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Review article

Growth kinetic models for microalgae cultivation: A review

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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.

Contents

1. Introduction

Increasing energy demand has led to concerns about fossil fuel depletion as well as anthropogenic carbon dioxide (CO_2) emissions which have contributed to global climate change [100,111,130]. To reduce the consumption of fossil fuel and associated CO_2 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, %

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C_p	Algal phosphorus content per unit algal dry weight, %
C_{pro}	Cell product concentration, mg L^{-1}
$C_{pro,m}$	Maximum cell product concentration, mg L^{-1}
C_x	Microalgae cell concentration, mg L^{-1}
$C_{x,m}$	Maximum microalgae cell concentration, mg L^{-1}
c	Fitting constant
d	Fitting constant
$f(C_p / C_n)$	Saturation ratio of the pooled phosphorus in algal cells
$f(I_{av})$	A function of average light intensity
$f(T)$	A function of temperature
I	Incident light intensity, μmol photon m^{-2} s^{-1}, W m^{-2}, μE m^{-2} s^{-1}, MJ $m^{-2}day^{-1}$, or g cal cm^{-2} d^{-1}
I_{abs}	Total light energy absorbed in reactor, mol d^{-1}
I_{av}	Average irradiance in the culture, W m^{-2}, μmol photon m^{-2} s^{-1}, or μE m^{-2} s^{-1}
I_c	Light intensity at the center measured from one direction with light shining from both direction, W m^{-2}
I_e	Average irradiance at the energy compensation point, μE m^{-2} s^{-1} or μmol photon m^{-2} s^{-1}
I_{in}	Light intensity at the front with shining from one side, W m^{-2}
I_k	Microalgal affinity for light, μE m^{-2} s^{-1}
$I_{\max}$	Maintenance rate, mol (kg d)$^{-1}$
I_{opt}	I at $\mu = \mu_{\max}$, μmol photon m^{-2} s^{-1}, W m^{-2}, μE m^{-2} s^{-1}, MJ m^{-2} day^{-1}, or g cal cm^{-2} d^{-1}
I_{out}	Light intensity at the back with shining from one side, W m^{-2}
K	Proportionality constant which is akin in meaning to growth yield, (see Eq. (14) of Table 2), kg mol^{-1}
K_a	Attenuation constant kg m^{-3}
K_c	Curve-fitting constant, g g^{-1} Carbon, mol mol^{-1} Carbon, or mol $cell^{-1}$
K_I	Photo-saturation constant, μmol photon m^{-2} s^{-1}, E m^{-2} s^{-1}, W m^{-2}, klx, or KJ cm^{-2} h^{-1}
K_i	Inhibition constant, mg L^{-1}
$K_{i,CO2}$	Inhibition constant of CO_2, mg L^{-1}
$K_{i,L}$	Photoinhibition constant, klx, kJ cm^{-2} h^{-1}, or μE m^{-2} s^{-1}
$K_{i,OC}$	Sodium acetate inhibition constant of cell growth, mg L^{-1}
$K_{S,nu}$	Monod half-saturation constant of limiting nutrients, mg L^{-1}
K_S	Monod half-saturation constant, mg L^{-1}
$K_{S,CO2}$	Monod half-saturation constant of CO_2, mg L^{-1}
$K_{S,N}$	Monod half-saturation constant of nitrogen, mg L^{-1}
$K_{S,OC}$	Monod half-saturation constant of sodium acetate, mg L^{-1}
$K_{S,P}$	Monod half-saturation constant of phosphorus, mg L^{-1}
K_q	Dimensionless parameter to set the curve form, $K_q = Kc / (Q_{\max} - Q_{\min})$
k	Parameter
k_d	Consumption rate of photosynthesis products per unit dry weight of the functional substance, mg (mg d)$^{-1}$
m	Shape parameter
n	Exponent
p	Length of light path inside the photobioreactor, m
Pho	photosynthetic rate
$Pho_{\max}$	Light-saturated photosynthesis rate
