Mathematical Biosciences and Engineering

http://www.aimspress.com/journal/mbe

MBE, 20(4): 6591–6611.
DOI: 10.3934/mbe.2023283
Received: 06 November 2022
Revised: 17 January 2023
Accepted: 27 January 2023
Published: 02 February 2023

Research article

Mathematical analysis of a two-tiered microbial food-web model for the anaerobic digestion process

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Abstract: In this research paper, we presented a four-dimensional mathematical system modeling the anaerobic mineralization of phenol in a two-step microbial food-web. The inflowing concentrations of the hydrogen and the phenol are considered in our model. We considered the case of general class of nonlinear growth kinetics, instead of Monod kinetics. Due to some conservative relations, the proposed model was reduced to a two-dimensional system. The stability of the steady states was carried out. Based on the species growth rates and the three main operating parameters of the model, represented by the dilution rate and input concentrations of the phenol and the hydrogen, we showed that the system can have up to four steady states. We gave the necessary and sufficient conditions ensuring the existence and the stability for each feasible equilibrium state. We showed that in specific cases, the positive steady state exists and is stable. We gave numerical simulations validating the obtained results.

Keywords: anaerobic digestion; chemostat; phenol mineralisation; food-web; local stability; global stability; optimal strategy

1. Introduction

Methanisation (also called biomethanisation or anaerobic digestion) is the natural biological process of degradation of organic matter in the absence of oxygen (anaerobic). It occurs naturally in certain sediments, marshes, rice fields, landfills, as well as in the digestive tract of certain animals, such as insects (termites) or ruminants. Part of the organic matter is broken down into methane, and another part is used by methanogenic microorganisms for their growth and reproduction. The decomposition is not complete, and leaves the ”digestate” (partly comparable to a compost).

Methanization is also a technique implemented in methanizers, where the process is accelerated and maintained to produce usable methane (biogas, called biomethane after purification). Organic waste (or products from energy crops, solid, or liquid) can thus be recovered in the form of energy.

Microbial anaerobic digestion plays an important role in the carbon cycle in nature with an advantage of producing hydrogen and methane. Methanisation results from the action of certain groups of interacting microbial microorganisms constituting a food web. We classically distinguish four successive phases: hydrolysis, acidogenesis, acetogenesis and methanogenesis.

Since the Anaerobic Digestion Model No.1.(ADM1) [1] is highly parametrized, only some numerical investigations are done [2]. More simpler mathematical models of microbial interaction are studied [3–9] in order to understand this microbial process.

In this paper, we consider a two-tiered model including substrate inhibition of the second population. The organisms involved in the resulting two-tiered model are the phenol degrader and the hydrogenotrophic methanogen. The phenol degrader grows on the phenol to form hydrogen, which inhibits its growth. The hydrogenotrophic methanogen grows on the produced hydrogen. This work is a generalization of a previous study [3]. An analytical approach, using a general representation of the specific growth rates, is given in [3], in the particular case with only influent phenol in the model. We included the inflow of hydrogen into the model, which was assumed to be equal to 0 in [3]. When there is no influent phenol and influent hydrogen, the system has only three steady states. However, the model in [3] was previously extended into several directions in the existing literature. Xu et al. [4] considered the same model but with the specific growth functions of type Monod (Holding type 2) and without inflow of hydrogen where the authors added decay terms of the species. Sari and Harmand [5] extended [3] by considering general growth functions. They extended also [4] by considering decay terms. Daoud et al. [6] extended [5] by adding the infow of hydrogen. Fekih-Salem et al. [7] extended [6] by considering the case where the rate of consumption of hydrogen is not necessarily an increasing function. The operating diagrams that show how the system behaves when varying the two control parameters (the dilution rate and the influent phenol) were obtained in [4–7]. We have, then, generalized the approach presented in [3] by including multiple substrate inflow into the model, and characterizing the stability of steady state. We have extended [3] by giving analytic results on the existence and stability of the four steady states and with general growth functions.

