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Ecophysiological modeling of the impact of light intensity and quality on microalgal growth in outdoor high-density open ponds

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ABSTRACT

Light is a critical factor governing microalgal growth, with both intensity (photosynthetically active radiation, PAR) and spectral composition (wavelength distribution) exerting significant influence. In high-density open raceway ponds, light attenuation creates pronounced vertical gradients in both PAR and spectral quality, though the specific effects of spectral composition on phytoplankton growth remain insufficiently characterized. This investigation examined the combined impacts of light intensity, spectral quality, and temperature on *Dunaliella salina* cultivated in greenhouse-based raceway ponds under natural irradiance. Outdoor experiments spanned two seasonal conditions (winter and summer), with cultures exposed to four spectral treatments: raceways equipped with neutral, red, and green filters, along with an unfiltered control system.

Experimental data were used to parameterize a growth model integrating light intensity, spectral quality, and temperature dependencies. The model reproduced biomass dynamics under all spectral conditions and seasons. Notably, when normalized for PAR and initial biomass, green light promoted superior biomass conversion efficiency—attributed to its enhanced vertical penetration in high-light conditions. These findings highlight the potential of spectral optimization in raceway cultivation systems. The model provides a valuable tool for selecting semi-transparent photovoltaic filters or colored panels to simultaneously enhance microalgal productivity and harness unused wavelengths for energy generation.

1. Introduction

Microalgae are an emerging natural resource becoming popular for producing molecules of interest, such as pigments, antioxidants, lipids or proteins [1]. They can grow at a rate an order of magnitude larger than terrestrial plants, making them good candidates for large-scale production of commodities [2]. Numerous culturing systems have been developed for microalgal production at high density, from closed photobioreactors to open raceway ponds [3]. In these culturing systems, high production yields are usually optimized through strain selection (e.g., [4,5]) or by controlling culturing conditions, including medium (e.g., [6]), temperature (e.g., [7–9]), or light (e.g., [10–12]).

Light impacts microalgal photosynthesis and growth in various ways, through light intensity, light frequency (e.g., day/night, flash), and light quality (i.e., wavelengths of spectral light). Low light intensity limits microalgal growth, while increasing light intensity positively impacts growth until photosynthesis reaches a maximum [13]. High light can then have a negative impact by damaging the photosystems, a process called photo-inhibition [14]. This reduction in productivity, especially at the surface of the reactor, lead to the idea of shadowing the culture with semi-transparent photovoltaic (STPV) panels [15,16], also reducing temperature to reach more productive growth conditions [17], i.e. temperature closer to the optimal growth temperature (34 °C), while the maximum bearable temperature is 43 °C [18].

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The integration of STPV into agricultural and microalgal production systems has emerged as a promising strategy to co-generate renewable energy while optimizing biomass productivity. In agrivoltaics, STPV panels balance light transmission for crops and electricity generation, maintaining 60–80 % of crop yields while producing 50–100 W/m² of power [19]. Recent advances in semi-transparent organic photovoltaics (ST-OPVs) leverage tunable bandgaps in organic semiconductors to selectively transmit photosynthetically active radiation (PAR, 400–700 nm) while harvesting underutilized ultraviolet and near-infrared wavelengths [20]. Non-fullerene acceptors have enabled opaque OPV efficiencies of 18 %, with ST-OPVs achieving above 13 % power conversion efficiency and more than 20 % average visible transmittance, alongside roll-to-roll manufacturability and compatibility with flexible greenhouse claddings (e.g., low-density polyethylene). However, spectral overlap between OPV absorption and microalgae pigments remains a challenge, with chlorophyll preferentially absorbing blue (440 nm) and red (650–700 nm) light, while accessory pigments like β -carotene absorb broader ranges (400–500 nm). Self-shading in conventional reactors reduces incident light to 10–20 % of surface irradiance, causing photo-limitation at depth [12,21,22], and this effect should be reduced by playing on the transmitted light wavelength and the way they become extinct in dense cultures. Spectral optimization - using underutilized wavelengths (e.g., green/yellow) or tailored filters - can enhance light penetration and productivity. For instance, red light improves growth in *Chlamydomonas reinhardtii* [23], orange in *Chlorella vulgaris* [24], and fluorescent red filters boost productivity in mixed cultures (*Chlorella*, *Dunaliella*, *Botryococcus*) under natural light [25]. Microalgae further adjust pigment content via photoacclimation to optimize light capture at varying intensities and spectra [26,27], which make optimization more challenging.

Outdoor systems introduce additional complexities, as temperature fluctuations interact with light effects on growth kinetics [9,28]. While mathematical models exist for light- and temperature-dependent growth [28–32], most neglect spectral composition, focusing instead on bulk irradiance. Only a few models consider the spectrum of solar light in photobioreactors (for cyanobacteria [33] or microalgae [34]), leaving a critical gap in modeling spectral effects for raceway-cultivated microalgae. Bridging this gap could unlock tailored STPV designs that dynamically match microalgal spectral needs while maximizing energy output.

This study combines experimental and modeling approaches to assess the effects of light quality on microalgal productivity. Growth experiments were conducted with *Dunaliella salina* in high-density open ponds under greenhouse conditions, subjecting cultures to natural fluctuations in temperature and light typical of Mediterranean climates. Spectral light conditions were manipulated using commercial colored filters mimicking colored STPV. A novel microalgal growth model was developed, incorporating the combined effects of light intensity, spectral quality, and temperature. In addition to simulating temperature-dependent growth, photoacclimation, and photoinhibition, the model accounts for spectral light attenuation through the culture depth and its subsequent influence on algal growth dynamics. Simulations of *D. salina* productivity under both experimental and idealized conditions provided insights into the underlying mechanisms governing growth optimization.

2. Materials and methods

2.1. Experimental setup

2.1.1. Outdoor raceway ponds

Outdoors cultures of the green algae *Dunaliella salina* (CCAP 19/18, Culture Collection of Algae and Protozoa, United Kingdom) were carried out under the greenhouse of the FullSpectrum platform (Laboratoire d'Océanographie de Villefranche-sur-Mer, French Riviera, France). Two 14-d experiments were carried out: one in winter (November 2015) and

the other one in summer (July 2016). Four open raceway ponds were used, with a length of 3.5 m, a width of 0.9 m and a depth of 0.25 m, for a surface of 2.61 m² (Fig. 1a-b).

Cultures were grown in a nutrient-enriched natural seawater based on f/2 medium composition [35,36]. Pre-filtered natural seawater was first sterilized using sodium hypochlorite (4 %) and transferred in the raceways. Stock solutions (1 L) of trace elements (f/2), nitrogen (NaNO₃, 9f) and phosphorus (NaH₂PO₄·2H₂O, 9f) were prepared in deionized water and autoclaved before inoculation. Salinity was also adjusted to 100 mg.L⁻¹ with NaCl in order to limit potential contamination of the cultures, which was regularly monitored by microscope observation.

The algae were acclimated to the growing conditions in the greenhouse, by first growing them in a closed bioreactor in fed-batch mode (100-L plastic bags) for 10 d. This culture was then inoculated into the control raceway for 1 week. At the beginning of the experiment, this culture was equally distributed in each raceway to reach a final volume of 350 L of diluted algal suspension, corresponding to a water depth of 0.14 m.

The cultures were continuously agitated with a paddle wheel located at one extremity of the pond. Tap water was added daily to compensate for evaporation. Water temperature and pH were continuously recorded (Inpro 4800 ISM, Metler Toledo, France). To ensure both optimal pH condition and non-limiting CO₂ supply,

The pH of each raceway was maintained at 7.5 through automated CO₂ injection, regulated by a pH controller coupled to an electrovalve and inline pH sensors [37]. This value represents an optimal trade-off. Ensuring non-limiting CO₂ conditions for microalgal growth while minimizing outgassing losses, thereby maximizing CO₂ transfer efficiency into the liquid phase.

