Adaptive control of light attenuation for optimizing microalgae production

Francis Mairet, Rafael Muñoz-Tamayo, Olivier Bernard

A preliminary version of this work has been presented in the 12th Symposium on Computer Applications in Biotechnology (CAB 2013), Mumbai.

Corresponding author. Tel.: +33 4 92 38 71 80; fax: +33 4 92 38 78 58.
E-mail addresses: francis.mairet@inria.fr (F. Mairet), rafaun@yahoo.com (R. Muñoz-Tamayo), olivier.bernard@inria.fr (O. Bernard).

1 The reactor is permanently fed with an inflow of nutrients, while the same outflow keeps the culture volume constant.

Contents lists available at ScienceDirect

Journal of Process Control

journal homepage: www.elsevier.com/locate/jprocont

Abstract

The light attenuation factor, defined by the ratio between the incident light and the light at the bottom of the reactor, is a key operating parameter for light-limited phototrophic culture. Here, two nonlinear control laws have been proposed in order to regulate this ratio: a static controller, which is input-to-state stable with respect to measurement noise, and an adaptive controller. Then, we propose a set-point for the light attenuation factor in order to optimize microalgae productivity under constant illumination. Finally, numerical simulations illustrate how the adaptive controller can be used to optimize biomass productivity under realistic day–night cycles.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Microalgae are emerging as a promising solution to address a number of markets including feed, food, green chemistry, and bioenergy [1–3]. Nonetheless, the productivities recorded in outdoor conditions are often disappointing with respect to the actual potential of these fast growing microorganisms. This is mainly due to low photosynthetic yields resulting from a non optimal conversion of light into energy fueling biomass and reserve compounds synthesis [4]. In this context, the control of phototrophic culture is a key feature to improve economic and environmental yields [5,6,4,7,8]. The use of continuous cultures is of particular interest since it allows to drive the process to a desired state by manipulating adequately the dilution rate (ratio between the input flow rate and the reactor volume). Light absorption by pigments and scattering by the particles creates a light gradient in these phototrophic cultures. For light-limited growth (assuming that all nutrients are supplemented in excess), apprehending the light distribution inside the reactor is a keystone for productivity optimization. At high biomass, dark zones where photosynthetic growth is lower than respiration appear. On the other hand, at low biomass, a large part of the photons are not absorbed. Both phenomena lead to reduced productivity. It is therefore crucial to correctly represent light attenuation inside the reactor, and to adapt the dilution rate in order to regulate microalgae concentration.

For one-dimensional light distribution geometry (e.g. flat panel or raceways) and under constant illumination, a criteria has been proposed in order to optimize microalgae production: the steady-state biomass productivity is optimal when the light at the bottom of the culture is such that the specific growth rate equals the respiration [9]. The biomass concentration should be regulated, through the dilution rate, in order to satisfy this condition.

The optimization of biomass production under day–night cycles is more challenging. Indeed, the aforementioned criteria could not be maintained during a full day [10]. In [11], an optimal biomass concentration has been determined experimentally in order to optimize biomass productivity under natural sunlight. Given the high complexity of the problem, mathematical modeling of microalgae culture [4,12] can be helpful. Based on a dynamic model considering the effects of light, nutrient and temperature, [13] have determined numerically an optimal strategy. By
following the approach of self-optimizing control, the authors have shown that near optimal productivity can be obtained through the regulation of the light attenuation factor, defined by the ratio between the incident light and the light at the bottom of the reactor. The main idea is to find a trade-off over the day/night cycle between maximizing light capture and minimizing respiration losses, by manipulating adequately the dilution rate. At first glance, this attenuation factor is proportional to the biomass concentration. Nonetheless, the pigment content of microalgae can vary because of nitrogen limitation or light change (photoacclimation), leading to a more complex relationship between light attenuation factor and biomass. This operating mode – using the dilution rate to regulate the light attenuation factor – is generally called turbidostat or luminostat.2

Our objective is to propose closed loop control laws to automatically reach near optimal biomass productivity for light-limited cultures. To this end, we design a controller which regulates the light attenuation factor. The structure of the control law, based on the work of [14,15], is of particular interest for bioprocesses since it does not require any knowledge of the growth rate kinetics. Then, we show that this controller optimizes microalgae production.

