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BILINEAR SYSTEM AS A MODELLING FRAMEWORK FOR ANALYSIS OF MICROALGAL GROWTH

Štěpán Papáček, Sergej Čelikovský, Dalibor Štys and Javier Ruiz-León

A mathematical model of the microalgal growth under various light regimes is required for the optimization of design parameters and operating conditions in a photobioreactor. As its modelling framework, bilinear system with single input is chosen in this paper. The earlier theoretical results on bilinear systems are adapted and applied to the special class of the so-called intermittent controls which are characterized by rapid switching of light and dark cycles. Based on such approach, the following important result is obtained in the present paper: as the light/dark cycle frequency is going to infinity, the value of resulting production rate in the microalgal culture goes to a certain limit value, which depends on average irradiance in the culture only. As a case study, the so-called three-state model of photosynthetic factory, being a simple four-parameter model, is analyzed. The present paper shows various numerical simulations for the model parameters previously published and analyzed experimentally in the biotechnological literature. These simulation results are in a very good qualitative compliance with the well-known flashing light experiments, thereby confirming viability of the approach presented here.

Keywords: bilinear system, model of photosynthetic factory, microalgae, light/dark cycles, flashing light experiments

AMS Subject Classification: 93C10, 37N25

1. INTRODUCTION AND PROBLEM STATEMENT

Delivering the light in an optimal manner and achieving maximum productivity is a key issue as far as the control of photobioreactors (further PBR) is concerned. When microalgal cells are grown in PBR, photon flux density (PFD) decreases exponentially (according to the Lambert–Beer's law) with the growing distance from irradiated side of the PBR. The cells near the front are exposed to high PFD (some authors prefer to use the equivalent term "irradiance"), which usually allows a high growth rate. At the core, the cells receive less or no light and will thus have a lower growth rate. Nevertheless, it was observed experimentally that higher PFD does not automatically mean higher growth rate. The phenomenon, when for the increasing PFD the growth rate decreases, is called in the biotechnological literature as the photoinhibition [11, 15, 16]. Consequently, there is a certain value of constant PFD, for which this growth is the highest possible. That is not surprising from the system theory point of view, as the response to irradiance is described, later on, by dynamical system modelled by ordinary differential equations with controlled input.

For this reason, in the real PBR the cells are mixed between the front and core of the PBR thereby achieving more uniform irradiance for all cells. As a consequence, the cell moving between the front and core of the PBR receives the light intermittently. Both intuitively expected and experimentally confirmed hypothesis is that intermittent (flashing) regimes may do the same job as the average constant irradiance equal to integral average of intermittent regime.

In the present paper, this expectation will be confirmed also theoretically, based on the properties of the so-called bilinear systems with single input. It is interesting to see, that the biotechnological "intermittent principle" is mathematically a consequence of Lipschitz dependence of trajectories of bilinear system on input, with respect to certain special functional norm of an input space. This is the main original contribution of the present paper to the topic previously treated only experimentally, or by computer simulations.

These experimental treatments have achieved a lot of attention, especially in biotechnological literature. Terry in [18] presented an excellent experimental work leading to the elucidation of dependence of photosynthetic growth enhancement on flashing rate, but he did not explain the mechanism of growth enhancement by means of mathematical modelling. Whereas photosynthesis by microalgal cells in small laboratory systems under "deterministic" light/dark cycles has been studied since 1953 (see e. g. [9, 10, 14, 18, 19]), no structured mathematical model describing the flashing light enhancement has been proposed till now.

The theory of photosynthetic microorganisms growth modelling has long been regarded as a well-defined discipline in algal biotechnology, consisting of the adequate coupling between photosynthesis and irradiance, resulting in the light response curve (so-called *P–I curve*), which represents the microbial kinetics. However, several phenomena, e. g. just mentioned flashing light enhancement, cannot be explained by a simple kinetic relation. The main difficulty in considering the role of light/dark cycles induced by algal suspension flow in PBR consists in different time scales of both processes. While the time constant of algal growth is in order of hours, the transport of cells from light to dark zone and viceversa occurs generally in seconds.

Nevertheless, a simple dynamic model of photosynthetic factory (further PSF model), proposed by Eilers and Peeters [5], has proved to be an effective means to model both relevant phenomena, i. e. microalgal growth under both constant and intermittent light regime. The PSF model is a lumped parameter model of microalgal growth in the form of the bilinear system, see Eq. (1), which is linear in state x (state vector x has three components representing three states of a photosynthetic unit), linear in control variable u (single scalar input u represents the irradiance in the culture), but not jointly linear in both.

Our paper is organised as follows: Section 2 begins with an announcement of the Lipschitzean dependence of trajectories of bilinear systems on control, which is based on the earlier studies on bilinear systems [1, 2, 3]. Then, considering the following application to microalgal growth modelling, a new theorem is formulated and proved. Further we investigate the dynamic behaviour of a special model of microalgal growth (so-called three-state model of photosynthetic factory) in form of bilinear system. In Section 3, the relation for photosynthetic production rate is derived and the condition for optimal control is announced as a special theorem. Subsequently, the most relevant results of numerical simulations are presented in a graphical form and some consequences are depicted. The final Section 4 presents our conclusions and future prospects in microalgal growth modelling and control.

2. MODEL DEVELOPMENT

2.1. Bilinear systems with single input

Let us consider the following control system called in the sequel as the *bilinear system with single input (BLSSI)*:

$$\dot{x} = Ax + (Bx + c)u, \qquad x(t_0) = x_0, \tag{1}$$

where A, B are $(n \times n)$-dimensional constant matrices and c is vector in $\mathbb{R}^n$ space. Scalar control u is assumed to be a measurable function on every finite time interval $[t_0, t_f]$ such that almost everywhere on $[t_0, t_f]$ it holds

$$u_{\min} \leq u(t) \leq u_{\max},$$

where $u_{\min}, u_{\max}$ are given real numbers. Such a control is further denoted as the admissible one. Finally, $x \in \mathbb{R}^n$ is the vector of state variables and $x_0 \in \mathbb{R}^n$ is the given initial state of the system. More general forms of bilinear systems are described in [13].

2.2. Estimate for Lipschitzean dependence of trajectories of BLSSI on control

Here, we aim to briefly recall the validity of the following estimate:

$$\max{}_{t_0 \leq t \leq t_f} \|x_d(t) - x_e(t)\|_{\mathbb{R}^n} \leq K \ \max{}_{t_0 \leq t \leq t_f} \left| \int_{t_0}^{t} (u_d(s) - u_e(s))\,\mathrm{d}s \right|, \tag{2}$$

where $x_d(t)$ and $x_e(t)$ are solutions of (1) for $u_d(t)$ and $u_e(t)$ respectively, K is a constant depending only on $A, B, c, t_0, t_f, u_{\min}$, and $u_{\max}$. Let us note that the above estimate means, in fact, Lipschitzean dependence of the trajectories of the bilinear systems on the inputs with respect to the special input space norm

$$\left| \int_{t_0}^{t} u(s)\,\mathrm{d}s \right|$$

and the usual uniform convergence norm for state trajectories space

$$\max{}_{t_0 \leq t \leq t_f} \|x(t)\|_{\mathbb{R}^n}.$$

Theorem 1. Let us consider system (1), defined on the time interval $[t_0, t_f]$, with the initial state $x(t_0) = x_0$ and let $x_d(t)$ and $x_e(t)$ be trajectories of this system for admissible control $u_d(t)$ and $u_e(t)$ respectively. Then the estimate (2) is valid, where

$$\begin{aligned} K = {} & K_1 K_2 \|x_0\|_{\mathbb{R}^n} + 2K_1 K_2^2 K_3 K_4 \|A\|_s \|c\|_{\mathbb{R}^n} (t_f - t_0) \\ & + K_2^2 K_4 \|A\|_s \|c\|_{\mathbb{R}^n} (t_f - t_0) + K_4 \|c\|_{\mathbb{R}^n}. \end{aligned} \tag{3}$$