This paper is organized as the following: in Section 2, we present the mathematical model with a two-tiered microbial food-web, which takes into account the phenol and the hydrogen inflowing concentrations. We give the general assumptions on the microbial growth functions and some preliminary results on positivity and boundedness of solutions. Next, in Section 3, the model was reduced to a two-dimensional system. The necessary and sufficient conditions of existence, and local and global stability of the steady states are determined using the operating parameters and the species growth rates. In Section 4, we give the global behaviour of the main four-dimensional model. In Section 5, we propose an optimal strategy to maximise the size of both populations while minimising the input concentration of the hydrogen. In Section 6, we discuss some numerical simulations confirming the obtained theoretical results.

2. Mathematical model and properties

2.1. Mathematical model

The proposed normalised mathematical model is given by

$$\begin{cases} \dot{x}_1 &= (\theta f_1(p,h) - D)x_1, \\ \dot{x}_2 &= (f_2(h) - D)x_2, \\ \dot{p} &= D(p_{in} - p) - f_1(p,h)x_1, \\ \dot{h} &= D(h_{in} - h) + (1-\theta)f_1(p,h)x_1 - f_2(h)x_2, \end{cases} \tag{2.1}$$

where p_{in} and h_{in} are the input concentrations of phenol and hydrogen into the chemostat, respectively. D is the dilution rate. $\theta \in (0,1)$ is the part of the phenol consumed by the species 1, which is devoted to the growth of the species, the other part is transformed into hydrogen. $p(t)$ and $h(t)$ are the concentrations of phenol and hydrogen in the chemostat at time t, respectively. $x_i(t), i = 1,2$ is the i^{th} species concentration in the chemostat at time t.

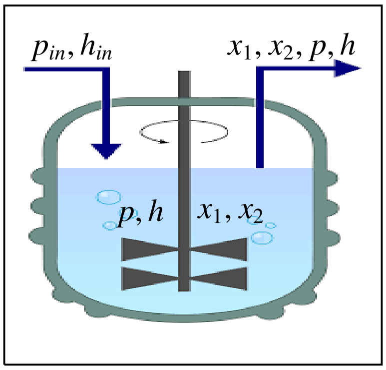

Figure 1. A chemostat is a continuous stirring mechanism (bioreactor) to which a limiting phenol concentration (p_{in}) and hydrogen concentration (h_{in}) are continuously added, while culture liquid (x_1, x_2, p, h) is continuously removed at the same flow rate (D) [10].

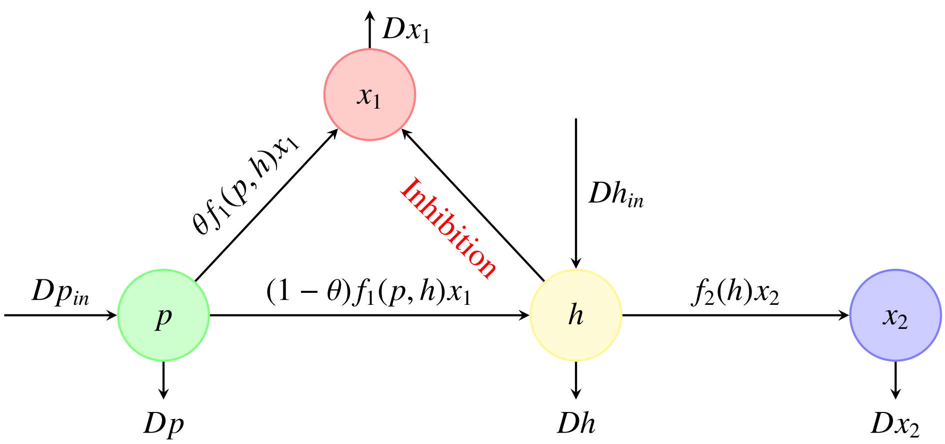

Figure 2. Two-tiered microbial food-web diagram.

$f_1(p,h)$: is the rate of consumption of phenol by species 1, depending on phenol and hydrogen.
$f_2(h)$: is the species 2 growth rate, depending only on hydrogen.
The functional responses $f_1 : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $f_2 : \mathbb{R}_+ \to \mathbb{R}_+$ are of class C^1, and satisfy

A1 $f_1(0,h) = f_2(0) = 0, \quad \forall\ h \in \mathbb{R}_+$,

A2 $\dfrac{\partial f_1}{\partial p}(p,h) > 0,$ and $\dfrac{\partial f_1}{\partial h}(p,h) < 0, \quad \forall\ (p,h) \in \mathbb{R}_+^2$.