The paper is organized as follows. We first describe a model for light-limited cultures [16]. In Section 3, we present the design of the control laws which regulate the light attenuation factor. Then, we show that this controller can be used in order to optimize biomass production in light/dark cycles. Finally, we illustrate our approach with numerical simulations of a – more realistic – extended version of the model (presented in appendix).

2. Modelling light-limited growth of microalgae

This section presents a simple model for light-limited growth of microalgae, based on the research work developed by Huisman and co-workers [16–18] for competition. Originally developed for natural systems (lake, ocean, etc.), this theoretical approach can be used for microalgae culture systems (planar photobioreactor or raceways).

2.1. Model development

Let us consider a phototrophic continuous culture of depth \( L \) in which microalgae grow (whose concentration is denoted \( x \)). We assume that the system is completely homogeneous, i.e. every concentration (microalgae, nutrients) is the same at any point. Due to light absorption and scattering by the algae, a spatial gradient of light occurs: the light intensity in the reactor decreases along the depth.

Let us assume that the light decrease in the water column can be described by the Lambert–Beer law. Thus, for a given position \( z \in [0, L] \), the corresponding light intensity \( I(x, z, t) \) satisfies

\[
I(x, z, t) = I_{\text{out}}(t) \exp(-\alpha x),
\]

where \( I_{\text{out}}(t) \) is the incident light, and \( \alpha \) is the mass extinction coefficient resulting from absorption and scattering. The light at the bottom of the water column is called \( I_{\text{out}}(x, t) = I(x, L, t) \).

We consider here that the growth of microalgae is only limited by light, so the specific growth rate is defined by a continuous function \( \mu(I) > 0 \), \( \forall I > 0 \). The total growth \( G \) of microalgae is obtained by integrating the local growth over depth:

\[
G(x, t) = \frac{x}{L} \int_0^L \mu(I(x, z, t)) dz
\]

Given Eq. (1), we obtain

\[
G(x, t) = \frac{1}{L} \int_{I_{\text{out}}(x,t)}^{I_{\text{out}}(t)} f(l)dl
\]

with \( f(l) = \mu(l)/l \).

Considering a dilution rate \( u \) and a constant basal respiration rate \( r \),3 the dynamic evolution of the microalgae concentration \( x \) is therefore given by

\[
\dot{x} = G(x, t) - (u + r)x.
\]

More accurate models [4] have been proposed in order to consider the effects of temperature, nutrient or photo-acclimation. Nonetheless, despite its relative simplicity, Eq. (4) has been able to represent quite accurately experimental data [19].

2.2. Model analysis in open loop

In this subsection, we consider a constant light supply \( I_{\text{in}} \), and a constant dilution rate \( u \).

First, note that \( G(x) \) is an increasing function whose derivatives write:

\[
G'(x) = \frac{\mu(I_{\text{out}}(x))}{I_{\text{out}}(x)} > 0
\]

\[
G''(x) = -aL \mu(I_{\text{out}}(x))
\]

Thus, the asymptotic behavior of the model depends on the specific growth rate. In the following subsections we consider various typologies of growth functions.

2.2.1. For an increasing growth rate \( \mu(I) \) [16,17]

Proposition 1. For increasing growth rate, if \( (u + r) < \mu(I_{\text{in}}) \), then Eq. (4) has one non-trivial equilibrium, which is globally stable.

Proof. For increasing growth rate, \( G(x) \) is increasing and concave given Eq. (5) (see Fig. 1). Thus, Eq. (4) is bounded and has two equilibria if \( (u + r) < \mu(I_{\text{in}}) = G'(0) \):

• a trivial equilibrium which is unstable,
• a non-trivial stable equilibrium. \( \square \)

For example, assuming a kinetics of Michaelis–Menten type, the specific growth rate writes:

\[
\mu(I) = \frac{\bar{\mu} I}{I + K_s},
\]

where \( \bar{\mu} \) and \( K_s \) are respectively the maximum growth rate and the half-saturation coefficient.

