



Review article

Growth kinetic models for microalgae cultivation: A review

Eunyoung Lee^a, Mehregan Jalalizadeh^b, Qiong Zhang^{a,*}^a Department of Civil and Environmental Engineering, University of South Florida, 4202 E Fowler Avenue, Tampa, FL 33620, USA^b Department of Chemical, Biochemical, and Environmental Engineering, University of Maryland, Baltimore County, 1000 Hilltop Circle, Baltimore, MD 21250, USA

ARTICLE INFO

Article history:

Received 5 May 2015

Received in revised form 3 September 2015

Accepted 6 October 2015

Available online 4 November 2015

Keyword:

Kinetic model

Microalgal growth

Light intensity

Nutrients

Carbon

ABSTRACT

Microalgae-based biofuel has received increasing attention as one of the alternative energy sources because of its many advantages. Cultivation of microalgae is a crucial step for successful applications in the biofuel industry. Growth kinetic models are needed to provide an understanding of microalgal growth so that cultivation conditions can be optimized. This review study aims to provide an overview of the existing growth kinetic models for microalgae cultivation and identify knowledge gaps. The existing models were compiled and organized into three groups: those considering a single substrate factor, a light factor, or multiple factors including both substrate and environment. Three major knowledge gaps were identified in this review. For models considering multiple factors, the trade-off between the complexity of the model structure and the usability of the model must be managed. There is a need for appropriate incorporation of light and temperature in the growth model. This can be accomplished through developing an appropriate expression for temporally varying culture temperature and improving light expressions by considering the light attenuation and variation in sunlight intensity. Lastly, developing a generalized growth model for incorporation of species diversity is necessary for more realistic modeling of actual systems.

© 2015 Elsevier B.V. All rights reserved.

Contents

1. Introduction	497
2. Growth kinetic models considering a single substrate factor	499
3. Growth kinetic models considering a light factor	502
4. Growth kinetic models considering multiple factors	505
5. Current challenges in microalgae growth models	507
5.1. Adequately considering co-limiting factors in algae growth	507
5.2. Appropriately integrating temperature and light in the growth model	508
5.3. Incorporating diversity of the species in the growth model	508
6. Future research	508
7. Conclusion	509
Acknowledgements	510
References	510

1. Introduction

Increasing energy demand has led to concerns about fossil fuel depletion as well as anthropogenic carbon dioxide (CO₂) emissions which have contributed to global climate change [100,111,130]. To reduce the consumption of fossil fuel and associated CO₂ emissions, sustainable and renewable energy sources, including wind, tidal, solar, and

Nomenclature

a	Fitting constant
a'	Optical cross section of chlorophyll a, m ² g ⁻¹ chl
b	Fitting constant
C_n	Algal nitrogen content per unit algal dry weight, %
$C_{n,max}$	Maximum algal nitrogen content or nitrogen content of the functional substance per unit algal dry weight, %

* Corresponding author.

E-mail address: qiongzhang@usf.edu (Q. Zhang).

C_p	Algal phosphorus content per unit algal dry weight, %	$Q_{\max,N}$	Maximum N cell quota for algal existence, g g^{-1} Carbon, mol N mol^{-1} Carbon or g cell^{-1}
C_{pro}	Cell product concentration, mg L^{-1}	$Q_{\max,P}$	Maximum P cell quota for algal existence, g g^{-1} Carbon, mol P mol^{-1} Carbon or g cell^{-1}
$C_{pro,m}$	Maximum cell product concentration, mg L^{-1}	Q_{\min}	Minimum nutrient cell quota for algal existence, g g^{-1} Carbon, $\text{mol nutrient mol}^{-1}$ Carbon, or g cell^{-1}
C_x	Microalgae cell concentration, mg L^{-1}	$Q_{\min,N}$	Minimum N cell quota for algal existence, g g^{-1} Carbon, mol N mol^{-1} Carbon, or g cell^{-1}
$C_{x,m}$	Maximum microalgae cell concentration, mg L^{-1}	$Q_{\min,P}$	Minimum P cell quota for algal existence, g g^{-1} Carbon, mol P mol^{-1} Carbon, or g cell^{-1}
c	Fitting constant	Q_P	P cell quota, g g^{-1} Carbon, mol P mol^{-1} Carbon, or g cell^{-1}
d	Fitting constant	S	Nutrient concentration, mg L^{-1}
$f(C_p / C_n)$	Saturation ratio of the pooled phosphorus in algal cells	S_{CO_2}	Carbon dioxide concentration in the medium, mg L^{-1}
$f(I_{av})$	A function of average light intensity	S_N	Nitrogen concentration in the medium, mg L^{-1}
$f(T)$	A function of temperature	S_{nu}	Limiting nutrient concentration, mg L^{-1}
I	Incident light intensity, $\mu\text{mol photon m}^{-2} \text{s}^{-1}$, W m^{-2} , $\mu\text{E m}^{-2} \text{s}^{-1}$, $\text{MJ m}^{-2} \text{day}^{-1}$, or $\text{g cal cm}^{-2} \text{d}^{-1}$	S_{OC}	Sodium acetate concentration in the medium, mg L^{-1}
I_{abs}	Total light energy absorbed in reactor, mol d^{-1}	S_P	Phosphorus concentration in the medium, mg L^{-1}
I_{av}	Average irradiance in the culture, W m^{-2} , $\mu\text{mol photon m}^{-2} \text{s}^{-1}$, or $\mu\text{E m}^{-2} \text{s}^{-1}$	T	Temperature, $^{\circ}\text{C}$
I_c	Light intensity at the center measured from one direction with light shining from both direction, W m^{-2}	T_{ref}	Reference temperature (20°C)
I_e	Average irradiance at the energy compensation point, $\mu\text{E m}^{-2} \text{s}^{-1}$ or $\mu\text{mol photon m}^{-2} \text{s}^{-1}$	V	Liquid volume in the reactor, m^3
I_{in}	Light intensity at the front with shining from one side, W m^{-2}	V_F	Illuminated volume fraction of the reactor
I_k	Microalgal affinity for light, $\mu\text{E m}^{-2} \text{s}^{-1}$	X	Cell concentration, kg m^{-3}
I_{\max}	Maintenance rate, mol (kg d)^{-1}	x	Carbon subsistence quota, $\text{g Carbon g}^{-1} \text{dw}$
I_{opt}	I at $\mu = \mu_{\max}$, $\mu\text{mol photon m}^{-2} \text{s}^{-1}$, W m^{-2} , $\mu\text{E m}^{-2} \text{s}^{-1}$, $\text{MJ m}^{-2} \text{day}^{-1}$, or $\text{g cal cm}^{-2} \text{d}^{-1}$	x_e^*	Steady-state fraction of functional activated PSUs under continuous illumination
I_{out}	Light intensity at the back with shining from one side, W m^{-2}	y_c	Yield coefficient of the functional substance from the storage substance, mg mg^{-1}
K	Proportionality constant which is akin in meaning to growth yield, (see Eq. (14) of Table 2), kg mol^{-1}	α	Initial slope of the light response curve
K_a	Attenuation constant kg m^{-3}	α'	Parameter, $\text{E m}^{-2} \text{s}^{-1}$
K_c	Curve-fitting constant, g g^{-1} Carbon, mol mol^{-1} Carbon, or mol cell^{-1}	$\alpha_{C\max}$	Maximum affinity for growth at carbon dioxide limiting condition
K_I	Photo-saturation constant, $\mu\text{mol photon m}^{-2} \text{s}^{-1}$, $\text{E m}^{-2} \text{s}^{-1}$, W m^{-2} , klx , or $\text{KJ cm}^{-2} \text{h}^{-1}$	$\alpha_{P\max}$	Maximum affinity for growth at phosphorus limiting condition
K_i	Inhibition constant, mg L^{-1}	β	Sharpness coefficient (from -1 to ∞)
K_{i,CO_2}	Inhibition constant of CO_2 , mg L^{-1}	β'	Slope of the light response curve beyond the onset of photoinhibition
$K_{i,L}$	Photoinhibition constant, klx , $\text{kJ cm}^{-2} \text{h}^{-1}$, or $\mu\text{E m}^{-2} \text{s}^{-1}$	δ	Parameter, $\mu\text{E}^{-0.5} \text{m s}^{-0.5}$
$K_{i,OC}$	Sodium acetate inhibition constant of cell growth, mg L^{-1}	Θ	Temperature coefficients for growth
$K_{S,nu}$	Monod half-saturation constant of limiting nutrients, mg L^{-1}	ϕ	Quantum efficiency $\text{g C mol}^{-1} \text{photons}$
K_S	Monod half-saturation constant, mg L^{-1}	μ	Specific growth rate, day^{-1} or h^{-1}
K_{S,CO_2}	Monod half-saturation constant of CO_2 , mg L^{-1}	$\mu_{c,\max}$	Maximum of synthesis rate of the storage substance per unit dry weight of the functional substance, mg (mg d)^{-1}
$K_{S,N}$	Monod half-saturation constant of nitrogen, mg L^{-1}	$\mu_{f,\max}$	Maximum of synthesis rate of the functional substance per unit dry weight of the functional substance, mg (mg d)^{-1}
$K_{S,OC}$	Monod half-saturation constant of sodium acetate, mg L^{-1}	μ_{\max}	Maximum specific growth rate, day^{-1} or h^{-1}
$K_{S,P}$	Monod half-saturation constant of phosphorus, mg L^{-1}	$\mu_{\max,\min}$	The most limiting nutrient's maximum growth rate, day^{-1} or h^{-1}
K_q	Dimensionless parameter to set the curve form, $K_q = K_c / (Q_{\max} - Q_{\min})$	μ_{m1}	Maximum value for μ , day^{-1}
k	Parameter	μ_{m2}	Specific growth rate at the absence of nutrient in the culture medium, day^{-1}
k_d	Consumption rate of photosynthesis products per unit dry weight of the functional substance, mg (mg d)^{-1}	μ_{m3}	Specific growth rate at high nutrient concentration in the culture medium, day^{-1}
m	Shape parameter	μ'_{\max}	Hypothetical maximum growth rate at infinite Q , day^{-1}
n	Exponent	$\mu'_{\max,\min}$	Hypothetical maximum growth rate at infinite Q for the most limiting nutrient, day^{-1}
p	Length of light path inside the photobioreactor, m	μ^*_{\max}	Maximum growth rate at the maximum value of Q , day^{-1}
Pho	photosynthetic rate		
Pho_{\max}	Light-saturated photosynthesis rate		
Q	Nutrient cell quota, g g^{-1} Carbon, $\text{mol nutrient mol}^{-1}$ Carbon, or g cell^{-1}		
Q_N	N Cell quota, g g^{-1} Carbon, mol N mol^{-1} Carbon, or g cell^{-1}		
Q_{\max}	Maximum nutrient cell quota for algal existence, g g^{-1} Carbon, $\text{mol nutrient mol}^{-1}$ Carbon, or g cell^{-1}		

biofuel, have received much attention [101]. Since biofuels can be stored and used directly in existing vehicle engines, they become an attractive source for transportation fuels. In particular, biofuels derived from

microalgae have been considered as one of the most promising renewable energy sources, due to the unique traits of microalgae [4,21].

Microalgae are photosynthetic microorganisms capable of rapid adaptation to new environments [24,50]. They exhibit high growth rates, high lipid production capacity, high CO₂ fixation rates, and low land use, compared to other energy crops [4,128]. They can thrive under conditions with high levels of CO₂ [81]. This attribute makes microalgae suitable for using CO₂ contained in waste flue gases emitted from industrial facilities or power plants for its growth. Moreover, microalgae are capable of thriving in poor-quality water, such as municipal, industrial, or agricultural wastewaters. Thus, microalgae can efficiently recover nutrients such as nitrogen (N) and phosphorus (P) from wastewater streams, improving wastewater quality [7,67,69,97,121]. In addition, microalgal biomass can be used to produce a broad portfolio of fuels, such as biodiesel, bioethanol, and biogas [52,98,125].

Many research studies have been carried out to develop technologies for the production of microalgae-based biofuel [19,70]. However, some challenges in terms of technical feasibility and economic viability remain in the full-scale implementation of microalgae cultivation [3,42,77]. In particular, scaling up cultivation systems is a challenge due to difficulty in controlling the optimum conditions for microalgae growth [42]. Ahmad et al. [3] reported that the development of microalgal biofuels is currently limited by the high production cost compared with both first and second generation biofuels. Murphy and Allen [77] pointed out that the energy required for cultivating algae exceeded the energy content of the algae produced. To better estimate and optimize microalgae productivity under different conditions, process modeling is needed to provide useful information about the performance of microalgae cultivation systems. In a process model simulating microalgae cultivation systems, a growth kinetic model is a crucial element. Numerous kinetic models have been developed to understand microalgae growth in natural habitats. These models can be categorized as two types of models: descriptive and explanatory models. Explanatory models are developed primarily to explain the causal relationship or underlying system behavior. Most of these models have complex structure and mathematical formulations, but they may be simplified to reduce complexity using some rules. For example, some models can be simplified by adopting conceptual rules about simplified predator–prey interaction [114]. Most mechanistic models belong to explanatory models. Descriptive models, on the other hand, are developed to predict system performance rather than to explain mechanisms. Most kinetic models that were empirically developed fall into this category. These models are developed based on regression analysis of measured data and are difficult to generalize. Previous kinetic models are expressed as a function of a single factor or multiple factors affecting microalgae growth, including light intensity, nutrient availability, dissolved CO₂ concentration, temperature, and dissolved oxygen concentration. Some models take into account the interactions or relationships among factors, resulting in complex mathematical formulas. For example, models considering multi-nutrients and their co-limitation on microalgae growth frequently have complex forms. Such models often experience overfitting issues because they involve many parameters. To reduce this inherent problem, models are preferred to have compact and comprehensible forms with a small set of assumptions, while applicable for a wide range of environmental and nutrient conditions [114].

