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Maria Teresa Gutierrez-Wing[1]
Athens Silaban[1]
Jonathan Barnett[1]
Kelly A. Rusch[2]

[1] Department of Civil and Environmental Engineering, and Sea Grant College Program, Louisiana State University, Baton Rouge, LA, USA

[2] Office for Research and Creative Activity, North Dakota State University, Fargo, ND, USA

Review

Light irradiance and spectral distribution effects on microalgal bioreactors

The irradiance and light spectral distribution affect the growth and productivity of microalgal cultures. In extensive open pond cultures, the light control has limited options, mainly the culture depth. In photobioreactors, besides the culture depth, the light source, configuration of the reactor, light pathway, and flow rate can be used to control the characteristics of the light available to the cultures. The change of light conditions can also be used to modify the composition of the microalgal biomass produced to optimize the production of bioproducts of interest. Additionally, in mixed cultures, the species composition can be influenced by the light quantity and quality. Determining the effect of the light quantity and quality in photosynthetic cultures will help to develop strategies to optimize the production of biomass, lipids, pigments, proteins, and other compounds of interest in photosynthetic microorganisms. Information obtained from bench scale cultures can rarely be applied directly to large-scale bioreactors. Nonetheless, determining the kinetic parameters of microalgal cultures at bench scale will reduce the time needed to optimize the cultures in photobioreactors. In this work, a review of the main factors is presented, along with specific examples of the effect of light quality and quantity in cultures with single and multiple species. Additionally, some models to predict the effect of light on microalgal productivity are discussed.

Keywords: Co-culture / Irradiance / Microalgal productivity / Mixotrophic growth / Spectral distribution

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1 Introduction

Photobioreactors (PBRs), have higher productivity than open ponds. The higher productivity is influenced by the typically larger surface area that maximizes the illumination received by the microalgal cells. PBR designs include flat plates, tubular, helical, column PBR, and stirred tank reactor among others [1–4].

Light is one of the most important parameters in the control of microalgal cultures. The quality and quantity of light can affect not only the growth rates, but also the partition of carbon toward diverse bioproducts such as lipids, pigments and proteins, among others. The relationship between light and the growth rate and productivity of microalgal cultures is complex and the response of different species is not homogeneous. The response of each species and strains to the light spectrum varies with their genetic characteristics and adaptation to growth conditions.

There has been considerable effort in determining the effect of light irradiance and spectral distribution in batch cultures at laboratory scale. The information obtained in these cultures can provide an indication of the response of microalgae to light conditions, but in many cases, it cannot be translated directly to larger scale PBRs. The difference of lab scale cultures can be more pronounced when comparing it with continuous flow systems.

Photosynthetic microorganisms (microalgae and cyanobacteria) contain three major pigment groups, chlorophylls, carotenoids, and phycobilins. Each pigment has a characteristic light absorption range. The chlorophylls, the most abundant of the pigment groups have two major absorption ranges. The first one is in the range of the blue light (450–475 nm) and the second and most significant is in the red light range (630–675 nm). The carotenoids, which include α-carotenes and β-carotenes and xanthophylls including lutein, violaxanthin, zeaxanthin, and fucoxanthin, among others. Carotenoids have an absorption range from 400 to 550 nm [5]. The group of the phycobilins that includes phycoerythrin and phycocyanin are found in

Correspondence: Dr. Maria Teresa Gutierrez-Wing (mgutie5@lsu.edu), Department of Civil and Environmental Engineering, Sea Grant College Program, Louisiana State University, 3520A Patrick Taylor Hall, Baton Rouge, LA 70803, USA

Abbreviations: HISTAR, hydraulically integrated serial turbidostat algal reactor; **HPS**, high-pressure sodium; **PBRs**, photobioreactors

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cyanobacteria and red algae. Phycobilins have an absorption range of 500–650 nm.

The photosynthetic efficiency in terms of energy is affected by the total irradiance and wavelength distribution of the light. Although some photosynthetic organisms can grow in heterotrophic regimes, their growth will be limited [6]. Low irradiances result in light limitation and impaired growth and high irradiances can induce photoinhibition and in severe cases photobleaching, that can be irreversible and result in the destruction of the photosynthetic pigments. In terrestrial plants, the highest growth rates have been observed by some authors using red and blue lights, matching the absorbance peaks of the chlorophylls. Similarly, experiments conducted using LED lights have found that microalgal growth is higher in many species using red light [7–9].