The total growth \( G \) is obtained by integration along the depth:

\[
G(x) = \frac{\bar{\mu}}{L} \ln \left( \frac{I_{\text{in}} + K_s}{I_{\text{out}}(x) + K_s} \right).
\]

The nontrivial equilibrium of Eq. (4) is obtained by solving

\[
\frac{\bar{\mu}}{L} \ln \left( \frac{I_{\text{in}} + K_s}{I_{\text{out}}(x) \exp(-\alpha x L) + K_s} \right) = (u + r)x^*.
\]

where \( x^* \) is the biomass concentration at steady state. This allows to define the light at the bottom of the water column at equilibrium \( I_{\text{out}} = I_{\text{in}} \exp(-\alpha x L) \).

\[ ^2 \text{ Note that the definition of these operating modes diverge between authors, in particular under day/night cycles.} \]

\[ ^3 \text{ We consider that the respiration due to the biosynthetic cost is already included in the specific growth rate } \mu(I) \]
3. Design of control laws

Now, we propose to use the dilution rate \( u \) as a control in order to regulate, in closed loop, the light attenuation factor to a desired set-point. The specific growth rate \( \mu(I) \) can be either increasing or non-monotone (photoinhibition).

First, we consider a constant incident light \( I_{in} \) such that \( r < \mu(I_{in}) \). Under this assumption, we can define \( \bar{x} \) the unique solution of \( G(x) = rx \), and then show that the trajectories are bounded.

**Lemma 1.** The set \([0, \bar{x}]\) is positively invariant for Eq. (4), \( \forall u(t) \geq 0 \).

**Proof.** It is easy to check that the solutions stay positive. Now, if \( x = \bar{x} \), then \( \dot{x} \leq G(\bar{x}) - \bar{x} = 0 \), \( \forall u \), $\Box$

In the following, we will assume initial conditions within this set.

3.1. Static controller

We assume that the net growth can be on-line measured or indirectly estimated:

**Hypothesis 1.** Net growth \( G(x) - rx \) is measured with a noise of multiplicative nature:

\[
y_1(t) = (G(x) - rx)(1 + \delta(t))
\]

where the noise \( \delta(t) \) is such that \( |\delta(t)| < 1 - \epsilon \), with \( 0 \leq \epsilon < 1 \).

Actually, the net growth can be estimated using observer-based estimator [21,22] based on oxygen production [23] or \( CO_2 \) consumption for example. Since such estimate is corrupted with noise, we will study the robustness of the controller with respect to this uncertainty.

In order to stabilize Eq. (4) towards the set-point \( x^* \), we consider the static controller:

\[
u = \frac{1}{x^*} y_1(t)
\]  

(11)

Note that we have \( y_1(t) > 0 \) for all \( x \in (0, \bar{x}] \).

This controller has been proposed for the classical substrate-limited chemostat in [14]. Robustness of this control law with respect to fluctuations in the input substrate concentration and with respect to the presence of other species has been considered respectively in [24] and in [25]. Here, we apply this controller for a light-limited chemostat, and we show its robustness with respect to noise in the measurement.

Under Control law (11), Eq. (4) becomes:

\[
\dot{x} = (G(x) - rx) \left[ 1 - \frac{1 + \delta(t)}{x^*} \right]
\]

(12)

The following proposition characterizes the stability of this system and the robustness of the controller with respect to measurement noise.

**Proposition 3.** Considering \( \delta(t) \) as a (bounded) perturbation input, System (12) is input-to-state stable (ISS), i.e. there exists a class $\mathcal{K}_\infty$
function $\beta$ and a class $\mathcal{K}$ function $\lambda$ such that for any initial state $x(t_0) \in (0, \bar{x})$ and any bounded input $\delta(t)$, the solution $x(t)$ satisfies:

$$||x(t) - x^*|| \leq \beta(||x(t_0) - x^*||, t - t_0) + \lambda\left(\sup_{t_0 \leq t \leq t} ||\delta(t)||\right)$$

where $\lambda(r) = \frac{\sqrt{7}}{\beta}(r)$, with $0 < \theta < 1$.

**Proof.** Recalling that $r < \mu(I_{in})$, we have $G(x) - r x > 0$. For $x \in (0, \bar{x})$ (see Section 2.2.2), this allows us to take

$$V = x^* \int_x^\infty \frac{w - x^*}{G(w) - r w} dw$$

as an ISS-Lyapunov function candidate. We obtain:

$$\dot{V} = -(x - x^*)^2 - \delta(t)x(x - x^*)$$

$$= -\left(1 - \frac{\theta}{\bar{x}}\right)(x - x^*)^2 - x(x - x^*) \left[\delta(t) + \frac{\theta}{\bar{x}}(x - x^*)\right].$$

Thus, $\forall(x - x^*) \geq \frac{\bar{x}}{\theta} \delta(t)$, we have

$$\dot{V} \leq -(1 - \theta)(x - x^*)^2. $$

Therefore, applying Theorem 4.19 from [26], the system is ISS with $\lambda(r) = \frac{\sqrt{7}}{\beta}(r)$.