To date, one review has been published on the kinetic models considering light and temperature for algae growth for outdoor cultivation [9]. In Béchet et al.'s study, forty models have been reviewed focusing on the effect of light and temperature on algae growth; however, the models considering other growth factors such as nutrients which could be critical for algae growth depending on cultivation conditions were not included in the study. Due to high environmental impacts associated with energy and fertilizer consumption for microalgae cultivation, integrating cultivation systems with wastewater treatment systems has gained attention to improve the sustainability of current

microalgae cultivation systems [61,71]. Since wastewater has an imbalanced condition for microalgae growth, other factors such as nutrients and dissolved CO₂ concentrations may become limiting factors for microalgae growth [18,83]. Currently, a comprehensive overview of algae growth kinetic models is still lacking. In particular, no review paper has been published on algae growth kinetic models considering major factors, such as N, P, CO₂ and light, which are directly related with photosynthesis and endogenous respiration [56].

This paper aims to provide an overview of the existing kinetic models (listed in Tables 1–3), which were classified as three groups considering: 1) a single substrate factor (N, P, and CO₂), 2) a light intensity factor, and 3) multiple factors (e.g. both substrate and light). This paper also discusses the current challenges in the area of microalgae growth kinetic models and provides a direction for future research in this area.

2. Growth kinetic models considering a single substrate factor

Microalgae growth generally has six different phases in batch culture, which is the same as the growth of microorganism: lag phase, exponential phase, linear phase, declining growth phase, stationary phase, and death phase (See Fig. 1) [58,70,95,117]. In the lag phase, the growth is delayed due to the presence of non-viable cells or physiological adjustments in new environments. This is followed by an exponential phase, where cells grow and divide as an exponential function of time. During this period, light intensity and nutrients do not limit microalgae growth. In the linear growth phase, microalgae cell division slows down because light becomes limiting, so microalgae biomass accumulates at a constant rate until nutrients or inhibitors in culture medium become the limiting factors. The declining growth phase is characterized by the reduction of the cell division rate due to limiting factors, such as nutrients, carbon dioxide, and others. The growth rate then reaches zero in the stationary phase because nutrients in the culture medium are exhausted. In this phase, storage carbon products, such as starch, and neutral lipid are accumulated. The microalgae cell concentration declines rapidly in the death phase, also called the crash phase, due to a depletion of nutrients, overheating, pH disturbance, or contamination.

Under light-saturating conditions, microalgae growth depends on the availability of nutrients such as N, P, and carbon (C) sources in aquatic environments. Most kinetic models for growth are expressed as a function of a single nutrient concentration, which is presented in Table 1. These models are categorized into two groups (Group A-I and Group A-II).

Group A-I model assumes that the growth rate is controlled by an external nutrient concentration: that is, the growth rate depends

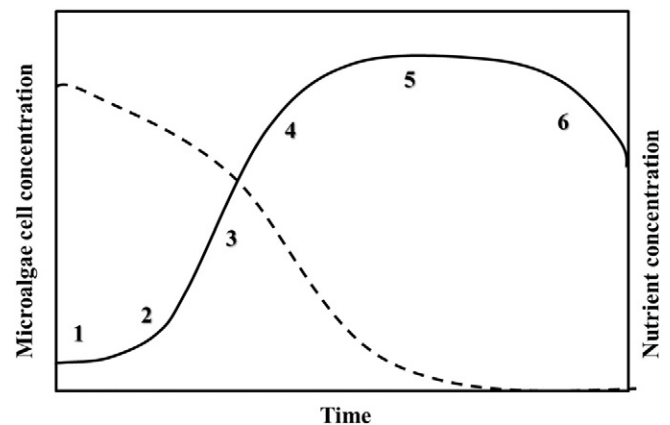


Fig. 1. Growth phases in microalgae batch culture (solid line) and nutrient concentration (dashed line); (1) lag phase; (2) exponential phase; (3) linear phase; (4) declining growth phase; (5) stationary phase; and (6) death phase [58,70,95].

Table 1
Microalgal growth kinetic models as a function of a single substrate.

Category	Source	Formula	Consideration	Applications	Parameters values
Group A-I: Model considering external nutrient concentration	Monod [72]	$\mu = \mu_{\max} \frac{S}{K_s + S}$	(1) Nutrient limitation	CO ₂ : 0–13.1 mg L ⁻¹ as TIC [35] 0–880 mg L ⁻¹ as CO ₂ [78] 0–0.2 mg L ⁻¹ as HCO ₃ ⁻ [119] 206–4150 mg L ⁻¹ as TIC [50] N: 0–0.4 mg L ⁻¹ DIN-N [102] 13.2–410 mg L ⁻¹ as NH ₄ -N [7] 2.5–25 mg L ⁻¹ as NO ₃ -N [121] P: 7.7–199 mg L ⁻¹ as PO ₄ -P [7] 0.1–2 mg L ⁻¹ as PO ₄ -P [121]	CO ₂ : <i>S. quadricauda</i> (at 400 fc, 27 °C) $\mu_{\max} = 2.29 \text{ d}^{-1}$ at pH 7.10–7.61 [35] $K_s = 0.30 \text{ mg L}^{-1}$ at pH 7.10–7.21 [35] $K_s = 0.36 \text{ mg L}^{-1}$ at pH 7.25–7.39 [35] $K_s = 0.71 \text{ mg L}^{-1}$ at pH 7.44–7.61 [35] <i>S. carpicornulum</i> (at 400 fc, 27 °C) $\mu_{\max} = 2.45 \text{ d}^{-1}$ at pH 7.05–7.57 [35] $K_s = 0.40 \text{ mg L}^{-1}$ at pH 7.05–7.23 [35] $K_s = 1 \text{ mg L}^{-1}$ at pH 7.25–7.39 [35] $K_s = 1.2 \text{ mg L}^{-1}$ at pH 7.43–7.59 [35] <i>Chlorella</i> (at 600 fc, 27 °C) $\mu_{\max} = 0.070 \text{ h}^{-1}$ [78] $K_s = 0.26 \text{ mg L}^{-1}$ [78] <i>Anabaena flos aquae</i> (at 600 fc, 27 °C) $\mu_{\max} = 0.045 \text{ h}^{-1}$ [78] $K_s = 0.17 \text{ mg L}^{-1}$ [78] <i>Selenastrum capricornutum</i> (at 600 fc, 27 °C) $\mu_{\max} = 0.057 \text{ h}^{-1}$ [78] $K_s = 0.18 \text{ mg L}^{-1}$ [78] <i>Senedesmus quadricauda</i> (at 600 fc, 27 °C) $\mu_{\max} = 0.057 \text{ h}^{-1}$ [78] $K_s = 0.17 \text{ mg L}^{-1}$ [78] <i>Oscillatoria</i> (at 600 fc, 27 °C) $\mu_{\max} = 0.028 \text{ h}^{-1}$ [78] $K_s = 0.43 \text{ mg L}^{-1}$ [78] <i>Microcoleus vaginatus</i> (at 600 fc, 27 °C) $\mu_{\max} = 0.031 \text{ h}^{-1}$ [78] $K_s = 3.22 \text{ mg L}^{-1}$ [78] <i>Thermosynechococcus</i> sp. CL-1 (at 10,000 lx, pH 9.5, 50 °C) $\mu_{\max} = 3.5 \text{ d}^{-1}$ [50] $K_s = 1.9 \text{ mM}$ [50] N: <i>Chlorella vulgaris</i> (at 4100 lx, pH 7.0, 20 °C) $k = \mu_{\max}/Y_N = 1.5 \text{ mg mg}^{-1} \text{ d}^{-1}$ [7] $K_s = 31.5 \text{ mg L}^{-1}$ [7] <i>Scenedesmus</i> sp. (at 55–60 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$, light/dark ratio = 14:10, 25 °C) $\mu_{\max} = 1.78 \times 10^6 \text{ cells} \cdot (\text{mL d})^{-1}$ [121] $K_s = 11.8 \text{ mg L}^{-1}$ [121] P: <i>Chlorella vulgaris</i> (at 4100 lx, pH 7.0, 20 °C) $k = \mu_{\max}/Y_P = 0.5 \text{ mg mg}^{-1} \text{ d}^{-1}$ [7] $K_s = 10.5 \text{ mg L}^{-1}$ [7] <i>Scenedesmus</i> sp. (at 55–60 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$, light/dark ratio = 14:10, 25 °C) $\mu_{\max} = 1.02 \times 10^6 \text{ cells} \cdot (\text{mL d})^{-1}$ [121] $K_s = 0.28 \text{ mg L}^{-1}$ [121]

Table 1 (continued)

Category	Source	Formula	Consideration	Applications	Parameters values
Group A-II: Model considering internal nutrient storage	Andrews [5]	$\mu = \mu_{\max} \frac{S}{K_s + S + \frac{S^2}{K_I}}$	(2) Nutrient limitation and inhibition	CO ₂ : 0–0.2 mg L ⁻¹ as HCO ₃ ⁻ [119] 0–0.2 pCO ₂ [63] Acetate: 0–10 mg L ⁻¹ [74]	CO ₂ : <i>Chlorococcum littorale</i> (at >300 μmol photon m ⁻² s ⁻¹ , pH 5.5, 25 °C) $\mu_{\max} = 0.12 \text{ h}^{-1}$ [63] $K_s = 0.00048 \text{ pCO}_2$ [63] $K_I = 0.31 \text{ pCO}_2$ [63] <i>Haematococcus lacustris</i> (at 23 °C) $\mu_{\max} = 21.30 \text{ h}^{-1}$ [74] $K_s = 1320 \text{ g dm}^{-3}$ [74] $K_I = 3.170 \text{ g dm}^{-3}$ [74] P: <i>Scenedesmus obliquus</i> (at 11.334 klx, 30 °C) $\mu_{m1} = 0.0466 \text{ h}^{-1}$ [67] $\mu_{m2} = 0.0256 \text{ h}^{-1}$ [67] $K_s = 0.20 \text{ μM}$ [67] P: <i>Scenedesmus obliquus</i> (at 11.334 klx, 30 °C) $\mu_{m1} = 0.0471 \text{ h}^{-1}$ [67] $\mu_{m2} = 0.0350 \text{ h}^{-1}$ [67] $\mu_{m2} = 0.0272 \text{ h}^{-1}$ [67] $K_s = 0.25 \text{ μM}$ [67] $K_I = 0.955.72 \text{ μM}$ [67] N: <i>Ceratium hirundinella</i> $\mu'_{\max}: 0.26 \text{ d}^{-1}$ [102] $Q_{\min}: 0.033 \text{ mol mol}^{-1}$ [102] <i>Peridinium</i> sp. $\mu'_{\max}: 0.31 \text{ d}^{-1}$ [102] $Q_{\min}: 0.036 \text{ mol mol}^{-1}$ [102] <i>Sphaerocystis Schroeteri</i> $\mu'_{\max}: 0.79 \text{ d}^{-1}$ [102] $Q_{\min}: 0.046 \text{ mol mol}^{-1}$ [102] P: <i>Scenedesmus</i> (at 10 ¹⁶ quanta cm ⁻² s ⁻¹ , pH 7.2, 12 °C) $\mu'_{\max}: 0.755 \text{ d}^{-1}$ [39] $Q_{\min}: 5.16 \text{ fmol cell}^{-1}$ [39] <i>Chlorella</i> (at 10 ¹⁶ quanta cm ⁻² s ⁻¹ , pH 7.2, 12 °C) $\mu'_{\max}: 0.842 \text{ d}^{-1}$ [39] $Q_{\min}: 0.352 \text{ fmol cell}^{-1}$ [39] P: <i>S. quadricauda</i> (at 3000 lx, light: dark ratio = 12:12, 25 °C) $\mu^*_{\max}: 0.0002 \text{ min}^{-1}$ [123] $Q_{\min}: 0.25 \times 10^{-8} \text{ μmol cell}^{-1}$ [123] $K_c: 0.25 \times 10^{-8} \text{ μmol cell}^{-1}$ [123] P: <i>Alexandrium minutum</i> (at 200 μmol photon m ⁻² s ⁻¹ , light/dark ratio = 14:10, 18 °C) $\mu'_{\max}: 0.55 \text{ d}^{-1}$ [17] $Q_{\min}: 3.7 \text{ gP cell}^{-1}$ [17] $Q_{\max}: 32.6 \text{ gP cell}^{-1}$ [17] $K_q: 4.24$ [17] <i>Heterocapsa triquetra</i> (at 200 μmol photon m ⁻² s ⁻¹ , light/dark ratio = 14:10, 18 °C) $\mu'_{\max}: 0.67 \text{ d}^{-1}$ [17] $Q_{\min}: 5.5 \text{ gP cell}^{-1}$ [17] $Q_{\max}: 15.6 \text{ gP cell}^{-1}$ [17] $K_q: 1.34$ [17]
	Martínez Sancho et al. [69]	$\mu = \frac{\mu_{m1}S + \mu_{m2}K_s}{K_s + S}$	(3) Nutrient limitation and absence	P: 0–10.1 mg L ⁻¹ as PO ₄ -P [67]	
	Martínez et al. [67]	$\mu = \frac{\mu_{m1}S + \mu_{m2}K_s + \mu_{m3}S^2/K_I}{K_s + S + S^2/K_I}$	(4) Nutrient absence, limitation, and inhibition	P: 0–10.1 mg L ⁻¹ as PO ₄ -P [67]	
	Droop [26]	$\mu = \mu'_{\max} (1 - \frac{Q_{\min}}{Q})$	(5)	N: 0.014–0.061 mol mol ⁻¹ [102] P: 0.352–324 × 10 ⁻¹⁵ mol cell ⁻¹ [39]	
	Caperon and Meyer [13,14]	$\mu = \mu^*_{\max} \frac{Q - Q_{\min}}{Q - Q_{\min} + K_c}$	(6) Integrated Michaelis-Menten function	P: 0–5.6 × 10 ⁻⁶ mol cell ⁻¹ [123]	
	Flynn [28]	$\mu = \mu'_{\max} \frac{(1 + K_q)(Q - Q_{\min})}{(Q - Q_{\min}) + K_q(Q_{\max} - Q_{\min})}$	(7) Normalized Michaelis-Menten function	N: 0–0.25 g g ⁻¹ Carbon [30] P: 0–0.14 g g ⁻¹ Carbon [30] 0–0.04 g g ⁻¹ Carbon [55] 0–1.3 × 10 ⁻¹² mol cell ⁻¹ [17]	
		$\mu = \mu'_{\max} \frac{Q - Q_{\min}}{Q_{\max} - Q_{\min}}$	(8) Simplified quota model		

on a nutrient concentration in culture solution. The models in this group are widely applied because it is easy to measure an external nutrient concentration (S). The Monod model [72] is a representative model in group A-I, which considers only nutrient limitation conditions (Eq. 1, Table 1). Many researchers have applied the Monod model to describe the relationship between microalgae growth and a single nutrient concentration (N , P , or CO_2) because of its simple formula [7,35,50,78,90,115,121]. Aslan and Kapdan [7] applied the Monod model to determine the effects of initial N and P concentrations (7.7 – 199 $mgP\ L^{-1}$ and 13.2 – 410 $mgN\ L^{-1}$ with an N/P ratio of around $2/1$) on nutrient uptake by microalgae *Chlorella vulgaris* from synthetic wastewater, and found that the growth of *C. vulgaris* in a batch reactor was limited when N and P concentrations were below 31.5 $mgN\ L^{-1}$ and 10.5 $mgP\ L^{-1}$, respectively. Xin et al. [121] reported that the growth of *Scenedesmus* sp. was in agreement with the Monod model under different N and P concentrations (2.5 – 25 $mgN\ L^{-1}$ with 1.3 $mgP\ L^{-1}$; 0.1 – 2.0 $mgP\ L^{-1}$ with 10 $mgN\ L^{-1}$). Goldman et al. [35] reported that the Monod model described well the growth of the *Scenedesmus quadricauda* and *Selenastrum capricornulum* with consideration of aqueous CO_2 concentration (Total Inorganic Carbon concentration (TIC) = 0 – 13.1 $mg\ L^{-1}$). Similarly, Hsueh et al. [50] were able to explain the rate of growth of *Thermosynechococcus* sp. and *Nannochloropsis oculata* under different total inorganic carbon concentrations (4.7 – 94.3 mM) using the Monod model.