Q	Nutrient cell quota, g g^{-1} Carbon, 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, mol nutrient mol^{-1} Carbon, or g $cell^{-1}$
$Q_{\max,N}$	Maximum N cell quota for algal existence, g g^{-1} Carbon, mol N mol^{-1} Carbon or g $cell^{-1}$
$Q_{\max,P}$	Maximum P cell quota for algal existence, g g^{-1} Carbon, mol P mol^{-1} Carbon or g $cell^{-1}$
$Q_{\min}$	Minimum nutrient cell quota for algal existence, g g^{-1} Carbon, mol nutrient mol^{-1} Carbon, or g $cell^{-1}$
$Q_{\min,N}$	Minimum N cell quota for algal existence, g g^{-1} Carbon, mol N mol^{-1} Carbon, or g $cell^{-1}$
$Q_{\min,P}$	Minimum P cell quota for algal existence, g g^{-1} Carbon, mol P mol^{-1} Carbon, or g $cell^{-1}$
Q_P	P cell quota, g g^{-1} Carbon, mol P mol^{-1} Carbon, or g $cell^{-1}$
S	Nutrient concentration, mg L^{-1}
S_{CO2}	Carbon dioxide concentration in the medium, mg L^{-1}
S_N	Nitrogen concentration in the medium, mg L^{-1}
S_{nu}	Limiting nutrient concentration, mg L^{-1}
S_{OC}	Sodium acetate concentration in the medium, mg L^{-1}
S_P	Phosphorus concentration in the medium, mg L^{-1}
T	Temperature, °C
T_{ref}	Reference temperature (20 °C)
V	Liquid volume in the reactor, m^3
V_F	Illuminated volume fraction of the reactor
X	Cell concentration, kg m^{-3}
x	Carbon subsistence quota, g Carbon g^{-1} dw
x_e^*	Steady-state fraction of functional activated PSUs under continuous illumination
y_c	Yield coefficient of the functional substance from the storage substance, mg mg^{-1}
α	Initial slope of the light response curve
α'	Parameter, E m^{-2} s^{-1}
$\alpha_{C\max}$	Maximum affinity for growth at carbon dioxide limiting condition
$\alpha_{P\max}$	Maximum affinity for growth at phosphorus limiting condition
β	Sharpness coefficient (from −1 to ∞)
β'	Slope of the light response curve beyond the onset of photoinhibition
δ	Parameter, $\mu E^{-0.5}$ m $s^{-0.5}$
Θ	Temperature coefficients for growth
ϕ	Quantum efficiency g C mol^{-1} photons
μ	Specific growth rate, day^{-1} or h^{-1}
$\mu_{c,\max}$	Maximum of synthesis rate of the storage substance per unit dry weight of the functional substance, mg (mg d)$^{-1}$
$\mu_{f,\max}$	Maximum of synthesis rate of the functional substance per unit dry weight of the functional substance, mg (mg d)$^{-1}$
$\mu_{\max}$	Maximum specific growth rate, day^{-1} or h^{-1}
$\mu_{\max,\min}$	The most limiting nutrient's maximum growth rate, day^{-1} or h^{-1}
μ_{m1}	Maximum value for μ, day^{-1}
μ_{m2}	Specific growth rate at the absence of nutrient in the culture medium, day^{-1}
μ_{m3}	Specific growth rate at high nutrient concentration in the culture medium, day^{-1}
$\mu'_{\max}$	Hypothetical maximum growth rate at infinite Q, day^{-1}
$\mu'_{\max,\min}$	Hypothetical maximum growth rate at infinite Q for the most limiting nutrient, day^{-1}
$\mu^*_{\max}$	Maximum growth rate at the maximum value of Q, day^{-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 CO_2 fixation rates, and low land use, compared to other energy crops [4,128]. They can thrive under conditions with high levels of CO_2 [81]. This attribute makes microalgae suitable for using CO_2 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 CO_2 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 CO_2 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, CO_2 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 CO_2), 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