A3 $f_2'(h) > 0, \quad \forall\ h \in \mathbb{R}_+$.

Hypothesis **A1** expresses that no growth can take place without phenol for species 1, and no growth can take place without hydrogen for species 2; hypothesis **A2** expresses that species 1 growth increases with the phenol concentration, but is inhibited by the hydrogen concentration. Hypothesis **A3** expresses that the species 2 growth increases with the hydrogen concentration.

Note that our model is a special case of the model considered by Sari et al. [9] when neglecting the dependence of the growth of species 2 on the phenol, and is also a special case of the model considered by Daoud et al. [6] when neglecting the decay terms.

2.2. *General properties*

Let us recall two fundamental well-known properties of the model of the chemostat [11].

Proposition 1. *1) For every initial condition* $(x_1(0), x_2(0), p(0), h(0)) \in \mathbb{R}_+^4$, *the corresponding solution admits positive and bounded components, and is then definite for all* $t \geq 0$.

2) The set $\Omega = \{(x_1, x_2, p, h) \in \mathbb{R}_+^4\ / x_1 + x_2 + p + h = p_{in} + h_{in}; x_1 + \theta p = \theta p_{in}; x_2 + (1-\theta)p + h = (1-\theta)p_{in} + h_{in}\}$ *is invariant and is an attractor of all solutions of system (2.1).*

Proof. The positivity of the solution is proved by the fact that:

If $x_i = 0$, then $\dot{x}_i = 0$ for $i = 1, 2$. If $p = 0$, then $\dot{p} = Dp_{in} > 0$, and if $h = 0$, then $\dot{h} = Dh_{in} > 0$.

Next, we have to prove the boundedness of solutions of (2.1). Consider $T_1(t) = x_1(t) + x_2(t) + p(t) + h(t) - p_{in} - h_{in}$, $T_2(t) = x_1(t) + \theta p(t) - \theta p_{in}$ and $T_3(t) = x_2(t) + (1-\theta)p(t) + h(t) - (1-\theta)p_{in} - h_{in}$.

$$\dot{T}_1(t) = \dot{x}_1(t) + \dot{x}_2(t) + \dot{p}(t) + \dot{h}(t) = D\Big(p_{in} + h_{in} - x_1(t) - x_2(t) - p(t) - h(t)\Big) = -DT_1(t),$$

$$\dot{T}_2(t) = \dot{x}_1(t) + \theta\dot{p}(t) = D\Big(\theta p_{in} - x_1(t) - \theta p(t)\Big) = -DT_2(t)$$

and

$$\dot{T}_3(t) = \dot{x}_2(t) + (1-\theta)\dot{p}(t) + \dot{h}(t) = D\Big((1-\theta)p_{in} + h_{in} - x_2(t) - (1-\theta)p(t) - h(t)\Big) = -DT_3(t)$$

then

$$T_1(t) = T_1(0)e^{-Dt}, T_2(t) = T_2(0)e^{-Dt} \text{ and } T_3(t) = T_3(0)e^{-Dt}.$$

Therefore,

$$x_1(t) + x_2(t) + p(t) + h(t) = p_{in} + h_{in} + (x_1(0) + x_2(0) + p(0) + h(0) - p_{in} - h_{in})e^{-Dt}, \tag{2.2}$$

$$x_1(t) + \theta p(t) = \theta p_{in} + (x_1(0) + \theta p(0) - \theta p_{in})e^{-Dt}, \tag{2.3}$$

and

$$x_2(t) + (1-\theta)p(t) + h(t) = (1-\theta)p_{in} + h_{in} + (x_2(0) + (1-\theta)p(0) + h(0) - (1-\theta)p_{in} - h_{in})e^{-Dt}. \tag{2.4}$$

Since all terms of the sum are positive, then the solution of system (2.1) is bounded.
The second point is a direct consequence of Eqs (2.2)–(2.4).

