbid cultures is derived for any net growth rate satisfying the following assumptions.

Assumption 4. *There exists a light intensity $I^* > 0$ such that μ is strictly increasing for $I \in [0, I^*]$ and strictly decreasing for $I \in [I^*, \infty)$.*

Assumption 4 states that phytoplankton can suffer from photoinhibition. Here, I^* is the light intensity at which μ reaches its maximum value.

Assumption 5. $\mu(0) = \lim_{I\to\infty} \mu(I)$.

[2] By a Haldane-type model, we mean $p(I) = \frac{I}{aI^2+bI+c}$ with $a, c > 0$.

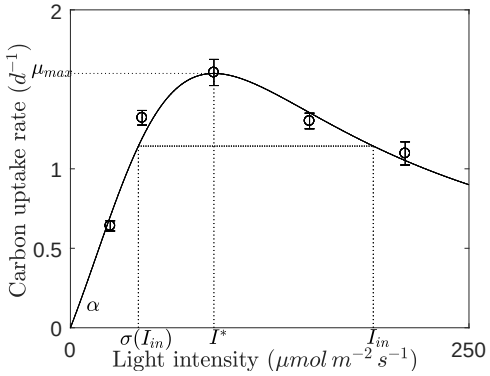

Figure 4: Carbon uptake rate (see Eq.(25)) for *Chlorella vulgaris* with kinetic parameters from Table 2, experimental data from [29], and graphical description of σ.

Assumption 5 states that for high light intensities ($I \to \infty$) phytoplankton grows similarly as under absence of light ($I = 0$). Indeed, when p is given by 25 we have $\mu(0) = \lim_{I\to\infty} \mu(I) = -m$.

When p is given by Eq.(25) or Eq.(24) it is possible to obtain explicit expressions for the AGR (see Appendix B).

Symmetry of p. We note that for any $I > 0$ different from I^*, there exists another light intensity, that will be denoted $\sigma(I)$, such that

$$p(I) = p(\sigma(I)). \tag{26}$$

A graphic representation of σ is shown in Fig.4. It seems clear to define $\sigma(I^*) = I^*$ which ensures the continuity of σ. As we will see below, σ is relevant when describing the AGR. In the case that p is given by Eq.(25) we obtain a simple expression for $\sigma(I)$

$$\sigma(I) = \frac{I^{*2}}{I}. \tag{27}$$

Critical optical depth. Consider that the incident light intensity I_{in} is fixed and lower than or equal to I^*. According to Lemma A1, the AGR (or the function g) increases as the light intensity at the bottom I_{out} increases. Consequently, the maximum value of the AGR is obtained when I_{out} equals I_{in}. Recalling Eq.(1), this equality is only possible if $\theta = 0$ (i.e. the medium is transparent). Consider now that I_{in} is fixed at a value higher than I^*. According to Lemma A1, there exists $\gamma(I_{in}) < I^*$ such that the AGR is maximal when $I_{out} = \gamma(I_{in})$, or, in terms of the optical depth, when $\theta = \ln(I_{in}/\gamma(I_{in}))$.

Following these ideas we define the *critical optical depth*, denoted by $\tilde{\theta}(I_{in})$, as

$$\tilde{\theta}(I_{in}) := \begin{cases} \ln\left(\frac{I_{in}}{\gamma(I_{in})}\right) & if \quad I_{in} > I^*, \\ 0 & if \quad I_{in} \leq I^*. \end{cases} \tag{28}$$

The critical optical depth (associated to a critical value if biomass) reflects the value of the optical depth for which the AGR is maximal. Fig.5A shows how the AGR varies with the optical depth for different incident light intensities. When $I_{in} = I^*$ (or $I_{in} < I^*$), the AGR decreases with θ. When $I_{in} > I^*$, the AGR increases with θ until reaching its maximum value at $\theta = \tilde{\theta}(I_{in})$ and then decreases. As θ tends to be too high, the AGR approaches the value of the specific growth rate in absence of light ($\lim_{\theta\to\infty} \bar{\mu}(\cdot) = \mu(0)$). Proposition A2 states in detail this behavior. We note that $\tilde{\theta}$ increases with I_{in}, which is true in general as stated in Proposition A4. When p is given by Eq.(25), according to Proposition A4, we have that for any $I_{in} > I^*$

$$\ln\left(\frac{I_{in}}{I^*}\right) < \tilde{\theta}(I_{in}) < 2\ln\left(\frac{I_{in}}{I^*}\right). \tag{29}$$

This inequality shows that $\tilde{\theta}$ increases logarithmically. Fig.6 shows $\tilde{\theta}(I_{in})$ as a function of I_{in} for three different microalgae species with kinetic parameters from Table 2.

Critical incident light. Fig.5B shows the AGR as a function of the incident light for different values of the optical depth. According to Lemma A2, there is an incident light intensity $\mathcal{I}(\theta)$, that we call *critical incident light intensity*, at which the AGR is maximal. When $\theta = 0$, the AGR coincides with the specific growth rate. As θ increases, the form of the AGR becomes wider and reaches its maximum at a higher incident light intensity. At low incident light intensity (i.e. for $I_{in} < \mathcal{I}(\theta)$), light is a limiting factor in the sense that increasing light enhances the growth rate. This notion is not straightforward since some cells (in surface) can be photoinhibited. At high light (and especially for low θ), light is globally inhibiting.