Here we use the notation

$$K_1 = (2\|A\|_s \|B\|_s (t_f - t_0) + \|B\|_s) \tag{4}$$
$$K_2 = \exp\left((\|B\|_s u_p + \|A\|_s)(t_f - t_0)\right) \tag{5}$$
$$K_3 = \{\exp\left(\|B\|_s u_p (t_f - t_0)\right) - 1\} / \|B\|_s \tag{6}$$
$$K_4 = \exp\left(\|B\|_s u_p (t_f - t_0)\right) \tag{7}$$
$$u_p = \max\{|u_{\min}|, |u_{\max}|\}. \tag{8}$$

Finally, $\|\cdot\|_s$ stands for the matrix norm compatible with the Euclidean norm in $\mathbb{R}^n$ and $\|\cdot\|_{\mathbb{R}^n}$ for the Euclidean vector norm.

Proof. The proof is performed in detail in [3]. □

Remark 1. Theorem 1 in fact establishes not only continuous dependence of trajectory of system (1) on control with respect to norms $\max_{t_0 \le t \le t_f} \left| \int_{t_0}^{t} u(s)\, \mathrm{d}s \right|$ and $\max_{t_0 \le t \le t_f} \|x(t)\|_{\mathbb{R}^n}$, but even Lipschitzean dependence of a trajectory of a bilinear system on control with respect to these norms. Notice that the norm in the input space is a special one, as the absolute value is taken *outside* the integral. Consequently, two inputs, closed each to other with respect to this norm, may have even very different values.

2.3. Dependence of trajectories and states of BLSSI on intermittent input signal

In this subsection we formulate and prove Theorem 2 mathematically supporting the experimental observation that rapidly flashing light gives practically the same microalgae growth as would some its average constant irradiance equivalent. This theorem is closely related with the well-known Filipov theorem on differential inclusion and is proved by a very similar technique as used in [1, 2, 3]. Nevertheless, neither of these results directly imply our Theorem 2.

Definition 1. *(Intermittent controlled input)* Let u_a, u_b, $u_a \le u_b$, be given real numbers. The controlled input $u^{**}(s) \in [u_{\mathrm{a}}, u_{\mathrm{b}}]$, $s \in [t_0, t_f]$, will be called as the *intermittent* one if there exist real numbers h and h_a, $h > h_a > 0$, such that (see Figure 1):

1) $u^{**}(s) = u_a$ on each subinterval of the form $[t_0 + (i-1)\, h, t_0 + (i-1)\, h + h_a]$,
2) $u^{**}(s) = u_b$ on each subinterval of the form $[t_0 + (i-1)\, h + h_a, t_0 + ih]$.

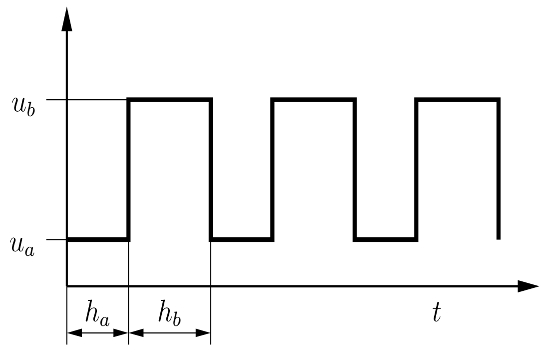

Fig. 1. Schematic presentation of the periodic intermittent input signal u^{**}, where u_a is the irradiance level during time period h_a and u_b is the irradiance level during time period h_b. The total cycle period is $h = h_a + h_b$.

Definition 2. Let us consider the system (1) with the initial state $x(t_0) = x_0$ and let us use the notation of Definition 1. By $X^{**}(t_0, t, x_0, u_a, u_b)$ we denote the set of all points reachable from x_0 using the intermittent controlled inputs $u^{**}(s) \in [u_\mathrm{a}, u_\mathrm{b}]$, $s \in [t_0, t]$. Analogously, $X_c(t_0, t, x_0, u_a, u_b)$ stands for the set of all points reachable from x_0 using the constant controlled inputs $u_c(s) \in [u_\mathrm{a}, u_\mathrm{b}]$, $s \in [t_0, t]$. For the sake of brevity, when obvious from the context, u_a, u_b might be omitted.

Theorem 2. Let us consider the system (1) with initial state $x(t_0) = x_0$. Then for any $t \in [t_0, t_f]$

$$X_c(t_0, t, x_0, u_a, u_b) = \overline{X^{**}(t_0, t, x_0, u_a, u_b)}.$$

The proof of Theorem 2 is based on the following

Lemma 1. Let be $u_c = \frac{h_a}{h} u_a + \frac{h-h_a}{h} u_b$ and let $u^{**}(s)$ is the intermittent controlled input defined in Definition 1. Then it holds for all $t \in [t_0, t_f]$

$$\left| \int_{t_0}^{t} u_c(s)\,\mathrm{d}s - \int_{t_0}^{t} u^{**}(s)\,\mathrm{d}s \right| \le (u_\mathrm{b} - u_\mathrm{a}) \frac{h_a}{h} \left(1 - \frac{h_a}{h} \right) h. \tag{9}$$

P r o o f. The straightforward computations show that

$$|w_c(t) - w^{**}(t)| \le h_a(u_c - u_a), \tag{10}$$

where

$$w_c(t) := \int_{t_0}^{t} u_c(s)\,\mathrm{d}s, \quad w^{**}(t) := \int_{t_0}^{t} u^{**}(s)\,\mathrm{d}s.$$

Taking into account the assumption $u_c = \frac{h_a}{h} u_a + \frac{h-h_a}{h} u_b$ one has

$$h_a(u_c - u_a) = h_a \left(\frac{h_a}{h} u_a + \frac{h - h_a}{h} u_b - u_a \right) = (u_\mathrm{b} - u_\mathrm{a}) \frac{h_a(h - h_a)}{h}, \tag{11}$$

which completes the proof. □

Proof of Theorem 2. By Lemma 1 every constant controlled input $u_c(s) \in [u_\mathrm{a}, u_\mathrm{b}]$, $s \in [t_0, t]$, is the limit of the suitable sequence of the intermittent controlled inputs $u^{**}(s) \in [u_\mathrm{a}, u_\mathrm{b}]$, $s \in [t_0, t]$, where the corresponding convergence is in the norm

$$\left| \int_{t_0}^{t} u(s)\, \mathrm{d}s \right| .$$

At the same time, Theorem 1 establishes the Lipschitzean dependence of trajectories of bilinear systems on inputs with respect to the above norm of the input space and the usual norm of the uniform convergence in the state trajectories space. As a consequence, for every trajectory generated by some constant input there exists a suitable sequence of the trajectories generated by the intermittent inputs converging to it in the usual uniform convergence norm. In particular,

$$X_c(t_0, t, x_0, u_a, u_b) = \overline{X^{**}(t_0, t, x_0, u_a, u_b)}$$

and Theorem 2 have been proved. □

Remark 2. Theorem 2 establishes that the state trajectory of a bilinear system for a constant control signal u_c can be approximated by the state trajectory corresponding to the intermittent control signal u^{**} with an arbitrary precision. Moreover, thanks to Theorem 1, establishing the Lipschitz dependence of trajectories of bilinear systems on inputs with respect to the appropriate norms, this approximation can be even made uniform with respect to parameters $h > h_a > 0$ and the constant inputs[1] which is another useful aspect for practical computations later on. In particular, Theorem 2 will be used to set out a simple strategy for the open loop control of microalgal growth to achieve "intermittently" optimal light regime, see Theorem 3 in Subsection 3.2.