The Monod model is suitable to describe growth under low and moderate nutrient concentrations, but this model is limited in describing microalgae growth inhibition due to high nutrient concentrations. In particular, the inhibition for microalgae growth occurs when concentrations of NH_3 are above 300 $mg\ L^{-1}$ in culture solution [82,109]. To overcome such a limitation, a modification of the Monod model that is based on the Haldane inhibition model [44] for enzymes has been introduced. In the context of microbial growth, it is referred to as the Andrews model [5] (Eq. 2, Table 1), which includes a term of $\frac{S^2}{K_i}$ in the denominator to describe the inhibitory effect of the nutrient on the growth rate at high concentrations. Kurano and Miyachi [63] and Wijanarko et al. [119] applied the Andrews model to examine the effect of high CO_2 concentrations on algae growth. Kurano and Miyachi [63] reported that the Andrews model was able to explain the growth rate of *Chlorococcum littorale* under 0 – 20% CO_2 enrichment of feed air. Similarly, Wijanarko et al. [119] concluded that the Andrews model is preferable to the Monod model to describe the effect of CO_2 concentrations on the growth of *C. vulgaris* under 0 – 30% CO_2 enrichment of feed air.

The Monod model is also limited in explaining growth under nutrient absence in growth media. In reality, when a nutrient is absent from the growth medium, algae can still grow because of nutrient storage in the cell. It is reported that microalgae growth does not directly respond to the external nutrient concentrations [26,29,92]. For example, when extracellular phosphorus was absent, microalgae growth was supported by the intracellular stored phosphorus [124]. In order to describe this phenomenon, Martínez Sancho et al. [69] (Eq. 3, Table 1) has modified the Monod model by adding a maximum specific growth rate (μ_{m2}) in the absence of an external nutrient. Thus, when there is no nutrient in the culture ($S = 0$), the specific growth rate μ is not equal to zero but to μ_{m2} . Another modified model by Martínez et al. [67] incorporates all three concepts in one formulation: growth under nutrient absence, growth limited by low nutrient concentration, and growth inhibited by high nutrient concentration by adding the inhibition constant (K_i) and two maximum specific growth rates (μ_{m2} and μ_{m3}). When the nutrient is absent in the culture, the equation becomes $\mu = \mu_{m2}$. When the nutrient is present at high concentrations ($S > K_i$), the value of μ decreases with the increase of nutrient concentration because μ_{m3} is smaller than 1. Although these modifications by Martínez et al. [67] overcome the drawbacks of the Monod model as well as provide a better description of the relationship between

microalgae growth and a single nutrient, they are rarely applied due to additional parameters to be determined (K_i , μ_{m2} and μ_{m3}).

Group A-II models are based on the assumption that the growth rate depends on the internal nutrient concentration in the cell, measured by cell quota, which is the amount of intercellular nutrient per cell. These models are expressed as a function of the cell quota of the limiting nutrient. Thus, this group's models are applicable to both steady-state and unsteady-state conditions. Steady-state, in the context of these models, refers to the state where the nutrient transfer rate from the culture medium into the cell is equal to the nutrient consumption rate in the cell. This group's models may describe the growth rate more realistically because it can explain the growth in the absence of external nutrients due to accumulated nutrients in the cell. These models have been applied to describe resource competition among algae species and physiological changes of algae due to resource limitations in natural environments [39,40,59]. However, comparing with group A-I, the applicability of the group A-II models is limited, because of the technological difficulty in measuring the nutrient quota, as well as a lack of clear interpretation of the quota (i.e. the quota is changed by both limiting nutrient content in the cell and carbon per cell) [28,102]. To address these issues, the quota expression was modified as a nutrient cell quota per carbon biomass [29]. In this group, the Droop model [26] and Caperon and Meyer model [13,14] are representative. The Droop model (Eq. 5, Table 1) has been applied successfully to describe algae growth in natural ecosystems including rivers, lakes, and oceans [39,40,65,102] with N or P as a limiting nutrient [34]. For example, Grover [39] reported that the Droop model provided a better description of the relationship between P cell quota and the growth rate of *Chlorella* sp. and *Scenedesmus* sp. in continuous cultures when compared to the Monod model. Similarly, Sommer [102] compared the Monod and Droop models to describe algae growth rates in eutrophic lakes and concluded that the Droop model provides a better description of the growth behavior under the natural eutrophic condition where N was a limiting nutrient.

The Droop model, however, has an inherent problem with their mathematical formula; when the growth rate (μ) is equal to the μ'_{max} , quota (Q) would approach an infinite value that is impossible in reality. To address this, Caperon and Meyer [13,14] suggested a simple combination of the droop function ($1 - Q_{min} / Q$) and Michaelis-Menten equation (Eq. 6, Table 1), which introduces a curve-fitting constant (K_C) that is akin to a half saturation constant of the Monod model. This model better describes the growth than the Droop model, but requires the determination of an additional parameter (K_C) that increases the difficulty of applying the model [126]. Two other models (Eqs. 7 and 8) have been proposed as a modification to the Droop model [28]. Eq. (7) was introduced by normalizing Eq. (6) using a factor of $Q_{max} - Q_{min}$ and reported as a good representation of the relationship between nutrients (N , P) and growth rate [30]. For N , it was observed that the growth curve becomes a straight line when K_Q is greater than 5. Under this condition, Eq. (7) was simplified to the form of the Eq. (8).

3. Growth kinetic models considering a light factor

For photoautotrophic microalgae under nutrient saturation conditions, light is a critical factor for photosynthetic activity related to energy metabolism, because insufficient light limits microalgae growth [45,100]. Microalgae require a specific light level in order to reach the maximum growth rate, referred to as a saturated light level. If light intensity is far above the saturation level, the growth will be inhibited by light (called photoinhibition). On the other hand, if light intensity is below the saturation level, the growth will be limited by light (called light-limitation). For example, in outdoor mass culture systems (cultivation systems with high concentrations of microalgae), microalgae growth is limited due to light scattering by a thick top layer where high areal productivity of microalgae occurs [127]. Therefore, the

growth kinetic models considering the light's effect are critical for the design of both photobioreactors and outdoor ponds to optimize the performance. The growth kinetic models considering the single factor of the light intensity are summarized in Table 2, and these models are characterized into three groups.

Group B-I models consider light-limitation conditions and assume algae exist as individual cells. The models in this group have simple structures with two or three parameters so that they are easy to implement which is in agreement with the statement from Béchet et al. [9]. In particular, they have often been applied in lab-scale studies. In this group, the Tamiya model is a well-known theoretical model as well as the most widely applied model, which is analogous to a Monod-type expression in describing the effect of light on microalgae growth [110]. In the model, the growth rate is related to the incident light intensity with two parameters μ_{\max} (maximum specific growth rate) and K_I (saturation constant with respect to the light intensity). When the incident light intensity (I) is lower than K_I , the growth is limited by light according to first order kinetics. When I is far above K_I , the growth is independent of light and μ approaches to μ_{\max} . Chae et al. [15] reported that the Tamiya model was able to describe the growth of *Euglena gracilis* under laboratory conditions using fluorescent lamps (about 0–550 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) with kinetic parameters of μ_{\max} as 0.06 h^{-1} and K_I as 178 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. Similarly, under continuous illumination of fluorescent light, Huang and Chen [51] reported that the growth of *Spirulina platensis* followed the Tamiya model with the $K_I = 0.2 \text{ klx}$ (about 124 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) and $\mu_{\max} = 2.0 \text{ day}^{-1}$. Using the Tamiya model, Sasi et al. [100] was able to accurately explain the growth rate of *C. vulgaris* in the circulating loop photobioreactor under different incident light intensities (0–71.8 mW L^{-1}).

In addition to the theoretical model, several empirical models have been developed by van Oorschot [116], Bannister [8], and Chalker [16]. van Oorschot [116] used a Poisson function ($1 - e^{-I/K_I}$) (Eq. 10, Table 2) describing light-limitation. The Poisson function was also applied in the Webb model [118], a commonly used model for predicting photosynthetic rates in literature. Bannister [8] adopted the same structure of the Tamiya model with incorporation of a shape parameter (m) depending on the algae species. Jassby and Platt [53] tested eight kinetic models to describe the population of marine phytoplankton and reported that a hyperbolic tangent model was the best fit to their data. Since a hyperbolic tangent function is the most popular mathematical form to explain the photosynthetic activity as a function of light intensity [16], Kurano and Miyachi [63] used this formula (Eq. 12, Table 2) to explain the relationship between the algae growth rate and incident light intensity assuming that photosynthetic activity is the only limiting mechanism of microalgae growth. To determine the best expression of microalgae growth rate, Kurano and Miyachi [63] compared several expressions including the Poisson, hyperbolic tangent, and Tamiya models, and concluded that the hyperbolic tangent function was the best mathematical expression for *C. littorale* growth kinetics under the incident light intensity ranging from 2.3 to 1060 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. On the other hand, Martínez et al. [68] who compared the Tamiya and Poisson models concluded that the Poisson model provided a better fit to the experimental data of *Chorella pyrenoidosa* under the incident light intensity of 400–2000 lx; however, the differences in the goodness of fit between two models were very small. The differences of the experimental conditions such as illumination range and species make it difficult to compare different studies and render consistent conclusions.

The models in group B-I appear to be preferable for low and moderate algae concentrations under laboratory conditions, assuming that each individual cell equally receives incident light intensity, i.e., there is minimal self-shading by the microalgae cells. In reality, light attenuation is commonly observed in microalgae cultivation systems which typically have high algae concentrations for biofuel feedstock production. To account for light attenuation, an average light intensity or absorbed light intensity has been adopted, as listed in group B-II. The average light intensity (or absorbed light intensity) is determined by

the light path, culture density, and incident light intensity, which represents the average light absorption of algae cells in the system [1]. Béchet et al. [9], however, pointed out that the average light intensity might not be the appropriate parameter to represent light intensity because it does not account for heterogeneity of light intensity received by individual cells in the system and its effect on the overall algae growth. Grima et al. [36] modified the Tamiya model with the average light intensity and introduced an exponent (n) in the formula (Eq. 13, Table 2), which is similar to Bannister's shape parameter. This model was often applied in the optimization of the photobioreactors for both indoor and outdoor culture [22,94]. On the other hand, the Ogbonna model [79] is akin to a linear formula, and this model includes a cell concentration (X) and reactor volume (V) to account for the impact of cell concentrations on the light attenuation. In addition, this model uses the non-illuminated volume fraction ($1 - V_f$) to incorporate the effect of dark zones on growth.

In order to reduce the energy cost from artificial illumination, outdoor mass culture systems have been adopted. In outdoor culture systems, however, microalgae can experience photoinhibition during the mid-day peak light period. Group B-III consists of models that consider both light-limitation and photoinhibition. In this group, the models developed by Aiba [2], Lee et al. [64], Steele [104], Talbot et al. [108], and Bernard and Rémond [11] have a relatively less complex formula with two or three parameters. In particular, the Steele model (Eq. 15) is widely used and is able to describe the effects of light-limitation using I / I_{opt} and photoinhibition using an exponential expression ($\exp(1 - I / I_{\text{opt}})$) [80,104,105]. Platt et al. [89] also used the exponential expression by expanding the Webb model to include the effects of photoinhibition at high irradiances. This model ($P = P_{\max}[1 - e(-\alpha I/P_{\max})] \cdot e(-\beta I/P_{\max})$) is frequently used to predict photosynthesis rates, when photoinhibition is present. The structure of the Aiba, Lee, Talbot, and Bernard and Rémond models is similar to the Andrews model's structure, which incorporated an inhibition term (expressed as a function of light intensity²) in the denominator. Different light intensities were used in these models: incident light intensity (I) in the Aiba model (Eq. 16), average light intensity (I_{av}) in the Lee model (Eq. 17), normalized incident light intensity (I / I_{opt}) in the Talbot model (Eq. 18), and both I and I / I_{opt} in the Bernard and Rémond model (Eq. 19).