2.1.2. Light conditions

The greenhouse was covered by a neutral plastic cover, while different dyed polyester filters (Eurofilter) were located above the ponds, in order to modify both the direct solar light spectrum and intensity (Fig. 1b). These commercial filters were selected among others based on their spectral properties, which were measured with a radio-spectrometer (USB400-UV-VIS, Ocean Optics, USA) from filter and greenhouse cover samples using natural sunlight as incoming light (Fig. 1c). The red filter (#247 Full Minus Green) reduced the light intensity between 500 and 600 nm. The green filter (#088 Lime Green) eliminated the light intensity between 475 and 600 nm. The neutral filter (#298 0.15 Neutral Density) decreased the entire light intensity uniformly. The fourth pond had no light filter, playing the role of control experiment. The greenhouse cover decreased light intensity uniformly across the PAR spectrum (Table 1). Downwelling irradiance at the surface of the raceways were also recorded with a hyperspectral radiometer (SAM-820E RAMSES, TriOS Mess, Germany) every hour over the course of one day on October 29th (data not shown). For each basin, an averaged spectrum of light intensities between 400 nm to 700 nm representative of daytime illumination conditions spectrum was estimated from hourly spectral measurements taken between 10:00 am and 3:00 pm. The spectra thus obtained for each condition were used to estimate relative spectral intensities, i.e., the partition of the total PAR every 5 nm over the 400 nm to 700 nm wavelength range (the integration of every relative spectral intensity between 400 nm and 700 nm yields 1 for a given condition; Fig. 1d). As total light intensity received by each raceway was measured continuously by a sensor placed under the filter (PAR Quantum Sensor, SKYE Instruments, UK), hourly estimations of the incoming light spectrum at the surface of each raceway over the course of the experiments were obtained by multiplying the relative spectral intensities by the continuous measures of total light intensity.

2.1.3. Nitrogen biomass estimation and chlorophyll measurements

Algal cell counts were carried out on 50-mL samples with an optical cell counter (HIAC, model 9703, Pacific Scientific Instruments) after

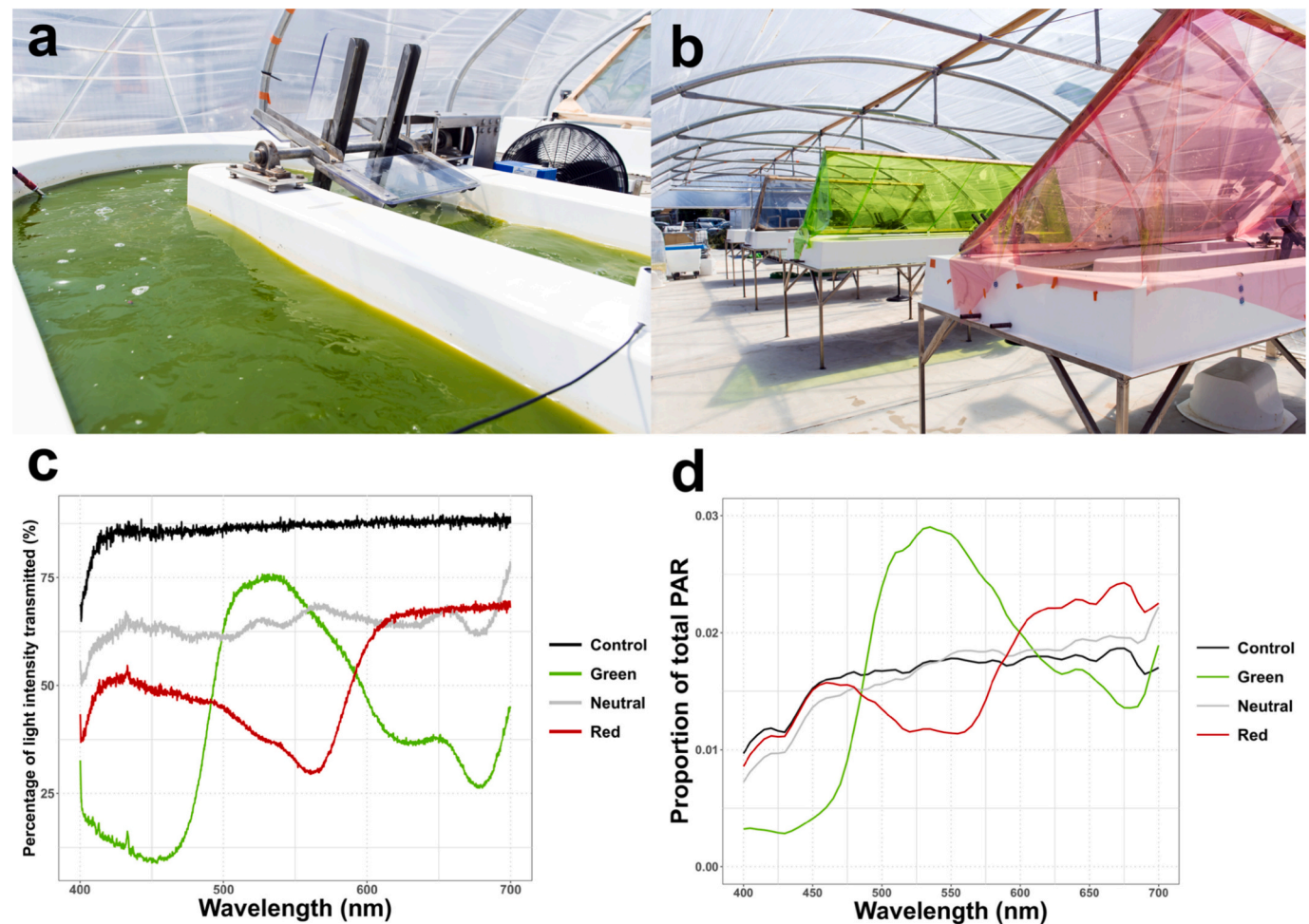


Fig. 1. Experimental setup of the FullSpectrum Platform. (a, b) Algal cultures are grown in open raceway ponds located in a greenhouse and under different commercial color filters. (c) Transmission spectra (400–700 nm) measured for the three colored filters and the control raceway relative to natural sunlight. (d) Spectral decomposition of the total incoming light intensity at the surface of each raceway every five nm over the 400 nm to 700 nm range.

Table 1
Percentage of incoming natural sunlight transmitted to each raceway, averaged over the entire PAR spectrum, the purple-blue portion (400–500 nm), the green-yellow portion (500–600 nm) and the red portion (600–700 nm) of the PAR spectrum.

Filter	Total (400–700 nm)	400–500 nm	500–600 nm	600–700 nm
Control	86.4	84.2	87.1	88
Neutral	64.1	61.5	65.2	65.5
Red	51.3	47.9	39.3	66.7
Green	40.7	19.8	66.5	35.9

dilution of the culture with 0.22 μm filtered seawater. Concentration and biovolumes (in $\mu\text{m}^3.\text{mL}^{-1}$) were calculated counting all the particles whose diameters range from 2.65 μm to 20 μm . The measured biovolumes were converted into nitrogenous biomass (in $\text{mgN}.\text{m}^{-3}$) using a conversion factor of $3.5.10^{-5} \text{ mg}.\text{mL}^{-1}.\mu\text{m}^{-3}$, estimated with previous studies from the same species cultivated in photobioreactor [38].

Samples were also collected (5–10 mL depending on biomass abundance) and then filtered through a 1.2 μm glass fiber filter (GF/C, Whatman). Chlorophyll *a* measurements were carried out by HPLC (1200 Series HPLC System, Agilent Technologies, USA) after pigment extraction in 100 % methanol containing vitamin E acetate as internal standard for 2 h. Cells were disrupted by sonication and clarified by filtration (Whatman glass microfiber filters, Grade GF/F). These measures yielded chlorophyll concentration (in $\text{mg Chl}.\text{m}^{-3}$) at the 8th, 11th

and 15th days of winter experiment (Fig. Suppl.2). While chlorophyll measurements were initially also carried out during the summer experiment, those samples were mishandled and could not be used in subsequent analyses.

2.2. Model development

2.2.1. Ecophysiological model of light- and temperature-limited algal growth

An ecophysiological model was developed, assuming that only the quantity of photosynthetically usable radiations (*PUR* as initialed used by Morel [39]), and temperature influence the net growth rate $\mu_{\text{net}}(\text{PUR}, T)$:

$$\frac{dP_N}{dt} = \mu_{\text{net}}(\text{PUR}, T).P_N \tag{1}$$

This model simulates the temporal evolution of the algal biomass described in particulate nitrogen concentration P_N ($\text{mgN}.\text{m}^{-3}$) and takes into account both photoacclimation and photoinhibition. The gross growth is assumed to be the product of a light-limitation term $F_{\text{PUR}}(\text{PUR})$ which depends on the *PUR* and a temperature-limitation term $F_T(T)$ [28], while the biomass loss is due to temperature-dependent respiration term $R(T)$. This leads to the following equation:

$$\mu_{\text{net}}(\text{PUR}, T) = \mu_{\text{max}}.F_{\text{PUR}}(\text{PUR}).F_T(T) - R(T) \tag{2}$$

where μ_{max} is the maximum gross growth rate.