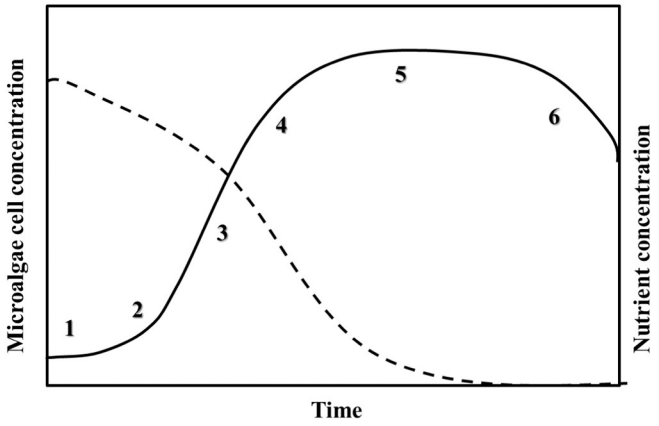

Fig. 1. Growth phases in microalgae batch culture (solid line) and nutrient concentration (dashed line); (1) lag phase; (2) exponential phase; (3) linear phase; (4) declining growth phase; (5) stationary phase; and (6) death phase [58,70,95].

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^{-1} [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: *S. quadricauda* (at 400 fc, 27 °C) $\mu_{max} = 2.29\ d^{-1}$ at pH 7.10–7.61 [35] $K_s = 0.30$ mg L^{-1} at pH 7.10–7.21 [35] $K_s = 0.36$ mg L^{-1} at pH 7.25–7.39 [35] $K_s = 0.71$ mg L^{-1} at pH 7.44–7.61 [35] *S. carpricornulum* (at 400 fc, 27 °C) $\mu_{max} = 2.45\ d^{-1}$ at pH 7.05–7.57 [35] $K_s = 0.40$ mg L^{-1} at pH 7.05–7.23 [35] $K_s = 1$ mg L^{-1} at pH 7.25–7.39 [35] $K_s = 1.2$ mg L^{-1} at pH 7.43–7.59 [35] *Chlorella* (at 600 fc, 27 °C) $\mu_{max} = 0.070\ h^{-1}$ [78] $K_s = 0.26$ mg L^{-1} [78] *Anabaena flos aquae* (at 600 fc, 27 °C) $\mu_{max} = 0.045\ h^{-1}$ [78] $K_s = 0.17$ mg L^{-1} [78] *Selenastrum capricornutum* (at 600 fc, 27 °C) $\mu_{max} = 0.057\ h^{-1}$ [78] $K_s = 0.18$ mg L^{-1} [78] *Senedesmus quadricauda* (at 600 fc, 27 °C) $\mu_{max} = 0.057\ h^{-1}$ [78] $K_s = 0.17$ mg L^{-1} [78] *Oscillitoria* (at 600 fc, 27 °C) $\mu_{max} = 0.028\ h^{-1}$ [78] $K_s = 0.43$ mg L^{-1} [78] *Microcoleus vaginatus* (at 600 fc, 27 °C) $\mu_{max} = 0.031\ h^{-1}$ [78] $K_s = 3.22$ mg L^{-1} [78] *Thermosynechococcus* sp. CL-1 (at 10,000 lx, pH 9.5, 50 °C) $\mu_{max} = 3.5\ d^{-1}$ [50] $K_s = 1.9$ mM [50] N: *Chlorella vulgaris* (at 4100 lx, pH 7.0, 20 °C) $k = \mu_{max}/Y_N = 1.5$ mg $mg^{-1}\ d^{-1}$ [7] $K_s = 31.5$ mg L^{-1} [7] *Scenedesmus* sp. (at 55–60 μmol photon $m^{-2}\ s^{-1}$, light/dark ratio = 14:10, 25 °C) $\mu_{max} = 1.78 \times 10^6$ cells·(mL d)$^{-1}$ [121] $K_s = 11.8$ mg L^{-1} [121] P: *Chlorella vulgaris* (at 4100 lx, pH 7.0, 20 °C) $k = \mu_{max}/Y_P = 0.5$ mg $mg^{-1}\ d^{-1}$ [7] $K_s = 10.5$ mg L^{-1} [7] *Scenedesmus* sp. (at 55–60 μmol photon $m^{-2}\ s^{-1}$, light/dark ratio = 14:10, 25 °C) $\mu_{max} = 1.02 \times 10^6$ cells·(mL d)$^{-1}$ [121] $K_s = 0.28$ mg L^{-1} [121]

Table 1 (*continued*)