Several models with more complex formulas have also been proposed. Rubio et al. [96] introduced a mechanistic model to account for photadaptation, photoinhibition and the flashing light effect. This model assumes that photosynthesis occurs in the photosynthetic unit (PSU, a minimum unit leading to the generation of NADPH and ATP), and PSUs are based on a metabolic control of energy consumption through an enzyme-mediated process such as Michaelis–Menten-type kinetics. In addition, this model uses a square-root dependence on irradiance to explain photoinhibition. Among other complex models, the modified Grima model [37] and Muller-Feuga model [75] are commonly applied to estimate the growth rate of algae. Grima et al. [37] and García-Malea et al. [32] improved the Grima model (Eq. 13, Table 2) to account for photoinhibition on the microalgae growth by modifying the parameters of microalgal affinity for light (I_K) and n as a function of incident light intensity (I). These models are able to describe the effect of photoinhibition, light-limitation, and light attenuation. On the other hand, the Muller-Feuga model (Eq. 22, Table 2) introduced three parameters, including the minimum light intensity for survival (I_e), optimum light intensity to achieve the maximum growth rate (I_{opt}), and average light intensity (I_{av}). This model described the effect of light-limitation using $(I_{\text{av}} / I_{\text{opt}} - I_e / I_{\text{opt}})$ in the nominator and the effect of photoinhibition using $(I_{\text{av}} / I_{\text{opt}} - I_e / I_{\text{opt}})^2$ in the denominator. Martínez et al. [66] compared the model's prediction of García-Malea et al. [32] (Eq. 21, Table 2) and Muller-Feuga [75] for the growth of *Synechocystis* sp. They concluded that the Muller-Feuga model was able to give a closer estimation than the García-Malea model because the García-Malea model could not predict the diminution in growth rate of *Synechocystis* sp. at high irradiances.

Table 2
Microalgal growth kinetic models for a function of light intensity.

Model	Source	Formula		Applications	Parameters values
Group B-I: Model considering light-limitation	Tamiya et al. [110]	$\mu = \mu_{\max} \frac{I}{K_I + I}$	(9)	0–1000 lx ^[51] 0–550 μmol photon m ^{−2} s ^{−1} ^[15] 0–71.8 mW m ^{−2} ^[100] 0–65 W m ^{−2} ^[20] 0–2000 lx ^[68] 0–1060 μmol photon m ^{−2} s ^{−1} ^[63]	<i>Spirulina platensis</i> $\mu_{\max} = 2.0 \text{ d}^{-1}$ ^[51] $K_I = 9.2 \text{ klx}$ ^[15] <i>Euglena gracilis</i> $\mu_{\max} = 0.06 \text{ h}^{-1}$ ^[15] $K_I = 178.7 \text{ μmol photon m}^{-2} \text{ s}^{-1}$ ^[15] <i>Chlorella vulgaris</i> $\mu_{\max} = 0.040 \text{ h}^{-1}$ ^[100] $K_I = 2.8 \text{ mW L}^{-1}$ ^[100] <i>Chlorella pyrenoidosa</i> $\mu_{\max} = 0.116 \text{ h}^{-1}$ ^[68] $K_I = 1011 \text{ lx}$ ^[68] <i>Chlorococcum littorale</i> $\mu_{\max} = 0.134 \text{ h}^{-1}$ ^[63] $K_I = 95.8 \text{ μmol photon m}^{-2} \text{ s}^{-1}$ ^[63]
				0–2000 lx ^[68] 0–1060 μmol photon m ^{−2} s ^{−1} ^[63]	<i>Chlorella pyrenoidosa</i> $\mu_{\max} = 0.076 \text{ h}^{-1}$ ^[68] $K_I = 708 \text{ lx}$ ^[68] <i>Chlorococcum littorale</i> $\mu_{\max} = 0.116 \text{ h}^{-1}$ ^[63] $K_I = 114 \text{ μmol photon m}^{-2} \text{ s}^{-1}$ ^[63]
					<i>Chlorella pyrenoidosa</i> (at 25 °C) $\mu_{\max} = 2.48 \text{ d}^{-1}$ $K_I = 5.7 \text{ μE m}^{-2} \text{ d}^{-1}$ $m = 3$
					<i>Chlorococcum littorale</i> $\mu_{\max} = 0.115 \text{ h}^{-1}$ ^[63] $K_I = 150 \text{ μmol photon m}^{-2} \text{ s}^{-1}$ ^[63]
Group B-II: Model considering light-limitation associated with light attenuation by cells	Grima et al. [36]	$\mu = \mu_{\max} \frac{I_{av}^n}{I_k^n + I_{av}^n}$ $I_{av} = \frac{I}{K_a p X} [1 - e(-K_a p X)]$	(13)	0–84 μE m ^{−2} s ^{−1} ^[22] 0–1620 μE m ^{−2} s ^{−1} ^[94]	<i>S. platensis</i> $\mu_{\max} = 2.06 \times 10^{-5} \text{ s}^{-1}$ ^[22] $I_k = 160 \text{ μE m}^{-2} \text{ s}^{-1}$ ^[22] $n = 1.49$ ^[22] <i>Phaeodactylum tricornutum</i> $\mu_{\max} = 0.075 \text{ h}^{-1}$ ^[94] $I_k = 120 \text{ μE m}^{-2} \text{ s}^{-1}$ ^[94] $n = 2.02$ ^[94]
					<i>Chlorella pyrenoidosa</i> $K = 0.8 \text{ kg mol}^{-1}$ $X = 0.01905 \text{ kg m}^{-3}$ $V = 0.00075 \text{ m}^3$ $I_{\max} = 0.13 \text{ mol kg}^{-1} \text{ d}^{-1}$
					<i>Chlorococcum littorale</i> $\mu_{\max} = 0.134 \text{ h}^{-1}$ ^[63] $I_{opt} = 505 \text{ μmol photon m}^{-2} \text{ s}^{-1}$ ^[63]
					<i>Cryptomonas 976/67</i> $\mu_{\max} = 1.37 \text{ d}^{-1}$ at 26 °C ^[80] <i>Cryptomonas 976/62</i> $\mu_{\max} = 0.72 \text{ d}^{-1}$ at 21 °C ^[80] $I_{opt} < 100 \text{ μmol photon m}^{-2} \text{ s}^{-1}$ ^[80]
Group B-III: Model considering both light-limitation and photoinhibition	Aiba [2]	$\mu = \mu_{\max} \frac{I}{K_I + I + \frac{I^2}{K_{IL}}}$	(16)	0–83 W m ^{−2} ^[64]	<i>Spirulina platensis</i> $\mu_{\max} = 5.4849 \text{ h}^{-1}$ ^[64] $K_I = 959.2 \text{ W m}^{-2}$ ^[64] $K_{IL} = 0.5817 \text{ m}^2 \text{ W}^{-1}$ ^[64]
					<i>Spirulina platensis</i> $K_I = 177.9 \text{ m}^2 \text{ W}^{-1} \text{ h}^{-1}$ ^[64] $K_{IL} = 0.1083 \text{ m}^2 \text{ W}^{-1} \text{ h}^{-1}$ ^[64]
					<i>Porphyridium cruentum</i> (at 30 °C) $\mu_{\max} = 1.06 \text{ d}^{-1}$ ^[25] $I_{opt} = 350 \text{ μmol photon m}^{-2} \text{ s}^{-1}$ ^[25] $\beta = 2.06$ ^[25]
					<i>Chlorella pyrenoidosa</i> $\mu_{\max} = 2.0 \text{ d}^{-1}$ $I_{opt} = 275 \text{ μE m}^{-2} \text{ s}^{-1}$ $\alpha = 0.05$
	Grima et al. [37]	$\mu = \mu_{\max} \frac{I_{av}^{\beta + \frac{\alpha}{K_{IL}}}}{[\mu_{K+} (\frac{I_{av}^{\beta + \frac{\alpha}{K_{IL}}}}{I_{opt}^{\beta + \frac{\alpha}{K_{IL}}}} + I_{av}^{\beta + \frac{\alpha}{K_{IL}}})]}$	(20)	0–1.2 × 10 ⁸ μE m ^{−2} s ^{−1} ^[1] 0–3426 μE m ^{−2} s ^{−1} ^[38] 0–2500 μE m ^{−2} s ^{−1} ^[93]	<i>Phaeodactylum tricornutum</i> $\mu_{\max} = 0.063 \text{ h}^{-1}$ ^[1] $I_k = 94.3 \text{ μE m}^{-2} \text{ s}^{-1}$ ^[1]

Table 2 (continued)

Model	Source	Formula	Applications	Parameters values
				$K_{i,L} = 768.4 \mu\text{E m}^{-2} \text{s}^{-1}$ [1] $a = 3.04$ [1] $b = 1.209$ [1] $c = 514.6$ [1]
				<i>Phaeodactylum tricornutum</i> $\mu_{\text{max}} = 0.063 \text{ h}^{-1}$ [38] $I_k = 94.3 \mu\text{E m}^{-2} \text{s}^{-1}$ [38] $K_{i,L} = 3426 \mu\text{E m}^{-2} \text{s}^{-1}$ [38] $a = 3.04$ [38] $b = 1.209$ [38] $c = 514.6$ [38]
				<i>Phaeodactylum tricornutum</i> $\mu_{\text{max}} = 0.00385 \text{ h}^{-1}$ [93] $I_k = 94.3 \mu\text{E m}^{-2} \text{s}^{-1}$ [93] $K_{i,L} = 2000 \mu\text{E m}^{-2} \text{s}^{-1}$ [93] $a = 3.04$ [93] $b = 1.209$ [93] $c = 514.5$ [93]
García-Malea et al. [32]		$\mu = \mu_{\text{max}} \frac{\frac{I}{I_{\text{opt}}}}{(c+df) \left(\frac{I}{I_{\text{opt}}} \right) + \frac{I}{I_{\text{opt}}}}$	(21) 400–2400 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ [66]	<i>Haematococcus pluvialis</i> $\mu_{\text{max}} = 0.11 \text{ h}^{-1}$ $a = 2.32$ $b = -0.00008 \mu\text{E m}^{-2} \text{s}^{-1}$ $c = 98.7 \mu\text{E m}^{-2} \text{s}^{-1}$ $d = 0.034$
Muller-Feuga [76]		$\mu = 2 \mu_{\text{max}} \frac{(1 - \frac{I}{I_{\text{opt}}}) (\frac{I}{I_{\text{opt}}} - \frac{I_c}{I_{\text{opt}}})}{(1 - \frac{I}{I_{\text{opt}}})^2 + (\frac{I}{I_{\text{opt}}} - \frac{I_c}{I_{\text{opt}}})^2}$	(22) 400–2400 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ [66] 0–236 $\mu\text{E m}^{-2} \text{s}^{-1}$ [75]	<i>Porphyridium cruentum</i> $\mu_{\text{max}} = 1.415 \text{ d}^{-1}$ [75] $I_{\text{opt}} = 385 \mu\text{E m}^{-2} \text{s}^{-1}$ [75] $I_c = 3.5 \mu\text{E m}^{-2} \text{s}^{-1}$ [75]
Rubio et al. [96]		<p>$\mu = \mu_{\text{max}} \cdot \frac{I}{\alpha'} (1 - X_e^*)$</p> <p>Light limitation:</p> $\mu = \mu_{\text{max}} \cdot \frac{I}{\alpha'} [(1 - k - \frac{\alpha'}{I}) - \sqrt{(1 - k - \frac{\alpha'}{I})^2 + 4k}]$ <p>Photoinhibition:</p> $\mu = \mu_{\text{max}} \cdot \frac{I}{\alpha'} (1 - X_e^*) \cdot (\frac{1}{1 + \beta \sqrt{I}})$	(23) 0–800 $\mu\text{E m}^{-2} \text{s}^{-1}$	<i>Chorella</i> sp. (light limitation) $\mu_{\text{max}} = 0.12 \text{ h}^{-1}$ $\alpha' = 91 \mu\text{E m}^{-2} \text{s}^{-1}$ $k = 0.24$

4. Growth kinetic models considering multiple factors

Limitation of both multi-nutrients and light on microalgae growth, called co-limitation, was commonly observed in natural environments [6,60,85]. The co-limitation of N, P, and organic C for heterotrophic bacteria has been discussed by Thingstad [113]. Thereafter, the growth kinetics of microorganisms including the growth controlled by multiple nutrients have been reviewed by Kovárová-Kovar and Egli [60]. The concept of co-limitation for microalgae growth was further explained by Arrigo [6] and Saito et al. [99]. To provide accurate estimations of microalgae growth as well as a better understanding of the growth, this concept has been applied in the development of kinetic models. The basic assumption behind the co-limitation is that both multiple nutrient resources and light, and their interactions control overall microalgae growth [112]. The models based on co-limitation can be organized as two distinctive types of models, threshold and multiplicative models (shown in Table 3).

The threshold model, also called the minimum law, is based on the hypothesis that the overall growth rate is affected by the most limited resource among all resources required for cell growth. Thus, the final mathematical expression of the model is similar to the growth models considering a single factor. However, the theory behind the threshold model is based on the concept of co-limitation because all possible resources were considered to construct the kinetic models for the growth. The framework of the threshold models is:

$$\mu = \mu_{\text{max}, \min}(f(x_1), f(x_2), f(x_3) \cdots f(x_i))$$

where $\mu_{\text{max}, \min}$ is a maximum growth rate with respect to the most limited resource and $f(x_i)$ is a function of multiple limited resources such as N, P, CO₂ and light intensity.

The threshold models presented in Table 3 are most commonly used to describe effects of two resources on the growth, especially the co-

limitation of N and P [12,41,59]. In the threshold models, the Droop formulas were frequently adopted as rate expressions for the limited resources. In Table 3, Eqs. 24, 25, 27, and 28 used the Droop expression to describe the effect of N on the growth, while Eqs. 24, 25, and 28 adopted it for a rate expression of P. In the threshold models, the Monod equations were also applied as rate expression for CO₂ and P (Eq. 26).