The wavelength distribution of the light in the PBRs affect not only the photosynthetic efficiency, but will also modify the bioproducts that can be obtained from the microalgal cultures. As an example, red and infrared light has been found necessary for the production of hydrogen by *Rodobacter sphaeroides* [10]. Biomass productivity from the cyanobacteria *Spirulina platensis* is greater under red light, compared with blue light. The results obtained by Ravelonandro et al. [11] show that the green light at high intensities resulted in better growth of *S. platensis*. Das et al. [12] found that *Nannochloropsis sp.* productivity was higher with LED lights of 470 nm (blue), but the fatty acid content was higher at 550 nm (green) light. For mixed cultures of *Chlorella sp.* with *Saccharomyces cerevisiae*, Shu et al. [13] obtained a higher growth rate with red light and higher lipid productivity with blue light.

Detailed experimental data from large scale cultures have been obtained for bioreactors by several researchers [14–18]. Most of the data generated have focused on the total scalar photosynthetic available radiation irradiance. Although in recent years the study of the effects of the light quality on the microalgal cultures has increased, few model efforts have been done to relate quality with growth and productivity of the cultures. The data obtained in these systems have been used to develop models that allow the prediction of the effect of irradiance on microalgal growth [19–22].

2 Irradiance-dependent growth models

The ability of the microalgae to use the light energy available for biomass formation can be represented by the biomass yield based on the light energy input [1, 23] according to Eq. (1):

$$Y_{dw,E} = \frac{P_{dw}}{PFD_d} \times \frac{V}{A} \quad (1)$$

where $Y_{dw,E}$ (g[mol photon] $^{-1}$) is the biomass yield per light energy, P_{dw} (g m^{-3} d^{-1}) is the microalgal biomass productivity, PFD_d (mol photon m^{-2} d^{-1}) is the photon flux density, received from all directions (scalar irradiance), and V/A (m^3 m^{-2}) is the volume to surface area ratio of the microalgal culture. The photosynthetic efficiency (%), which represents the percentage of light energy converted into energy stored in the microalgal biomass, can be calculated using Eq. (2):

$$PE = Y_{dw,E} \times \frac{C_B}{E} \times 100\% \quad (2)$$

where PE (%) is the photosynthetic efficiency, C_B (kJ g^{-1}) is the microalgal caloric content, and E (kJ [mol photon] $^{-1}$) is the conversion of the scalar irradiance to energy input. Microalgae have been reported to have a much higher photosynthetic efficiency compared to higher plants (vascular plants) [1,24]. Based on the photosynthesis process mentioned before, a minimum of 8 moles of light photons is required to produce 1 mole of carbohydrate (CH_2O), 1 mole of O_2, and 1 mole of H_2 [25]. The energy content of 1 mole of photons is 218 kJ, which means to produce 1 mole of CH_2O the potential light energy captured is 1744 kJ. The energy contained in 1 mole of CH_2O is about 467 kJ, which results in a theoretical solar to chemical energy conversion of approximately 27%. However, not all the light spectrum is available to be used for photosynthesis and there are other factors that significantly reduce the photosynthetic efficiency, such as photosaturation and photoinhibition, photorespiration, poor light respiration, and rate limitations due to factors other than light. The theoretical case of maximum photosynthetic efficiency that a perfectly efficient microalgal can achieve as reported by Weyer et al. [26] is around 26.7%, although in practice the efficiency is lower (5–11%) but is still higher than photosynthetic efficiency levels achieved by terrestrial plants, which are around 1–2% . The culture growth and photosynthetic efficiency will depend on the scalar irradiance received by each cell in the reactor.