Category	Source	Formula		Consideration	Applications	Parameters values
	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^{-1} [119] 0–0.2 pCO_2 [63] Acetate: 0–10 mg L^{-1} [74]	CO_2: *Chlorococcum littorale* (at >300 μmol photon m^{-2} s^{-1}, pH 5.5, 25 °C) $\mu_{max} = 0.12$ h^{-1} [63] $K_s = 0.00048$ pCO_2 [63] $Ki = 0.31$ pCO_2 [63] *Haematococcus lacustris* (at 23 °C) $\mu_{max} = 21.30$ h^{-1} [74] $K_s = 1320$ g dm^{-3} [74] $Ki = 3.170$ g dm^{-3} [74]
	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]	P: *Scenedesmus obliquus* (at 11.334 klx, 30 °C) $\mu_{m1} = 0.0466$ h^{-1} [67] $\mu_{m2} = 0.0256$ h^{-1} [67] $K_s = 0.20$ μM [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]	P: *Scenedesmus obliquus* (at 11.334 klx, 30 °C) $\mu_{m1} = 0.0471$ h^{-1} [67] $\mu_{m2} = 0.0350$ h^{-1} [67] $\mu_{m2} = 0.0272$ h^{-1} [67] $K_s = 0.25$ μM [67] $K_i = 0.955.72$ μM [67]
Group A-II: Model considering internal nutrient storage	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]	N: *Ceratium hirundinella* μ'_{max}: 0.26 d^{-1} [102] Q_{min}: 0.033 mol mol^{-1} [102] *Peridinium* sp. μ'_{max}: 0.31 d^{-1} [102] Q_{min}: 0.036 mol mol^{-1} [102] *Sphaerocystis schroeteri* μ'_{max}: 0.79 d^{-1} [102] Q_{min}: 0.046 mol mol^{-1} [102] P: *Scenedesmus* (at 10^{16} quanta cm^{-2} s^{-1}, pH 7.2, 12 °C) μ'_{max}: 0.755 d^{-1} [39] Q_{min}: 5.16 fmol $cell^{-1}$ [39] *Chlorella* (at 10^{16} quanta cm^{-2} s^{-1}, pH 7.2, 12 °C) μ'_{max}: 0.842 d^{-1} [39] Q_{min}: 0.352 fmol $cell^{-1}$ [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]	P: *S. quadricauda* (at 3000 lx, light: dark ratio = 12:12, 25 °C) μ^*_{max}: 0.0002 min^{-1} [123] Q_{min}: 0.25 × 10^{-8} μmol $cell^{-1}$ [123] K_c: 0.25 × 10^{-8} μmol $cell^{-1}$ [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]	P: *Alexandrium minutum* (at 200 μmol photon m^{-2} s^{-1}, light/dark ratio = 14:10, 18 °C) μ'_{max}: 0.55 d^{-1} [17] Q_{min}: 3.7 gP $cell^{-1}$ [17] Q_{max}: 32.6 gP $cell^{-1}$ [17] K_q: 4.24 [17] *Heterocapsa triquetra* (at 200 μmol photon m^{-2} s^{-1}, light/dark ratio = 14:10, 18 °C) μ'_{max}: 0.67 d^{-1} [17] Q_{min}: 5.5 gP $cell^{-1}$ [17] Q_{max}:15.6 gP $cell^{-1}$ [17] K_q: 1.34 [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 oculta* 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. 7and 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 Kq 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 μmol photon m^{-2} s^{-1}) with kinetic parameters of μ_{max} as 0.06 h^{-1} and K_I as 178 μmol photon m^{-2} 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 $K_I = 0.2$ klx (about 124 μmol photon m^{-2} s^{-1}) and $\mu_{max} = 2.0$ 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 μmol photon m^{-2} s^{-1}. 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 ($exp(1 - I / I_{opt})$) [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 intensity^2) 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 ($I_{av} / I_{opt} - I_e/I_{opt}$) in the nominator and the effect of photoinhibition using $(I_{av} / I_{opt} - I_e / I_{opt})^2$ 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]	*Spirulina platensis* $\mu_{\max} = 2.0\ d^{-1}$ [51] $K_I = 9.2$ klx [15] *Euglena gracilis* $\mu_{\max} = 0.06\ h^{-1}$ [15] $K_I = 178.7$ μmol photon m^{-2} s^{-1} [15] *Chlorella vulgaris* $\mu_{\max} = 0.040\ h^{-1}$ [100] $K_I = 2.8$ mW L^{-1} [100] *Chlorella pyrenoidosa* $\mu_{\max} = 0.116\ h^{-1}$ [68] $K_I = 1011$ lx [68] *Chlorococcum littorale* $\mu_{\max} = 0.134\ h^{-1}$ [63] $K_I = 95.8$ μmol photon m^{-2} s^{-1} [63]