Unlike the threshold model, the multiplicative model assumes that all resources equally contribute to microalgae growth. In other words, all major resources can simultaneously affect the overall growth rate:

$$\mu = \mu_{\text{max}} f(x_1) \cdot f(x_2) \cdot f(x_3) \cdots f(x_i)$$

where μ_{max} is the overall maximum specific growth rate. Goldman [33] introduced the multiplicative model for microalgae growth considering multiple environmental factors such as light intensity, temperature, nutrients, and pH. This type of models was frequently applied to describe co-limitation of N, CO₂, and light on the growth. In the multiplicative models, the Monod formula is the most common rate expressions for individual growth factors. It was used as the rate expression for N in Eqs. 29, 31, 37, 41, and 42 and for P in Eqs. 31, 34, and 36 in Table 3. The Droop formula was less used in the multiplicative models, only in Eq. 32 for N and Eq. 42 for P. Rate expressions for CO₂ were often expressed by the Monod (Eqs. 33, 34, 35, 37, and 38) or Andrews equations (Eqs. 39, 40 and 41), while the Tamiya model is often employed as the rate expressions for light intensity (Eqs. 30, 31, 33, 38, and 39). In addition, several studies include the temperature as another major factor that is expressed by the Arrhenius equation (Eqs. 31, 38, 40, and 41) [32,44,58,87]. Spijkerman et al. [102] attempted to compare four kinetic models based on threshold and multiplicative theory with the Monod formula to describe the effect of P and CO₂ on the growth (Eqs. 26, 34, 35, and 36, Table 3), and revealed that the multiplicative model gave the best fit to describe the P and CO₂ co-limitation (Eq. 34). Most of the rate expressions

Table 3
Microalgal growth kinetic models for a function of multiple factors.

Model structure	Source	Formula	Factor consideration	Parameters values
Threshold model	Klausmeier et al. [59]	$\mu = \mu'_{\max, \min} \left(1 - \frac{Q_{\min, N}}{Q_N}, 1 - \frac{Q_{\min, P}}{Q_P} \right)$	(24) N, P	<i>Scenedesmus</i> sp. $\mu'_{\max, \min} = 1.35 \text{ d}^{-1}$ $Q_{\min, N} = 45.4 \times 10^{-9} \mu\text{mol cell}^{-1}$ $Q_{\min, P} = 1.64 \times 10^{-9} \mu\text{mol cell}^{-1}$
	Bougaran et al. [12]	$\mu = \mu'_{\max, \min} \left(\frac{1 - \frac{Q_{\min, N}}{Q_N}}{1 - \frac{Q_{\min, N}}{Q_{\max, N}}}, \frac{1 - \frac{Q_{\min, P}}{Q_P}}{1 - \frac{Q_{\min, P}}{Q_{\max, P}}} \right)$	(25) N, P	<i>Isochrysis affinis galbana</i> $\mu'_{\max, \min} = 1.5 \text{ d}^{-1}$ $Q_{\min, N} = 6.5 \times 10^{-2} \text{ molN molC}^{-1}$ $Q_{\max, N} = 0.14 \text{ molN molC}^{-1}$ $Q_{\min, P} = 0.9 \times 10^{-3} \text{ molP molC}^{-1}$ $Q_{\max, P} = 0.006 \text{ molP molC}^{-1}$
	Spijkerman et al. [103]	$\mu = \mu_{\max, \min} \left(\frac{S_P}{K_{S,P} + S_P}, \frac{S_{CO_2}}{K_{S,CO_2} + S_{CO_2}} \right)$	(26) CO ₂ , P	<i>Selenastrum minutum</i> $\mu'_{\max, \min} = 1.58 \text{ d}^{-1}$ $Q_{\min, N} = 6 \times 10^{-2} \text{ molN molC}^{-1}$ $Q_{\max, N} = 0.21 \text{ molN molC}^{-1}$ $Q_{\min, P} = 1.8 \times 10^{-3} \text{ molP molC}^{-1}$ $Q_{\max, P} = 0.015 \text{ molP molC}^{-1}$
	Packer et al. [84]	$\mu = \mu'_{\max, \min} \left(1 - \frac{Q_{\min, N}}{Q_N}, \text{Pho}/x \right)$ $\text{Pho} = \text{Pho}_{\max} (1 - e^{-a' I_d / \text{Pho}_{\max}})$	(27) N, light intensity	<i>Pseudochlorococcum</i> sp. $\mu'_{\max, \min} = 3.26 \text{ d}^{-1}$ $Q_{\min, N} = 0.0278 \text{ gN g}^{-1} \text{ dw}$ $Q_{\min, P} = 1.8 \times 10^{-3} \text{ molP molC}^{-1}$ $a' = 4.82 \text{ m}^2 \text{ g}^{-1} \text{ chl}$ $\phi = 9.84 \times 10^{-2} \text{ molC mol}^{-1} \text{ photon}$
Multiplicative models	Guest et al. [41]	$\mu = \mu'_{\max, \min} \left[1 - \left(\frac{Q_{N, \min}}{Q_N} \right)^4, 1 - \left(\frac{Q_{P, \min}}{Q_P} \right)^4 \right] \cdot f(I_{av})$	(28) N, P, light intensity	<i>Chlamydomonas reinhardtii</i> $\mu'_{\max, \min} = 0.82 \text{ h}^{-1}$ $Q_{\min, N} = \text{NA}$ $Q_{\min, P} = \text{NA}$
	Kunikane and Kaneko [62]	$\mu = [\mu_{c, \max} \cdot \{f(\frac{C_c}{C_n})\}^a - (\frac{1}{y_c} - 1) \cdot \mu_{f, \max} \cdot \{f(\frac{C_c}{C_n})\}^b \cdot (\frac{S_N}{K_{S,N} + S_N}) - k_d] \cdot (\frac{C_n}{C_{n, \max}})$	(29) N, P	<i>Scenedesmus dimorphus</i> $\mu_{c, \max} = 7.0 \text{ mg mg}^{-1} \text{ d}^{-1}$ $\mu_{f, \max} = 5.0 \text{ mg mg}^{-1} \text{ d}^{-1}$ $k_d = 0.5 \text{ mg mg}^{-1} \text{ d}^{-1}$ $C_{n, \max} = 12\%$ $K_{S,N} = 18 \mu\text{g N L}^{-1}$ as NO ₃ -N $a = 0.18$ $b = 0.35$ $y_c = 0.8 \text{ mg mg}^{-1}$
	Zhang et al. [129]	$\mu = \mu_{\max} \left(\frac{S_{OC}}{K_{S,OC} + S_{OC} + \frac{S_{OC}^2}{K_{I,OC}}} \right) \left(\frac{I}{K_I + I} \right) \left(1 - \frac{C_x}{C_{x, \max}} \right) \left(1 - \frac{C_{pro}}{C_{pro, \max}} \right)$	(30) Acetate, cell concentration, Cell product, light intensity	<i>Haematococcus pluvialis</i> $\mu_{\max} = 0.5258 \text{ d}^{-1}$ $C_{x, \max} = 2.92 \text{ g L}^{-1}$ $C_{pro, \max} = 55.6 \text{ mg L}^{-1}$ $K_{S,OC} = 0.0211 \text{ g L}^{-1}$ $K_{I,OC} = 56.6813 \text{ g L}^{-1}$ $K_I = 53.26 \mu\text{mol m}^{-2} \text{ s}^{-1}$
	Haario et al. [43]	$\mu = \mu_{\max} \cdot \theta^{T - T_{\text{ref}}} \left(\frac{I}{K_I + I} \right) \left(\frac{S_P}{K_{S,P} + S_P} \right) \left(\frac{S_N}{K_{S,N} + S_N} \right)$	(31) N, P, light intensity, temperature	Wild type algae (Chrysophyceae) $\mu_{\max} = 0.0465 \text{ d}^{-1}$ $\theta = 1.137$ $T_{\text{ref}} = 20 \text{ }^{\circ}\text{C}$ $K_{S,P} = 8.27 \text{ g L}^{-1}$ $K_{S,N} = 32.9 \text{ g L}^{-1}$ (total N) $K_I = 115 \text{ W m}^{-2}$
	Bernard [10]	$\mu = \mu_{\max} \left(\frac{I_{av}}{K_I + I_{av} + \frac{I_{av}^2}{K_{I,L}}} \right) \left(1 - \frac{Q_{\min, N}}{Q_N} \right)$	(32) Light intensity, N	<i>Isochrysis galbana</i> $\mu_{\max} = 1.7 \text{ d}^{-1}$ $K_I = 1.4 \mu\text{mol m}^{-2} \text{ s}^{-1}$ $K_{I,L} = 295 \mu\text{mol m}^{-2} \text{ s}^{-1}$ $Q_{\min, N} = 0.050 \text{ gN gC}^{-1}$
	Filali et al. [27]	$\mu = \mu_{\max} \left(\frac{I_{av}}{K_I + I_{av}} \right) \left(\frac{S_{CO_2}}{K_{S,CO_2} + S_{CO_2}} \right)$	(33) CO ₂ , light intensity	<i>Chlorella vulgaris</i> $\mu_{\max} = 0.8 \text{ h}^{-1}$ $K_I = 0.14 \mu\text{E s}^{-1} 10^9 \text{ cell}^{-1}$ $K_{S,CO_2} = 1.28 \times 10^{-5} \text{ mol } 10^9 \text{ cell}^{-1}$
	Spijkerman et al. [103]	$\mu = \mu_{\max} \left(\frac{S_P}{K_{S,P} + S_P}, \frac{S_{CO_2}}{K_{S,CO_2} + S_{CO_2}} \right)$	(34) CO ₂ , P	<i>Chlamydomonas acidophila</i> $\mu_{\max} = 0.073 \text{ h}^{-1}$ $K_{S,CO_2} = 0.38 \mu\text{M}$ $K_{S,P} = 1.09 \text{ nM}$
		$\mu = \mu_{\max} \frac{S_{CO_2}}{\frac{S_P + K_{S,P}}{S_P} \frac{\mu_{\max}}{\alpha_{C, \max}} + S_{CO_2}}$	(35)	<i>Chlamydomonas acidophila</i> $\mu_{\max} = 0.059 \text{ h}^{-1}$ $K_{S,P} = 0.70 \text{ nM}$ $\alpha_{C, \max} = 0.039$
		$\mu = \mu_{\max} \frac{S_P}{\frac{S_{CO_2} + K_{S,CO_2}}{S_{CO_2}} \frac{\mu_{\max}}{\alpha_{P, \max}} + S_P}$	(36)	<i>Chlamydomonas acidophila</i> $\mu_{\max} = 0.066 \text{ h}^{-1}$ $K_{S,CO_2} = 0.77 \mu\text{M}$ $\alpha_{P, \max} = 0.075$

Table 3 (continued)

Model structure	Source	Formula	Factor consideration	Parameters values
	Yang [122]	$\mu = \mu_{\max} \left(\frac{S_{CO_2}}{K_{S,CO_2} + S_{CO_2}} \right) \left(\frac{S_N}{K_{S,N} + S_N} \right) \frac{I_{av}}{I_{opt}} \exp(1 - \frac{I_{av}}{I_{opt}})$	(37) CO ₂ , light intensity, N	Wild type algae $\mu_{\max} = 0.9991 \text{ d}^{-1}$ $K_{S,CO_2} = 0.001 \text{ mol m}^{-3}$ $K_{S,N} = 0.001 \text{ mol m}^{-3}$ as NH ₄ -N $I_{opt} = 14.63 \text{ MJ m}^{-2} \text{ d}^{-1}$
	Franz et al. [31]	$\mu = \mu_{\max} \left(\frac{I}{K_I + I} \right) \left(\frac{S_{CO_2}}{K_{S,CO_2} + S_{CO_2}} \right) \left(\frac{S_{nu}}{K_{S,nu} + S_{nu}} \right) f(T)$	(38) CO ₂ , light intensity, nutrient, temperature	<i>Chlamydomonas reinhardtii</i> $\mu_{\max} = 1.4 \text{ d}^{-1}$ $K_I = 215 \mu\text{mol m}^{-2} \text{ s}^{-1}$ $K_{S,CO_2} = 0 \text{ g L}^{-1}$ $K_{S,nu} = 0 \text{ g L}^{-1}$ $f(T) = 1$
	He et al. [48]	$\mu = \mu_{\max} \left(\frac{I_{av}}{K_I + I_{av}} \right) \left(\frac{S_{CO_2}}{K_{S,CO_2} + S_{CO_2} + \frac{S_{CO_2}^2}{K_{I,CO_2}}} \right)$	(39) CO ₂ , light intensity	<i>Chlorella</i> sp. <i>Synechocystis</i> PCC 6803 <i>Tetraselmis suecica</i> $\mu_{\max} = 0.041 \text{ d}^{-1}$ $K_I = 14 \mu\text{mol m}^{-2} \text{ s}^{-1}$ $K_{S,CO_2} = 0.00021 \text{ mol m}^{-3}$ $K_{I,CO_2} = 10 \text{ mol m}^{-3}$
	Pegallapati and Nirmalakhandan [88]	$\mu = \mu_{\max} \cdot 1.066^{T-20} \left(\frac{I_{av}}{K_I + I_{av}} \right) \left(\frac{S_{CO_2}}{K_{S,CO_2} + S_{CO_2} + \frac{S_{CO_2}^2}{K_{I,CO_2}}} \right)$	(40) CO ₂ , light intensity, temperature	<i>Nannochloropsis salina</i> <i>Scenedesmus</i> sp. $\mu_{\max} = 1.2 \text{ d}^{-1}$ $K_I = 181 \mu\text{E m}^{-2} \text{ s}^{-1}$ $m = 1.75$ $K_{S,CO_2} = 2.316 \times 10^{-6} \text{ mol L}^{-1}$ $K_{I,CO_2} = 0.0046 \text{ mol L}^{-1}$
	Ketheesan and Nirmalakhandan [57]	$\mu = \mu_{\max} \cdot 1.066^{T-20} \left(\frac{S_N}{K_{S,N} + S_N} \right) \left(\frac{S_{CO_2}}{K_{S,CO_2} + S_{CO_2} + \frac{S_{CO_2}^2}{K_{I,CO_2}}} \right) \left(\frac{I_{av}}{K_I + I_{av} + \frac{I_{av}^2}{K_{I,L}}} \right)$	(41) N, CO ₂ , light intensity, temperature	<i>Nannochloropsis salina</i> <i>Scenedesmus</i> sp. $\mu_{\max} = 2.0 \text{ d}^{-1}$ $K_I = 200 \mu\text{E m}^{-2} \text{ s}^{-1}$ $K_{I,L} = 2800 \mu\text{E m}^{-2} \text{ s}^{-1}$ $m = 1.75$ $K_{S,CO_2} = 9.0 \times 10^{-4} \text{ mol m}^{-3}$ $K_{I,CO_2} = 180 \text{ mol m}^{-3}$ $K_{S,N} = 0.02 \text{ g m}^{-3}$ as NO ₃ -N
	Wu et al. [120]	$\mu = \mu_{\max} \left(\frac{S_N}{K_{S,N} + S_N} \right) \left(1 - \frac{Q_{min,P}}{Q_P} \right) \frac{I}{I_{opt}} \exp(1 - \frac{I}{I_{opt}})$	(42) N, P, light intensity	<i>Scenedesmus</i> sp. $\mu_{\max} = 0.79 \text{ d}^{-1}$ $I_{opt} = 5227 \text{ lx}$ $K_{S,N} = 9.5 \text{ mg L}^{-1}$ (total dissolved N) $Q_{min,P} = 0.019\%$

considering multiple factors were based on either external nutrient concentrations such as the Monod model or internal nutrient concentrations such as the Droop model. However, Kunikane and Kaneko [62] developed a multiplicative model with a rate expression that combined internal P, internal N, and external N concentrations for the growth of *Scenedesmus dimorphus* (Eq. 29). It is difficult to apply this model due to its complex structure and the difficulty of parameter estimation.