The light limitation term follows a Haldane type formulation accounting for photoinhibition at high light, with the parameterization proposed by Bernard & Rémond [28]:

$$F_{PUR}(PUR) = \frac{PUR}{PUR + \frac{\mu_{max}}{\alpha} \left(\frac{PUR}{PUR_{opt}} - 1 \right)^2} \quad (3)$$

where PUR_{opt} is the optimal PUR and α the initial slope of the light-dependent growth curve. The amount of photosynthetically usable radiation (PUR) is estimated from the total light intensity PAR , as the probability that a given photon is absorbed by a microalgae cell depends on its wavelength. The PUR value is obtained by applying a wavelength-specific ponderation function to PAR [40,41]:

$$PUR = \int_{\lambda=400}^{700} PAR(\lambda)A(\lambda)d\lambda \quad (4)$$

where $A(\lambda)$ is the *D. salina* absorption spectrum measured on a low cell density culture (2.10^5 cell.mL⁻¹), with an acquisition step increment of 1 nm, using a dual-beam UV/visible spectrophotometer (Varian DMS1005 UV Visible; Intelligent Instrumentation) equipped with an integrating sphere [42]. This absorption spectrum was normalized by the absorbance value at $\lambda = 680$ nm which was fixed at 0.7, the ratio between the absorption maxima at $\lambda = 680$ nm and $\lambda = 440$ nm (the absorption maxima of chlorophyll *a* and chlorophyll *b* respectively) commonly measured in cultures of *D. salina* (Fig. Suppl.1).

The value of PUR_{opt} was obtained from the optimal PAR value for growth ($PAR_{opt} = 866$ μ mol photons.m⁻².s⁻¹) estimated in Combe et al. [43] by computing the associated PUR from the light spectrum measured at the surface of the control raceway weighted by $A(\lambda)$.

The effect of temperature (T , in °C) follows the cardinal temperature model with inflexion (CTMI) adapted by Bernard & Rémond [28] to describe the growth of microalgae:

$$F_T(T) = \begin{cases} 0 & \text{for } T < T_{min} \\ \frac{\theta(T)}{\Psi(T)} & \text{for } T_{min} < T < T_{max} \\ 0 & \text{for } T > T_{max} \end{cases} \quad (5)$$

With

$$\theta(T) = \frac{(T - T_{max})(T - T_{min})^2}{(T_{opt} - T_{min})} \quad (6)$$

$$\Psi(T) = (T_{opt} - T_{min})(T - T_{min}) - (T_{opt} - T_{max})(T_{opt} + T_{min} - 2T) \quad (7)$$

where T_{opt} is the optimal temperature, T_{max} the maximum temperature beyond which there is no growth, and T_{min} the minimum temperature for growth. The temperature-dependant respiration rate $R(T)$ follows an Arrhenius law (with T in Kelvin) as in Geider et al. [31]:

$$R(T) = R_{ref} \cdot e^{-A_E \left(\frac{1}{T+c_K} - \frac{1}{T_{opt}+c_K} \right)} \quad (8)$$

where R_{ref} is the respiration rate at T_{opt} , c_K is the constant to convert temperature from the Celsius degree to Kelvin ($c_K = 273.15$) and A_E is the slope of the Arrhenius function.

2.2.2. Modeling chlorophyll content

The algal biomass in carbon (P_C) is assumed to be proportional to P_N using the Redfield ratio r_d [44] as follows:

$$P_C = r_d \cdot P_N \quad (9)$$

Since the chlorophyll *a* content varies with light due to photo-acclimation [45], the algal biomass in chlorophyll P_{chl} is obtained from the chlorophyll-to-carbon ratio $R_{chl:C}$ as follows:

$$P_{chl} = R_{chl:C}(PAR_D, T) \cdot r_d \cdot P_N \quad (10)$$

where the chlorophyll to carbon ratio $R_{chl:C}$ is defined using the formulation of Cloern et al. [46]. It depends on T_D and on PAR_D , respectively the mean temperature and the mean total light intensity for the current simulation day:

$$R_{chl:C}(PAR_D, T) = R_{min\ chl:C} + \mu' \cdot c_1 \cdot e^{c_2 \cdot T_D} \cdot e^{-c_3 \cdot PAR_D} \quad (11)$$

where μ' is the nutrient-limited growth rate (set at 1 in this study since the nutrients are not limiting the growth in the raceways), and c_1 , c_2 and c_3 the parameters defined empirically by Cloern et al. [46].

2.2.3. Simulating vertical profiles of light quantity and quality in the raceways

The originality of the proposed model lies in the fact that the vertical light absorption in the raceway ponds due to both water and algal cells was simulated for each wavelength λ following Morel [47] and Morel & Maritorena [48]. Hence, the vertical profiles of both light intensity and quality were simulated. The raceway was discretized vertically, with layer heights increasing exponentially with depth to better represent the process at the surface (10 layers were used, with a layer width of 0.3 cm at the surface and 5.31 cm at the bottom). The spectral light intensity $PAR(\lambda, z, P_{chl}(z))$ for a wavelength λ at depth z , where the chlorophyll concentration was $P_{chl}(z)$, was estimated from the spectral light intensity $PAR(\lambda, z-\Delta z, P_{chl}(z-\Delta z))$ in the layer above $z-\Delta z$ using an exponential decrease of light intensity following a Beer-Lambert law with an extinction factor $k(\lambda, P_{chl}(z))$ resulting from absorption and scattering from cells and background medium:

$$PAR(\lambda, z, P_{chl}(z)) = PAR(\lambda, z - \Delta z, P_{chl}(z - \Delta z)) \cdot e^{-k(\lambda, P_{chl}(z)) \cdot \Delta z} \quad (12)$$

where $k(\lambda, P_{chl}(z))$ is the attenuation coefficient for downward irradiance at depth z . It is estimated for each wavelength λ as the sum of the light attenuation coefficient due to water $k_0(\lambda)$ and the light attenuation coefficient due to algal biomass $k_{alg}(\lambda, P_{chl}(z))$ [47]:

$$k(\lambda, z, P_{chl}(z)) = k_0(\lambda) + k_{alg}(\lambda, P_{chl}(z)) \quad (13)$$

$$k_{alg}(\lambda, P_{chl}(z)) = k_p(\lambda) \cdot (P_{chl}(z)/r_p)^{L(\lambda)} \quad (14)$$

where k_p is the attenuation coefficient at the wavelength λ by the algal pigment, r_p is the contribution of chlorophyll to total algal pigments, and $L(\lambda)$ an exponential coefficient that varies with λ . The total light intensity $PAR(\lambda, z, P_{chl}(z))$ at a given depth z was hence calculated as the sum of the light intensities estimated for each wavelength at that depth:

$$PAR(z, P_{chl}(z)) = \int_{\lambda_{min}}^{\lambda_{max}} PAR(\lambda, z, P_{chl}(z)) \quad (15)$$

With $\lambda_{min} = 400$ nm and $\lambda_{max} = 700$ nm. The light attenuation parameters were taken from Morel & Maritorena [48].

At each time step, the algal chlorophyll content and algal growth were estimated successively in each layer using Eqs. 1 to 12 with $PAR = PAR(z, P_{chl}(z))$, starting from the layer closest to the surface down to the bottom of the raceway (i.e., following the direction of the vertical light gradient). The vertical decrease of PAR_D (see Eq. 11) was estimated at each time step in the same manner. Biomass was then averaged over the vertical dimension before the beginning of the next time step to reflect the constant homogenization of the medium inside the raceway.

2.2.4. Model simulations and parameter sensitivity

The model was simulated using the R software version 4.4.1 [49] with the *lsoda* function of the package *deSolve* version 1.40 [50]. For each of the four raceways, the simulated time duration was 14 days (as the experiments) with a time step of 1 h. The R function *lsoda* solves initial value problems for stiff or non-stiff systems of first-order ordinary

differential equations (ODEs) and provides an interface to the FORTRAN ODE solver of the same name. Initial microalgal concentrations in each raceway were set to the concentrations experimentally measured under the greenhouse for both seasons (Table 2). For each season, the water temperature recorded under the green filter was used as forcing temperature for all the raceways, whereas the light intensity measured experimentally at the surface of each raceway was used as forcing light intensity (cf. Fig. 3). The initial Chl concentration for a given condition was set equal in all vertical layers and was estimated from Eq. 10 using the mean temperature and the mean total surface PAR measured during the first day of the modeled season/color combination. The outputs of the model were the vertically integrated algal concentration (P_N in nitrogen, P_C in carbon, and P_{Chl} in chlorophyll), as well as total light intensity (PAR) at each layer depth and the limiting factors F_{PUR} (PUR) et F_T (T). Plots were produced using the ggplot2 package [51].