	van Oorschot [116]	$\mu = \mu_{\max}(1-e^{-I/K_I})$	(10)	0–2000 lx [68] 0–1060 μmol photon m^{-2} s^{-1} [63]	*Chlorella pyrenoidosa* $\mu_{\max} = 0.076\ h^{-1}$ [68] $K_I = 708$ lx [68] *Chlorococcum littorale* $\mu_{\max} = 0.116\ h^{-1}$ [63] $K_I = 114$ μmol photon m^{-2} s^{-1} [63]
	Bannister [8]	$\mu = \mu_{\max}\frac{I}{(K_I^m+I^m)^{1/m}}$	(11)		*Chlorella pyrenoidosa* (at 25 °C) $\mu_{\max} = 2.48\ d^{-1}$ $K_I = 5.7$ μE m^{-2} d^{-1} $m = 3$
	Chalker [16]	$\mu = \mu_{\max}\tanh\frac{I}{K_I}$	(12)	0–1060 μmol photon m^{-2} s^{-1} [63]	*Chlorococcum littorale* $\mu_{\max} = 0.115\ h^{-1}$ [63] $K_I = 150$ μmol photon m^{-2} 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]	*S. platensis* $\mu_{\max} = 2.06\times10^{-5}\ s^{-1}$ [22] $I_k = 160$ μE m^{-2} s^{-1} [22] $n = 1.49$ [22] *Phaeodactylum tricornutum* $\mu_{\max} = 0.075\ h^{-1}$ [94] $I_k = 120$ μE m^{-2} s^{-1} [94] $n = 2.02$ [94]
	Ogbonna et al. [79]	$\mu = K\{\frac{I_{abs}}{X\,V} - I_{\max}(1-V_F)\}$	(14)		*Chlorella pyrenoidosa* K = 0.8 kg mol^{-1} X = 0.01905 kg m^{-3} V = 0.00075 m^3 I_{max} = 0.13 mol kg^{-1} d^{-1}
Group B-III: Model considering both light-limitation and photoinhibition	Steele [104]	$\mu = \mu_{\max}\frac{I}{I_{opt}}e(1-\frac{I}{I_{opt}})$	(15)	0–1060 μmol photon m^{-2} s^{-1} [63] 0–300 μmol photon m^{-2} s^{-1} [80]	*Chlorococcum littorale* $\mu_{\max} = 0.134\ h^{-1}$ [63] $I_{opt} = 505$ μmol photon m^{-2} s^{-1} [63] *Cryptomonas* 976/67 $\mu_{\max} = 1.37\ d^{-1}$ at 26 °C [80] *Cryptomonas* 976/62 $\mu_{\max} = 0.72\ d^{-1}$ at 21 °C [80] $I_{opt} < 100$ μmol photon m^{-2} s^{-1} [80]
	Aiba [2]	$\mu = \mu_{\max}\frac{I}{K_I+I+\frac{I^2}{K_{i,L}}}$	(16)	0–83 W m^{-2} [64]	*Spirulina platensis* $\mu_{\max} = 5.4849\ h^{-1}$ [64] $K_I = 959.2$ W m^{-2} [64] $K_{i,L} = 0.5817$ m^2 W^{-1} [64]
	Lee et al. [64]	$\mu = \mu_{\max}\frac{I_{av}}{K_I+K_{I,L}I_{av}^2}$ $I_{av} = \frac{I_{in}+I_{out}+2I_c}{2}$	(17)	0–83 W m^{-2} [64]	*Spirulina platensis* $K_I = 177.9$ m^2 W^{-1} h^{-1} [64] $K_{i,L} = 0.1083$ m^2 W^{-1} h^{-1} [64]
	Talbot et al. [108]	$\mu = 2\mu_{\max}(1+\beta)\frac{I/I_{opt}}{(I/I_{opt})^2+2\beta(I/I_{opt})+1}$	(18)	0–1200 μmol photon m^{-2} s^{-1} [25]	*Porphyridium cruentum* (at 30 °C) $\mu_{\max} = 1.06\ d^{-1}$ [25] $I_{opt} = 350$ μmol photon m^{-2} s^{-1} [25] $\beta = 2.06$ [25]
	Bernard and Rémond [11]	$\mu = \mu_{\max}\frac{I}{I+\frac{\mu_{\max}}{\alpha}(\frac{I}{I_{opt}}-1)^2}$	(19)		*Chlorella pyrenoidosa* $\mu_{\max} = 2.0\ d^{-1}$ $I_{opt} = 275$ μE m^{-2} s^{-1} $\alpha = 0.05$
	Grima et al. [37]	$\mu = \mu_{\max}\frac{I_{av}^{(b+\frac{c}{I})}}{[I_K+(\frac{I}{K_{I,L}})^{a_1(b+\frac{c}{I})}]+I_{av}^{(b+\frac{c}{I})}}$	(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]	*Phaeodactylum tricornutum* $\mu_{\max} = 0.063\ h^{-1}$ [1] $I_k = 94.3$ μE m^{-2} s^{-1} [1]