According to Lemma A2, the critical incident light intensity is such that μ is the same at the top and at the bottom of the PBR (see Eq. (40)). In terms of σ this can be written as

$$\sigma(\mathcal{I}(\theta)) = \mathcal{I}(\theta)e^{-\theta}. \tag{30}$$

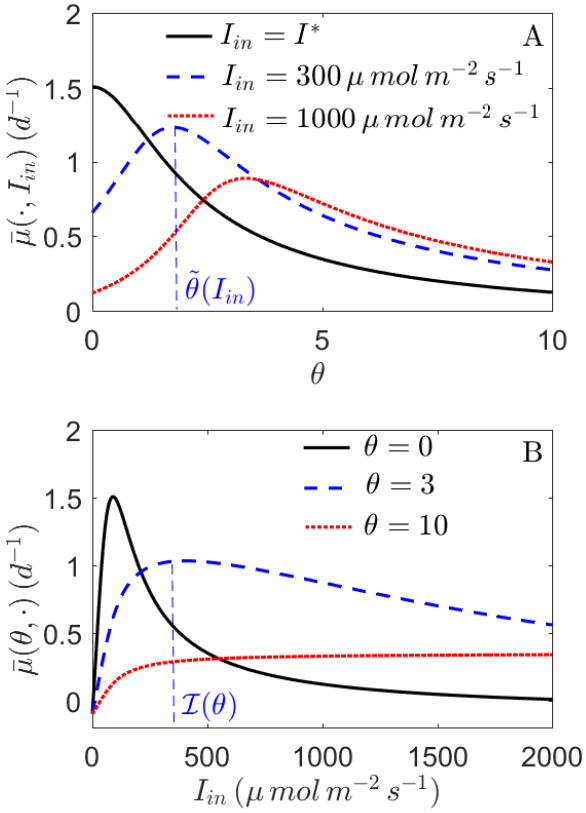

Figure 5: A. Plot of the AGR as a function of the optical depth for three different values of the incident light. B. Plot of the AGR as a function of the incident light intensity for three different values of the optical depth. We consider p given by (25) with the kinetic parameters of *C. vulgaris* given in Table 2 and $m = 0.1\,d^{-1}$.

Thus, if p is given by Eq.(25), then

$$\mathcal{I}(\theta) = I^* e^{\theta/2}. \tag{31}$$

If p is given by Eq.(24), we cannot determine an explicit expression for σ, but we can determine directly from Eq.(40) (Appendix A) the form of the critical incident light intensity

$$\mathcal{I}(\theta) = I^* \frac{\theta}{1 - e^{-\theta}},$$

These expressions show that the critical incident light increases with the optical depth. This is true in the general case according to Proposition A5.

4. Discussion

AGR as a function of the microalgae population density. Let us consider a flat-plate PBR, and as-

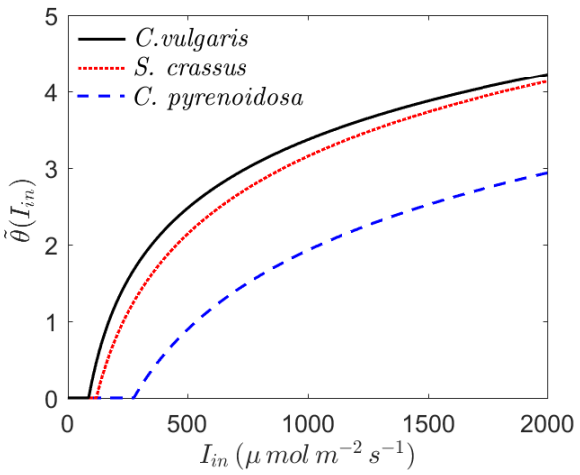

Figure 6: Critical optical depth $\tilde{\theta}$ as a function of the incident light I_{in} for three different microalgae species. Kinetic parameters are taken from Table 2.

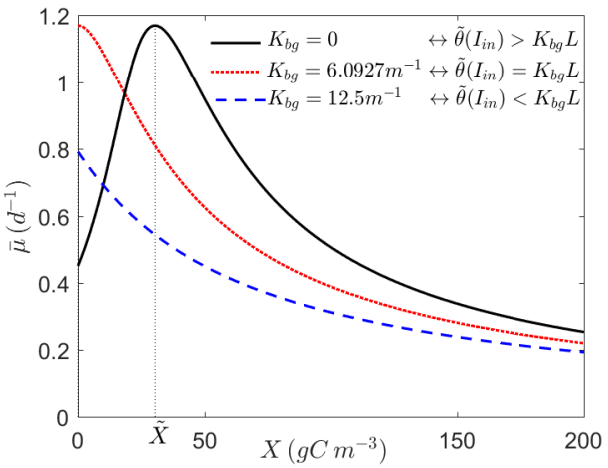

Figure 7: Plot of the AGR as a function of X. We consider p given by (25) with the kinetic parameters of *C. vulgaris* given in Table 2. The other parameters are taken to be $I_{in} = 500\,\mu\,mol\,m^{-2}\,s$, $k = 0.2\,m^2\,gC^{-1}$, $L = 0.4\,m$, and $m = 0.1\,d^{-1}$.