### 3.2. Adaptive control

#### 3.2.1. Controller design

In the previous section, we have seen that Control law (11) allows to globally stabilize Eq. (4). Nevertheless, a static error can remain in the case of a poor estimation of the net growth. Thus, following the work of [14, 27], we introduce an adaptive gain $\gamma(t)$ in the feedback law.

We now assume that the two following quantities can be measured:

**Hypothesis 2.** We consider that the following measurements are available:

- the net growth $y_1(t) = G(x, t) - r x$,
- the light attenuation factor: $y_2(t) = ax$.

The light attenuation factor $y_2$ can be easily computed from light measurements by online sensors at two places in the reactor. A straightforward way is to measure the light at the top and bottom of the culture:

$$y_2(t) = \frac{1}{I_0} \ln \left(\frac{I_{in}(t)}{I_{out}(x, t)}\right).$$

but the sensor can also be positioned inside the culture at a depth $z_m < L$ in order to increase measurement precision in case of low incident light and/or high biomass concentration (when $I_{out}$ is almost zero)

$$y_2(t) = \frac{1}{z_m} \ln \left(\frac{I_{in}(t)}{I(x, z_m, t)}\right),$$

We consider a possibly time varying incident light $I_{in}(t)$, but we first neglect the respiration rate. Given a set-point $y_2^* = ax^*$ for the light attenuation, we define $\gamma' = a/y_2^*$.

**Proposition 4.** Consider an incident light $I_{in}(t) > \epsilon > 0$, $\forall t \geq 0$. Assuming Hypothesis 2 and $r > 0$, the adaptive feedback control law

$$(13) \begin{cases} u(t) = \gamma(t)y_1(t) \\ \dot{y} = Ky_1(t)y_2(t) - \gamma - y_m \gamma_m - \gamma \end{cases}$$

with $0 < \gamma_m < \gamma < \gamma_M$ and $K > 0$ globally stabilizes Eq. (4) towards the positive set point $x^* = y_2^*/a$.

**Proof.** Given that $y_2 = ax$, Eq. (4) under Control law (13) rewrites:

$$\begin{cases} \dot{y}_1 = G(x, t) - r y_2 + y_1 \\ \dot{y} = Kg(x, t)y_2 - \gamma - y_m \gamma_m - \gamma \end{cases}$$

Since $G(x, t) \geq 0$, the set $\mathbb{R}^+ \times [y_m, y_M]$ is positively invariant (in the following, we assume initial conditions belonging to this set). Given its dynamics, one can show that $y_2(t) \geq y_\gamma \forall t \geq 0$, with:

$$y = \min\left(y_2(0), \frac{a}{\gamma_M}\right).$$

So we have $I_{in}(t) - I_{out}(t) \exp(-\gamma L), \forall t \geq 0$. Using Eq. (3), we deduce that $G(x, t)$ is lower bounded (since $f(I) > 0, \forall I > 0$). Thus, we can introduce the time change $t' = \int_0^t G(x(t), t) dt$. Denoting with a prime the derivatives with respect to $t'$, System (14) rewrites:

$$\begin{cases} \dot{y}'_1 = a - y_2' \\ \dot{y}' = Kg(x, t)y'_2 - \gamma - y_m \gamma_m - \gamma \end{cases}$$

Now consider the following Lyapunov candidate function $V[14]$:

$$V = \int_{y_2'}^{y_2} \frac{w - y_2'}{w - y_2'} dw + \int_{y_2'}^{y_2} \frac{w - y'}{w - y_2'} dw.$$

The derivative of $V$ along the trajectories of System (15) is given by

$$\dot{V} = -a\frac{(y_2 - y_2')^2}{y_2'^2}.$$

$V$ is a continuously differentiable, radially unbounded, positive definite function with $V(y_2, y') \leq 0, \forall(y_2, y') \in \mathbb{R}^+ \times [y_m, y_M]$. Moreover, one can easily check that the largest invariant set defined by $V = 0$ is actually the set-point $(y_2^*, \gamma^*)$. Therefore, using Krasovskii theorem [26], the set-point $(y_2^*, \gamma^*)$ is globally asymptotically stable.