Table 2 (*continued*)

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

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

where $\mu_{max,min}$ 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, CO_2 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 CO_2 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:

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

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, CO_2, 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 CO_2 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 CO_2 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 CO_2 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	*Scenedesmus* sp. $\mu'_{\max,\min} = 1.35\ d^{-1}$ $Q_{\min,N} = 45.4\times10^{-9}$ μmol cell^{-1} $Q_{\min,P} = 1.64\times10^{-9}$ μmol 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	*Isochrysis affinis galbana* $\mu'_{\max,\min} = 1.5\ d^{-1}$ $Q_{\min,N} = 6.5\times10^{-2}$ molN molC^{-1} $Q_{\max,N} = 0.14$ molN molC^{-1} $Q_{\min,P} = 0.9\times10^{-3}$ molP molC^{-1} $Q_{\max,P} = 0.006$ molP molC^{-1} *Selenastrum minutum* $\mu'_{\max,\min} = 1.58\ d^{-1}$ $Q_{\min,N} = 6\times10^{-2}$ molN molC^{-1} $Q_{\max,N} = 0.21$ molN molC^{-1} $Q_{\min,P} = 1.8\times10^{-3}$ molP molC^{-1} $Q_{\max,P} = 0.015$ 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	*Chlamydomonas acidophila* $\mu_{\max,\min} = 0.076\ h^{-1}$ $K_{S,CO2} = 1.43$ μM $K_{S,P} = 1.46$ nM
	Packer et al. [84]	$\mu = \mu'_{\max,\min}\left(1-\frac{Q_{\min,N}}{Q_N}, Pho/x\right)$, $Pho = Pho_{\max}\left(1-e^{-a'I\phi/Pho_{\max}}\right)$	(27)	N, light intensity	*Pseudochlorococcum* sp. $\mu'_{\max,\min} = 3.26\ d^{-1}$ $Q_{\min,N} = 0.0278$ gN g^{-1}dw $Q_{\min,P} = 1.8\times10^{-3}$ molP molC^{-1} $a' = 4.82$ m^2 g^{-1} chl $\phi = 9.84\times10^{-2}$ molC mol^{-1} photon
	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	*Chlamydomonas reinhardtii* $\mu'_{\max,\min} = 0.82\ h^{-1}$ $Q_{\min,N} =$ NA $Q_{\min,P} =$ NA