5. Current challenges in microalgae growth models

Based on a review of microalgae growth kinetic models described in Sections 2–4, several challenges have been identified.

5.1. Adequately considering co-limiting factors in algae growth

As previously stated, the models considering multiple factors have emerged due to a recognition of a co-limitation of resources on microalgae growth [6,103]. Table 4 provides a summary of the factors considered in the models based on the co-limitation theory, which is arranged in chronological order. Due to different algae species and different environmental conditions considered in previous studies, these models have different mathematical forms (shown in Table 3) involving different factors (shown in Table 4). In terms of selected factors, the early models considered N, P, and light as major factors to provide better understanding of cell metabolism in the natural environments; however, CO₂ and light factors have become dominant factors for recent model development due to interest in CO₂ sequestration and microalgae photobioreactor design. There is a lack of consistency in selecting the

factors and there is no clear consensus on the mathematical framework for explaining the effect of multiple growth factors. For example, when considering N and P, De Groot [23] concluded that they follow the threshold relationship; however, the multiplicative model has still been applied to explain the effect of these two factors on the growth of microalgae [43,120].

The parameters in the models considering a single factor can be easily determined by an experimental approach. In this case, a reductionist approach is typically used, which is to control variables and reduce all sources of variability, so a single variable can be studied in a quantified manner. Although sources of variability are reduced, there is still tremendous variability. For example, it is observed that values of the Monod half saturation constant (K_S) for N are different among studies, because algal growth efficiency varies depending on the N source such as NH₄-N or NO₃-N. Therefore, it is important to understand the applicable range of variables as well as growth conditions for the models developed. On the other hand, determination of model parameters for models considering multiple factors may not be easy because it is difficult to simulate co-limitation conditions (e.g. experimental design and setup) [62,86]. Furthermore, due to the many parameters that need to be fitted with experimental data, these models often result in overfitting issues [9,47]. Overfitting is recognized as a common problem in model development. Complex models with many parameters often suffer from overfitting because they are too specific or sensitive to the dataset that are used to develop the model. Therefore, the predictive power of such models is questionable for application and there are few true predictive models that can be applied under different conditions without parameter fitting.

Table 4
Existing models using multiple factors.

Source	Species	Considered factors in the models						
		N	P	CO ₂	OC ^a	Light	Temp ^b	Others
Kunikane and Kaneko [62]	<i>Scenedesmus dimorphus</i>	✓	✓					
Zhang et al. [129]	<i>Haematococcus pluvialis</i>				✓	✓		✓
Klausmeier et al. [59]	<i>Scenedesmus</i> sp.	✓	✓					
Haario et al. [43]	Wild type algae (Chrysophyceae)	✓	✓			✓	✓	
Bougaran et al. [12]	<i>Selenastrum minutum</i>	✓	✓					
	<i>Isochrysis affinis galbana</i>							
Bernard [10]	<i>Isochrysis galbana</i>	✓				✓		
Filali et al. [27]	<i>Chlorella vulgaris</i>			✓		✓		
Packer et al. [84]	<i>Pseudochlorococcum</i> sp.	✓				✓		
Spijkerman et al. [103]	<i>Chlamydomonas acidophila</i>		✓	✓				
Yang [122]	Wild type algae	✓		✓		✓		
Franz et al. [31]	<i>Chlamydomonas reinhardtii</i>	✓		✓		✓	✓	
He et al. [48]	<i>Chlorella</i> sp.			✓		✓		
	<i>Synechocystis</i> PCC 6803							
	<i>Tetraselmis suecica</i>							
Pegallapati and Nirmalakhandan [88]	<i>Nannochloropsis salina</i>			✓		✓	✓	
	<i>Scenedesmus</i> sp.							
Guest et al. [41]	<i>Chlamydomonas reinhardtii</i>	✓	✓			✓		
Ketheesan and Nirmalakhandan [57]	<i>Nannochloropsis salina</i>	✓		✓		✓	✓	
Wu et al. [120]	<i>Scenedesmus</i> sp.	✓		✓		✓		

^a Organic carbon.

^b Temperature.

5.2. Appropriately integrating temperature and light in the growth model

Under nutrient saturation conditions, the growth of autotrophic algae depends directly on temperature and the amount of light received by the cell. Although microalgae growth is highly dependent on temperature, it is often not taken into account in microalgae growth models. However, there are a few models that consider temperature effects on microalgae growth [31,43,57,88,108]. Most of these models adopted the Arrhenius equation to describe the effect of temperature on microalgae growth as an independent factor in the models, while the Talbot model accounts for the interdependence of light and temperature on the microalgae growth rate. In the Talbot model, μ_{\max} and β are expressed as functions of temperature.

Apart from temperature effect on growth, the light is considered as another main constraint on the mass cultivation of microalgae. In terms of model development, the models commonly use incident or average light intensity as a variable, as shown in Table 5. Incident light intensities have often been applied in models developed under lab scale conditions, while models for dense cell culture systems (mass cultivation systems) typically use average light intensity in order to account for light attenuation. Although light attenuation should be considered in models for mass cultivation systems, it was observed that incident light intensity has still been used in such models [31,84,120,129].

Light intensity was commonly measured by photosynthetically active radiation (PAR) or photosynthetically usable radiation (PUR). PAR refers to radiant energy available within the wavelengths between 400 and 700 nm [46], while PUR is the fraction of radiant energy absorbed by algae [73]. PUR differs between species and environments because it relies on the pigment composition of the algae cells as well as the spectral composition of the submerged radiant energy [73,87]. Thus, PAR is generally larger than PUR [87]. PUR or PAR are often expressed by units of photon flux (e.g. $\mu\text{mol photon m}^{-2} \text{s}^{-1}$, $\mu\text{E m}^{-2} \text{s}^{-1}$). However, PAR is sometimes expressed as energy flux. Some older models have used energy flux (e.g. W m^{-2} , cal m^{-2} , kJ m^{-2}) or luminous flux (e.g. $\text{lx} = \text{lumen m}^{-2}$) because of the absence of instruments for measuring quanta. Although photon flux as a light intensity expression is most commonly used today, some recent models still use luminous flux [120]. These units are not easily converted to each other (i.e., energy or luminous flux to photon flux) because additional information, such as wavelength of light sources, is required. As a result, it is difficult to compare different

studies and reach a consensus on the most suitable model to describe the relationship between algae growth and light intensity.

Another issue of growth models considering light intensity is associated with the application of sunlight in the cultivation. Most commercial cultivation systems use sunlight as the light source due to the high cost associated with artificial light [19]. However, the light intensity of sunlight changes daily and seasonally, which creates difficulties in representing it in a kinetic model. Additionally, photoinhibition may occur during the day due to high light intensity [32,38]. Most of the models considering photoinhibition have a complex structure (see Table 2), involving many parameters that are difficult to be accurately estimated.

5.3. Incorporating diversity of the species in the growth model

In reality, microalgae cultivation systems may contain several different species. This is especially true for open systems, due to a higher chance of contamination [101]. It is important to note that most models were developed and validated with respect to a specific species, as shown in Table 4. Among them, *Scenedesmus* sp. is the most commonly used species in the growth kinetic studies. However, the predictability of these models in the cultivation system with different species is questionable. When there are various algae species in the system (called as polyculture), nutrient and light competitions may occur and impact algae growth. There is limited information on the impact of light competition in polycultures [107]. On the other hand, Stockenreiter et al. [106] reported that microalgae use light more efficiently and also produce higher algal lipid content in polyculture systems. If the cultivation system includes microalgae and heterotrophic bacteria, microalgae may compete with bacteria for nutrient uptake, but symbiotic interaction may also occur. For example, oxygen generated by microalgae can be transferred to the bacteria and CO₂ produced by the bacteria can be used by microalgae for their growth [122]. Such competition and symbiotic relationships have not been considered in the algae growth model.

6. Future research

The development of growth models has changed from considering a single limiting factor to multiple limiting factors. Although major factors affecting microalgae growth have been identified, the specific mechanism behind them remains unclear. Because of this, there are no

Table 5
The models considering light factor.

Models		Light intensity			Unit	
		Incident	Average	Photon flux	Energy flux	Lumen flux
Light as a single factor	Tamiya et al. [110]	✓		✓		
	van Oorschot [116]	✓			✓	
	Steele [103]	✓			✓	
	Bannister [8]	✓		✓		
	Chalker [16]	✓		✓		
	Aiba [2]	✓			✓	✓
	Lee et al. [64]		✓		✓	
	Talbot et al. [108]	✓		✓		
	Grima et al. [36]		✓	✓		
	Ogbonna et al. [79]		✓	✓		
	Grima et al. [37]	✓	✓	✓		
	Muller-Feuga [76]		✓	✓		
	García-Malea et al. [32]	✓	✓	✓		
	Bernard and Rémond [11]	✓		✓		
Light as one of multiple factors	Zhang et al. [129]	✓		✓		
	Haario et al. [43]	✓			✓	
	Bernard [10]		✓	✓		
	Filali et al. [27]		✓	✓		
	Packer et al. [84]	✓		✓		
	Yang [122]		✓		✓	
	Franz et al. [31]	✓		✓		
	He et al. [48]		✓	✓		
	Pegallapati and Nirmalakhandan [88]		✓	✓		
	Guest et al. [41]		✓	✓		
	Ketheesan and Nirmalakhandan [57]		✓	✓		
	Wu et al. [120]	✓				✓

guidelines for selecting the factors in the development of microalgae growth models considering multi-factors. Furthermore, the relationship between these factors and microalgae growth (e.g., threshold or multiplicative) is not well understood. Thus, the development of a detailed guideline based on a better understanding of the specific contribution of different factors to algae growth for selecting the factors, the model framework, and the appropriate expression to incorporate each factor under different conditions will contribute greatly to the field of algae growth models.

Incorporating light, in particular, is important and challenging. Future studies should focus on investigating appropriate expressions of light intensity in a kinetic model. In cases of outdoor cultivation systems, the expression should incorporate both cell density in culture solution and variations in sunlight intensity during the day (e.g. a function of cell density and a function of time) instead of a fixed value in the kinetic models. The spectrum of the light sources and the light spectrum that different algae species prefer should be considered in the kinetic model. This might be achieved through shape parameters used in some existing kinetic models [36]. Furthermore, a uniform unit of light intensity will be of benefit to the research community in order to compare different studies. Since the photon is used in photosynthesis, the unit of the photon flux would be an appropriate unit for light intensity in the algae kinetic models.

From an application perspective, models considering multiple factors face several challenges, such as complex model structures and parameter determination. The complex model structure typically involves many parameters, making the application of the model not practical since it is difficult to determine parameters from existing experimental methods [43]. From a practical perspective, commercial full-scale cultivation systems are generally not limited by factors including N, P, CO₂, and pH, because the cultivation system can be designed to control these factors easily. However, temperature and light intensity are difficult to control, especially for outdoor cultivation systems, because these two factors vary with time and location. Therefore, a robust model for commercial cultivation systems should focus on incorporating the effect of temporal variations in sunlight intensity and temperature. In the case of coupling microalgae production systems with wastewater treatment, future studies should consider how to manage

the trade-off between accuracy of the model representation and real-world usability of the model by considering inhibition factors only in wastewater. Providing a user-friendly interface and a range of parameter values could potentially improve the applicability of complex models.

Most of the developed models are based on one or two species under strictly controlled conditions. As a result, little is known about the predictability of existing models for real applications. In particular, open systems are more vulnerable to contamination by other species or strains that may contribute to competition and symbiotic relationships. In order to better represent the real systems, it is necessary to develop generalized growth models, like an ecological algae bloom model [54,49,91]. The ecological algae bloom model considers various species and involves the concept of competition and symbiosis in lakes and rivers. Therefore, the knowledge gained from the ecological model might be incorporated into microalgae kinetic models.

7. Conclusion

Microalgae growth is a complex process that is affected by various limiting resources and environmental factors. Many growth kinetic models have been developed to describe the rate of microalgae growth. In this paper, the models were classified and reviewed in three groups: a single nutrient, light factors, and multiple factors. The models considering a single nutrient or light intensity are easiest to use, and these models are often applied at lab scale. Models considering multiple factors were developed based on either threshold or multiplicative theory. These models offer a better description for microalgae growth, but have a more complex structure compared to the models considering only one limiting factor. Based on the review, this paper identified several challenges in the development of algae growth models: adequate consideration of co-limiting factors, appropriate integration of light and temperature, and incorporation of species diversity in the growth model. Although there are many models considering multiple factors, there is no guideline for selecting the factors, the model framework, and the appropriate expression in model development. In addition, the applications of the models considering multiple factors are limited due to their complex mathematical forms and the difficulty in model

parameter estimation. Therefore, future research should focus on developing a guideline for model selection based on the understanding of microalgae growth under different environmental conditions, managing the trade-off between accuracy of the model representation and real-world usability of the model by eliminating non-limiting factors. For models considering light and temperature as factors, the light intensity and temperature expressions do not consider temporal variations in sunlight intensity and culture temperature. Furthermore, they often exclude light attenuation in model formulation, even though these elements play a crucial role in outdoor mass cultivation. Thus, future research must provide a better mathematical expression of light by considering light attenuation as well as temporal variation of light intensity if natural light is used. In addition, research is needed to incorporate the effect of temporal variations in culture temperature in the model. Lastly, the existing models are based on a monoculture of microalgae that are not applicable for real open systems with diverse species. Therefore, developing a generalized growth model considering diverse species will better represent real systems.