sume that ξ is given by (4). In that case the optical depth is given by

$$\theta(X) = (kX + K_{bg})L.$$

From the previous section, we know that the AGR is maximal if $\theta(X)$ equals the critical optical depth $\tilde{\theta}$. Thus, if the optical depth in absence of microalgae $\theta(0) = K_{bg}L$ is lower than $\tilde{\theta}$, there is a microalgae population density $\tilde{X} = \frac{\tilde{\theta}-K_{bg}L}{kL}$ maximizing the AGR. This shows the existence of an Allee effect, i.e. the AGR is maximal at an intermediate population density. This is illustrated in Fig. (7) that shows the AGR as a function of X for different values of K_{bg}. Now, if $\theta(0) = K_{bg}L \geq \tilde{\theta}$, any increase in the microalgae population will move the optical depth further away from its optimal value. In consequence, the AGR rate is maximal when $X = 0$. In that case there is no Allee effect.From Proposition A4, $\tilde{\theta}$ increases with I_{in}, thus, high values of I_{in} and low values of $K_{bg}L$ (low optical depth associated to the background turbidity) favor the presence of an Allee effect.

Experimental evidence of a positive optimal population density is for example described in [31]. The optimal density is $2.5\,g/L$ for a culture of *Spirulina platensis* in a glass column photobioreactor illuminated with an incident light intensity of $2000\,\mu\,mol\,m^{-2}\,s^{-1}$.

Incident light intensity as a limiting factor. By a limiting factor we understand a factor such that the AGR increases with any increase of it. Fig.5B shows that when $\theta = 10$, the incident light intensity is a limiting factor on the range $0 - 2000\,\mu\,mol\,m^{-2}\,s^{-1}$. This does not mean that microalgae does not suffer from photoinhibition, in fact, they do near the surface. It only means that the AGR increases. To determine if in outdoor cultures illuminated with natural light the light is a limiting factor, let us assume that I_{max} is the maximal incident light intensity (at midday) that the culture can receive. Thus, if $I_{max} \leq \mathcal{I}(\theta)$, then light is a limiting factor during all the day. If p is given by Eq.(25), recalling Eq.(31), this is equivalent to

$$\theta \geq 2\ln\left(\frac{I_{max}}{I^*}\right). \qquad (32)$$

Thus, if $I_{max} = 2000\,\mu\,mol\,m^{-2}\,s^{-1}$, and $I^* = 90\,\mu\,mol\,m^{-2}\,s^{-1}$, condition (32) says that for cultures with $\theta \geq 6.1$, the light is a limiting factor. In terms of microalgae concentration, if ξ is given by Eq.(4), Eq.(32) can be put as

$$LX \geq \left(2\ln\left(\frac{I_{max}}{I^*}\right) - LK_{bg}\right)/k. \qquad (33)$$

If $K_{bg} = 0\,m^{-1}$ and $k = 0.2\,gC\,m^{-2}$, the previous condition says that for cultures with an areal microalgal concentration higher than $30.5\,gC\,m^{-2}$

light is a limiting factor.

AGR in different geometries. In section 3, we described some properties of the AGR in vertical cylindrical (or flat-plate) PBRs illuminated over one base. Even if we did not provide any formal demonstration for these different cases, these properties are expected to be valid for PBRs with a different shape. For sake of simplicity, we will refer to the different PBRs as flat-plate (Eq.(9)), triangular (Eq.(11)), semicircular (Eq.15)), and cylindrical PBR (Eq.(18)). Fig.8A shows the AGR for different PBRs as a function of the optical depth. We can see that for low values of θ the AGR is higher in the flat-plate PBR while for high values of θ it is higher in the triangular PBR. Fig.8B shows the AGR for the different PBRs as a function of the incident light intensity. We can see that for high values of I_{in} the AGR is higher in the flat-plate PBR while for low values of I_{in} it is higher in the cylindrical PBR. These differences can be justified by the distribution of the microalgal culture with respect to the light gradient.