3. Reduction to the two-dimensional space

The solutions of the model (2.1) converge exponentially into the set Ω, and since we aim to study the asymptotic behavior of the system (2.1), it is sufficient to only study the asymptotic behavior of the restriction (2.1) on Ω. Therefore, thanks to Thieme's results [12], we can conclude on the asymptotic behavior of the complete system (2.1). Thus, in this section, we will study the restriction of system (2.1) on Ω which is simply the projection on the plane (x_1, x_2).

$$\left\{\begin{array}{lcl} \dot{x}_1 & = & (\theta f_1(p_{in} - \frac{x_1}{\theta}, h_{in} - x_2 + \frac{1-\theta}{\theta}x_1) - D)x_1, \\ \dot{x}_2 & = & (f_2(h_{in} - x_2 + \frac{1-\theta}{\theta}x_1) - D)x_2\ , \end{array}\right. \tag{3.1}$$

where the solution (x_1, x_2) of the reduced system (3.1) belongs to the following two-dimensional set:

$$\mathcal{S} = \left\{(x_1, x_2) \in \mathbb{R}_+{}^2 : 0 \leq x_1 \leq \theta p_{in};\ 0 \leq x_2 \leq h_{in} + \frac{1-\theta}{\theta}x_1\right\}.$$

3.1. Local analysis

Define $D_1 = \theta f_1(p_{in}, h_{in})$ and $D_2 = f_2(h_{in})$.

Lemma 1. *If $D < D_1$, then there exists a unique value $\bar{x}_1 \in (0, \theta p_{in})$ solution of the following equation:*

$$\theta f_1(p_{in} - \frac{x_1}{\theta}, h_{in} + \frac{1-\theta}{\theta}x_1) = D\ . \tag{3.2}$$

Proof. Let $\psi_1(x_1) = \theta f_1(p_{in} - \frac{x_1}{\theta}, h_{in} + \frac{1-\theta}{\theta}x_1) - D$. Since $\psi_1'(x_1) = -\frac{\partial f_1}{\partial p}(p_{in} - \frac{x_1}{\theta}, h_{in} + \frac{1-\theta}{\theta}x_1) + (1-\theta)\frac{\partial f_1}{\partial h}(p_{in} - \frac{x_1}{\theta}, h_{in} + \frac{1-\theta}{\theta}x_1) < 0$, $\psi_1(0) = D_1 - D$, $\psi_1(\theta p_{in}) = \theta f_1(0, h_{in} + (1-\theta)p_{in}) - D = -D < 0$, equation (3.2) admits a positive solution $\bar{x}_1 \in (0, \theta p_{in})$, if and only if, $D < D_1$. If this condition is satisfied, then (3.2) admits a unique solution since the function $\psi_1(.)$ is decreasing.

Lemma 2. *If $D < D_2$, then the equation $f_2(h) = D$ admits a unique solution $h^* \in (0, h_{in})$.*

Proof. The proof is evident since $f_2 : \mathbb{R}_+ \to \mathbb{R}_+$ is a continuous increasing function, and $f_2(0) = 0 < D < D_2 = f_2(h_{in})$, meaning there exists a unique value $h^* \in (0, h_{in})$ solution of $f_2(h) = D$.

Let $D_3 = \theta f_1(p_{in}, h^*)$ and $D_4 = f_2(h_{in} + \frac{1-\theta}{\theta}\bar{x}_1)$. Note that $D_1 < D_3$ and $D_2 < D_4$.

The equilibrium points of system (3.1) are given by $F_0 = (0,0), F_1 = (\bar{x}_1, 0)$, $F_2 = (0, h_{in} - h^*)$ and $F^* = (x_1^*, x_2^*)$, where x_1^* and x_2^* satisfy

$$\begin{cases} \theta f_1(p_{in} - \frac{x_1^*}{\theta}, h_{in} - x_2^* + \frac{1-\theta}{\theta}x_1^*) = D, \\ f_2(h_{in} - x_2^* + \frac{1-\theta}{\theta}x_1^*) = f_2(h^*) = D. \end{cases} \tag{3.3}$$

The Jacobian matrix J of system (3.1) on a point (x_1, x_2) is given by :

$$J = \begin{bmatrix} \theta f_1 - D - \frac{\partial f_1}{\partial p}x_1 + (1-\theta)\frac{\partial f_1}{\partial h}x_1 & -\theta\frac{\partial f_1}{\partial h}x_1 \\ \frac{1-\theta}{\theta}f_2' x_2 & f_2 - D - f_2' x_2 \end{bmatrix} \tag{3.4}$$

where f_1 is evaluated at $(p_{in} - \frac{x_1}{\theta}, h_{in} - x_2 + \frac{1-\theta}{\theta}x_1)$ and f_2 is evaluated at $h_{in} - x_2 + \frac{1-\theta}{\theta}x_1$.