The parameter values of the algal growth model were either measured experimentally or estimated from the literature and are given in Table 3. A preliminary sensitivity analysis indicated that the value of T_{opt} and μ_{max} both had a large influence on model results in both season and for all color conditions (data not shown). Dedicated simulations were thus performed to estimate the best value for μ_{max} and T_{opt} . The chosen values of μ_{max} and T_{opt} minimized a cost function F , i.e., the weighted sum of squared differences between measured biomasses and simulation outputs [52]. F is as follow:

$$F = \sum_{n=1}^{N=7} \frac{1}{T_n} \sum_{t_n} \frac{[obs_n(t_n) - mod_n(t_n)]^2}{\sigma_n} \quad (16)$$

where N is the number of season/color combinations for which experimental data were available (seven in total; three in winter, four in summer); T_n is the number of experimental measurement points for the season/color combination n ; $obs_n(t_n)$ is the biomass measurements at day t_n for the season/color combination n ; $mod_n(t_n)$ is the averaged simulated biomass P_N at day t_n for the season/color combination n ; and σ_n is the standard deviation of the experimental measurements for the season/color combination n , i.e. a weighting factor to control for the differences in biomass production from one season/color combination to another. F was minimized when $\mu_{max} = 1.5d^{-1}$ and $T_{opt} = 29^\circ C$ (Fig. Suppl.3). This value of μ_{max} was below the range proposed by Bernard & Rémond [28] for a green algae of the same genus, *Dunaliella tertiolecta*. The calibrated value of T_{opt} was also below the value of $34^\circ C$ reported for *D. salina* by Béchet et al. [18] from growth experiments in photobioreactors.

To further estimate the sensitivity of the simulations to the parameters of the model, the elasticity of total biomass production in nitrogen (N) for relevant model parameter p was computed as follows. The

elasticity e_p was defined as $e_p = \left(\frac{\frac{dP_N}{P_N}}{\frac{dp}{p}} \right)$ when the parameter p increases

by 10 %. An elasticity of 1 would then indicate a change in 10 % in the biomass production in nitrogen. The elasticity was calculated for each

Table 2

Initial microalgal concentrations (in $mgN.m^{-3}$) in the four raceways during the two seasonal experiments (November 4th, 2015, in winter and July 4th, 2016, in summer).

	Control raceway	Green filter raceway	Red filter raceway	Neutral filter raceway
Winter experiment	1310 (*)	1310 (*)	1437	1310
Summer experiment	11,845	5489	6028	5678

(*) No data was available for the control and green raceways at t_0 in the winter experiment. The initial concentration measured under the neutral filter was used instead.

Table 3

Parameters used in the model. The symbols, default values, units, and sources are indicated.

Symbol	Parameter	Value	Unit	Source
I_0	Light irradiance at the surface of the raceway	–	$\mu mol photons. m^{-2}.s^{-1}$	Measure experimentally
T	Water temperature in the raceway	–	$^\circ C$	Measure experimentally
P_{NO}	Initial algal concentration	–	$mgN.m^{-3}$	Measure experimentally
h	Water height in the raceway	0.25	m	Measure experimentally
n_z	Number of vertical layers in the model	10	unitless	–
μ_{max}	Maximum growth rate	1.5	d^{-1}	Calibration (Range reported by Bernard & Rémond [28] for <i>Dunaliella tertiolecta</i> : $2.7d^{-1}$ to $3.9d^{-1}$)
α	Initial slope of the light-dependant growth curve	0.05	d^{-1}	[28] (for <i>Chlorella pyrenoidosa</i>)
R_{ref}	Respiration rate for optimal light and temperature values conditions	0.1	d^{-1}	[31,53]
A_E	Slope of the Arrhenius curve	7000/8.3	K	[31,53]
PUR_{Opt}	Optimal light intensity for algal growth (based on PAR_{Opt} from Combe et al. [43]).	442.8	$\mu mol photons. m^{-2}.s^{-1}$	[43]
r_d	Redfield C:N stoichiometric ratio	(106/16)(12/14)	$mgC. mgN^{-1}$	[44]
T_{opt}	Optimal temperature for algal growth	29	$^\circ C$	Calibration (Value reported by Béchet et al. [18] for <i>Dunaliella salina</i> : $34^\circ C$) [28] (for <i>D. tertiolecta</i>)
T_{min}	Minimum temperature for algal growth	5	$^\circ C$	[18]
T_{max}	Maximum temperature for algal growth	43	$^\circ C$	[46]
$R_{min Chl:C}$	Minimum Chl:C ratio	0.003	$mgChl. mgC^{-1}$	[46]
c_1	First constant of the Chl:C equation	0.0154	$mgChl.j. mgC^{-1}$	[46]
c_2	Second constant of the Chl:C equation	0.05	$^\circ C^{-1}$	[46]
c_3	Third constant of the Chl:C equation	$0.059 \times 10^{-6} \times 86,400$	$(\mu mol photons. m^{-2}. s^{-1})^{-1}$	[46]
μ'	Nutrient-limited growth rate in the Cloern equation	1	d^{-1}	The nutrients are not limiting cultures.
r_p	Contribution of chlorophyll to total pigments	0.7	unitless	[54]
k_0	Light absorption coefficient by water	varies with λ	m^{-1}	[48]
k_p	Light absorption coefficient by the algal pigments	varies with λ	$m^{-1}. (mgChl. m^{-3})^{-1}$	[48]
L	Exponential factor for light absorption by the algal pigments	varies with λ	unitless	[48]

season and each raceway.

3. Results

3.1. Experimental data and physical forcing of the model

Temperature and light forcing varied due to the weather conditions during the 14 days of the experiments (Fig. 2). Between day and night, the water temperature varied between 15 °C and 25 °C in winter and between 17 °C and 39 °C in summer. Light intensity also varied during the day-night cycle and with the season. At the surface of the control raceway, it reached a maximum value of about 700 $\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$ in winter and 1600 $\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$ in summer. In comparison to the control, mean daily incoming light intensity was reduced on average to 71 %, 86 % and 58 % in winter, and to 64 %, 69 % and 52 % in summer for the neutral, red and green raceways, respectively. This means that filters not only alter incoming light quality, but also the total light quantity. The difference in the light regime between the two seasons was likely due to meteorological differences (with more clouds and a shorter period of exposure to sunlight during winter).

3.2. Sensitivity analyses of the model parameters

The algal biomass simulated by the model was mainly sensitive to the values of the parameters T_{opt} and μ_{max} for both seasons (Fig. Suppl.4a). The sensibility of T_{max} was also very pronounced under winter conditions. The effect of T_{max} and T_{opt} on model outputs was further tested. Changing the value of either parameter by a few degrees yielded marked changes in biomass production (Fig. Suppl.4b, Fig. Suppl.4c). For example, decreasing the value of T_{max} from 43 °C (the basal value) to 38 °C reduces the predicted final biomass in winter in the control raceway by 30.1 %. While decreasing T_{opt} also yielded a reduction in the biomass produced under summer conditions, by contrast it increased the predicted algal biomass after 14 days under winter conditions.

3.3. Algal biomass production

3.3.1. Experimental cultures

Both winter and summer experiments were affected by culture crashes: the agitation system failed in the control raceway at the beginning of winter experiment as well as in the red raceway after day nine of summer experiment, thus yielded no usable results.