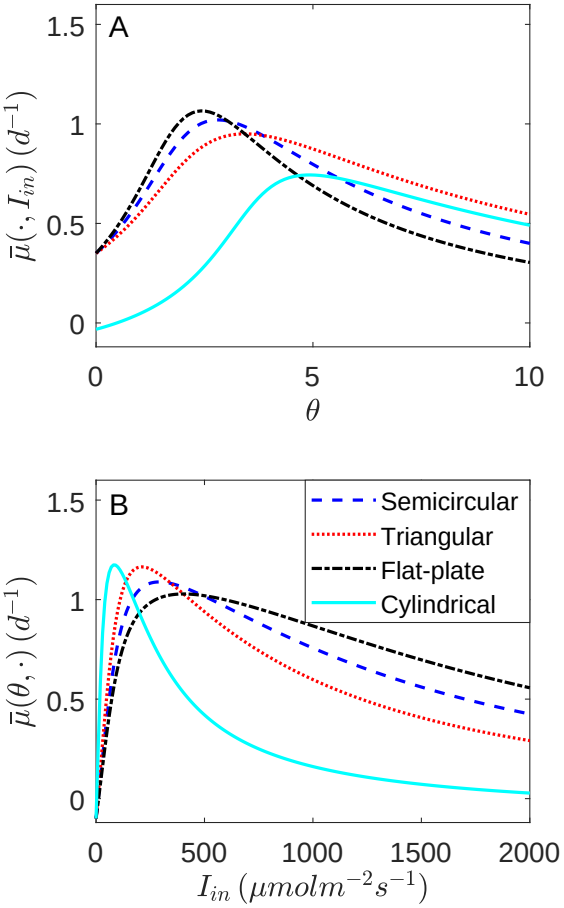

Figure 8: Plots of the AGR for different shapes of the PBR. A. $I_{in} = 500\,\mu\,mol\,m^{-2}\,s^{-1}$ is fixed. B. $\theta = 3$ is fixed. We consider p given by (25) with the kinetic parameters of *C. vulgaris* given in Table 2 and $m = 0.1\,d^{-1}$.

Productivity. In order to compare the productivity of the different PBRs presented in this paper, we benchmark them considering that they all have the same volume V and the same irradiated culture area A. The depth of the flat-plate, the triangular, and the semicircular PBRs are V/A, $2V/A$, and $\frac{4}{\pi}V/A$ respectively. For the cylindrical PBR the radius is $2V/A$. $B = XV/A$ corresponds to the biomass concentration per unit of irradiated area. Thus, the biomass productivity per unit of irradiated area is

$$P := B\bar{\mu}(I_{in}, \theta). \tag{34}$$

Writing the AGR as a function of the optical depth and the incident light intensity is justified by Theorems 2 and 3. Let us assume that the extinction coefficient is given by Eq. (4). Then, in the flat-plate PBR, the optical depth is given by

$$\theta = (kX + K_{bg})V/A = kB + K_{bg}V/A. \tag{35}$$

Consequently, P depends on V/A but not on the values of V and A separately. The same is valid for the other PBRs. In the case that $K_{bg} = 0$, the productivity P is independent of V/A. Figure 9 shows the productivity as a function of B. We note that when $I_{in} > I^*$ the highest productivity is reached in the rectangular PBR. However, when $I_{in} < I^*$ the highest productivity is reached in the column PBR. The microalgae population density that yields maximal productivity is known as optimal population (or cell) density (OCD). The OCD has been studied experimentally in many works [31, 32, 33, 34].

In practice, background turbidity is not zero. It can even be very high if algae are used in wastewater treatment. In that case, the productivity varies with V/A (or with the light path-length). Figure 10 shows the maximal productivity for different values of V/A. As shown experimentally in [34], the productivity decreases as the light path-length

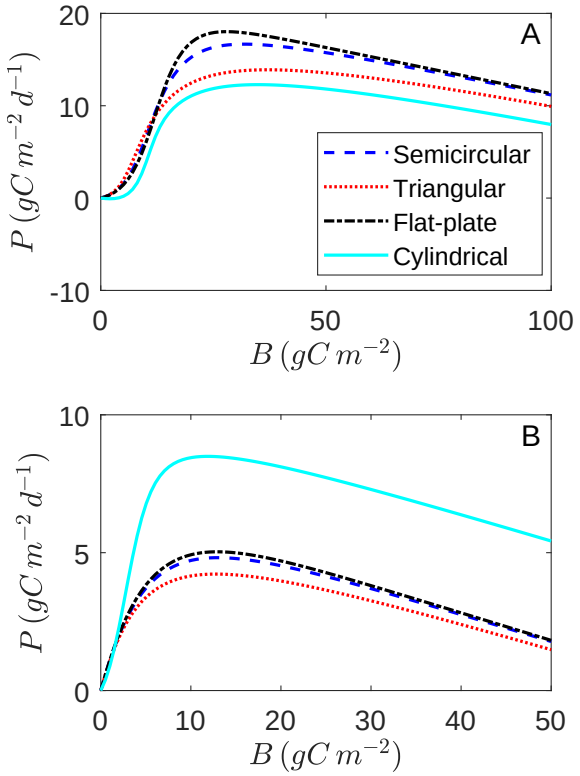

Figure 9: Productivity as a function of the biomass concentration per illuminated surface. A. $I_{in} = 1000\,\mu mol\,m^{-2}\,s^{-1}$ B. $I_{in} = 50\,\mu mol\,m^{-2}\,s^{-1}$. We consider p given by (25) with the kinetic parameters of *C. vulgaris* given in Table 2. The other parameters are taken to be $k = 0.2\,m^2\,gC^{-1}$, $m = 0.1\,d^{-1}$, and $K_{bg} = 0$.

increases. Note that the optical depth depends on $K_{bg}V/A$ and not on K_{bg} and V/A separately. Thus, the operational parameters determining the productivity are the incident light intensity I_{in} and the dimensionless parameter $K_{bg}V/A$ describing the background optical depth.