Multiplicative models	Kunikane and Kaneko [62]	$\mu = [\mu_{c,\max}\cdot\{f(\frac{C_P}{C_n})\}^a - (\frac{1}{y_c}-1)\cdot\mu_{f,\max}\cdot\{f(\frac{C_P}{C_n})\}^b\cdot(\frac{S_N}{K_{S,N}+S_N}) - k_d]\cdot(\frac{C_n}{C_{n,\max}})$	(29)	N, P	*Scenedesmus dimorphus* $\mu_{c,\max} = 7.0$ mg mg^{-1} d^{-1} $\mu_{f,\max} = 5.0$ mg mg^{-1} d^{-1} $k_d = 0.5$ mg mg^{-1} d^{-1} $C_{n,\max} = 12\%$ $K_{S,N} = 18$ μg N L^{-1} as NO_3–N $a = 0.18$ $b = 0.35$ $y_c = 0.8$ mg mg^{-1}
	Zhang et al. [129]	$\mu = \mu_{\max}\left(\frac{S_{OC}}{K_{s,OC}+S_{OC}+\frac{S_{OC}^2}{K_{i,OC}}}\right)(\frac{I}{K_I+I})\ (1-\frac{C_x}{C_{x,m}})(1-\frac{C_{pro}}{C_{pro,m}})$	(30)	Acetate, cell concentration, Cell product, light intensity	*Haematococcus pluvialis* $\mu_{\max} = 0.5258\ d^{-1}$ $C_{x,m} = 2.92$ g L^{-1} $C_{pro,m} = 55.6$ mg L^{-1} $K_{S,OC} = 0.0211$ g L^{-1} $K_{i,OC} = 56.6813$ g L^{-1} $K_I = 53.26$ μmol m^{-2} s^{-1}
	Haario et al. [43]	$\mu = \mu_{\max}\cdot\theta^{T-T_{ref}}(\frac{I}{K_I+I})(\frac{S_P}{K_{S,P}+S_P})(\frac{S_N}{K_{s,N}+S_N})$	(31)	N, P, light intensity, temperature	Wild type algae (Chrysophycea) $\mu_{\max} = 0.0465\ d^{-1}$ $\theta = 1.137$ $T_{\text{ref}} = 20$ °C $K_{S,P} = 8.27$ g L^{-1} $K_{S,N} = 32.9$ g L^{-1} (total N) $K_I = 115$ Wm^{-2}
	Bernard [10]	$\mu = \mu_{\max}\left(\frac{I_{av}}{K_I+I_{av}+\frac{I_{av}^2}{K_{i,L}}}\right)(1-\frac{Q_{\min,N}}{Q_N})$	(32)	Light intensity, N	*Isochrysis galbana* $\mu_{\max} = 1.7\ d^{-1}$ $K_I = 1.4$ μmol m^{-2} s^{-1} $K_{i,L} = 295$ μmol m^{-2} s^{-1} $Q_{\min,N} = 0.050$ gN gC^{-1}
	Filali et al. [27]	$\mu = \mu_{\max}(\frac{I_{av}}{K_I+I_{av}})(\frac{S_{CO_2}}{K_{S,CO_2}+S_{CO_2}})$	(33)	CO_2, light intensity	*Chlorella vulgaris* $\mu_{\max} = 0.8\ h^{-1}$ $K_I = 0.14$ μE s^{-1} 10^9 cell^{-1} $K_{S,CO2} = 1.28\times10^{-5}$ mol 10^9 cell^{-1}
	Spijkerman et al. [103]	$\mu = \mu_{\max}(\frac{S_P}{K_{S,P}+S_P})(\frac{S_{CO_2}}{K_{S,CO_2}+S_{CO_2}})$	(34)	CO_2, P	*Chlamydomonas acidophila* $\mu_{\max} = 0.073\ h^{-1}$ $K_{S,CO2} = 0.38$ μM $K_{S,P} = 1.09$ nM
		$\mu = \mu_{\max}\frac{S_{CO_2}}{\frac{S_P+K_{S,P}}{S_P\alpha_{C,\max}}\mu_{\max}+S_{CO_2}}$	(35)		*Chlamydomonas acidophila* $\mu_{\max} = 0.059\ h^{-1}$ $K_{S,P} = 0.70$ nM $\alpha_{C,\max} = 0.039$
		$\mu = \mu_{\max}\frac{S_P}{\frac{S_{CO_2}+K_{S,CO_2}}{S_{CO_2}\alpha_{P,\max}}\mu_{\max}+S_P}$	(36)		*Chlamydomonas acidophila* $\mu_{\max} = 0.066\ h^{-1}$ $K_{S,CO2} = 0.77$ μM $\alpha_{P,\max} = 0.075$