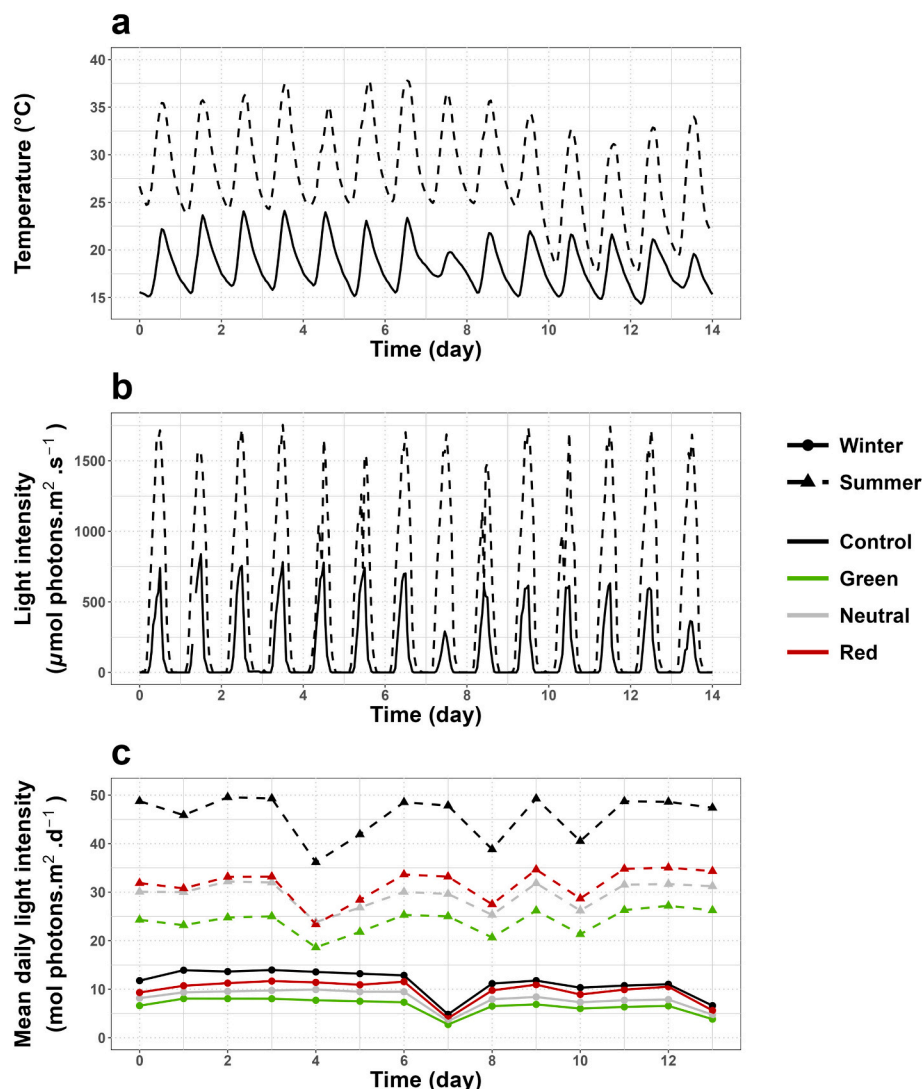


Fig. 2. (a) Water temperature (°C) and (b) light intensity (PAR, in $\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$) at the surface of the control raceway in winter (Nov. 2015, solid lines) and in summer (July 2016, dashed lines). (c) Mean daily incoming light intensity (PAR, in $\text{mol photons.m}^{-2}.\text{d}^{-1}$) at the water surface of each raceway (control, neutral, red and green) during the two experiments (winter: solid lines, summer: dashed lines). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Notwithstanding these missing measurements, the experimental results showed a clear effect of season and light conditions on biomass production (Fig. 3). The summer experiment yielded significantly higher biomass across all conditions compared to the winter experiment, with roughly an order-of-magnitude difference (e.g., close to 3.10^5 mgN.m⁻³ in summer vs. $2.3.10^4$ mgN.m⁻³ in winter in the red raceway). The observed algal production also differed between the four conditions: for both seasons, the red raceway yielded the highest biomass after 14 days (with a similar amount of biomass being produced in the control raceway during summer) while the lowest biomass was obtained under the green filter.

3.3.2. Simulated biomasses

The seasonal disparity in production was well reproduced by the model. The model predictions also yielded contrasted algal biomass predictions across conditions, although those differences did not necessarily exactly match the observed data. The model correctly predicted the lowest algal biomass in the green raceway, although predictions for winter conditions underestimated measurements both for algal biomass (Fig. 3a) and chlorophyll *a* (Fig. Suppl.2). More surprisingly, the model predicted much higher production levels in the control raceway compared to the other conditions, a pattern that is not apparent from summer experimental data (Fig. 3b). Summer production in the red

raceway was predicted to be much lower compared to the control raceway, although the measured biomasses in the two conditions at the end of the experiment were close. More generally, the model overestimated production in the control during summer, while production in the other raceways was adequately reproduced.

3.4. Dynamic of algal growth

3.4.1. Growth rate

Predicted daily growth rates at the beginning of the simulations were significantly higher under summer conditions in all conditions (Fig. 4a). The seasonal difference in mean daily growth rates (and consequently the difference in production) can be attributed to temperature limitation, as the model predicts noticeably higher limitation due to temperature (FT) values in summer (Fig. 4b). Predicted growth rates decreased over time, especially during summer (Fig. 4a). This appears to be caused by a decrease in light availability over the course of the simulations (Fig. 4c): the increase in algal biomass over time caused self-shading and amplified light attenuation with depth (Fig. Suppl.5), thus inducing a decrease in the algal growth rate.

The predicted differences in the mean daily growth rate between raceways can also be attributed to variations in biomass densities impacting self-shading across color conditions. Indeed, the control

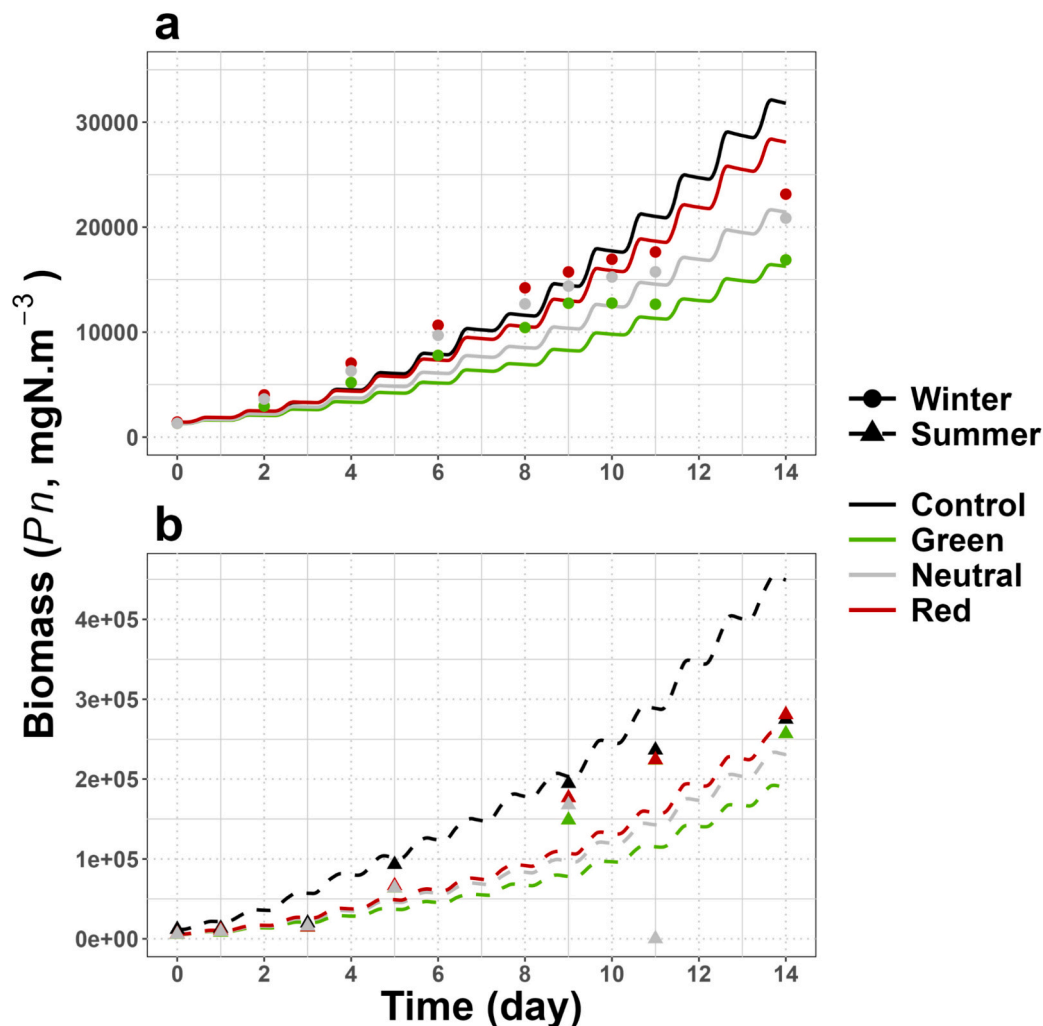


Fig. 3. Simulated and measured algal biomass (in mgN.m⁻³) in winter (a) and summer (b) experiments. Lines represent the simulated biomass, while dots (in winter) and triangles (in summer) represent experimental measurements. Colors indicate the raceways with black, grey, red and green for the control, neutral, red and green raceways, respectively. NB: experimental data (dots and triangles) are missing due to culture crashes for the control (winter, from day 0) and the neutral (summer, from day 11) raceways. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