Acknowledgements

This material is based in part upon work supported by a National Science Foundation Partnerships for International Research and Education (PIRE) grant (No. 1243510). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

References

- [1] F.G. Acien-Fernández, F. García-Camacho, J.A. Sánchez-Pérez, J.M. Fernández-Sevilla, E. Molina-Grima, Modeling of biomass productivity in tubular photobioreactors for microalgal cultures: effects of dilution rate, tube diameter and solar irradiance, *Biotechnol. Bioeng.* 58 (1998) 605–616.
- [2] S. Aiba, Growth kinetics of photosynthetic microorganisms: in microbial reactions, *Adv. Biochem. Eng.* 23 (1982) 85–156.
- [3] A. Ahmad, N. Yasin, C. Derek D, J. Lim, Microalgae as a sustainable energy source for biodiesel production: a review, *Renew. Sust. Energ. Rev.* 15 (1) (2011) 584–593.
- [4] S. Amin, Review on biofuel oil and gas production processes from microalgae, *Energy Convers. Manag.* 50 (7) (2009) 1834–1840.
- [5] J.F. Andrews, A mathematical model for the continuous culture of microorganisms utilizing inhibitory substrates, *Biotechnol. Bioeng.* 10 (6) (1968) 707–723.
- [6] K.R. Arrigo, Marine microorganisms and global nutrient cycles, *Nature* 437 (7057) (2005) 349–355.
- [7] S. Aslan, I.K. Kapdan, Batch kinetics of nitrogen and phosphorus removal from synthetic wastewater by algae, *Ecol. Eng.* 28 (1) (2006) 64–70.
- [8] T. Bannister, Quantitative description of steady state, nutrient-saturated algal growth, including adaptation, *Limnol. Oceanogr.* 24 (1) (1979) 76–96.
- [9] Q. Béchet, A. Shilton, B. Guieysse, Modeling the effects of light and temperature on algae growth: state of the art and critical assessment for productivity prediction during outdoor cultivation, *Biotechnol. Adv.* 31 (8) (2013) 1648–1663.
- [10] O. Bernard, Hurdles and challenges for modelling and control of microalgae for CO₂ mitigation and biofuel production, *J. Process Control* 21 (2011) 1378–1389.
- [11] O. Bernard, B. Rémond, Validation of a simple model accounting for light and temperature effect on microalgal growth, *Bioresour. Technol.* 123 (2012) 520–527.
- [12] G. Bougaran, O. Bernard, A. Sciandra, Modeling continuous cultures of microalgae colimited by nitrogen and phosphorus, *J. Theor. Biol.* 265 (3) (2010) 443–454.
- [13] J. Caperon, J. Meyer, Nitrogen-limited growth of marine phytoplankton—I. Changes in population characteristics with steady-state growth rate, *Deep Sea Res. Oceanogr. Abstr.* 19 (1972) 601–618.
- [14] J. Caperon, J. Meyer, Nitrogen-limited growth of marine phytoplankton—II. Uptake kinetics and their role in nutrient limited growth of phytoplankton, *Deep Sea Res. Oceanogr. Abstr.* 10 (1972) 619–632.
- [15] S. Chae, E. Hwang, H. Shin, Single cell protein production of *Euglena gracilis* and carbon dioxide fixation in an innovative photo-bioreactor, *Bioresour. Technol.* 97 (2) (2006) 322–329.
- [16] B.E. Chalker, Modeling light saturation curves for photosynthesis: an exponential function, *J. Theor. Biol.* 84 (2) (1980) 205–215.
- [17] A. Chapelle, C. Labry, M. Sourisseau, C. Lebreton, A. Youenou, M. Crassous, *Alexandrium minutum* growth controlled by phosphorus: an applied model, *J. Mar. Syst.* 83 (3) (2010) 181–191.
- [18] L. Christenson, R. Sims, Production and harvesting of microalgae for wastewater treatment, biofuels, and bioproducts, *Biotechnol. Adv.* 29 (6) (2011) 686–702.
- [19] Y. Chisti, Biodiesel from microalgae beats bioethanol, *Trends Biotechnol.* 26 (3) (2008) 126–131.
- [20] K. Chojnacka, A. Zielińska, Evaluation of growth yield of *Spirulina (arthrosira)* sp. in photoautotrophic, heterotrophic and mixotrophic cultures, *World J. Microbiol. Biotechnol.* 28 (2) (2012) 437–445.
- [21] A. Concas, M. Pisu, G. Cao, Novel simulation model of the solar collector of BIOCOIL photobioreactors for CO₂ sequestration with microalgae, *Chem. Eng. J.* 157 (2) (2010) 297–303.
- [22] A. Concas, L. Pisu, G. Cao, Mathematical modelling of *Chlorella vulgaris* growth in semi-batch photobioreactors fed with pure CO₂, *Chem. Eng. Trans.* 32 (2013) 1021–1026.
- [23] W. De Groot, Modelling the multiple nutrient limitation of algal growth, *Ecol. Model.* 18 (2) (1983) 99–119.
- [24] M.G. De Morais, J.A.V. Costa, Biofixation of carbon dioxide by *Spirulina* sp. and *Scenedesmus obliquus* cultivated in a three-stage serial tubular photobioreactor, *J. Biotechnol.* 129 (3) (2007) 439–445.
- [25] D. Dermoun, D. Chaumont, J.M. Thebault, A. Dauta, Modelling of growth of *Porphyridium cruentum* in connection with two interdependent factors: light and temperature, *Bioresour. Technol.* 42 (2) (1992) 113–117.
- [26] M. Droop, Vitamin B12 and marine ecology. IV. The kinetics of uptake, growth and inhibition in *Monochrysis lutheri*, *J. Mar. Biol. Assoc. UK* 48 (3) (1968) 689–733.
- [27] R. Filali, S. Tebbani, D. Dumur, A. Isambert, D. Pareau, F. Lopes, Growth modeling of the green microalga *Chlorella vulgaris* in an air-lift photobioreactor, *TIC* 10 (2) (2011).
- [28] K.J. Flynn, How critical is the critical n: P ratio? *J. Phycol.* 38 (5) (2002) 961–970.
- [29] K.J. Flynn, Modelling multi-nutrient interactions in phytoplankton; balancing simplicity and realism, *Prog. Oceanogr.* 56 (2) (2003) 249–279.
- [30] K.J. Flynn, The importance of the form of the quota curve and control of non-limiting nutrient transport in phytoplankton models, *J. Plankton Res.* 30 (4) (2008) 423–438.
- [31] A. Franz, F. Lehr, C. Posten, G. Schaub, Modeling microalgae cultivation productivities in different geographic locations—estimation method for idealized photobioreactors, *Biotechnol. J.* 7 (4) (2012) 546–557.
- [32] M. García-Malea, F. Acien, J. Fernández, M. Cerón, E. Molina, Continuous production of green cells of *Haematococcus pluvialis*: modeling of the irradiance effect, *Enzym. Microb. Technol.* 38 (7) (2006) 981–989.
- [33] J.C. Goldman, Outdoor algal mass cultures — II. Photosynthetic yield limitations, *Water Res.* 13 (1979) 119–136.
- [34] J.C. Goldman, J.J. McCarthy, Steady state growth and ammonium uptake of a fast-growing marine diatom, *Limnol. Oceanogr.* 23 (1978) 695–703.
- [35] J.C. Goldman, W.J. Oswald, D. Jenkins, The kinetics of inorganic carbon limited algal growth, *J. Water Pollut. Control Fed.* 46(3) (1974) 554–574.
- [36] E.M. Grima, F.G. Camacho, J. Pérez, J. Sevilla, F. Fernandez, A.C. Gomez, A mathematical model of microalgal growth in light-limited chemostat culture, *J. Chem. Technol. Biotechnol.* 61 (2) (1994) 167–173.
- [37] E.M. Grima, J.M. Sevilla, J.A. Pérez, F.G. Camacho, A study on simultaneous photolimitation and photoinhibition in dense microalgal cultures taking into account incident and averaged irradiances, *J. Biotechnol.* 45 (1) (1996) 59–69.
- [38] E.M. Grima, F. Acien Fernández, F. García Camacho, Y. Chisti, Photobioreactors: light regime, mass transfer, and scaleup, *Prog. Ind. Microbiol.* 35 (1999) 231–247.
- [39] J.P. Grover, Dynamics of competition among microalgae in variable environments: experimental tests of alternative models, *Oikos* (1991) 231–243.
- [40] J.P. Grover, Non-steady state dynamics of algal population growth: experiments with two chlorophytes, *J. Physiol.* 27 (1991) 70–79.
- [41] J.S. Guest, M.C. van Loosdrecht, S.J. Skerlos, N.G. Love, Lumped pathway metabolic model of organic carbon accumulation and mobilization by the alga *Chlamydomonas reinhardtii*, *Environ. Sci. Technol.* 47 (7) (2013) 3258–3267.
- [42] B. Guieysse, Q. Béchet, A. Shilton, Variability and uncertainty in water demand and water footprint assessments of fresh algae cultivation based on case studies from five climatic regions, *Bioresour. Technol.* 128 (2013) 317–323.
- [43] H. Haario, L. Kalachev, M. Laine, Reduced models of algae growth, *Bull. Math. Biol.* 71 (7) (2009) 1626–1648.
- [44] J.S.B. Haldane, *Enzymes*, Longmans, Green, UK/Republished by MIT Press, Cambridge, MA, 1930.
- [45] M. Hannon, J. Gimpel, M. Tran, B. Rasala, S. Mayfield, Biofuels from algae: challenges and potential, *Biofuels* 1 (5) (2010) 763–784.
- [46] L.J. Harmon, B. Matthews, S. Des Roches, J.M. Chase, J.B. Shurin, D. Schluter, Evolutionary diversification in stickleback affects ecosystem functioning, *Nature* 458 (7242) (2009) 1167–1170.
- [47] D.M. Hawkins, The problem of overfitting, *J. Chem. Inf. Comput. Sci.* 44 (2004) 1–12.
- [48] L. He, V.R. Subramanian, Y.J. Tang, Experimental analysis and model-based optimization of microalgal growth in photo-bioreactors using flue gas, *Biomass Bioenergy* 41 (2012) 131–138.
- [49] D.P. Hamilton, S.G. Schladow, Prediction of water quality in lakes and reservoirs. Part I—Model description, *Ecol. Model.* 96 (1) (1997) 91–110.
- [50] H. Hsueh, W. Li, H. Chen, H. Chu, Carbon bio-fixation by photosynthesis of *Thermosynechococcus* sp. CL-1 and *Nannochloropsis oculata*, *J. Photochem. Photobiol. B* 95 (1) (2009) 33–39.
- [51] S. Huang, C. Chen, Growth kinetics and cultivation of *Spirulina platensis*, *J. Chin. Inst. Eng.* 9 (4) (1986) 355–363.
- [52] E. Jacob-Lopes, L. Lacerda, T.T. Franco, Biomass production and carbon dioxide fixation by *Aphanethece microscopica năgeli* in a bubble column photobioreactor, *Biochem. Eng. J.* 40 (1) (2008) 27–34.
- [53] A.D. Jassby, T. Platt, Mathematical formulation of the relationship between photosynthesis and light for phytoplankton, *Limnol. Oceanogr.* 21 (4) (1976) 540–547.
- [54] S.E. Jørgensen, A eutrophication model for a lake, *Ecol. Model.* 2 (2) (1976) 147–165.