2.4. Three-state model of the photosynthetic factory

A structured three-state model of so-called photosynthetic factory (PSF) has been proposed by Eilers and Peeters in [5] and further developed in [6, 19, 20]. The authors of the paper [5] originally worked with the probabilities that a hypothetical photosynthetic factory is in one of the three states R, A or B: p_R represented the probability that PSF is in the resting state R, p_A the probability that PSF is in the activated state A, and p_B the probability that PSF is in the inhibited state B. The PSF can only be in one of these states, so:

$$p_R + p_A + p_B = 1\ . \tag{12}$$

[1] More precisely, for every required approximation precision there exist parameters $h > h_a > 0$, independent of particular constant input, guaranteeing that precision.

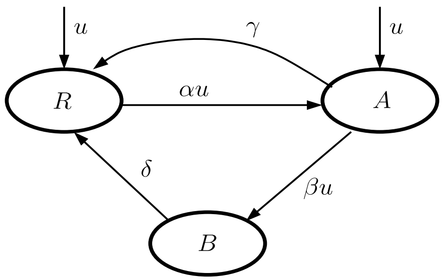

Fig. 2. Scheme of states and transition rates of the photosynthetic factory – Eilers and Peeters PSF model. The three states of the photosynthetic factory are:
R resting state, A activated state, B inhibited state. The transition rates are:
αu, βu, γ, δ (unit: s^{-1}). The input variable u is the irradiance (unit: $\mu\mathrm{E}\,\mathrm{m}^{-2}\,\mathrm{s}^{-1}$).

The possible transitions among states are supposed to be of zero or first order respective to the irradiance u. Hence from the PSF model, schematically depicted in Figure 2 directly follows

$$\begin{bmatrix} \dot{p_R} \\ \dot{p_A} \\ \dot{p_B} \end{bmatrix} = \begin{bmatrix} 0 & \gamma & \delta \\ 0 & -\gamma & 0 \\ 0 & 0 & -\delta \end{bmatrix} \begin{bmatrix} p_R \\ p_A \\ p_B \end{bmatrix} + u \begin{bmatrix} -\alpha & 0 & 0 \\ \alpha & -\beta & 0 \\ 0 & \beta & 0 \end{bmatrix} \begin{bmatrix} p_R \\ p_A \\ p_B \end{bmatrix} . \tag{13}$$

For given values of the model parameters α, β, γ, δ and the input variable, i. e. the irradiance u, the equation system (13) is a system of linear differential equations with constant coefficients, that can be solved explicitly by classical means. Many authors, e. g. Eilers and Peeters in [5], Zonneveld in [21], Han in [7], restrict themselves to the steady-state solution, when a constant irradiance is maintained long enough so that the PSF states do not change anymore. Taking into account the Eq. (12), further only two state variables will be evaluated, thus for the steady-state solution of PSF model the following equations hold:

$$p_{R_{ss}} = \frac{\delta\ (\gamma + \beta u)}{\alpha\beta u^2 + \delta\ (\alpha+\beta)u + \gamma\delta} , \tag{14}$$

$$p_{A_{ss}} = \frac{\delta\ \alpha u}{\alpha\beta u^2 + \delta\ (\alpha+\beta)u + \gamma\delta} . \tag{15}$$

According to [5], the rate of photosynthetic production (specific growth rate μ) is proportional (there is a proportional constant κ) to the transition rate from the resting to the activated state, i. e.:

$$\mu = \kappa\gamma p_{A_{ss}} = \frac{\kappa\ \gamma\delta\ \alpha u}{\alpha\beta u^2 + \delta\ (\alpha+\beta)u + \gamma\delta} . \tag{16}$$

Equation (16) gives the relation between irradiance and production (growth) rate in the steady state. This steady state growth kinetics is of Haldane type [17] or *Substrate inhibition kinetics* [4] and we realise that the value of irradiance to maximise growth rate is $u_{\mathrm{opt}} = \sqrt{\gamma\delta/(\alpha\beta)}$ (see Figure 3).

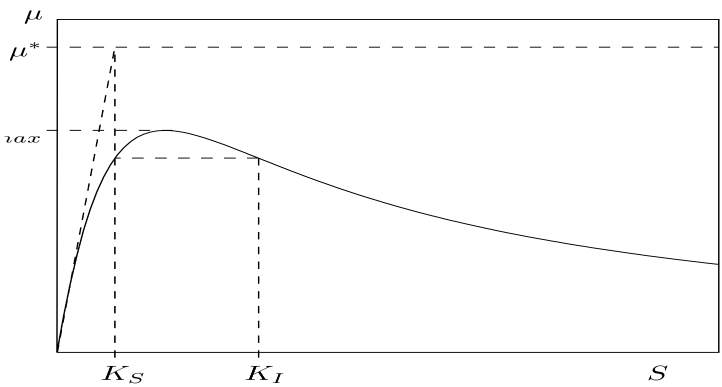

Fig. 3. Steady-state production curve of *Haldane* type or *Substrate inhibition kinetics*. The governing relation is: $\mu = \mu^* \ S/[K_S + S + S^2/K_I]$, where μ is specific growth rate and S is limiting substrate, $\mu^*,\ K_S,\ K_I$ are model constants. Maximum occurs at $S = (K_S\ K_I)^{0.5}$, when $\mu_{\max} = \mu^*/(2(K_S/K_I)^{0.5} + 1)$. The connection between PSF model and *Haldane kinetics* could be described as follows: $\mu^* = \kappa\gamma \cdot \frac{\alpha}{\alpha+\beta}$, $K_S = \gamma/(\alpha+\beta)$, and $K_I = \delta(\alpha+\beta)/(\alpha\beta)$. Note that for $K_I \to \infty$ (e. g. for $\frac{\beta}{\delta} \to 0$), the production curve is of Monod type.

Only three of the five parameters $(\kappa, \alpha, \beta, \gamma, \delta)$ could be estimated from the steady-state production curve of Haldane type. To estimate other two parameters corresponding to the time constants of two interconnected processes (i. e. photosynthetic light and dark reactions and photoinhibition), we need certain dynamic measurements.

Although Eilers and Peeters, in their first paper about PSF model [5], did not fully exploit the dynamic character of PSF model, precisely the simple connection between the growth process (specific growth rate μ) and the time averaged value of p_A is the most important advantage of PSF model, which permits e. g. modelling and simulations of the so-called flashing light experiments. The states of PSF model satisfactorily reflect the fluctuations of irradiance in time micro-scale and the averaging is made without loss of accuracy.