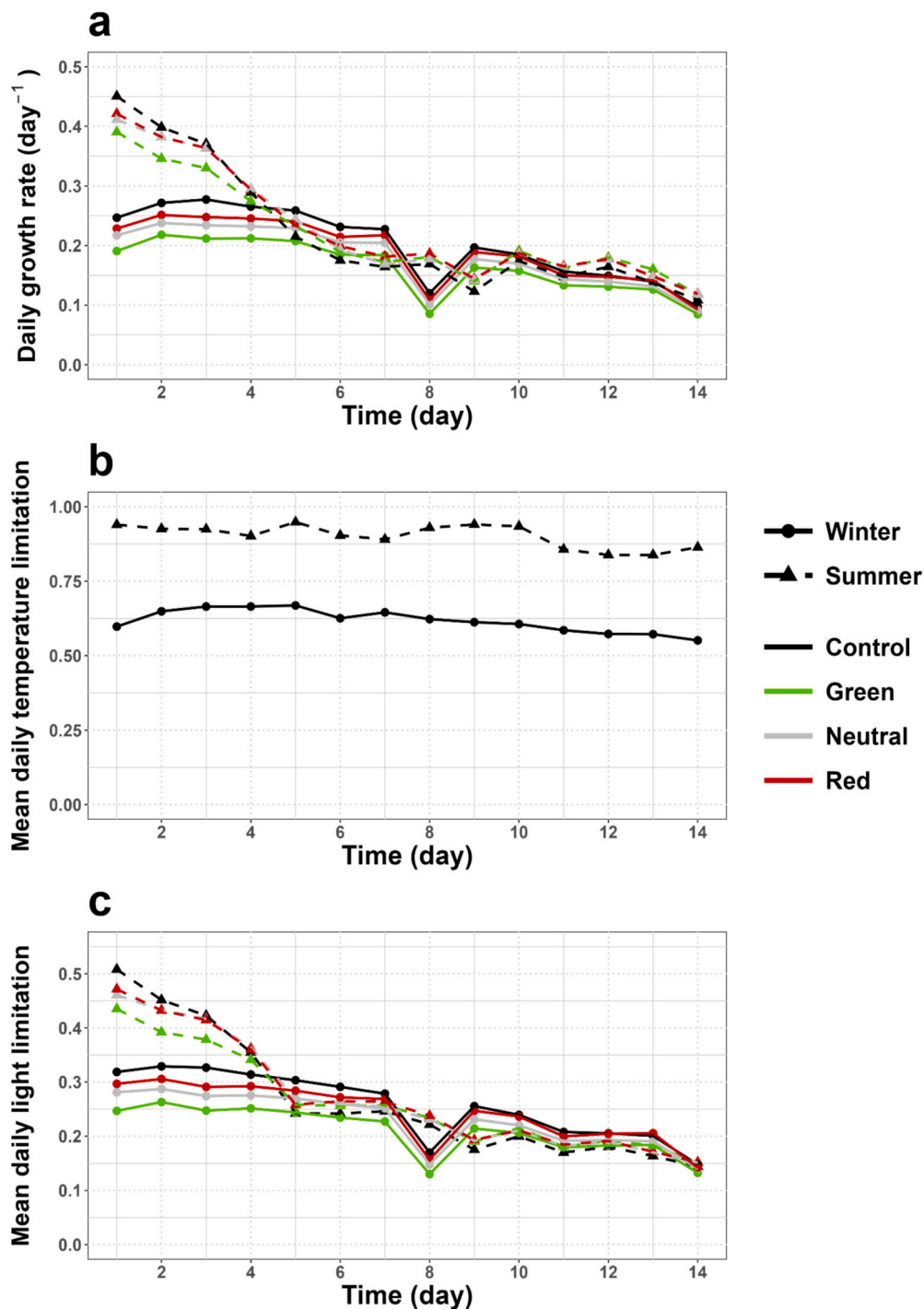


Fig. 4. (a) Daily growth rates (d^{-1}) for each season and each raceway during the simulation. (b) Mean daily temperature limitation and (c) light limitations for each season (solid lines, winter; dashed lines, summer) and each raceway during the simulations. Colors indicate the raceways with black, grey, red and green for the control, neutral, red and green raceways, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

condition showed, after day 4, the lowest predicted mean daily growth rate during summer. The initial and predicted biomasses in this raceway were the highest, so that shading was most prevalent. Investigating how the daily algal growth rates varied across color conditions thus offers a more nuanced view of the effect of filters than the total biomass outputs. Indeed, although total biomass production was the lowest in the raceway under the green filter for both seasons, the growth rate predicted was fairly close to the growth rates in the other raceways during winter, and it was not the lowest for summer conditions after the 5th day of the

simulation.

3.4.2. Growth efficiency

In addition to spectral differences, the flux of incoming photons varied across conditions. A direct comparison of daily growth rates is thus not possible to identify the optimal light spectrum for algal production. Another way to compare productivity across raceways is to investigate the growth efficiency with respect to the PAR at the culture surface, i.e., to divide the mean daily growth rate by the surface PAR.

Using this metric of productivity, the green raceway outperforms the other conditions in both experimental seasons (Fig. 5). Thus, while the transmittance of the green filter was the lowest, meaning that the PAR at the surface of the raceway was lower than for the other conditions, the conversion efficiency into biomass was higher. According to model predictions, the mean growth efficiency in winter was 10.1 % higher with the green filter than with the neutral filter, which reached the second-best efficiency. The magnitude of this predicted difference was even higher in summer (16.3 %), although growth efficiency was noticeably lower in summer than in winter across all conditions. The condition with the lowest predicted growth efficiency in both seasons was the control raceway (Fig. 5), which happened to be the condition with the highest incoming PAR. Predicted growth efficiency gradually decreased from the beginning to the end of winter experiment, and it decreased more sharply over time during summer.

3.5. Model predictions for an ideal experimental set up

The difference in the usage of green light vs. the usage of natural PAR (the control) was especially acute in summer, when incoming light and culture density was high and photoinhibition prevalent at the surface of the raceway. However, by simulating the model solely using the incoming light intensities measured in each raceway, it is difficult to determine whether this benefit was due to the difference in spectral composition and light vertical penetration properties caused by the filters, or because the green filter cut a higher proportion of total incoming light intensity and was thus less likely to induce photoinhibition at the surface of the pond.

Additional simulations were run assuming a situation with the same initial biomass densities and identical PAR after the colored filter (Fig. 6; Fig. Suppl.6). These simulations further highlighted the more efficient green light at high PAR: biomass production was predicted to be almost 12 % higher in the green raceway than in the control raceway for

summer conditions (Fig. 6b). In contrast, production was lower in the green raceway than in the control for winter conditions, although this difference was low (3 %) after 14 days of production (Fig. 6a). Under these simulated normalized PAR for winter, biomass production was maximized under the red filter. The differences in light conversion efficiency between the raceways stemmed from the specificity of the light absorption spectra. Indeed, the green wavelengths are less attenuated (see Eqs. 13 and 14) and as a result green light intensity was higher in the darkest layers of the raceway. Simulations showed that green light penetrated deeper in the water with relatively higher intensities of PUR and PAR at intermediate depths when compared to the control (Fig. Suppl.7). In contrast, red light intensity decreased over depth when compared to the control by the end of the simulations for summer conditions.