The conditions of existence of the equilibria are stated in the following lemmas.

Lemma 3. *The trivial equilibrium point F_0 exists always. F_0 is an unstable node if $D < \min(D_1, D_2)$. F_0 is a saddle point if $\min(D_1, D_2) < D < \max(D_1, D_2)$. It is a stable node if $D > \max(D_1, D_2)$.*

Proof. The Jacobian matrix J_0 of system (3.1) on $F_0 = (0,0)$ is then given by :

$$J_0 = \begin{bmatrix} \theta f_1(p_{in}, h_{in}) - D & 0 \\ 0 & f_2(h_{in}) - D \end{bmatrix} = \begin{bmatrix} D_1 - D & 0 \\ 0 & D_2 - D \end{bmatrix}.$$

Their eigenvalues are given by $\lambda_1 = D_1 - D$ and $\lambda_2 = D_2 - D$. Therefore, if $D < \min(D_1, D_2)$, then F_0 is an unstable node, and if $\min(D_1, D_2) < D < \max(D_1, D_2)$, then F_0 is a saddle point, and if $D > \max(D_1, D_2)$, then F_0 is a stable node.

Lemma 4. *The equilibrium point F_1 exists if, and only if, $D < D_1$. If F_1 exists, then it is a stable node if $D > D_4$, and it is a saddle point if $D < D_4$.*

Proof. An equilibrium F_1 exists, if and only if, $\bar{x}_1 \in]0, \theta p_{in}[$ is a solution of Eq (3.2), which admits a unique positive solution, if and only if, $D < D_1$.

Assume that F_1 exists ($D < D_1$). The Jacobian matrix J_1 of system (3.1) at $F_1 = (\bar{x}_1, 0)$ is given by:

$$J_1 = \begin{bmatrix} -\frac{\partial f_1}{\partial p}\bar{x}_1 + (1-\theta)\frac{\partial f_1}{\partial h}\bar{x}_1 & -\theta\frac{\partial f_1}{\partial h}\bar{x}_1 \\ 0 & f_2 - D \end{bmatrix} = \begin{bmatrix} -\frac{\partial f_1}{\partial p}\bar{x}_1 + (1-\theta)\frac{\partial f_1}{\partial h}\bar{x}_1 & -\theta\frac{\partial f_1}{\partial h}\bar{x}_1 \\ 0 & D_4 - D \end{bmatrix},$$

where the partial derivatives are evaluated at $p = p_{in} - \frac{\bar{x}_1}{\theta}$ and $h = h_{in} + \frac{1-\theta}{\theta}\bar{x}_1$. J_1 admits two eigenvalues given by $\lambda_1 = -\frac{\partial f_1}{\partial p}\bar{x}_1 + (1-\theta)\frac{\partial f_1}{\partial h}\bar{x}_1 < 0$ and $\lambda_2 = D_4 - D$. It follows that F_1 is a stable node if $D > D_4$, and it is a saddle point if $D < D_4$.

Lemma 5. *The equilibrium point F_2 exists if, and only if, $D < D_2$. If F_2 exists, then it is a stable node if $D > D_3$, and it is a saddle point if $D < D_3$.*

Proof. An equilibrium F_2 exists if, and only if $h^* \in]0, h_{in}[$ is a solution of the equation $f_2(h) = D$, which admits a unique positive solution if, and only if, $D < D_2$.

Assume that F_2 exists ($D < D_2$). The Jacobian matrix J_2 of system (3.1) at $F_2 = (0, h_{in} - h^*)$ is

$$J_2 = \begin{bmatrix} \theta f_1 - D & 0 \\ \frac{1-\theta}{\theta}(h_{in} - h^*)f_2' & -(h_{in} - h^*)f_2' \end{bmatrix} = \begin{bmatrix} D_3 - D & 0 \\ \frac{1-\theta}{\theta}(h_{in} - h^*)f_2' & -(h_{in} - h^*)f_2' \end{bmatrix},$$

where the partial derivatives are evaluated at $p = p_{in}$ and $h = h^*$. J_2 admits two eigenvalues given by $\lambda_1 = D_3 - D$ and $\lambda_2 = -f_2'(h^*)(h_{in} - h^*) < 0$. It follows that F_2 is a stable node if $D > D_3$, and it is a saddle point if $D < D_3$.