Note that this control scheme does not require any knowledge of the growth rate or the mass extinction coefficient. Moreover, the proposed controller can be used for multispecies culture, with interesting properties: it allows the selection of the fastest growing species under the condition fixed by the set-point [27].

### 3.2.2. Simulation

Eq. (4) with Haldane growth rate (Eq. (9)) under the Control law (13) is simulated with a periodic light supply:

$$I_{in}(t) = I_0[\max(0, \sin(2\pi t))]^2$$

where $I_0 = 1200 \mu mol \cdot m^{-2} \cdot s^{-1}$. Growth measurements $G$ are corrupted by an additive noise (up to $0.5 \text{ g L}^{-1} \cdot \text{d}^{-1}$). Model parameters are given in Table 1. The tuning of the control law parameters results from a trade-off between rapidity and smoothness: $K = 1$, $y_m = 0.01 \text{ L}^{-1}$, and $y_M = 4 \text{ L}^{-1}$. The set-point is $y^* = 1.5 \text{ dm}^{-1}$. Fig. 2 shows the good performance of the controller, even in presence of a periodic forcing and noise measurements. Recall that the controller...
implementation of the controller is proposed in the next subsection.

3.2.3. Practical implementation

When respiration is considered, given that \( Y_1 = G(x, t) - rx \) can be negative, the adaptive control law is modified as follows:

\[
\begin{align*}
    u(t) &= y(t) \max(y_1(t), 0) \\
    \dot{y} &= K \max(y_1(t), 0)(y_2 - y_2'y' - y_m(y - y')) 
\end{align*}
\]  

(17)

Although convergence is no longer guaranteed, the system moves faster during the light phase \((G(x, t) > 0)\) than the dark phase \((G(x, t) = 0)\) so we can expect that the system converges towards a periodic solution around the set-point.

4. Optimization of biomass productivity

In this section, we will show that the adaptive controller \((13)\) can be used in order to optimize biomass productivity \( P = ux \).

4.1. Under constant light

A criteria on the light at the bottom of the water column has been proposed in order to optimize biomass productivity \([9]\):

**Proposition 5.** Under constant illumination, the steady-state biomass productivity is optimal when the light at the bottom of the culture \( I_{\text{out}} \) is such that:

\[
    \mu(I_{\text{out}}) = r. 
\]  

(18)

**Proof.** At steady-state, we have \( P = ux = G(x) - rx \). The maximum of \( P \) is obtained for

\[
    \frac{dP}{dx} = G(x) - r = \mu(I_{\text{out}}(x)) - r = 0. 
\]

\( \Box \)

Thus, under constant illumination, the adaptive controller \((17)\) can be used to regulate the light attenuation factor at the set-point \( y_2' = (1/L) \ln(I_{\text{in}}/I_{\text{out}}) \) in order to optimize biomass productivity.

4.2. Under day–night cycle

The optimization of biomass production under day–night cycle is more challenging. Indeed, the culture could not be maintained in this condition \([10], [13]\) have shown by simulations that the regulation of the light attenuation allows to achieve near optimal productivity, and that this closed-loop strategy is quite robust towards environmental conditions and model uncertainties.

In \([15]\), Control law \((17)\) is used in simulations for the control of the light attenuation in order to optimize biomass production under day–night cycles. The adaptive controller reaches productivity close to the optimum (determined numerically). The choice of the set-point is a keystone which will be further discussed in the next section.

5. Simulation with a more accurate model

We test our approach via numerical simulations with an extended, yet more accurate, version of the microalgae model which also includes the effect of nitrogen limitation (based on Droop model) and temperature. This model, given in appendix, is based on \([4, 28, 13]\). It was calibrated with experimental data of *Tisochrysis lutea* (previously named as *Isochrysis aff. galbana*) culture.