4. Discussion

4.1. Influence of temperature on algal production

Seasonal disparities in biomass production reflected differences in temperature limitation between the two growing seasons. Indeed, the temperatures measured in winter were notably below the value of the optimal temperature for algal growth T_{opt} , resulting in unfavorable growing conditions for *D. salina* as lower temperatures negatively affect algal physiology [9]. The large differences in temperature limitation predicted by the model between the two rounds of experiment illustrate the necessity of considering the algal thermal niche to accurately model algal growth in outdoor culture systems year-round. The seasonal effect of temperature fluctuation on raceway productivity has been shown in other modeling studies [55,56]. The proposed model is able to adequately simulate algal growth both in summer and winter because of its realistic dependency to temperature. A misestimation of the cardinal parameters of the temperature niche could lead to a substantial

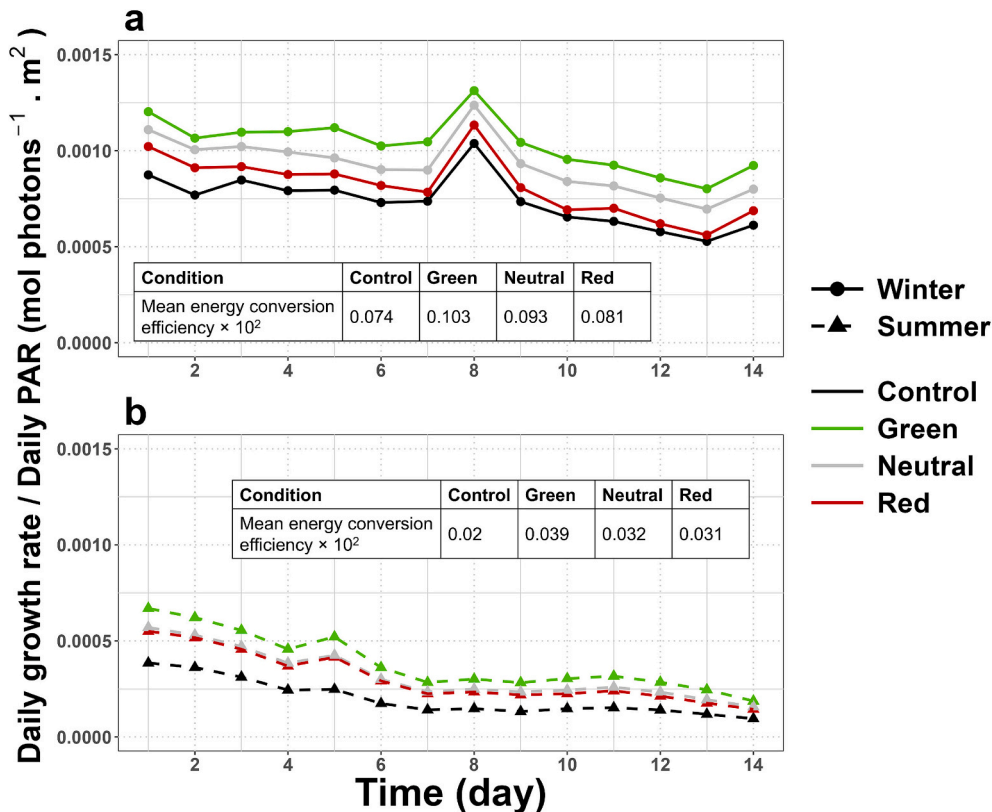


Fig. 5. Energy conversion efficiency (daily μ /daily PAR) in each raceway in winter (a) and summer (b). The mean value over the 14 days of simulation of this energy conversion efficiency are also indicated ($\frac{\text{mean daily } \mu}{\text{mean daily PAR}} \times 10^2$, from modeled data in (mol photons $\cdot$ m $^{-2}$) $^{-1}$).

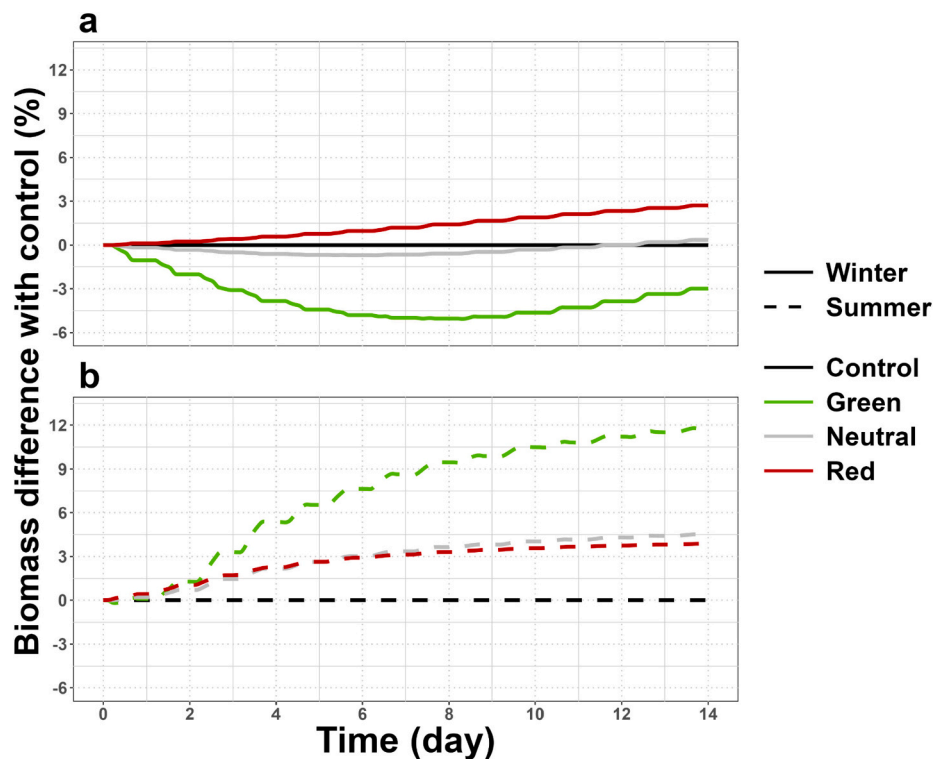


Fig. 6. Temporal evolution of the predicted differences in biomass concentrations between the raceways with filters compared to the control (expressed as a percentage) during winter (a) and during summer (b). For a given season, the total incoming light intensity (I_0) and the initial nitrogen biomasses were set to be identical across conditions.

deviation in production prevision. The model was especially sensitive to the parameters of the thermal niche (T_{max} and T_{opt}) in winter conditions when cultures experience cold temperatures with respect to T_{opt} . It is thus crucial to precisely characterize the thermal niche of the microalgae strain to accurately predict and optimize biomass production, especially for outdoor raceway cultures set in a greenhouse where diurnal and seasonal variations in temperature can be considerable (Fig. 2b). Combining a physical model of temperature in outdoor raceway ponds with the temperature-dependent algal growth model developed by Bernard and Rémond [28], Rodriguez-Miranda et al. [56] showed that, during summer, cultures can reach temperatures above T_{opt} , leading to cell mortality. The results of the sensitivity analysis further highlighted the importance of selecting algal strains that are productive over a broad thermal range. These strains should be able to withstand both the high temperatures commonly experienced under a greenhouse during summer, as well as lower, suboptimal temperatures in winter. Alternatively, the species should be adapted to the season to maintain the productivity along the year [17].

4.2. Influence of light quality on algal production

The observed differences in biomass production across light conditions were reasonably well reproduced by the model. They can be related to the PUR, i.e. to the fraction of light spectra absorbed by the cell pigments. Indeed, the lowest biomasses were obtained under the less absorbed green light condition, while the highest biomasses were measured under the red filter, i.e., for an incoming light spectrum that matches the absorption peak of Chl *a* more closely. These results are consistent with findings from other studies studying microalgae production under contrasting light conditions in high density cultivation settings. For example, in a study looking at the production of a cyanobacteria (*Arthrospira platensis*) in high density raceway ponds under translucent-colored PVC sheets, Kumar et al. [57] obtained greater algal biomasses under orange light (i.e., a light spectrum matching the

absorption maxima of the main pigment of their target microalgae) compared to blue light (i.e., wavelengths less absorbed by the pigment of *A. platensis*).

By the end of the simulations, as algal density increases in the raceways, the predicted differences in growth rates between conditions became negligible. This relatively weak effect of color contrasts with results from other studies of algal productivity. For instance, de Mooij et al. [34] reported fairly large differences of biomass productivity for *Chlamydomonas reinhardtii* cultures exposed to different light conditions: under yellow light (supplemented by a small amount of blue light), the average areal productivity was nearly double that of cultures under blue or red light. Looking at the growth rate of *D. salina* in photobioreactor under colored LEDs, Bredda et al. [58] measured similar (albeit significantly different) growth rates under green and red light and obtained much higher productivity levels for culture exposed to a mix of red and blue light. One major methodological difference with those studies, which were performed in photobioreactors exposed to artificial light via LEDs is that the flux of incoming photons was constant across their conditions (and relatively high at $1500 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ in de Mooij et al. [34]). In contrast, the colored filters transmitted different PAR at the surface of the raceways illuminated by natural light conditions (Fig. 2).