5. Conclusions

In this paper we have described the AGR of microalgae in perfectly mixed PBRs. We showed that, given a form of the reactor, the AGR is completely determined by the incident light intensity and the optical depth. This result is due to the Lambert-Beer law and to the fact that the extinction coefficient is independent of the location in the PBR. From a mathematical point of view, our assumptions over the specific growth rate are

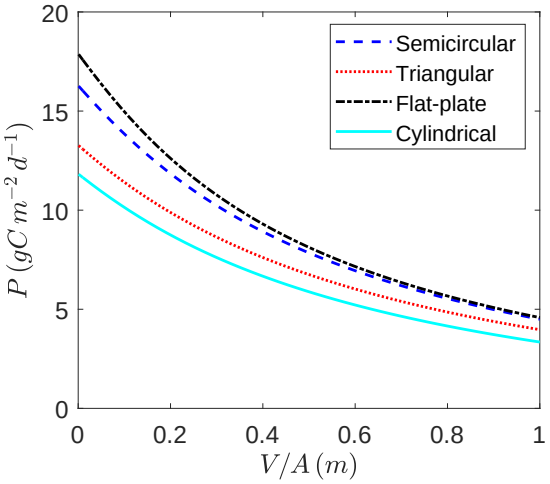

Figure 10: Maximal productivity as a function of V/A. p is given by (25) with kinetic parameters of *C. vulgaris* given in Table 2. Other parameters are taken to be $I_{in} = 1000\,\mu mol\,m^{-2}\,s$, $k = 0.2\,m^2\,gC^{-1}$, $m = 0.1\,d^{-1}$, $K_{bg} = 10\,m^{-1}$.

very general, in particular, we did not assume that the specific growth rate μ is differentiable as usually.

In the case of flat-plate PBRs illuminated from above, we studied in details the properties of the AGR. We showed the existence of values of the incident light intensity (critical light intensity) and the optical depth (critical optical depth) maximizing the AGR. We also studied how these values vary. These results are important for understanding how different environmental factors can affect the growth rate. In particular, they are useful for determining conditions for the occurrence of Allee effect or conditions such that the incident light intensity is a limiting factor.

6. Appendix A

These Appendix present the lemmas and propositions used in the two previous sections. We assume that assumptions 4 and 5 hold. The first lemma gives in detail the properties of the function g defined in (23). We note that Eq.(23) does not define g when I_{in} or I_{out} are equal to zero. However, from the definition of the AGR (Eq.(5)), it is natural to define

$$g(0, I_{out}) = g(I_{in}, 0) = \mu(0). \qquad (36)$$

In the reality I_{out} is never higher that I_{in}. However, we study the behavior of g for any value of I_{out}. This is necessary for proving Lemma A3.

Lemma A1. *(Properties of g) Let* $g : \mathbb{R}_+ \times \mathbb{R}_+ \longrightarrow \mathbb{R}$ *defined by Eq.(23) and Eq.(36).*

a) (Symmetry) $g(I_{in}, I_{out}) = g(I_{out}, I_{in})$ *for all* $I_{in}, I_{out} \geq 0$.

b) (Partial continuity) $g(I_{in}, \cdot)$ *is continuous on* $\mathbb{R}_+$ *for all* $I_{in} \in \mathbb{R}_+$.

c) (Unimodal function with respect to I_{out}*) For any* $I_{in} > 0$*, there exists a unique* $\gamma(I_{in}) > 0$ *satisfying*

$$g(I_{in}, \gamma(I_{in})) = \mu(\gamma(I_{in})). \tag{37}$$

It holds that $g(I_{in}, \cdot)$ *is strictly increasing on* $[0, \gamma(I_{in})]$ *and strictly decreasing on* $[\gamma(I_{in}), \infty)$*, moreover,*

- *if* $I_{in} > I^*$*, then* $\gamma(I_{in}) \in (\sigma(I_{in}), I^*)$,
- *if* $I_{in} = I^*$*, then* $\gamma(I_{in}) = I^*$*, and*
- *if* $I_{in} < I^*$*, then* $\gamma(I_{in}) \in (I^*, \sigma(I_{in}))$.

Proof. The proof of the part a) follows directly from the definition of g. For the part b), following [8], we can easily determine that $\lim_{I_{out} \to I_{in}} g(I_{in}, I_{out}) = \mu(I_{in})$ and $\lim_{I_{out} \to 0} g(I_{in}, I_{out}) = \mu(0)$. Thus c) is proved.

For the part c), let $I_{in} > 0$ be given. By using (23), we can determine the partial derivative of g with respect to I_{out};

$$\frac{\partial g(I_{in}, I_{out})}{\partial I_{out}} = \frac{1}{I_{out}[\ln(I_{in}) - \ln(I_{out})]^2} p(I_{out}), \tag{38}$$

with $p(I_{out}) = \int_{I_{out}}^{I_{in}} \frac{\mu(I) - \mu(I_{out})}{I} dI$. Since $I_{out}[\ln(I_{in}) - \ln(I_{out})]^2 > 0$ for any $I_{out} \in (0, I_{in})$, the sign of $\frac{\partial g(I_{in}, I_{out})}{\partial I_{out}}$ is determined by the sign of $p(I_{out})$.