We consider daily variation of temperature and solar irradiance in order to simulate realistic outdoor culture conditions. Nutrients

---

**Table 1**

Parameter values used for simulation in Section 3.2.2.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \mu )</td>
<td>5 d(^{-1} )</td>
</tr>
<tr>
<td>( K_{p} )</td>
<td>300 ( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} )</td>
</tr>
<tr>
<td>( K_{d} )</td>
<td>400 ( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} )</td>
</tr>
<tr>
<td>( a )</td>
<td>1 dm(^{2} \cdot \text{g}^{-1} )</td>
</tr>
<tr>
<td>( L )</td>
<td>2 dm</td>
</tr>
</tbody>
</table>

does not require any knowledge of model parameters. Note that we observe a decrease of growth \( G \) at noon because of photo-inhibition.

Nevertheless, in its present form, the controller requires the positivity of \( G \). This is no longer true in night or dim light when respiration is considered. To overcome this problem, a practical

---

**Fig. 2.** Simulation of Eq. (4) with the adaptive control \((13)\) under day-night cycles. The set-point is represented by the dashed line.
are in excess, but the day–night cycles leads to daily variation in the nitrogen quota, affecting cell chlorophyll and thus light attenuation, thus mimicking the periodic dynamics of chlorophyll synthesis (the chlorophyll content is assumed to be proportional to the nitrogen quota).

First, we test the controller (17) in this setting (see Fig. 3). We can observe oscillations, which are both due to the forcing light signal and to the respiration during the night, when the controller set the system in batch mode. In particular, the light attenuation factor cannot tend to an equilibrium point, contrary to the previous simulation without respiration (see Fig. 2). Although it has been designed on a simpler model, the adaptive controller presents good performance in terms of regulation. A periodic regime oscillating around the set-point is achieved. At day 20, we introduce a perturbation: the solar irradiance is reduced by 40%. Despite this perturbation, the light attenuation is maintained by the controller around its set-point. On the other hand, the nitrogen quota increases (because of the slow-down of carbon growth).

We now evaluate the biomass productivity obtained with the controller. For different set-points and maximum light intensities, simulations of Model (19) under Control (17) are performed until reaching a periodic regime. This allows us to determine an optimal set-point in order to maximize biomass productivity (see Fig. 4). An interesting result is that this optimal set-point is almost constant for different light intensities (around 10 m$^{-1}$). Thus, the proposed strategy appears to be robust with respect to weather variations.

![Fig. 3](image-url) Simulation of model (19) under Control law (17). The set-point for the adaptive controller is represented by the dotted line. At day 20, the solar irradiance is reduced by 40%.

![Fig. 4](image-url) Effect of the light attenuation set-point on biomass productivity in periodic regime for different light regimes (red: nominal, dash green: −25%, dot blue: −50%). The optimal set-point remains almost the same for the three light regimes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

6. Conclusion

In this paper, we have proposed nonlinear control laws which regulate the light attenuation factor in a microalgae culture. The global asymptotic stability of the closed-loop system has been
demonstrated using a simple model of light-limited growth. Then, it was shown through numerical simulations that the adaptive controller presents good performances in terms of regulation under constant light. The efficiency of the controller was also tested under day–night cycles using a more realistic growth model including the effects of temperature and nitrogen quota. Such operating mode, which remains rather simple to set up, is therefore of particular interest for optimizing biomass production in outdoor conditions.

Acknowledgements

This work benefited from the support of the Purple Sun research project ANR-13-BIME-004 funded by the French National Research Agency (ANR).

Appendix. A more realistic model

Variables and inputs

<table>
<thead>
<tr>
<th>Variable</th>
<th>Unit</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>s</td>
<td>g N m⁻³</td>
<td>Nitrogen concentration</td>
</tr>
<tr>
<td>qn</td>
<td>g N gC⁻¹</td>
<td>Internal nitrogen quota</td>
</tr>
<tr>
<td>x</td>
<td>g C m⁻³</td>
<td>Biomass concentration</td>
</tr>
<tr>
<td>s_w</td>
<td>g N m⁻³</td>
<td>Influent nitrogen conc.</td>
</tr>
<tr>
<td>u</td>
<td>d⁻¹</td>
<td>Dilution rate</td>
</tr>
</tbody>
</table>

Model equations

\[
\begin{align*}
\dot{s} &= u(s_{\text{in}} - s) - \rho(\cdot) \chi \\
\dot{q}_n &= \rho(\cdot) - (G(\cdot)/x - R(\cdot))q_n \\
\dot{x} &= G(\cdot) - (u + R(\cdot))x
\end{align*}
\]

(19)