One of the most common models used to describe the relationship of light irradiance and microalgal growth is the Steele's kinetics [27–29] model. This model is based on the description of the specific growth rate through an exponential function that peaks at the optimum irradiance (I_{opt}), where the maximum specific growth rate (μ_{max}) is obtained and declines at higher and lower levels of irradiance (Fig. 1A). The model is presented by the Eq. (3):

$$\mu = \mu_{max} \frac{I_a}{I_{opt}} e^{1-\frac{I_a}{I_{opt}}} \quad (3)$$

where μ (d^{-1}) is the specific growth rate, I_a (μmol m^{-2} s^{-1}) is the average scalar irradiance, I_{opt} (μmol m^{-2} s^{-1}) is the optimum irradiance that gives μ_{max}. This model shows that when irradiance is increased beyond the optimum irradiance (maximum μ) the specific growth rate of microalgae decreases. The model is appropriate for application with moderate density cultures [19,30]. The optimum irradiance varies with the species and strain cultured. For example, *Selenastrum minutum* has been reported to have the optimum irradiance of 365 μmol m^{-2} s^{-1} [31], *Selenastrum capricornutum* at 391 μmol m^{-2} s^{-1} [32], *Spirulina platensis* at 500 μmol m^{-2} s^{-1} [33], and *Chlorella sp.* at 200 μmol m^{-2} s^{-1} [34].

For more dense cultures, Molina Grima et al. [35] proposed an empirical hyperbolic function (Fig. 1B; Eq. (4), as the density of the culture makes less likely the onset of photoinhibition.

$$\mu = \frac{\mu_{max} \times I_a}{I_k + I_a} \quad (4)$$

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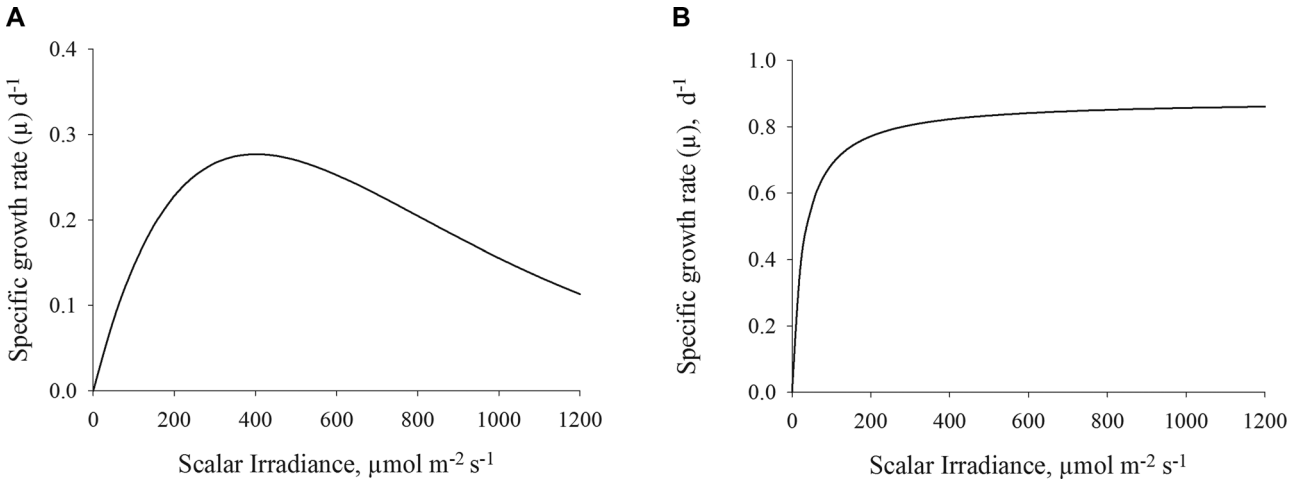

Figure 1. Curves fitted to experimental specific growth rate versus irradiance for a *Chlorella vulgaris*/*Leptolyngbya* sp. coculture under two culture conditions: (A) Steele kinetics and (B) hyperbolic function.

where I_k (μmol m^{-2} s^{-1}) is the light affinity constant for microalgae and represents the irradiance at which half μ_{max} is obtained. Although physiologically microalgal growth rates follow Steele kinetics with a μ_{max} peak at I_{opt}, the hyperbolic function can be used in a specific irradiance range. The results should not be extrapolated to higher irradiance values, because at some point the specific growth rate would finally decrease and the hyperbolic function cannot represent this decay.