Let us assume that $I_{in} > I^*$ and let $I_{out} \in [0, \sigma(I_{in})]$. Since μ is strictly increasing on $[0, \sigma(I_{in})]$, we have that $\mu(I) > \mu(I_{out})$ for all $I \in [I_{out}, \sigma(I_{in}))$. This implies that $p(I_{out}) > 0$. Since I_{out} was chosen arbitrarily we conclude that $p(I_{out}) > 0$ for all $I_{out} \in [0, \sigma(I_{in})]$. In the same way we can prove that $p(I_{out}) < 0$ for all $I_{out} \in [I^*, \infty)$ By the intermediate value theorem there exists $I' \in (\sigma(I_{in}), I^*)$ such that $p(I') = 0$. Suppose there exists another $I'' \in (\sigma(I_{in}), I^*)$ such that $p(I'') = 0$. By using elemental properties of integrals, it can be shown that the equality $p(I') = p(I'')$ implies

$$\int_{I''}^{I_{in}} \frac{\mu(I') - \mu(I'')}{I} dI = \int_{I'}^{I''} \frac{\mu(I) - \mu(I')}{I} dI. \tag{39}$$

Suppose that $I'' > I'$. Since μ is strictly increasing on $[0, I^*]$, we have that $\mu(I) \geq \mu(I')$ for all $I \in [I', I'']$. Thus the left side in (39) is negative, while the right side is positive. This contradiction shows that I' is the unique root of p. Hence p is positive on $[0, I')$ and negative on (I', ∞). Consequently, $g(I_{in}, \cdot)$ is strictly increasing on $[0, I')$ and strictly decreasing on (I', ∞). By taking $\gamma(I_{in}) = I'$ we conclude the proof. The case $I_{in} \leq I^*$ follows the same arguments. □

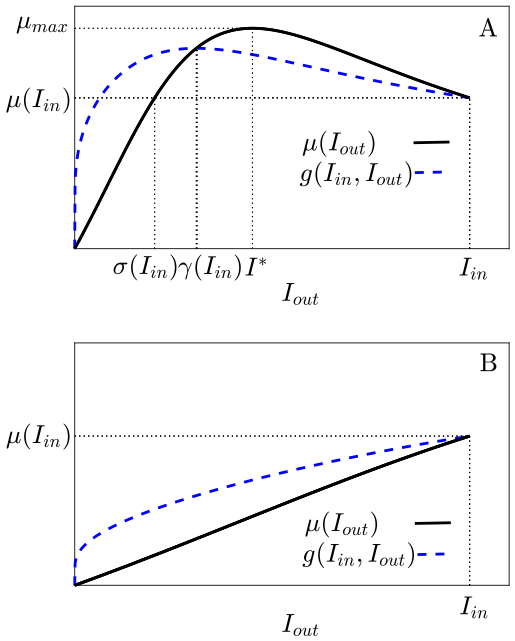

Figure 11: Plot of specific growth rate μ (continuous line) and the function $g(I_{in}, \cdot)$ (dotted line) as functions of I_{out}. a) $I_{in} > I^*$; the function μ has a peak at the optimal irradiance I^*, while the function $g(I_{in}, \cdot)$ has a peak at $\gamma(I_{in})$, where intersects μ. According to Lemma A1, $\sigma(I_{in}) < \gamma(I_{in}) < I^*$. Both functions reach the same value at I_{in}. b) $I_{in} \leq I^*$; both functions μ and $g(I_{in}, \cdot)$ are strictly increasing reaching the same value when $I_{out} = I_{in}$.

Fig.11 shows graphically the part c) of Lemma A1. The following proposition states the main

properties of the AGR (see Eq.(9) or Eq.(22)) as a function of the optical depth θ and the incident light intensity I_{in}.

Proposition A2. *(Properties of the AGR)*

a) $\bar{\mu}(\theta, 0) = \mu(0)$ *for all* $\theta \in \mathbb{R}_+$, *and* $\bar{\mu}(0, I_{in}) = \mu(I_{in})$ *for all* $I_{in} \in \mathbb{R}_+$.

b) If $I_{in} > 0$, *then* $\bar{\mu}(\cdot, I_{in})$ *is strictly increasing on* $[0, \tilde{\theta}(I_{in})]$ *and strictly decreasing on* $[\tilde{\theta}(I_{in}), \infty)$ *with* $\tilde{\theta}(I_{in})$ *defined by Eq.(28).*

c) If $\theta > 0$, *then* $\bar{\mu}(\theta, \cdot)$ *is strictly increasing on* $[0, \mathcal{I}(\theta)]$ *and strictly decreasing on* $[\mathcal{I}(\theta), \infty)$ *with* $\mathcal{I}(\theta)$ *defined by the equation*

$$\mu(\mathcal{I}(\theta)) = \mu(\mathcal{I}(\theta)e^{-\theta}). \tag{40}$$

d) $\lim_{\theta\to\infty} \bar{\mu}(\theta, I_{in}) = \mu(0)$ *for any* $I_{in} \in \mathbb{R}_+$.