Kinetic rates

- Growth:

\[
G(\cdot) = \frac{\phi(T)}{(b q_n x + c)l} \int_{l_{\text{mix}}(x,t)}^{l_{\text{mix}}(x,t)} \mu(I) \, dl \left(1 - \frac{q_n}{q_n}\right).
\]

(20)

with

\[
l_{\text{mix}}(x,t) = l_{\text{in}} \exp(- (b q_n x + c)l),
\]

\[
\mu(I) = \frac{\tilde{\mu}}{K_{\text{dil}} + I + P/K_{\text{H}}}
\]

- Nitrogen uptake rate:

\[
\rho(\cdot) = \tilde{\rho} \phi(T) \frac{s}{K_{\text{dil}}} \left( u + (1 - \tilde{\rho} m_{\text{in}} / m_{\text{in}} + c) \left(1 - q_n / q_n\right) \right)
\]

(21)

- Respiration rate:

\[
R(\cdot) = r_0 \phi(T) + \psi \rho(\cdot)
\]

(22)

- Temperature effect:

\[
\phi(T) = \begin{cases} 
0, & T < T_{\text{min}} \\
(T - T_{\text{min}})^2 / (T_{\text{max}} - T_{\text{min}})^2, & T_{\text{min}} \leq T \leq T_{\text{max}} \\
(T - T_{\text{min}})(T - T_{\text{min}})^2 / (T_{\text{opt}} - T_{\text{min}})(T_{\text{opt}} - T_{\text{min}})^2, & T_{\text{min}} < T < T_{\text{opt}} \\
(T - T_{\text{min}})(T - T_{\text{opt}})(T - T_{\text{max}})(T - T_{\text{max}})^2 / (T_{\text{max}} - T_{\text{min}})(T_{\text{opt}} - T_{\text{min}})(T_{\text{opt}} + T_{\text{max}} - 2T), & T_{\text{opt}} < T < T_{\text{max}} \\
0, & T > T_{\text{max}}.
\end{cases}
\]

Parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\mu)</td>
<td>6.6 d⁻¹</td>
<td>Theoretical maximum specific growth rate</td>
</tr>
<tr>
<td>(K_{\text{dil}})</td>
<td>150 µmol m⁻³ s⁻¹</td>
<td>Haldane saturation constant</td>
</tr>
<tr>
<td>(K_{\text{H}})</td>
<td>2000 µmol m⁻³ s⁻¹</td>
<td>Haldane inhibition constant</td>
</tr>
<tr>
<td>(Q_{\text{m}})</td>
<td>0.05 gN gC⁻¹</td>
<td>Minimum nitrogen quota</td>
</tr>
<tr>
<td>(Q_{\text{opt}})</td>
<td>0.20 gN gC⁻¹</td>
<td>Maximum nitrogen quota</td>
</tr>
<tr>
<td>(\hat{\mu})</td>
<td>0.1 gN gC⁻¹</td>
<td>Maximum nitrogen uptake rate</td>
</tr>
<tr>
<td>(K_{\text{n}})</td>
<td>0.018 gN m⁻³</td>
<td>Nitrogen uptake half saturation constant</td>
</tr>
<tr>
<td>(v)</td>
<td>0.19</td>
<td>Reduction factor of nitrogen uptake during the night</td>
</tr>
<tr>
<td>(r_0)</td>
<td>0.1 d⁻¹</td>
<td>Maintenance respiration rate</td>
</tr>
<tr>
<td>(\psi)</td>
<td>1.3 gC gN⁻¹</td>
<td>Biosynthesis cost coefficient</td>
</tr>
<tr>
<td>(b)</td>
<td>2 m² g⁻¹</td>
<td>Mass extinction coefficient linked to internal nitrogen</td>
</tr>
<tr>
<td>(c)</td>
<td>0.087 m⁻¹</td>
<td>Base light extinction coefficient</td>
</tr>
<tr>
<td>(T_{\text{min}})</td>
<td>273 K</td>
<td>Lower temperature for algae growth</td>
</tr>
<tr>
<td>(T_{\text{opt}})</td>
<td>299.8 K</td>
<td>Optimal temperature for algae growth</td>
</tr>
<tr>
<td>(T_{\text{max}})</td>
<td>306.4 K</td>
<td>Upper temperature for algae growth</td>
</tr>
</tbody>
</table>

References