Before to continue working with PSF model, we will transform the vector of state variables as follows

$$\begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix} = \begin{bmatrix} p_R - 1 \\ p_A \\ p_B \end{bmatrix}. \tag{17}$$

The purpose of such a transformation is twice:

- To formulate our problem of microalgal growth, with the initial condition $x(t_0) = [x_{10}, x_{20}, x_{30}]^T$, in form of bilinear system Eq. (1), as we did in Subsection 2.1, enabling an application of our Theorem 2.

- To have the "natural" initial condition for PSF model, an initial state of vector x, in form of $x(t_0) = [0, 0, 0]^T$, which corresponds to the steady-state value for

$u = 0$, i.e. this initial state is reachable after a long incubation in the dark, when PSF is in its resting state.

Taking into account the linear dependence of the three states of PSF model (i.e. $x_1 + x_2 + x_3 = 0$), further only two state variables x_1 and x_2 will be used. The resulting ODE system is then:

$$\begin{bmatrix} \dot{x_1} \\ \dot{x_2} \end{bmatrix} = \begin{bmatrix} -\delta & \gamma - \delta \\ 0 & -\gamma \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} + u \begin{bmatrix} -\alpha & 0 \\ \alpha & -\beta \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} + \begin{bmatrix} -\alpha \\ \alpha \end{bmatrix} u, \qquad (18)$$

where α, β, γ and δ are rate constants of PSF model and $u(t)$ is the known scalar function. It is assumed that $u(t)$ is at least piecewise continuous.

The analytical solution of an initial value (Cauchy) problem, and the problem of quasi steady-state under intermittent light regime will be performed in Subsection 2.5, and 2.6, respectively.

2.5. Model of PSF and initial value problem

Eilers and Peeters presented in [6] a solution of ODE (13) for constant irradiance u and for "natural" initial condition $p_R(t_0) = 1$, and $p_A(t_0) = 0$. In this subsection, we will briefly present the solution of an initial value problem for the system (18), constant control variable $u > 0$, and *general* initial condition $x(t_0) = [x_{10}, x_{20}]^T$. The results cannot be simply used for $u = 0$, thus the same proceeding (i.e. eigenvectors and fundamental matrix determination) for $u = 0$ will be briefly presented in the end of this subsection.

The system matrix from (18), which could be described as $(A + uB)$, is regular, i.e. $\det(A + uB) \neq 0$, for all $u \geq 0$. First of all, we will look for the eigenvalues of system matrix $(A + uB)$, and for steady state solution. The matrix $(A + uB)$ has two negative eigenvalues λ_1, λ_2; see Eq. (22) and Eq. (23). Let be $|\lambda_1| > |\lambda_2|$. After some simplification, aiming to avoid loss of the precision in the numerical calculation,[2] the next formulas hold

$$\lambda_1 = -\frac{(\alpha+\beta)u + \gamma + \delta}{2} - \frac{\sqrt{[(\alpha-\beta)u + \gamma - \delta]^2 + 4\beta u(\gamma - \delta)}}{2}, \qquad (19)$$

$$\lambda_2 = -\frac{(\alpha+\beta)u + \gamma + \delta}{2} + \frac{\sqrt{[(\alpha-\beta)u + \gamma - \delta]^2 + 4\beta u(\gamma - \delta)}}{2}. \qquad (20)$$

The steady-state solution of (18) for a constant $u \geq 0$, $x_{ss} = [x_{1ss}, x_{2ss}]^T$, which will be used in the next as a particular solution of the system (18), is

$$\begin{bmatrix} x_{1ss} \\ x_{2ss} \end{bmatrix} = \begin{bmatrix} \frac{-(\delta+\beta u)\alpha u}{\lambda_1 \lambda_2} \\ \frac{\delta \cdot \alpha u}{\lambda_1 \lambda_2} \end{bmatrix}. \qquad (21)$$

[2] The ODE system (18) is *stiff* and the stiffness ratio is about 10^3 (depending on u). The eigenvalues λ_1 and λ_2 were calculated for the values of PSF model parameters α=1.935 $\times 10^{-3}$ μE^{-1} m^2, β=5.785 $\times 10^{-7}$ μE^{-1} m^2, γ=1.460 $\times 10^{-1}$ s^{-1}, δ=4.796 $\times 10^{-4}$ s^{-1}, taken from [19] for the microalga *Porphyridium* sp. and for the irradiance u=250 μE m^{-2} s^{-1}, with the result: λ_1=-0.63, λ_2=-0.59 10^{-3}.

Note that the steady-state solution is stable, because the eigenvalues of system matrix (18) are negative for every $u \geq 0$:

$$\lambda_1 \lambda_2 = (\alpha u + \beta u + \gamma)\delta + \alpha\beta u^2 = \det(A + uB) \ > \ 0, \tag{22}$$

and

$$\lambda_1 + \lambda_2 = -(\alpha u + \beta u + \gamma + \delta) \ < \ 0. \tag{23}$$

Let $u > 0$, then the *eigenvectors* K_1, K_2 of system matrix $(A + uB)$, and the *fundamental matrix* $\Phi(u,t)$ of ODE (18) are:

$$K_1 = \begin{bmatrix} (\gamma + \beta u + \lambda_1) \\ \alpha u \end{bmatrix}, \tag{24}$$

$$K_2 = \begin{bmatrix} -(\gamma + \beta u + \lambda_2) \\ -\alpha u \end{bmatrix}, \tag{25}$$

$$\Phi(u,t) = \begin{bmatrix} (\gamma + \beta u + \lambda_1)\mathrm{e}^{\lambda_1 t} & -(\gamma + \beta u + \lambda_2)\mathrm{e}^{\lambda_2 t} \\ \alpha u \mathrm{e}^{\lambda_1 t} & -\alpha u \mathrm{e}^{\lambda_2 t} \end{bmatrix}. \tag{26}$$

For the standard form of the solution of Cauchy problem the matrix $\Phi^{-1}(u, t_0)$ is needed. Let t_0 be set to 0, without loss of generality, then:

$$\Phi^{-1}(u) = \frac{1}{\lambda_1 - \lambda_2} \begin{bmatrix} 1 & (1 + \frac{\delta + \lambda_1}{\alpha u}) \\ 1 & (1 + \frac{\delta + \lambda_2}{\alpha u}) \end{bmatrix}, \tag{27}$$

and the solution of Cauchy problem can be presented in the standard form:

$$x(t) = \Phi(u,t)\ \Phi^{-1}(u)(x_0 - x_{ss}) + x_{ss}\ . \tag{28}$$

Further by the following equation:

$$U(u,t) = \Phi(u,t)\ \Phi^{-1}(u), \tag{29}$$

we define the matrix of transition or standard form of fundamental matrix.[3]

Now the special case for $u = 0$ will be treated: The ODE (18) is reduced to the form $\mathrm{d}x/\mathrm{d}t = Ax$, hence the eigenvalues are (-γ) and (-δ) and the matrices $\Phi(0,t)$ and $\Phi^{-1}(0)$ are:

$$\Phi(0,t) = \begin{bmatrix} \mathrm{e}^{-\gamma t} & \mathrm{e}^{-\delta t} \\ -\mathrm{e}^{-\gamma t} & 0 \end{bmatrix}, \tag{30}$$

$$\Phi^{-1}(0) = \begin{bmatrix} 0 & -1 \\ 1 & 1 \end{bmatrix}. \tag{31}$$

The matrix of transition $U(0,t)$ is now very simple:

$$U(0,t) = \begin{bmatrix} \mathrm{e}^{-\delta t} & (\mathrm{e}^{-\delta t} - \mathrm{e}^{-\gamma t}) \\ 0 & \mathrm{e}^{-\gamma t} \end{bmatrix}. \tag{32}$$

[3] Note that the product of fundamental matrices $\Phi(u,t)\ \Phi^{-1}(u)$ is unique, i. e. independent on the form of fundamental matrix $\Phi(u,t)$.