Proof. Part a) follows directly from the definition of the AGR. For the part b), first we note that I_{out} is always decreasing as a function of θ. This implies that for any interval $J \subset [0, I_{in}]$, if $g(I_{in}, \cdot)$ is strictly increasing (decreasing)in J, then $\bar{\mu}(\cdot, I_{in})$ is strictly decreasing (increasing) in J^{-1} (as a function of θ), where $J^{-1} = \{\theta \geq 0\,;\, I_{out}(\theta, I_{in}) \in J\}$. If $I_{in} \leq I^*$, then $\tilde{\theta}(I_{in}) = 0$, hence we have to prove that $\bar{\mu}(\cdot, I_{in})$ is strictly decreasing on $\mathbb{R}_+$. From Lemma A1 we have that $g(I_{in}, \cdot)$ is strictly increasing in $J = \mathbb{R}_+$, then $\bar{\mu}(\cdot, I_{in})$ is strictly decreasing in $J^{-1} = \mathbb{R}_+$. If $I_{in} > I^*$, then $\tilde{\theta}(I_{in}) = \ln\left(\frac{I_{in}}{\gamma(I_{in})}\right) > 0$. From Lemma A1 we have that $g(I_{in}, \cdot)$ is strictly increasing in $J = [0, \gamma(I_{in})]$, then $\bar{\mu}(\cdot, I_{in})$ is strictly decreasing in $J^{-1} = [0, \tilde{\theta}(I_{in})]$. In the same way we prove that $\bar{\mu}(\cdot, I_{in})$ is strictly increasing in $[\tilde{\theta}(I_{in}), \infty)$.

For the part c), first we note that for any $\theta > 0$, $\frac{\partial \bar{\mu}(\theta, I_{in})}{\partial I_{in}} = \frac{1}{\theta I_{in}} h(I_{in})$ with $h(I) = \mu(I) - \mu(Ie^{-\theta})$. Since μ is strictly increasing on $(0, I^*]$, we have that

$$h(I) > 0 \text{ for all } I \in (0, I^*]. \tag{41}$$

In the same way, since μ is strictly decreasing on $[I^*, \infty)$, we have that

$$h(I) < 0 \text{ for all } I \in [I^* e^{\theta}, \infty). \tag{42}$$

From (41) and (42), we conclude that there exists $\mathcal{I}(\theta) \in J := (I^*, I^* e^{\theta})$ such that $h(\mathcal{I}(\theta)) = 0$. Now let $I_1, I_2 \in J$ such that $I_1 < I_2$. It is not difficult to note that

$$h(I_2) - h(I_1) = \underbrace{\mu(I_2) - \mu(I_1)}_{<0} + \underbrace{\mu(I_1 e^{-\theta}) - \mu(I_2 e^{-\theta})}_{<0} < 0,$$

from where h is strictly decreasing on J. Combining this result with the inequalities (41) and (42), we conclude that h is positive on $(0, \mathcal{I}(\theta))$ and negative on $(\mathcal{I}(\theta), \infty)$. Part c) follows directly from this result.

For the part d), if $\theta \to \infty$, then $I_{out}(\theta, I_{in}) \to 0$. Thus, $\bar{\mu}(\theta, I_{in}) \to g(0, I_{in}) = \mu(0)$. □

The following lemma states how γ (defined in Lemma A1) varies with I_{in}. This lemma is necessary for proving Proposition A4.

Lemma A3. γ *is continuous and strictly decreasing as a function of* I_{in} *on* $[I^*, \infty)$.

Proof. Let $I_{in}, I'_{in} > I^*$ such that $I_{in} < I'_{in}$. For any $I_{out} \in [\gamma(I_{in}), I^*)$, the function $g(I_{out}, \cdot)$ is strictly decreasing on $[\gamma(I_{out}), \infty)$. Since $I_{out} < I^*$, we have that $\gamma(I_{out}) \in (I^*, \sigma(I_{out}))$. We also note that $I_{out} > \gamma(I_{in}) > \sigma(I_{in})$, therefore $\sigma(I_{out}) < I_{in}$. The last inequality implies that the function $g(I_{out}, \cdot)$ is strictly decreasing on $[I_{in}, \infty)$. By symmetry of g, we conclude that the function $g(\cdot, I_{out})$ is strictly decreasing on $[I_{in}, \infty)$. Thus, we have that

$$g(I_{in}, I_{out}) > g(I'_{in}, I_{out}), \text{ for all } I_{out} \in [\gamma(I_{in}), I^*).$$

This shows that $g(I_{in}, \cdot)$ cannot intersect μ on $[\gamma(I_{in}), I^*)$, therefore $\gamma(I'_{in}) < \gamma(I_{in})$. Consequently, γ is strictly decreasing on (I^*, ∞).