4.3. Benefits of algal cultivation under a green filter

Contrary to initial expectations, neither biomass production nor productivity was maximized in the raceway pond equipped with the green filter, as this filter induced the strongest attenuation of incident light. This confirms that photosynthetically active radiation is the primary driver of growth and productivity, with its reduction directly impairing process performance. However, the green filter configuration exhibited the highest growth efficiency (Fig. 5), supporting the hypothesis that a less absorbed light spectrum enhances light penetration and thus improves the conversion efficiency of light into biomass. Model

simulations further predicted that under high light intensities—typical of summer conditions—the green filter system would achieve maximal production (Fig. 6). This effect arises from an optimized vertical light distribution, as green wavelengths are only moderately absorbed by the culture.

Specifically, modeling results revealed that light availability (PAR and PUR) remained comparatively higher at the bottom of the raceway with the green filter under normalized summer conditions, particularly during the early growth phase (Fig. Suppl.7). Thus, at equivalent incident summer irradiance, algal cells in deeper layers of the raceway with the green filter experienced reduced light limitation compared to those under other spectral filters.

The observed enhancement of growth efficiency under spectrally filtered light conditions aligns with previous productivity findings reported by Mattos et al. [59] and de Mooij et al. [34]. In particular, Mattos et al. [59] demonstrated increased biomass production of *Scenedesmus* sp. under green light in high-density photobioreactor cultures, attributing this effect to improved light penetration of green wavelengths compared to more strongly absorbed spectra. Similarly, de Mooij et al. [34] predicted through modeling a 50 % productivity increase under yellow light (with marginal blue supplementation) relative to natural sunlight, resulting from reduced photosystem oversaturation and consequently lower photoinhibition. Fuente et al. [33] further supported these observations in their modeling study of cyanobacterial cultures, showing lower light attenuation for green wavelengths compared to blue and red spectra. However, their model unexpectedly predicted the lowest light attenuation under white LED illumination. This counterintuitive result may reflect specific model parameters or uncharacterized physical artifacts in the simulation. This observation requires experimental validation as biomass production was not investigated.

It is worth noting that for simulated normalized summer conditions, the predicted difference of vertical penetration of the light spectrum under the green filter was less pronounced than at the beginning of the experiment (compare vertical light profile at day 1 and day 10 in Fig. Suppl.7). The relative benefit of green light thus decreased when algal density reached a critical threshold (i.e., when shading was high).

4.4. Limitations and perspectives

The modeling approach relied on parameter values for *D. salina* from previous studies [18,38]. In particular, an earlier version of this model (without photoacclimation and calibrated for solar light) was successfully validated for *Dunaliella salina* cultivation in 250 m² raceway ponds [18]. This version achieved strong predictive accuracy (± 2.7 mg DW L⁻¹) for biomass dynamics and included a validated sub-model for β -carotene production - which, critically, should remain applicable under spectrally modified light conditions given its mechanistic basis. The current work extends this framework by incorporating photoacclimation dynamics and spectral light effects, addressing key limitations for scalability. While large-scale experimental validation presents logistical challenges, it represents the essential next phase of model development.

The modeling framework described here can be extended to other strains of microalgae, providing the absorption spectrum of a given candidate species is available and a dedicated calibration work of species- and cultivation system-specific parameter values is performed. Given the sensitivity of the modeling results to the cardinal parameters of the thermal niche, dedicated experiments to assess microalgae growth response to temperature would also be needed, as in Pessi et al. [17].

It is important to keep in mind that commercially available filters are not very discriminative in the specific light wavelengths. Indeed, because of both filter non selectivity and diffuse light, high levels of non-green light in the 600–700 nm interval of the PAR spectrum were recorded under the green filter (Fig. 1c). The advantage of cultivating algae under a green light could potentially be higher for filters whose

associated transmission spectra show more pronounced peaks between 500 nm and 550 nm, adapting the average transmittance to keep light intensity at the surface of the basin similar to the intensity transmitted by the current filter.

Future developments could explore harnessing the portion of natural PAR spectrum absorbed by colored filters for photovoltaic electricity generation [15,60]. Colored photovoltaic cells represent a promising technology for converting non-transmitted wavelengths into electrical energy [25], with potential to reduce the environmental impact of cultivation systems through localized electricity production [60]. The current findings may also inform the design of artificial lighting systems for improved spectral control. For instance, Bredda et al. [58] demonstrated enhanced cultivation performance using tunable LED systems that precisely regulate spectral treatments. However, the energy-intensive nature of artificial lighting may constrain its scalability for commercial microalgae production.

Data for cultivation of microalgae at large scale under Semi-Transparent Photovoltaic (STPV) panels are missing. Agrivoltaic systems involve higher initial costs compared to conventional solar installations [16]. Capital expenditures (CAPEX) for agrivoltaics are 30 % higher due to increased labor and planning expenses. Operational costs (OPEX), however, remain similar. While traditional solar photovoltaic systems achieve payback in under 5 years, the review of Al Mamun et al. [16] for agrivoltaics show that 4–9 years are expected, depending on crop type and system design. Some studies suggest that integrating agrivoltaics can recover 50 % of land investment within two years, highlighting long-term economic potential. These figures are probably still optimistic, especially for the more expensive Semi-Transparent Organic Photovoltaic (ST-OPV) technologies with transmission spectrum adjustment, which are rapidly progressing in performance and cost [20].

The study of Morales et al. [60] evaluates through a Life cycle Analysis (LCA) the environmental impact of microalgae biodiesel produced in a solar greenhouse with varying photovoltaic (PV) coverage (0–90 %) using Copper Indium Gallium Selenide (CIGS) panels. It turns out that the Optimal PV coverage is 10–20 % for maximizing the Net Energy Ratio (NER). The authors recommended 20 % PV coverage to balance energy output with algal productivity, making it the most viable solution for sustainable microalgae production. Advances in OPV development are expected to further reduce the economic and environmental costs of photovoltaics, making their integration with algae cultivation even more compelling.

The present study focused primarily on light-mediated effects on biomass productivity. However, light quality and quantity also significantly influence metabolite biosynthesis, as microalgal physiology exhibits dynamic responses to spectral composition [61]. For instance, Nwoba et al. [62] demonstrated that *Dunaliella salina* cultivated in raceway ponds equipped with colored filters showed distinct biochemical profiles: systems with red filters enhanced biomass, lipid, and carotenoid yields, while those with blue filters increased cell density, protein content, and chlorophyll *a* concentration. Consequently, the optimal spectral conditions for high-density algal cultures depend on production objectives, whether prioritizing total biomass accumulation or targeting specific valuable compounds.

5. Conclusions

High-density raceway ponds operated under greenhouse conditions present a promising strategy for reducing algal cultivation costs while enabling combined biomass and photovoltaic electricity production. Experimental and modeling results indicate that coupling microalgae cultures with spectral filters, particularly those transmitting less attenuated wavelengths such as green light, can enhance biomass productivity under temperate summer conditions. Although this productivity advantage decreases with greater shading in the raceway, green light exposure maintains beneficial effects during early growth phases prior

to peak biomass accumulation.

The spatially explicit model effectively captured temporal growth dynamics while providing mechanistic insights into production-controlling factors. Through vertical discretization of light penetration, the model quantified spectral growth effects - a critical parameter in raceway systems that would be difficult to evaluate experimentally. While focusing on light quality and intensity, model predictions showed notable sensitivity to thermal niche parameters (T_{opt} and T_{max}), emphasizing the importance of accounting for temperature variability in outdoor cultivation systems.

This modeling framework represents a robust tool for assessing raceway productivity across variable light regimes, temperature conditions, and filter configurations. The approach could facilitate optimal spectral filter selection for maximizing productivity in outdoor high-density raceway systems. Future investigations should examine the integration of adaptive filter technologies with real-time environmental monitoring to further enhance productivity gains.

CRedit authorship contribution statement

Philippe Le Noac'h: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation. **Sakina-Dorothee Ayata**: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Eric Pruvost**: Methodology, Investigation. **Sabine Marty**: Writing – review & editing, Methodology, Investigation. **Olivier Bernard**: Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Martin Laviale**: Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Statement of informed consent, human/animal rights

No conflicts, informed consent, human or animal rights applicable.

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Declaration of authors' agreement

All authors agreed to the authorship and submission of the manuscript to Algal Research for peer review. For the purpose of open access, the authors have applied a CC-BY public copyright licence to any Author Accepted Manuscript (AAM) version arising from this submission.

Declaration of competing interest

The authors declare no conflict of interest. The authors report no commercial or proprietary interest in any product or concept discussed in this article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.algal.2025.104248>.

Data availability

The experimental data and the R code to reproduce the results are stored on a publicly available Zenodo archive (DOI: [10.5281/zenodo.15389340](https://doi.org/10.5281/zenodo.15389340)).

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