2.6. Model of PSF and periodic intermittent input signal

Having already resolved the initial value problem for the system with input variable u, we can advance to more specific case: the periodic intermittent input $u \in \{u_a, u_b\}$, with period $h = h_a + h_b$; see Figure 1.

In this case, as it will be seen during explicit computations later on, there exists a unique periodic solution of the system (18). Similar statement was obtained also e. g. in [8] (see Proposition 1) for the case of continuous periodic right hand side. Nevertheless, in our case the system (18) under influence of the intermittent input is the linear periodic system where the system matrix is discontinuous, but piecewise constant, so that our case is neither more, nor less general than the mentioned result in [8].

More specifically, we aim to prove that for every set of system parameters and parameters defining the intermittent input there exists an unique initial conditions, such that for the corresponding trajectory of (18) it holds that:

$$x(t) = x(t+h). \tag{33}$$

To show this property, let t_0 be the beginning of the "darker" a-interval of cycle, t_1 is the beginning of the "lighted" b-interval of cycle, and x_{ss_a}, resp. x_{ss_b} denotes the steady-state solution of (18), for $u = u_a$, resp. $u = u_b$. Then the above equation (33) to be proved is equivalent to the equality:

$$\begin{gathered} x(t_0) = \Phi(u_b, h_b)\ \Phi^{-1}(u_b)\times \\ \left\{\left[\Phi(u_a, h_a)\ \Phi^{-1}(u_a)(x(t_0) - x_{ss_a}) + x_{ss_a}\right] - x_{ss_b}\right\} + x_{ss_b}\ , \end{gathered} \tag{34}$$

where we set $t = t_0$ and after that the equation (28) have been used twice, first for $u = u_a$, then for $u = u_b$. For the common case of light/dark cycles, i. e. when u_a is actually equal to zero, taking into account that $x_{ss_a} = [0, 0]^T$, equation (34) can be rewritten as follows:

$$\left[I - U(u_b, h_b)U(0, h_a)\right] x(t_0) = \left[I - U(u_b, h_b)\right] x_{ss_b}. \tag{35}$$

Here, I is the (2×2)-dimensional identity matrix and $U(u_b, h_b)$, and $U(0, h_a)$ are matrices of transition defined by the equation (29), resp. by the equation (32).

Equation (35), which connects the unknown boundary value of state vector x with the model parameters $(\alpha, \beta, \gamma, \delta)$, the parameters of light/dark cycles $(h_a,\ h_b)$, and the value of input variable (u_b), is actually the system of two linear algebraic equations (LAE). The system matrix of LAE (35) is regular for every value of the light regime parameters, i. e. for every positive h_a, h_b, u_b, the determinant of system matrix (35) is positive:

$$\Delta_{\mathrm{Dir}} = \det\left[I - U(u_b, h_b)U(0, h_a)\right] >\ 0\ . \tag{36}$$

In other words, one can resolve uniquely the equation (35) with respect to $x(t_0)$ and therefore the periodic solution of ODE system (18) under periodic intermittent input signal exists and is unique.

After somewhat tedious calculation we receive the following symbolic expression for the determinant of the system matrix of LAE (35) and for the first and second component of state vector $x(t_0)$:

$$\begin{aligned}\Delta_{\mathrm{Dir}} &= 1+\mathrm{e}^{(h_b(\lambda_1+\lambda_2)-h_a(\gamma+\delta))}+\tfrac{\lambda_1+\delta}{\lambda_2-\lambda_1}\left(\mathrm{e}^{(\lambda_2 h_b-\delta h_a)}+\mathrm{e}^{(\lambda_1 h_b-\gamma h_a)}\right)\\ &\quad -\tfrac{\lambda_2+\delta}{\lambda_2-\lambda_1}\left(\mathrm{e}^{(\lambda_2 h_b-\gamma h_a)}+\mathrm{e}^{(\lambda_1 h_b-\delta h_a)}\right)\ ,\end{aligned} \tag{37}$$

$$\begin{aligned}x_1(t_0) &= -\tfrac{\alpha u_b}{(\lambda_2-\lambda_1)\ \Delta_{\mathrm{Dir}}}\{\,(\mathrm{e}^{\lambda_2 h_b}-\mathrm{e}^{\lambda_1 h_b})(1-\mathrm{e}^{-\delta h_a})\\ &\quad +(1-\mathrm{e}^{\lambda_1 h_b})\left[\tfrac{\delta}{\lambda_1}\,(1-\mathrm{e}^{(\lambda_2 h_b-\delta h_a)})+\tfrac{\beta u_b}{\lambda_1}\,(1-\mathrm{e}^{(\lambda_2 h_b-\gamma h_a)})\right]\\ &\quad -(1-\mathrm{e}^{\lambda_2 h_b})\left[\tfrac{\delta}{\lambda_2}\,(1-\mathrm{e}^{(\lambda_1 h_b-\delta h_a)})+\tfrac{\beta u_b}{\lambda_2}\,(1-\mathrm{e}^{(\lambda_1 h_b-\gamma h_a)})\right]\}\,,\end{aligned} \tag{38}$$

$$\begin{aligned}x_2(t_0) &= \tfrac{\alpha u_b}{(\lambda_2-\lambda_1)\ \Delta_{\mathrm{Dir}}}\,\{(\mathrm{e}^{\lambda_2 h_b}-\mathrm{e}^{\lambda_1 h_b})(1-\mathrm{e}^{-\delta h_a})\\ &\quad +\tfrac{\delta}{\lambda_1}\left(1-\mathrm{e}^{\lambda_1 h_b}\right)\left[1-\mathrm{e}^{(\lambda_2 h_b-\delta h_a)}\right]-\tfrac{\delta}{\lambda_2}\left(1-\mathrm{e}^{\lambda_2 h_b}\right)\left[1-\mathrm{e}^{(\lambda_1 h_b-\delta h_a)}\right]\}.\end{aligned} \tag{39}$$

The state vector x at the moment when the light is switched on, i.e. at the end of the first ("dark") interval of light/dark cycle when $t=t_1=t_0+h_a$, could be simply calculated using the Eq. (28). The other way is to use again the condition of periodicity (33) with new boundaries at $t=t_0+h_a$ and $t=t_0+h_a+h$. This represents more tedious calculation and served us as the proof of the next results:

$$\begin{aligned}x_1(t_1) &= -\tfrac{\alpha u_b}{(\lambda_2-\lambda_1)\ \Delta_{\mathrm{Dir}}}\,\{\mathrm{e}^{-\gamma h_a}(\mathrm{e}^{\lambda_2 h_b}-\mathrm{e}^{\lambda_1 h_b})(1-\mathrm{e}^{-\delta h_a})\\ &+(1-\mathrm{e}^{\lambda_1 h_b})\left[\tfrac{\delta}{\lambda_1}\ \mathrm{e}^{-\gamma h_a}\left(1-\mathrm{e}^{(\lambda_2 h_b-\delta h_a)}\right)+\tfrac{\beta u_b}{\lambda_1}\ \mathrm{e}^{-\delta h_a}\left(1-\mathrm{e}^{(\lambda_2 h_b-\gamma h_a)}\right)\right]\\ &-(1-\mathrm{e}^{\lambda_2 h_b})\left[\tfrac{\delta}{\lambda_2}\ \mathrm{e}^{-\gamma h_a}(1-\mathrm{e}^{(\lambda_1 h_b-\delta h_a)})+\tfrac{\beta u_b}{\lambda_2}\ \mathrm{e}^{-\delta h_a}(1-\mathrm{e}^{(\lambda_1 h_b-\gamma h_a)})\right]\},\end{aligned} \tag{40}$$

$$x_2(t_1)=\mathrm{e}^{-\gamma h_a}x_2(t_0)\ . \tag{41}$$

Once we have the values of state vector x at the moments when the light is switched on and off, the time course of state vector x in an arbitrary instant t of light/dark cycle could be easily determined by applying Eq. (28) with corresponding initial conditions and corresponding level of irradiance u. This will be used in the following section to calculate time-averaged value of state x_2.