Lemma 6. *If equilibria F_1, F_2 and F^* exist, then they satisfy $x_1^* > \bar{x}_1$ and $x_2^* > h_{in} - h^*$.*

Proof. Using the function ψ_1 one has :

$$\psi_1(x_1^*) = \theta f_1(p_{in} - \frac{x_1^*}{\theta}, h_{in} + \frac{1-\theta}{\theta}x_1^*) - D < \theta f_1(p_{in} - \frac{x_1^*}{\theta}, h_{in} - x_2^* + \frac{1-\theta}{\theta}x_1^*) - D = 0 = \psi_1(\bar{x}_1)$$

then $\psi_1(x_1^*) < \psi_1(\bar{x}_1)$ from where $x_1^* > \bar{x}_1$, since the $\psi_1(.)$ is decreasing. In the same way,

$$f_2(h_{in} - x_2^*) < f_2(h_{in} - x_2^* + \frac{1-\theta}{\theta}x_1^*) = D = f_2(h_{in} - (h_{in} - h^*)),$$

then $x_2^* > h_{in} - h^*$ since the function $f_2(.)$ is increasing.

Lemma 7. *The equilibrium point F^* exists if, and only if, $D < \min(D_3, D_4)$. If F^* exists, then it is always a stable node.*

Proof. An equilibrium F^* exists if, and only if, the following holds

$$\begin{cases} D = \theta f_1(p_{in} - \frac{x_1^*}{\theta}, h_{in} - x_2^* + \frac{1-\theta}{\theta}x_1^*) = \theta f_1(p^*, h^*), \\ D = f_2(h_{in} - x_2^* + \frac{1-\theta}{\theta}x_1^*) = f_2(h^*). \end{cases} \tag{3.5}$$

Since the function f_2 is increasing, then the equation $f_2(h) = D$ admits a unique solution $h^* \in (0, h_{in} + \frac{1-\theta}{\theta}\bar{x}_1)$ if, and only if, $D < D_4 = f_2(h_{in} + \frac{1-\theta}{\theta}\bar{x}_1)$. Now, since f_1 is an increasing function with respect to its first variable, p, then the equation $\theta f_1(p, h^*) = D$ admits a unique solution $p^* \in (0, p_{in})$ if, and only if, $D < D_3 = \theta f_1(p_{in}, h^*)$. Since $p^* \in (0, p_{in})$, therefore $0 < x_1^* = \theta(p_{in} - p^*) < \theta p_{in}$. Similarly, since $D = f_2(h^*) < D_4 = f_2(h_{in} + \frac{1-\theta}{\theta}\bar{x}_1) < f_2(h_{in} + \frac{1-\theta}{\theta}x_1^*)$ by Lemma 6. Therefore, $h^* < h_{in} + \frac{1-\theta}{\theta}x_1^*$, since f_2 is an increasing function. Then, $x_2^* = h_{in} + \frac{1-\theta}{\theta}x_1^* - h^* > 0$. Therefore, the equilibrium point F^* exists if, and only if, $D < \min(D_3, D_4)$.

Assume that F^* exists. The Jacobian matrix J^* of system (3.1) at $F^* = (x_1^*, x_2^*)$ is:

$$J^* = \begin{bmatrix} -\frac{\partial f_1}{\partial p} x_1^* + (1-\theta)\frac{\partial f_1}{\partial h} x_1^* & -\theta \frac{\partial f_1}{\partial h} x_1^* \\ \frac{1-\theta}{\theta} f_2' x_2^* & -f_2' x_2^* \end{bmatrix},$$

where the partial derivatives are evaluated at $p = p_{in} - \frac{x_1^*}{\theta}$ and $h = h^*$. Note that trace(J^*)= $-\frac{\partial f_1}{\partial p} x_1^* + (1-\theta)\frac{\partial f_1}{\partial h} x_1^* - f_2' x_2^* < 0$ and det(J^*)= $\frac{\partial f_1}{\partial p} f_2' x_1^* x_2^* > 0$. Then, J^* admits two eigenvalues with negative real parts. It follows that, if it exists, F^* is a stable node.