To prove that γ is continuous, it is enough to prove that γ is a bijection. Since γ is strictly decreasing, it is enough to prove that for any $y \in (0, I^*)$ there exist $I_y \in (I^*, \infty)$ such that $g(I_y, y) = \mu(y)$. For this purpose, we define the function $G : [I^*, \infty) \longrightarrow \mathbb{R}$ such that

$$\begin{aligned} G(I_{in}) &= \ln(I_{in}/y)[g(I_{in}, y) - \mu(y)] \\ &= \int_y^{I_{in}} \frac{\mu(I) - \mu(y)}{I} dI. \end{aligned}$$

It is clear that $G(I^*) > 0$ (see proof Lemma A1 c)). Let $M(I) = \frac{\mu(I) - \mu(y)}{I}$. Since $\lim_{I\to\infty} \frac{M(I)}{1/I} = \mu(0) - \mu(y) < 0$, we conclude that $\lim_{I_{in}\to\infty} G(I_{in}) = -\infty$. Thus, since G is

continuous, there is $I_y > I^*$ such that $G(I_y) = 0$.

From Lemma A1 c), we have that

$$\theta(I_{in}) < \gamma(I_{in}) < I^*.$$

By taking the limit when $I \to I^{*+}$ in the later inequality, we conclude that $\gamma(I_{in}) \to I^*$ as $I_{in} \to I^{*+}$. Therefore γ is continuous on $[I^*, \infty]$. □

The following proposition states some properties of the critical optical depth (defined in (28)).

Proposition A4. *(Properties of the critical optical depth.)*

a) For any $I_{in} \in [I^*, \infty)$ it holds

$$\ln\left(\frac{I_{in}}{I^*}\right) < \tilde{\theta}(I_{in}) < \ln\left(\frac{I_{in}}{\sigma(I_{in})}\right). \qquad (43)$$

b) $\tilde{\theta}$ is continuous on $\mathbb{R}_+$, strictly increasing on $[I^*, \infty)$, and $\lim_{I_{in}\to\infty} \tilde{\theta}(I_{in}) = \infty$.

Proof. From Lemma A1 part c), we have that for any $I_{in} > I^*$,

$$\sigma(I_{in}) < \gamma(I_{in}) < I^*.$$

This implies the inequality (43). For the part b), from Lemma A3 and the definition of $\tilde{\theta}$ (see Eq. 28), we conclude that $\tilde{\theta}$ is strictly increasing on $[I^*, \infty)$. By taking the limit when $I_{in} \to \infty$ in (43), we conclude that $\lim_{I_{in}\to\infty} \tilde{\theta}(I_{in}) = \infty$. For the continuity, we take the limit when $I_{in} \to I^{*+}$ in Eq.(43), we obtain $\lim_{I_{in}\to I^{*+}} \tilde{\theta}(I_{in}) = 0 = \tilde{\theta}(I^*)$, from where $\tilde{\theta}$ is continuous in I^*. The continuity over all $\mathbb{R}_+$ follows directly from the definition of $\tilde{\theta}$ and Lemma A3. □

The following proposition gives some properties of the critical light intensity

Proposition A5. *(Properties of the critical light intensity) $\mathcal{I}$ is strictly increasing and continuous.*

Proof. From Eq.(40) we obtain that

$$\frac{\mathcal{I}(\theta)}{\sigma(\mathcal{I}(\theta))} = e^{\theta}.$$

This equation shows that as θ increases the fraction on the left increases. Since σ is strictly decreasing, this is only possible if $\mathcal{I}(\theta)$ increases. Thus, $\mathcal{I}$ is strictly increasing as a function of θ. From Eq.(6), we also note that $\mathcal{I}$ is a bijection, indeed, it is inverse function $\mathcal{I}^{-1}(I) : [I^*, \infty) \longrightarrow [0, \infty)$ is given by

$$\mathcal{I}^{-1}(I) = \ln\left(\frac{I}{\sigma(I)}\right). \qquad (44)$$

Since $\mathcal{I}$ is strictly increasing and bijective, we conclude that is continuous. □

Appendix B

Assume that p is given by Eq.(25). Let $\Delta = 4\frac{\mu_{max}}{\alpha I^*} - 1$, then

- if $\Delta = 0$,

$$\bar{\mu}(\theta, I_{in}) = \frac{I_{in} - I_{out}}{\theta} \frac{4p_{max}I^*}{(I^* + I_{in})(I^* + I_{out})} - m$$

- if $\Delta > 0$,

$$\bar{\mu}(\theta, I_{in}) = \frac{2p_{max}/\sqrt{\Delta}}{\theta} \left[\arctan(\kappa(I_{in})) - \arctan(\kappa(I_{out}))\right] - m,$$

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

- if $\Delta < 0$,

$$\bar{\mu}(\theta, I_{in}) = \frac{p_{max}/\sqrt{-\Delta}}{\theta} \ln\left[\frac{(I_{in} - I^* + \xi_2)(I_{out} - I^* + \xi_1)}{(I_{in} - I^* + \xi_1)(I_{out} - I^* + \xi_2)}\right] - m,$$

where $\xi_1 = \frac{I^{*2}\alpha}{2p_{max}}(1 + \sqrt{-\Delta})$ and $\xi_2 = \frac{I^{*2}\alpha}{2p_{max}}(1 - \sqrt{-\Delta})$.

Assume that μ is given by Eq.(24). Then,

$$\bar{\mu}(\theta, I_{in}) = \frac{p_{max}}{\theta} e^{1 - \frac{I_{out}}{I^*}} \left(e^{\frac{I_{in} - I_{out}}{I^*}} - 1\right) - m$$

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