Remark 3. The variables λ_1 , λ_2, resp. $-\gamma$, $-\delta$, in the above equations (37) – (41) are the eigenvalues of system matrix (18) for $u=u_b$ and $u=0$, respectively. Note also that in Eqs. (37) – (41), the model parameters, the parameters of light/dark cycles and the variable u_b are put together to form dimensionless expressions.

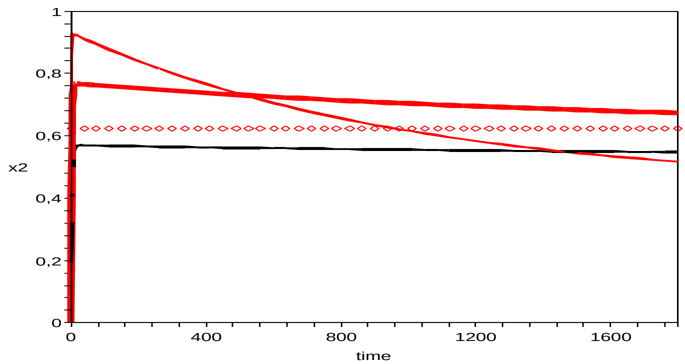

Fig. 4. Time course of the second component of state vector x under different values of irradiance (PFD). The dotted line represents the steady state value $x_{2_{ss}}$ for optimal value of PFD, i. e. for 250 μE m^{-2} s^{-1}. The bold line represents the case for $u_{\rm opt}$=250 μE m^{-2} s^{-1}. The bottom thin line corresponds to the case for u=100 μE m^{-2} s^{-1}. The line which firstly reaches the highest value of x_2 but finally falls to the lowest value of x_2 corresponds to the case for u =1000 μE m^{-2} s^{-1}. The simulations started from the "natural" initial condition $x = [0, 0]^T$, i. e. after a long time of incubation in the dark, and was stopped after $t = 1800$ s = 30 minutes. To reach the highest value of the state x_2 was necessary about 30 s.

3. RESULTS AND DISCUSSION

3.1. Relation for photosynthetic production of PSF Model

In this paper, we restrict ourselves to model the continuous reactor operation (e. g. chemostat or turbidostat, see [4, 17]). Hence, we work on previously not specified time interval. Further, in a real PBR, only the intermittent control signal u^{**}, i. e. the periodic switching between higher and lower irradiance induced by the flow regime (which depends either on the PBR design and on PBR operating conditions), is worth to consider. Applying the control signal u^{**}, the state vector x exhibits periodic behaviour after sufficiently large time of transition to so-called quasi–steady state. The quantification of the transient phenomena for PSF model and high–frequency light/dark cycles is governed by the relation:

$$x_{2av} = x_{2ss} + \frac{\alpha u_{av}}{\lambda_2 - \lambda_1}\left[-\mathrm{e}^{\lambda_1 t}\left(\frac{\delta}{\lambda_1}+1\right)+\mathrm{e}^{\lambda_2 t}\left(\frac{\delta}{\lambda_2}+1\right)\right], \tag{42}$$

and graphically depicted in Figure 4.

Accordingly to [5], the photosynthetic production is directly proportional to the average value of PSF closed state $x_{2_{av}}$; see Eq. (16), which represents the special case for $u = u_c$. The average value of state x_2 for the intermittent control signal u^{**}, when the "quasi–steady state" is reached, can be evaluated by the integration over one cycle period h:

$$x_{2_{av}} = \frac{1}{h}\int_{t_0}^{t_0+h} x_2(t)\,\mathrm{d}t = \frac{1}{h}\left(\int_{t_0}^{t_1} x_2(t)\,\mathrm{d}t \; + \int_{t_1}^{t_0+h} x_2(t)\,\mathrm{d}t\right). \tag{43}$$

Considering our previous results in Subsections 2.5 and 2.6, the further evaluation of Eq. (43) is straightforward and leads to the following result:

$$\begin{aligned} x_{2_{av}} &= \tfrac{h_b}{h} x_{2ss_b} + \tfrac{1-\mathrm{e}^{-\gamma h_a}}{\gamma h} x_2(t_0) + \tfrac{\alpha u_b}{\lambda_1\lambda_2\ h}\left(1 - \tfrac{\lambda_2 \mathrm{e}^{\lambda_1 h_b} - \lambda_1 \mathrm{e}^{\lambda_2 h_b}}{\lambda_2-\lambda_1}\right)(x_1(t_1) - x_{1ss_b}) \\ &+ \tfrac{\mathrm{e}^{\lambda_2 h_b} - \mathrm{e}^{\lambda_1 h_b}}{(\lambda_2-\lambda_1)\ h}(x_2(t_1) - x_{2ss_b}) + \tfrac{\alpha u_b + \delta}{\lambda_1\lambda_2\ h}\left(1 - \tfrac{\lambda_2 \mathrm{e}^{\lambda_1 h_b} - \lambda_1 \mathrm{e}^{\lambda_2 h_b}}{\lambda_2-\lambda_1}\right)(x_2(t_1) - x_{2ss_b})\ . \end{aligned} \tag{44}$$

This result could be expressed, accordingly to the Terry's work [18] in terms of light/dark cycle frequency $\nu = 1/h$, ratio $\phi_b = h_b/h$, and average irradiance $u_{av} = \phi_b u_b$. Such a choice of independent variables will be preferred in Subsection 3.3.

3.2. Intermittently optimal control

The main objective of our paper is to show that the bilinear system with single input models very well the behaviour of microalgal culture under both constant and intermittent light regime. The following Theorem 3 takes advantage of Theorem 2 and formulates a simple condition to achieve an extreme level of a performance index or cost functional. The motivation of Theorem 3 is more clear regarding to PSF model: It provides the tool for optimisation of intermittent input signal.[4]

Definition 3. Let us consider system (1) with initial state $x(t_0) = x_0$. Let have the constant control u_c on $[t_0, t_f]$, $u_c \in [u_\mathrm{a}, u_\mathrm{b}]$. By constant optimal control u_opt we denote such constant control that optimise (maximise or minimise) cost functional $J(u_c)$, given as

$$J(u_c) := \int_{t_0}^{t_f} f_0(x_c(t), u_c)\,\mathrm{d}t, \tag{45}$$

where $x_c(t)$ is the solution of system (1) with $u = u_c$. Let have the periodic intermittent piecewise constant control $u^{**}(t)$ on $[t_0, t_f]$, $u^{**}(t) \in \{u_\mathrm{a}, u_\mathrm{b}\}$. By ϕ_a, resp. ϕ_b let be denoted the ratios h_a/h, resp. h_b/h. By intermittently ϵ-optimal control $u^{**}_{\mathrm{opt},\epsilon}$ we denote such an intermittent control that

$$\frac{1}{t_f - t_0}\int_{t_0}^{t_f} \|x^{**}_\epsilon(t) - x_\mathrm{opt}(t)\|_{\mathbb{R}^n}\,\mathrm{d}t \le \epsilon. \tag{46}$$

where $x^{**}_\epsilon(t)$ and $x_\mathrm{opt}(t)$ are solutions of (1) for $u^{**}_{\mathrm{opt},\epsilon}(t)$ and u_opt respectively.