The Lemmas 3–7 are summarized in Table 1. The number of equilibrium points of system (3.1) and their nature are given hereafter.

Table 1. Existence and local stability of steady-states.

Steady-state	Existence condition	Stability condition
F_0	Always exists	$\max(D_1, D_2) < D$
F_1	$D < D_1$	$D_4 < D$
F_2	$D < D_2$	$D_3 < D$
F^*	$D < \min(D_3, D_4)$	Always stable

Theorem 1.

1) If $D < \min(D_1, D_2)$, then system (3.1) admits four equilibria F_0, F_1, F_2 and F^*. F_0 is an unstable node, F_1 and F_2 are saddle points, and F^* is a stable node.

2) If $D_2 < D < \min(D_1, D_4)$, then system (3.1) admits three equilibria F_0, F_1 and F^*. F_0 and F_1 are saddle points, and F^* is a stable node.

3) If $D_1 < D < \min(D_2, D_3)$, then system (3.1) admits three equilibria F_0, F_2 and F^*. F_0 and F_2 are saddle points, and F^* is a stable node.

4) If $D_4 < D < D_1$, then then system (3.1) admits two equilibria F_0, and F_1. F_0 is a saddle point and F_1 is a stable node.

5) If $D_3 < D < D_2$, then system (3.1) admits two equilibria F_0 and F_2. F_0 is a saddle point, and F_2 is a stable node.

6) If $\max(D_1, D_2) < D$, then system (3.1) admits a unique equilibrium point, F_0, which is a stable node.

3.2. Global analysis

We first prove that the reduced system (3.1) hasn't no periodic orbit nor poly-cycle on $\mathcal{S}$.

Theorem 2. *System (3.1) has no periodic orbits nor poly-cycles on $\mathcal{S}$.*

Proof. Consider a solution of system (3.1) on $\mathcal{S}$. Let $\xi_1 = \ln(x_1)$ and $\xi_2 = \ln(x_2)$, then the transformation of (3.1) gives the following new system:

$$\begin{cases} \dot{\xi}_1 &= h_1(\xi_1, \xi_2) := \theta f_1(p_{in} - \frac{e^{\xi_1}}{\theta}, h_{in} - e^{\xi_2} + \frac{1-\theta}{\theta} e^{\xi_1}) - D, \\ \dot{\xi}_2 &= h_2(\xi_1, \xi_2) := f_2(h_{in} - e^{\xi_2} + \frac{1-\theta}{\theta} e^{\xi_1}) - D. \end{cases} \tag{3.6}$$

We have

$$\frac{\partial h_1}{\partial \xi_1} + \frac{\partial h_2}{\partial \xi_2} = -e^{\xi_1} \frac{\partial f_1}{\partial p} + (1-\theta) e^{\xi_1} \frac{\partial f_1}{\partial h} - e^{\xi_2} f_2' < 0.$$

Thus, using Dulac criterion [11], system (3.6) has no periodic trajectory. Therefore, system (3.1) has no periodic orbit inside $\mathcal{S}$.

Theorem 3. *The solution of (3.1) converges asymptotically to :*

- F^* *if* $D < \min(D_3, D_4)$.
- F_1 *if* $D_4 < D < D_1$.
- F_2 *if* $D_3 < D < D_2$.
- F_0 *if* $\max(D_1, D_2) < D$.

Proof. We restrict the proof to the case where $D < \min(D_1, D_2)$. The other cases can be done similarly. The system (3.1) admits four equilibrium points F_0, F_1, F_2 and F^*. F_0 is an unstable node, F_1 and F_2 are two saddle points, and only F^* is a stable node. We aim to prove that F^* is globally asymptotically stable. Let $x_1(0) > 0, x_2(0) > 0$ and ω, the ω-limit set of $(x_1(0), x_2(0))$. ω is an invariant compact set and $\omega \subset \bar{\mathcal{S}}$. Assume that ω contains a point M on the x_1x_2 axis :