In order to calculate the irradiance available (I_a) to the microalgal cells, several variables have to be taken into account. Attenuation of the light by air, water, and the culture density will reduce the effective average scalar irradiance that an individual microalgal cell will receive in the culture. In static cultures, with little or no mixing, some cells can be either in the photolimited or photoinhibited. In cultures well mixed, by circulation or agitation by air, paddles or other methods, all cells will be exposed to similar average scalar irradiance, as they will cycle between low and high irradiance zones within the PBR.

Light attenuation in the reactors is not linear and it tends to decrease faster in the first few centimeters of the culture. Bioreactors with shorter light path lengths such as small diameter tubular reactors or shallow plate culture systems tend to have more homogeneous light distribution in the culture volume, but are more prone to photoinhibition. Deeper culture systems have considerably different scalar irradiances across the light path length, but provide a better buffer against photoinhibition and heat effects.

Although many models have been developed considering the light scattering and diffraction due to high culture densities, the effect of the light attenuation with the reactor depth (light path length) is most commonly modeled based on the Lambert–Beer law [18, 36–39]. The average scalar irradiance in the reactor can be obtained integrating Eq. (5) over the depth of the reactor [18, 40]:

$$I_a = \frac{1}{d}\int_0^d I(z)\mathrm{d}z = \frac{I_o(1-\mathrm{e}^{-k_0\cdot d})}{(k_0\cdot d)} \quad (5)$$

where I_a is the average scalar irradiance available to the microalgal cells, d is the total depth of the reactor, z is the depth for which the irradiance is calculated, I_o is the surface irradiance, and k_0 is the overall scalar irradiance attenuation coefficient that includes the attenuation due to water and attenuation due to biomass [18]:

$$k_0 = k_w + k_b X \quad (6)$$

where k_w is the attenuation coefficient due to the water, the k_b is the attenuation coefficient due to the biomass, and X is the biomass concentration (g m^{-3}).

3 Light control in PBRs

One of the difficulties in maintaining the optimum light irradiance in microalgal bioreactors is the change of light penetration as the culture density increases [41]. Short light paths and/or high irradiance increase the photon capture efficiency, but may lead to photoinhibition or even photobleaching (irreversible damage to the photosynthetic apparatus) in lower density cultures. Conversely, low average light levels may limit the photosynthesis in higher density cultures.

In order to optimize the efficiency of the light use in PBRs by controlling the total irradiance, several methods have been proposed. These methods follow two main strategies: (1) control of the exposure time or, (2) control of the irradiance supplied to the cultures. A combination of both strategies is commonly used in most systems. The control of light/dark periods to increase microalgal productivity has been explored for many years. Some authors [42–44] have used short periods or pulses of light. Grobbelaar et al., using frequencies from 0.5 to 5000 Hz showed that algae exposed to light pulses from 0.1 ms to 10 s have higher photosynthetic rates at higher frequencies. In general systems with shorter path lengths can benefit from higher pulse frequencies, by allowing the algae to limit the exposure time to high levels of incident light while increasing the total irradiance [41].

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The use of pulses of light requires precise control of the light source and the repeated cycles can limit the durability of the lamps. The control of the irradiance supplied can be achieved through modification of the intensity of the light source, partial shading, and the limit of the light path. The intensity of the light source can be controlled in systems using artificial illumination. Partial shading can be achieved through mixing regimes that limit the time the microalgal cell is exposed to light [44] or by the use of shade cloth [45, 46] or other materials such as semitransparent films. The light path can be modified by controlling the culture depth in the case of reactors illuminated from one direction (such as plates, tank, ponds, or raceways) or controlling the size of the elements, particularly the diameter of tubular reactors. Additionally, the distance of the light source can be modified, with some systems using the light source inside the reactors to increase the possibility of photon capture [47].