[4] The more cumbersome way to optimise light regime parameters of PSF model (i. e. mainly the optimisation of ratio $\phi_b = h_b/h$ for some value of light/dark cycle frequency and for some fixed value u_b) goes through the analysis of Eq. (44).

Theorem 3. Let system (1) with initial state $x(t_0) = x_0$ be given and let have the intermittent input signal $u^{**}_{u_a,u_b,h,\phi_a}$ determined by two constant parameters u_a, u_b and two variables h, ϕ_a. Then for any $\epsilon_J > 0$ exist h^{**} and ϕ_a^{opt} that for any $h \leq h^{**}$ it holds that the corresponding intermittent control $u^{**}_{u_a,u_b,h,\phi_a}$ is intermittently ϵ-optimal.

Proof. In order to prove assertion of Theorem 3 it only suffices to apply Theorem 1 and Theorem 2 and find the relations for h^{**} and ϕ_a^{opt} depending on ϵ_J. These relations we define in the following Lemma 2, thus proving Lemma 2, Theorem 3 will be proven too. □

Lemma 2. Let be done the relation between the values of u_{opt} and ϕ_a^{opt} as follows

$$u_{\mathrm{opt}} = \phi_a^{\mathrm{opt}}\ u_a + (1 - \phi_a^{\mathrm{opt}})\ u_b, \tag{47}$$

then estimate (46) is valid, if

$$h^{**} \leq \frac{\epsilon_J (u_b - u_a)}{K(u_b - u_{\mathrm{opt}})(u_{\mathrm{opt}} - u_a)}\ . \tag{48}$$

Proof. Lemma 2 will be proven in two steps:

1) Derivation of an auxiliary estimate using Theorem 1 and Theorem 2.
2) Derivation of the condition for maximal possible value of h (i. e. h^{**}), leading to the satisfaction of the condition (46), always when the ratio ϕ_a of light/dark cycles obeys the relation (47).

Let now proceed to each item separately:

Ad 1) Putting together the estimate Eq. (2) from Theorem 1 and estimate Eq. (9) from Lemma 1, the following estimate results:

$$\max{}_{t_0 \leq t \leq t_f} \|x^{**}(t) - x_c(t)\|_{\mathbb{R}^n} \leq K\ \ (u_{\mathrm{b}} - u_{\mathrm{a}})\frac{h_a}{h}\left(1 - \frac{h_a}{h}\right)\ h\ , \tag{49}$$

Further integration of this estimate (49) leads to

$$\int_{t_0}^{t_f} \|x^{**}(t) - x_c(t)\|_{\mathbb{R}^n}\, \mathrm{d}t \leq K\ \ (u_{\mathrm{b}} - u_{\mathrm{a}})\frac{h_a}{h}\left(1 - \frac{h_a}{h}\right)\ h\ (t_f - t_0)\ , \tag{50}$$

and finally

$$\frac{1}{t_f - t_0}\int_{t_0}^{t_f} \|x^{**}(t) - x_c(t)\|_{\mathbb{R}^n}\, \mathrm{d}t \leq K\ \ (u_{\mathrm{b}} - u_{\mathrm{a}})\frac{h_a}{h}\left(1 - \frac{h_a}{h}\right)\ h\ . \tag{51}$$

Ad 2) In order to satisfy the estimate (46) for an arbitrary $\epsilon_J > 0$, regarding the just derived estimate (51), we receive the following condition

$$\epsilon_J \leq K\ \ (u_{\mathrm{b}} - u_{\mathrm{a}})\frac{h_a}{h}\left(1 - \frac{h_a}{h}\right)\ h\ . \tag{52}$$

Then, after applying the relation (47), the condition for h^{**} in form of estimate (48) results and proof is completed. □

Remark 4. Theorem 3 seems to be an obvious extension of Theorem 2, i. e. also Theorem 3 states that for known constant optimal control u_{opt}, the corresponding trajectory of state vector x could be approximated by the trajectory of x under intermittent control $u^{**}_{u_a,u_b,h,\phi_a}$ on interval $[t_0, t_f]$ with an arbitrary precision (in sense of the Euclidean vector norm). Nevertheless, Theorem 3 and Lemma 2 give the answer about light-to-dark ratio and minimal light/dark cycle frequency (i. e. maximal h^{**}) to ensure intermittently optimal control for general BLSSI (1). Naturally, for a specific case, e. g. PSF model represented by ODE system (18), the constant K from estimate (2) and consequently h^{**} from estimate (48) could be evaluated exactly, e. g. employing Eq. (44). This problem and the problem of existence and finding of a ratio $\phi_a = h_a/h$, which optimise some functional J for some *given* h, is left to the near future.

3.3. Numerical simulations of growth experiments in flashing light

Many algal biotechnologists are still experimenting with influence of intermittent light on microalgal growth. These so-called *flashing light experiments* are described e. g. in [9, 14, 16, 18]. Although the first results of flashing light experiments were published some 50 years ago, no convincing conclusion was made in this topic.

The most relevant results of our numerical simulations based on data published in [19] are presented in the following figures.

Firstly, in Figure 5, the course of $x_{2_{av}}$ depending on frequency $\nu = 1/h$ is shown. The average value of irradiance is maintained constant and set to the characteristic value $u_{\text{opt}} = \sqrt{\gamma\delta/(\alpha\beta)}$, resulting in $250\,\mu\text{E}\,\text{m}^{-2}\text{s}^{-1}$ for model parameters taken from [19]. All three curves differing in value of ratio $\phi_b = h_b/h$ have the same superior limit, which is the steady state value of x_2 for $u = u_{\text{opt}}$ (the dotted curve). Hence, our general statement of Theorem 2 is confirmed in this special case of PSF model.

In Figure 6, the course of $x_{2_{av}}$ depending on ratio h_b/h is shown. Now, the value of incident irradiance u_b is set to $2000\,\mu\text{E}\,\text{m}^{-2}\,\text{s}^{-1}$ and ratio $\phi_b = h_b/h$ is the independent variable. Obviously, the average value of irradiance is varying accordingly to $u_b\phi_b$. Not all curves in this figure (differing in value of light/dark cycle frequency ν) show similar tendencies as the P–I curve of Haldane type kinetics (see Figure 3 of this paper). For lower light/dark cycle frequency (for periods h in order of tens of seconds) almost no light integration occurs (see the dotted curve), i. e. the photosynthetic growth could be calculated separately for light period and dark period.