Table 3 (*continued*)

Model structure	Source	Formula		Factor consideration	Parameters values
	Yang [122]	$\mu = \mu_{\max}\left(\frac{S_{CO_2}}{K_{S,CO_2}+S_{CO_2}}\right)\left(\frac{S_N}{K_{s,N}+S_N}\right)\frac{I_{av}}{I_{opt}}\exp\left(1-\frac{I_{av}}{I_{opt}}\right)$	(37)	CO_2, light intensity, N	Wild type algae $\mu_{\max} = 0.9991\ d^{-1}$ $K_{S,CO2} = 0.001\ mol\ m^{-3}$ $K_{S,N} = 0.001\ mol\ m^{-3}$ as NH_4–N $I_{opt} = 14.63\ MJ\ m^{-2}\ d^{-1}$
	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	*Chlamydomonas reinhardtii* $\mu_{\max} = 1.4\ d^{-1}$ $K_I = 215\ \mu mol\ m^{-2}\ s^{-1}$ $K_{S,CO2} = 0\ g\ L^{-1}$ $K_{S,nu} = 0\ g\ L^{-1}$ $f(T) = 1$
	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	*Chlorella* sp. *Synechocystis PCC 6803* *Tetraselmis suecica* $\mu_{\max} = 0.041\ d^{-1}$ $K_I = 14\ \mu mol\ m^{-2}\ s^{-1}$ $K_{S,CO2} = 0.00021\ mol\ m^{-3}$ $K_{i,CO2} = 10\ mol\ m^{-3}$
	Pegallapati and Nirmalakhandan [88]	$\mu = \mu_{\max}\cdot 1.066^{T-20}\left(\frac{I_{av}^m}{K_I^m+I_{av}^m}\right)\left(\frac{S_{CO2}}{K_{S,CO_2}+S_{CO_2}+\frac{S_{CO_2}^2}{K_{i,CO_2}}}\right)$	(40)	CO_2, light intensity, temperature	*Nannochloropsis salina* *Scenedesmus* sp. $\mu_{\max} = 1.2\ d^{-1}$ $K_I = 181\ \mu E\ m^{-2}\ s^{-1}$ $m = 1.75$ $K_{S,CO2} = 2.316\times10^{-6}\ mol\ L^{-1}$ $K_{i,CO2} = 0.0046\ mol\ L^{-1}$
	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	*Nannochloropsis salina* *Scenedesmus* sp. $\mu_{\max} = 2.0\ d^{-1}$ $K_I = 200\ \mu E\ m^{-2}\ s^{-1}$ $K_{i,L} = 2800\ \mu E\ m^{-2}\ s^{-1}$ $m = 1.75$ $K_{S,CO2} = 9.0\times10^{-4}\ mol\ m^{-3}$ $K_{i,CO2} = 180\ mol\ m^{-3}$ $K_{S,N} = 0.02\ g\ m^{-3}$ as NO_3–N
	Wu et al. [120]	$\mu = \mu_{\max}\left(\frac{S_N}{K_{s,N}+S_N}\right)\left(1-\frac{Q_{\min,P}}{Q_P}\right)\frac{I}{I_{opt}}\exp\left(1-\frac{I}{I_{opt}}\right)$	(42)	N, P, light intensity	*Scenedesmus* sp. $\mu_{\max} = 0.79\ d^{-1}$ $I_{opt} = 5227\ lx$ $K_{S,N} = 9.5\ mg\ L^{-1}$ (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, CO_2 and light factors have become dominant factors for recent model development due to interest in CO_2 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 NH_4–N or NO_3–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]	*Scenedesmus dimorphus*	✓	✓					
Zhang et al. [129]	*Haematococcus pluvialis*				✓	✓		✓
Klausmeier et al. [59]	*Scenedusmus* sp.	✓	✓					
Haario et al. [43]	Wild type algae (Chrysophycea)	✓	✓			✓	✓	
Bougaran et al. [12]	*Selenastrum minutum*	✓	✓					
	Isochrysis affinis galbana							
Bernard [10]	*Isochrysis galbana*	✓				✓		
Filali et al. [27]	*Chlorella vulgaris*			✓		✓		
Packer et al. [84]	*Pseudochlorococcum* sp.	✓				✓		
Spijkerman et al. [103]	*Chlamydomonas acidophila*		✓	✓				
Yang [122]	Wild type algae	✓		✓		✓		
Franz et al. [31]	*Chlamydomonas reinhardtii*	✓		✓		✓	✓	
He et al. [48]	*Chlorella* sp.			✓		✓		
	Synechocystis PCC 6803							
	Tetraselmis suecica							
Pegallapati and Nirmalakhandan [88]	*Nannochloropsis salina*			✓		✓	✓	
	Scenedesmus sp.							
Guest et al. [41]	*Chlamydomonas reinhardtii*	✓	✓			✓		
Ketheesan and Nirmalakhandan [57]	*Nannochloropsis salina Scenedesmus* sp.	✓		✓		✓	✓	
Wu et al. [120]	*Scenedesmus* 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. μmol photon m^{-2} s^{-1}, μE m^{-2} 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. lx = 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 CO_2 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, CO_2, 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.

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