Another strategy to optimize the light efficiency is to select the wavelength distribution according to the peak response of the photosynthetic pigments. Although this strategy may reduce the energy input and risk associated with photoinhibition, the application is not easy. As discussed before different species of microalgae and cyanobacteria respond to distinct wavelength, even when the primary photosynthetic pigment for all is the chlorophyll "a." Studies of each species are needed to optimize the light spectral distribution. As a general approach, light in the red spectrum seems to promote the highest biomass production, as the photons in this spectrum (either 680 or 700 nm for photosystem I and II) provide the energy that more closely matches the energy needed by the chlorophyll to reach the first excited stage [48]. Photons with lower energies may not allow the molecule to reach the necessary excited stage. Photons in the blue spectrum may take the molecule to the second excited stage, at which point, it will be necessary to dissipate some energy either as heat or fluorescence to transfer the electrons to the next step.

The control of wavelength distribution can be done through monochromatic lights such as narrow range LEDs [49–51]. Also, filters can be used to restrict the input of undesirable wavelengths [52]. Note that these strategies can be very costly for large-scale PBRs, but the possibility of controlling the output of valuable bioproducts, may offset the costs.

4 Light effect on photosynthetic microbial cultures growth

In this section, we will present an example of the light behavior in a HISTAR (hydraulically integrated serial turbidostat algal reactor) with a microalgae/cyanobacteria coculture. The coculture (here thereafter called Louisiana coculture) is composed of a microalgae (*Chlorella sp.*) and a cyanobacteria (*Leptolyngbya sp.*) native to the state of Louisiana (USA). The HISTAR bioreactor is a design concept that can be applied to systems from laboratory to industrial scale and is based on a triple mechanism of protection that includes: (1) continuous supply of high quality inoculum from turbidostats, (2) use of a series of continuous flow stirred tank reactors to amplify the biomass and improve the wash out of possible contaminants and, (3) a hydraulic disconnect of tanks in the system to prevent backflow of possible contaminants. The quality of the inoculum is maintained by using alternating turbidostats inoculated directly from stock cultures fed with high quality culture media. The continuous flow stirred tank reactors have a high local dilution rate in each tank to allow a rapid flow and wash out the possible contaminants to reduce their effects on the culture and low system dilution rate that allows for the biomass accumulation. In case of contamination of the tanks, the quasi plug-flow mode of the system will restrict the effect of the contaminant to a small volume of the system.

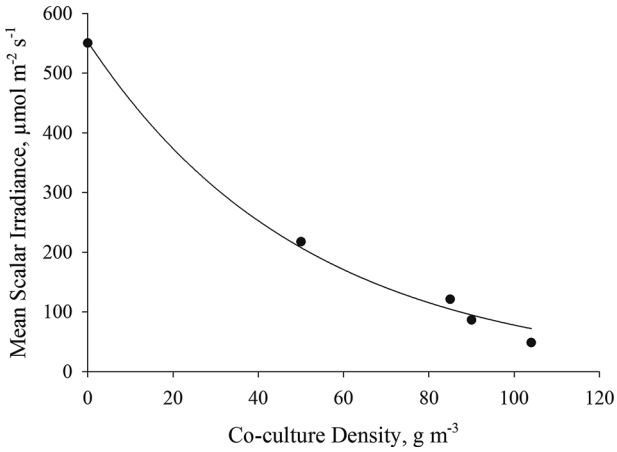

Figure 2. Effect of the *Chlorella vulgaris*/*Leptolyngbya* sp. coculture density on the average scalar irradiance in a HISTAR CFSTR.

The light dynamics of the HISTAR system illuminated by high-pressure sodium (HPS) lamps were described by Benson and Rusch, Benson et al. and Gutierrez-Wing et al. [16, 18, 40]. These authors showed that at culture with *S. capricornutum* biomass densities in the range of 41–142 g m^3, the surface irradiance of 400 μmol m^{-2} s^{-1} is reduced sharply in the first 10–20 cm of culture and the light penetration at 40 cm is almost null. In contrast, the attenuation by the water column alone is linear and more than half of the surface irradiance penetrates at a depth of 40 cm. Similar results but with higher attenuation were obtained in our laboratory with the Louisiana coculture where the incident irradiance of 550 μmol m^{-2} s^{-1} is reduced almost immediately in the first few centimeters by 30 % or more, depending on the biomass concentration. The average scalar irradiance decreases rapidly as the biomass concentration increases (Fig. 2). At lower scalar irradiance values, the percentage of cyanobacteria by cell counts increases in the coculture. If the light drops below 80 μmol m^{-2} s^{-1}, the coculture is cyanobacteria dominated. The photosynthetic pigments, including chlorophyll "a" increase, with decreasing scalar irradiance, with a marked decrease for nonaerated cultures at irradiances of 1200 μmol m^{-2} s^{-1}.