- [55] E.H. John, K.J. Flynn, Modelling phosphate transport and assimilation in microalgae; how much complexity is warranted? *Ecol. Model.* 125 (2) (2000) 145–157.
- [56] A. Juneja, R.M. Ceballos, G.S. Murthy, Effect of environmental factors and nutrient availability on the biochemical composition of algae for biofuel production: a review, *Energies* 6 (9) (2013) 4607–4638.
- [57] B. Ketheesan, N. Nirmalakhandan, Modeling microalgal growth in an airlift-driven raceway reactor, *Bioresour. Technol.* 136 (2013) 689–696.
- [58] S.K. Kim, *Handbook of Marine Microalgae: Biotechnology Advances* Retrieved from 2015 <http://www.ebilib.com>.
- [59] C.A. Klausmeier, E. Litchman, S.A. Levin, Phytoplankton growth and stoichiometry under multiple nutrient limitation, *Limnol. Oceanogr.* 49 (4) (2004) 1463–1470.
- [60] K. Kovárová-Kovar, T. Egli, Growth kinetics of suspended microbial cells: from single-substrate-controlled growth to mixed-substrate kinetics, *Microbiol. Mol. Biol. Rev.* 62 (3) (1998) 646–666.
- [61] A. Kumar, S. Ergas, X. Yuan, A. Sahu, Q. Zhang, J. Dewulf, F.X. Malcata, H. Van Langenhove, Enhanced CO₂ fixation and biofuel production via microalgae: recent developments and future directions, *Trends Biotechnol.* 28 (7) (2010) 371–380.
- [62] S. Kunikane, M. Kaneko, Growth and nutrient uptake of green alga, *Scenedesmus dimorphus*, under a wide range of nitrogen/phosphorus ratio—II. Kinetic model, *Water Res.* 18 (10) (1984) 1313–1326.
- [63] N. Kurano, S. Miyachi, Selection of microalgal growth model for describing specific growth rate–light response using extended information criterion, *J. Biosci. Bioeng.* 100 (4) (2005) 403–408.
- [64] H.Y. Lee, L.E. Erickson, S.S. Yang, Kinetics and bioenergetics of light-limited photoautotrophic growth of *Spirulina platensis*, *Biotechnol. Bioeng.* 29 (7) (1987) 832–843.
- [65] V. Lemesle, L. Mailleret, A mechanistic investigation of the algae growth “Droop” model, *Acta Biotheor.* 56 (1–2) (2008) 87–102.
- [66] L. Martínez, A. Morán, A.I. García, Effect of light on *Synechocystis* sp. and modelling of its growth rate as a response to average irradiance, *J. Appl. Phycol.* 24 (1) (2012) 125–134.
- [67] M. Martínez, J. Jimenez, F. El Yousfi, Influence of phosphorus concentration and temperature on growth and phosphorus uptake by the microalga *Scenedesmus obliquus*, *Bioresour. Technol.* 67 (3) (1999) 233–240.
- [68] M.E. Martínez, F. Camacho, J. Jimenez, J. Espinola, Influence of light intensity on the kinetic and yield parameters of *Chlorella pyrenoidosa* mixotrophic growth, *Process Biochem.* 32 (1997) 93–98.
- [69] M. Martínez Sancho, J. Jimenez Castillo, F. El Yousfi, Influence of phosphorus concentration on the growth kinetics and stoichiometry of the microalga *Scenedesmus obliquus*, *Process Biochem.* 32 (8) (1997) 657–664.
- [70] T.M. Mata, A.A. Martins, N.S. Caetano, Microalgae for biodiesel production and other applications: a review, *Renew. Sust. Energ. Rev.* 14 (1) (2010) 217–232.
- [71] E. Menger-Krug, J. Niederste-Hollenberg, T. Hillenbrand, H. Hiessl, Integration of microalgae systems at municipal wastewater treatment plants: implications for energy and emission balances, *Environ. Sci. Technol.* 46 (21) (2012) 11505–11514.
- [72] J. Monod, The growth of bacterial cultures, *Annu. Rev. Microbiol.* 3 (1) (1949) 371–394.
- [73] A. Morel, Available, usable, and stored radiant energy in relation to marine photosynthesis, *Deep-Sea Res.* 25 (8) (1978) 673–688.
- [74] M. Moya, M. Sánchez-Guardamino, A. Vilavella, E. Barbera, Growth of *Haematococcus lacustris*: a contribution to kinetic modeling, *J. Chem. Technol. Biotechnol.* 68 (3) (1997) 303–309.
- [75] A. Muller-Feuga, R. Le Guédes, J. Pruvost, Benefits and limitations of modeling for optimization of *Porphyridium cruentum* culture in annular photobioreactor, *J. Biotechnol.* 103 (2003) 153–163.
- [76] A. Muller-Feuga, Growth as a function of rationing: a model applicable to fish and microalgae, *J. Exp. Mar. Biol. Ecol.* 236 (1) (1999) 1–13.
- [77] C.C. Murphy, D.T. Allen, Energy–water nexus for mass cultivation of algae, *Environ. Sci. Technol.* 45 (2011) 5861–5868.
- [78] J.T. Novak, D.E. Brune, Inorganic carbon limited growth kinetics of some freshwater algae, *Water Res.* 19 (2) (1985) 215–225.
- [79] J.C. Ogonna, H. Yada, H. Tanaka, Kinetic study on light-limited batch cultivation of photosynthetic cells, *J. Ferment. Bioeng.* 80 (3) (1995) 259–264.
- [80] A. Ojala, Effects of temperature and irradiance on the growth of two freshwater photosynthetic cryptophytes, *J. Phycol.* 29 (3) (1993) 278–284.
- [81] E. Ono, J.L. Cuello, Selection of optimal microalgae species for CO₂ sequestration, In Second National Conference on Carbon Sequestration; 2003 May 5–8 Alexandria, VA.
- [82] J. Park, H. Jin, B. Lim, K. Park, K. Lee, Ammonia removal from anaerobic digestion effluent of livestock waste using green alga *Scenedesmus* sp., *Bioresour. Technol.* 101 (22) (2010) 8649–8657.
- [83] J.B.K. Park, R. Craggs, A.N. Shilton, Wastewater treatment high rate algal ponds for biofuel production, *Bioresour. Technol.* 102 (1) (2011) 35–42.
- [84] A. Packer, Y. Li, T. Andersen, Q. Hu, Y. Kuang, M. Sommerfeld, Growth and neutral lipid synthesis in green microalgae: a mathematical model, *Bioresour. Technol.* 102 (2011) 111–117.
- [85] H.W. Paerl, Factors Limiting Productivity of Freshwater Ecosystems. *Advances in Microbial Ecology*, Springer US, 1982 75–110.
- [86] M. Pahlow, A. Oschlies, Chain model of phytoplankton P, N and light colimitation, *Mar. Ecol. Prog. Ser.* 376 (2009) 69–83.
- [87] T.R. Parsons, M. Takahashi, B. Hargrave, “Chapter 3. Primary Formation of Particulate Materials” *Biological oceanographic processes*, Elsevier, 2013.
- [88] A.K. Pegallapati, N. Nirmalakhandan, Modeling algal growth in bubble columns under sparging with CO₂-enriched air, *Bioresour. Technol.* 124 (2012) 137–145.
- [89] T. Platt, C.L. Gallegos, W.G. Harrison, Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton, *J. Mar. Res.* 38 (1980) 687–701.
- [90] P. Popova, C. Boyadjev, About microalgae growth kinetics modeling, *Chem. Biochem. Eng. Q.* 22 (4) (2008) 491–497.
- [91] M.J. Riley, H.G. Stefan, MINLAKE: a dynamic lake water quality simulation model, *Ecol. Model.* 43 (3) (1988) 155–182.
- [92] A. Regaudie-de-Gioux, S. Sal, Á. López-Urrutia, Poor correlation between phytoplankton community growth rates and nutrient concentration in the sea, *Biogeosci. Discuss.* 11 (10) (2014) 14,797–14,818.
- [93] R.L.L. Ribeiro, A.B. Mariano, J.A. Souza, J.V.C. Vargas, Transient modeling and simulation of compact photobioreactors, *Thermal. Eng. (Brazil)* 7 (2) (2008) 66–71.
- [94] R.L.L. Ribeiro, A.B. Mariano, J.A. Souza, J.V.C. Vargas, J.C. Ordóñez, Numerical simulation of the biomass concentration of microalgae cultivated in a self-sustainable photobioreactor, *Proceedings of COBEM 2009 20th International Congress of Mechanical Engineering*, Gramado, Brazil 2009 Nov, pp. 15–20 ABCM, 2009.
- [95] A. Richmond, Q. Hu, *Handbook of Microalgal Culture: Biotechnology and Applied Phycology* (2nd Ed.) Retrieved from 2013 <http://www.onlinelibrary.wiley.com>.
- [96] F.C. Rubio, F.G. Camacho, J.M. Sevilla, Y. Chisti, E.M. Grima, A mechanistic model of photosynthesis in microalgae, *Biotechnol. Bioeng.* 81 (4) (2003) 459–473.
- [97] A. Ruiz-Marin, L.G. Mendoza-Espinosa, T. Stephenson, Growth and nutrient removal in free and immobilized green algae in batch and semi-continuous cultures treating real wastewater, *Bioresour. Technol.* 101 (1) (2010) 58–64.
- [98] B. Rusten, A.K. Sahu, Microalgae growth for nutrient recovery from sludge liquor and production of renewable bioenergy, *Water Sci. Technol.* 64 (6) (2011) 1195–1201.
- [99] M.A. Saito, T.J. Goepfert, J.T. Ritt, Some thoughts on the concept of colimitation: three definitions and the importance of bioavailability, *Limnol. Oceanogr.* 53 (1) (2008) 276–290.
- [100] D. Sasi, P. Mitra, A. Viguera, G.A. Hill, Growth kinetics and lipid production using *Chlorella vulgaris* in a circulating loop photobioreactor, *J. Chem. Technol. Biotechnol.* 86 (6) (2011) 875–880.
- [101] S.A. Scott, M.P. Davey, J.S. Dennis, I. Horst, C.J. Howe, D.J. Lea-Smith, A.G. Smith, Biodiesel from algae: challenges and prospects, *Curr. Opin. Biotechnol.* 21 (3) (2010) 277–286.
- [102] U. Sommer, A comparison of the Droop and the Monod models of nutrient limited growth applied to natural populations of phytoplankton, *Funct. Ecol.* (1991) 535–544.
- [103] E. Spijkerman, F. de Castro, U. Gaedke, Independent colimitation for carbon dioxide and inorganic phosphorus, *PLoS One* 6 (12) (2011), e28219.
- [104] J. Steele, Environmental control of photosynthesis in the sea, *Limnol. Oceanogr.* 7 (2) (1962) 137–150.
- [105] J. Steele, Notes on some theoretical problems in production ecology, *Primary Productivity in Aquatic Environments* 1966, pp. 383–398.
- [106] M. Stockenreiter, F. Haupt, A. Graber, J. Seppälä, K. Spilling, T. Tamminen, H. Stibor, Functional group richness: implications of biodiversity for light use and lipid yield in microalgae, *J. Physiol.* 49 (5) (2013) 838–847.
- [107] M. Striebel, S. Behl, S. Diehl, H. Stibor, Spectral niche complementarity and carbon dynamics in pelagic ecosystems, *Am. Nat.* 174 (1) (2009) 141–147.
- [108] P. Talbot, J.M. Thébault, A. Daut, J. De la Noüe, A comparative study and mathematical modeling of temperature, light and growth of three microalgae potentially useful for wastewater treatment, *Water Res.* 25 (4) (1991) 465–472.
- [109] N. Tam, Y. Wong, Effect of immobilized microalgal bead concentrations on wastewater nutrient removal, *Environ. Pollut.* 107 (2000) 145–151.
- [110] H. Tamiya, E. Hase, K. Shibata, A. Mituya, T. Iwamura, T. Nihei, T. Sasa, Kinetics of growth of *Chlorella*, with special reference to its dependence on quantity of available light and on temperature, *Algal culture from laboratory to pilot plant* 1953, pp. 204–234.
- [111] D. Tang, W. Han, P. Li, X. Miao, J. Zhong, CO₂ biofixation and fatty acid composition of *Scenedesmus obliquus* and *Chlorella pyrenoidosa* in response to different CO₂ levels, *Bioresour. Technol.* 102 (3) (2011) 3071–3076.
- [112] K. Terry, Nitrogen and phosphorus requirements of *Pavlova lutheri* in continuous culture, *Bot. Mar.* 23 (1980) 757–764.
- [113] T.F. Thingstad, Utilization of N, P, and organic C by heterotrophic bacteria. I. Outline of a chemostat theory with a consistent concept of “maintenance” metabolism, *Mar. Ecol. Prog. Ser.* 35 (1–2) (1987) 99–109.
- [114] T.F. Thingstad, A theoretical approach to structuring mechanisms in the pelagic food web, *Hydrobiologia* 363 (1998) 59–72.
- [115] L. Travieso, F. Benitez, E. Sanchez, R. Borja, A. Martín, M. Colmenarejo, Batch mixed culture of *Chlorella vulgaris* using settled and diluted piggery waste, *Ecol. Eng.* 28 (2) (2006) 158–165.
- [116] J.L.P. van Oorschot, Conversion of Light Energy in Algal Culture, H. Veenman, Wageningen, 1955.
- [117] D.A. Vaccari, P.F. Strom, J.E. Alleman, *Environmental Biology for Engineers and Scientists*, Wiley-Interscience, Hoboken, N.J., 2005.
- [118] W.L. Webb, M. Newton, D. Starr, Carbon dioxide exchange of *Alnus rubra*: a mathematical model, *Oecologia* 17 (1974) 281–291.
- [119] A. Wijanarko, A.Y. Sendjaya, H. Hermansyah, A.B. Witarto, M. Gozan, B.T. Sofyan, K. Asami, K. Ohtaguchi, R.W. Soemantojo, S.K. Song, Enhanced *Chlorella vulgaris* buntzenorg growth by photon flux density alteration in serial photobioreactors, *Biotechnol. Bioprocess Eng.* 13 (4) (2008) 476–482.
- [120] Y.H. Wu, X. Li, Y. Yu, H.Y. Hu, T.Y. Zhang, F.M. Li, An integrated microalgal growth model and its application to optimize the biomass production of *Scenedesmus* sp. LX1 in open pond under the nutrient level of domestic secondary effluent, *Bioresour. Technol.* 144 (2013) 445–451.
- [121] L. Xin, H. Hong-ying, G. Ke, S. Ying-xue, Effects of different nitrogen and phosphorus concentrations on the growth, nutrient uptake, and lipid accumulation of a freshwater microalga *Scenedesmus* sp., *Bioresour. Technol.* 101 (14) (2010) 5494–5500.

- [122] A. Yang, Modeling and evaluation of CO₂ supply and utilization in algal ponds, Ind. Eng. Chem. Res. 50 (19) (2011) 11,181–11,192.
- [123] B. Yao, B. Xi, C. Hu, S. Huo, J. Su, H. Liu, A model and experimental study of phosphate uptake kinetics in algae: considering surface adsorption and P-stress, J. Environ. Sci. (China) 23 (2) (2011) 189–198.
- [124] C. Yao, J. Ai, X. Cao, S. Xue, Characterization of cell growth and starch production in the marine green microalga *Tetraselmis subcordiformis* under extracellular phosphorus-deprived and sequentially phosphorus-replete conditions, Appl. Microbiol. Biotechnol. 97 (13) (2013) 6099–6110.
- [125] K. Yeh, J. Chang, Effect of light supply and carbon source on cell growth and cellular composition of a newly isolated microalga *Chlorella vulgaris* ESP-31, Eng. Life Sci. 10 (3) (2010) 201–208.
- [126] S.J. Yoo, S.K. Oh, J.M. Lee, Design of experiments and sensitivity analysis for microalgal bioreactor systems, 22nd European Symposium on Computer Aided Process Engineering; 2012 June 17–20, Elsevier, London, UK 2012, pp. 722–726 (30).
- [127] Y.S. Yun, J.M. Park, Kinetic modeling of the light-dependent photosynthetic activity of the green microalga *Chlorella vulgaris*, Biotechnol. Bioeng. 83 (3) (2003) 303–311.
- [128] X. Zeng, M.K. Danquah, X.D. Chen, Y. Lu, Microalgae bioengineering: from CO₂ fixation to biofuel production, Renew. Sust. Energ. Rev. 15 (6) (2011) 3252–3260.
- [129] X. Zhang, X. Gong, F. Chen, Kinetic models for astaxanthin production by high cell density mixotrophic culture of the microalga *Haematococcus pluvialis*, J. Ind. Microbiol. Biotechnol. 23 (1) (1999) 691–696.
- [130] B. Zhao, Y. Zhang, K. Xiong, Z. Zhang, X. Hao, T. Liu, Effect of cultivation mode on microalgal growth and CO₂ fixation, Chem. Eng. Res. Des. 89 (9) (2011) 1758–1762.