The purpose of Figure 6 is either to verify Theorem 3 and to illustrate the old concept of photosynthetic production enhancement due to the flashing light. In outdoor condition, the value of incident irradiance could not be easily changed, therefore, the idea of "cutting light" or "light dilution" appeared on the laboratories of algal researchers. Two curves for light/dark cycle frequency of 0.1 Hz and 0.5 Hz have the sharp maximum for certain value of ratio $\phi_b = h_b/h$, i. e. cutting the period in some way into light and dark period enhances the growth. For high light/dark cycle frequency, the optimal ratio ϕ_b^{opt} could be calculated accordingly to Theorem 3 (in Figure 6, see that the curve for $\nu = 0.5\,\text{Hz}$ is almost identical to bold curve

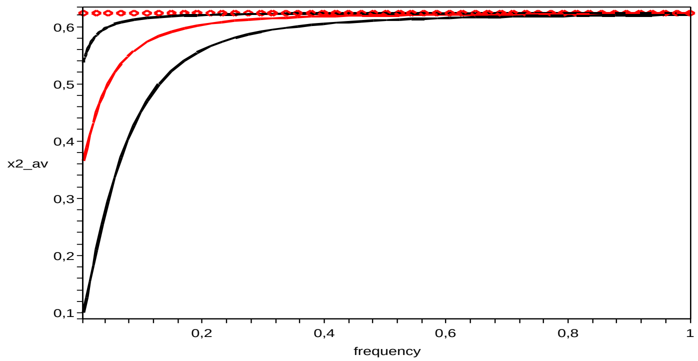

Fig. 5. Dependence of $x_{2_{av}}$, i. e. the second component of state vector x, on light/dark cycles frequency $\nu = 1/h$. For all curves the average value of irradiance was $250\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$. The dotted line represents the value of superior limit corresponding to the continuous light, $x_{2_{ss}}(250)$. Three full lines correspond from bottom to top to following values of light period-to-total period ratio h_b/h: 0.1, 0.5, and 0.8, respectively.

corresponding to the steady state relation).

The independent variable in the x-axis of Figure 7 is logarithm of light/dark cycle period duration $\log h$. The reason why is due to more evident comparison with experimental results published in work of Nedbal et al.; see Figure 2 in [14]. The average value of irradiance u_{av} is again maintained constant, but it is set to value of $500\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$, accordingly to [14]. All curves in Figure 7, differing in value of ratio h_b/h_a, show the same tendency as those in the Nedbal's paper, providing once again the perfect concordance with general Theorem 2, and at the same time proving the validity of our modelling approach based on bilinear systems.

4. CONCLUSIONS

The models describing microalgal growth are usually based on so-called P–I curve, i. e. on the empirical description of microbial kinetics. Thereafter, the interconnection between the steady state model and the dynamic one is often artificial, see e. g. the concept of *integration of light intensity – factor* Γ, introduced by Terry in [18].

In this paper, we have considered a bilinear system with single input as modelling framework for lumped parameter model of microalgal growth. We developed the earlier works [1, 2, 3] on bilinear systems and we studied its properties under periodic, piecewise constant input signal, i. e. under intermittent light regime. We have shown that the state trajectory of a bilinear system for a constant control signal can be approximated by the state trajectory corresponding to the intermittent control signal, with an arbitrary precision, depending on cycle period (see Theorem 2). Hence, the capacity described in [18] as the capacity of the "integration of light intensity" is inherent to bilinear systems.

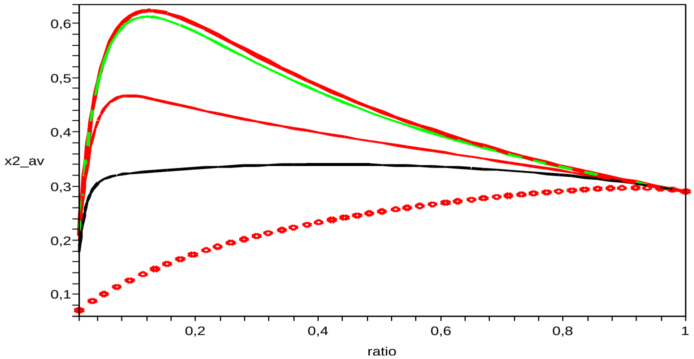

Fig. 6. Dependence of $x_{2_{av}}$ on ratio h_b/h for different values of light/dark cycles frequency ν. The maximal value of irradiance was $u_b = 2000\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$. The dotted line represents the case for $\nu = 0.01\,\mathrm{Hz}$, when almost no light integration occurs. Three full thin lines correspond from bottom to top to values of light/dark cycles with frequency 0.05 Hz, 0.1 Hz, and 0.5 Hz, respectively. Finally, the bold line corresponds to the steady state curve for continuous light and corresponding limits of irradiance (i. e. from 0 to $2000\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$).

In order to verify our theoretical results we have chosen the four-parameter model of photosynthetic factory as a model example. We first determined the steady state solution of PSF model, which leads to the substrate inhibition or Haldane type kinetics. Next we resolved an initial value (Cauchy) problem for the system of ordinary differential equations that qualitatively reproduces the dynamics of the states of photosynthetic factory. Then, knowing that the unique periodic solution of PSF model exists, we analytically resolved the time course of states of PSF under periodic intermittent input. Finally, the average value of state component x_2, which is directly proportional to the photosynthetic growth rate, was evaluated; see Eq. (44).

For the model parameters, published in [19], the numerical simulations of so-called flashing light experiments are presented as graphical outputs of calculations performed in the MAPLE programming environment [12]. We realise that our results are in good qualitative agreement with the experimental data measured by Nedbal et al. [14]. In all cases the asymptotic behaviour of growth rate was expected from Theorem 2, since the average value of input signal (i. e. the average irradiance in the culture) is normalised. The analysis of influence of light regime parameters on microalgal culture growth and the optimisation of parameters involved in cost functional related to average value of state component x_2, however, cannot be understood without a careful analysis of Eq. (44). Such analysis is currently under investigation. Nevertheless, Theorem 3 gives the answer to problem of light regime optimisation for the case when “sufficiently” high light/dark cycle frequency could be reached.

Resuming: our analytical modelling approach based on bilinear systems (leading to announcement of Theorem 2 and 3) reveals at the same time good qualitative properties and the coherence of model structure, permitting its further implementa-

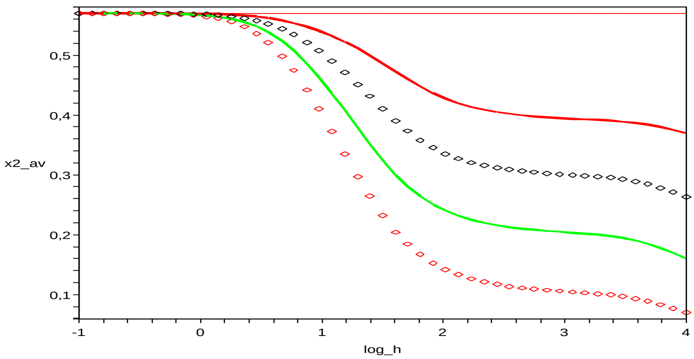

Fig. 7. Dependence of $x_{2_{av}}$ on light/dark cycle period h (in logarithmic scale) for different values of light-to-dark period h_b/h_a. Accordingly to [14], the average value of irradiance was $500\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$. Two dotted line correspond from bottom to top to the case for $h_b/h_a = 1:5$ and $h_b/h_a = 1:1$. Two full bold lines correspond from bottom to top to values of light-to-dark ratio 1:2 and 2:1, respectively. The thin line represents to the steady state value $x_{2_{ss}}$ for continuous light (i. e. for $500\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$).

tion into the distributed parameter model of microalgal growth.

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