The average scalar irradiance impact also the lipid and pigment accumulation in the biomass. For the Louisiana coculture, the highest lipid productivity is obtained in the

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range of 400–800 μmol m^{-2} s^{-1} and decreases rapidly outside of these values at aerations below 1.0 lpm. The maximum average lipid concentration (38 mg L d^{-1}) was observed at 400 μmol m^{-2} s^{-1}.

The total incident irradiance and average scalar irradiance are very important to determine the energy available for photosynthesis, but these do not reflect the effect of different wavelengths in the photosynthetic efficiency and carbon partition in the microalgae. In the HISTAR system a change in light source with the same intensity, but different spectral irradiance may lead to different productivity and/or fouling of the reactor walls, as observed by Benson et al. [17] who found an increased wall growth in cultures maintained under Son Agro® lights, with higher output in the blue spectrum, compared with the regular HPS lamps.

Given the higher penetration of blue light in water, it can be expected that fouling in the bottom and walls of light-limited culture systems will increase. In the case of the Louisiana coculture under HPS light, it was observed that when the optical density of the cultures reached an absorbance above 0.4, irrespective of the actual cell counts, the wall and bottom growth became difficult to control, eventually collapsing the culture. Current experiments are in progress to determine the possibility of reducing the fouling by supplying light with lower components in the blue spectrum.

5 Concluding remarks

Light irradiance and wavelength distribution have a large impact on the growth, productivity, and composition of microbial photosynthetic cultures (including microalgae and cyanobacteria).

Photoinhibition and photolimitation can be caused by inadequate irradiance. The photoinhibition can be controlled by (1) reducing the total irradiance input, increasing the cycling of the microbes between the light and dark zones of the culture either by aeration, mixing, flow, or the use of intermittent light pulses reduction of the light source power or increasing the distance to the culture, (2) increasing the depth of the cultures to provide longer dark periods and areas with lower irradiance levels, and (3) using filters to exclude unnecessary light wavelengths, thus reducing the total light energy to the system. Photolimitation can be controlled by increased total irradiance input and decrease of culture depth. Although nonusable wavelength can increase the effect of photoinhibition and the risk of heath damage, increasing the light in those spectrums will not reduce the photolimitation effectively.

The growth of different species of photosynthetic microorganisms can be manipulated through changes in light wavelength distribution. Providing the adequate spectrum of light will increase the lipid and pigment and other bioproducts productivity and reduce the cost of illumination. There is no single wavelength that will be useful for all species and all bioproducts. Bench scale assays coupled with numerical models can be used to reduce the cost of determining the optimum conditions for the accumulation of the target bioproducts.

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Nomenclature

$Y_{dw,E}$	[g (mol photon) $^{-1}$]	Biomass yield per light energy
P_{dw}	[g m^{-3} d^{-1}]	Microalgal biomass productivity
PFD_d	[mol photon m^{-2} d^{-1}]	Photon flux density measured as scalar irradiance
PE	[%]	Photosynthetic efficiency
C_B	[kJ g^{-1}]	Caloric content
E	[kJ (mol photon) $^{-1}$]	Conversion of the scalar irradiance to energy input
μ	[d^{-1}]	Specific growth rate
μ_{max}	[d^{-1}]	Maximum specific growth rate
I_a	[μmol m^{-2} s^{-1}]	Average scalar irradiance
I_{opt}	[μmol m^{-2} s^{-1}]	Optimum scalar irradiance
I_k	[μmol m^{-2} s^{-1}]	Light affinity constant
d	[m]	Depth of reactor
z	[m]	Depth coordinate for which irradiance is calculated
I_o	[μmol m^{-2} s^{-1}]	Surface irradiance
X	[g m^{-3}]	Microalgal biomass concentration

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