- M can't be F_0 because F_0 is an unstable node and can't be a part of the ω-limit set of $(x_1(0), x_2(0))$,
- If $M \in]\bar{x}_1, \theta p_{in}] \times \{0\}$ (respectively, $M \in \{0\} \times]h_{in} - h^*, h_{in} + (1-\theta) p_{in}]$). As ω is invariant, then $\gamma(M) \subset \omega$ which is impossible because ω is bounded and $\gamma(M) =]\bar{x}_1, +\infty[\times \{0\}$ (respectively, $\gamma(M) = \{0\} \times]h_{in} - h^*, +\infty[$),
- If $M \in]0, \bar{x}_1[\times \{0\}$ (respectively, $M \in \{0\} \, , \times]0, h_{in} - h^*[$). ω contains $\gamma(M) =]0, \bar{x}_1[\times \{0\}$ (respectively, $\gamma(M) = \{0\} \times]0, h_{in} - h^*[$). As ω is a compact, then it contains the adherence of $\gamma(M)$, $[0, \bar{x}_1] \times \{0\}$ (respectively $\{0\} \times [0, h_{in} - h^*]$). In particular, ω contains F_0, which is impossible,
- If $M = F_1$ (respectively, $M = F_2$), then ω is not reduced to F_1 (respectively, to F_2). By the Butler-McGehee theorem, ω contains a point P of $(0, +\infty) \times \{0\}$ other that F_1 (respectively, of $\{0\} \times (0, +\infty)$ other that F_2) which is impossible.

Finally, the ω-limit set does not contain any point on the x_1x_2 axis. System (3.1) has no periodic orbit inside $\mathcal{S}$. Using the Poincaré-Bendixon Theorem [11], F^* is a globally asymptotically stable equilibrium point for system (3.1).

4. Back to the four-dimensional space

In this section, we state and prove the main results of the paper. The equilibrium points of system (2.1) are $E_0 = (0, 0, p_{in}, h_{in})$, $E_1 = (\bar{x}_1, 0, \bar{p}, \bar{h})$, $E_2 = (0, h_{in} - h^*, p_{in}, h^*)$ and $E^* = (x_1^*, x_2^*, p^*, h^*)$, where $\bar{p} = p_{in} - \frac{\bar{x}_1}{\theta}$ and $\bar{h} = h_{in} + \frac{1-\theta}{\theta}\bar{x}_1$.

Theorem 4. *For every initial condition in $\mathbb{R}_+^4$, the trajectories of (2.1) converge asymptotically to :*

- *E^* if $D < \min(D_3, D_4)$.*
- *E_1 if $D_4 < D < D_1$.*
- *E_2 if $D_3 < D < D_2$.*
- *E_0 if $\max(D_1, D_2) < D$.*

Proof. Let $(x_1(t), x_2(t), p(t), h(t))$ be a solution of (2.1). From (2.3) and (2.4), we deduce that

$$p(t) = p_{in} - \frac{x_1}{\theta} + K_1 e^{-Dt} \quad \text{and} \quad h(t) = h_{in} - x_2 + \frac{1-\theta}{\theta}x_1 + K_2 e^{-Dt},$$

where $K_1 = p(0) + \frac{x_1(0)}{\theta} - p_{in}$ and $K_2 = h(0) + x_2(0) - \frac{1-\theta}{\theta}x_1(0) - h_{in}$. Hence, $(x_1(t), x_2(t))$ is a solution of the non-autonomous system of two differential equations :

$$\begin{cases} \dot{x}_1 &= \left(\theta f_1(p_{in} - \frac{x_1}{\theta} + K_1 e^{-Dt}, h_{in} - x_2 + \frac{1-\theta}{\theta}x_1 + K_2 e^{-Dt}) - D\right)x_1, \\ \dot{x}_2 &= \left(f_2(h_{in} - x_2 + \frac{1-\theta}{\theta}x_1 + K_2 e^{-Dt}) - D\right)x_2. \end{cases} \tag{4.1}$$

This system (4.1) is an asymptotically, non-autonomous differential system that converges to the autonomous system (3.1). It turns out that system (3.1) contains only, locally exponentially stable and unstable equilibria, and neither periodic orbits nor cyclic chains. Thus, Thiemes's results [12] can be applied to deduce the asymptotic behaviours of the solutions of the complete system (4.1) from the asymptotic behaviours of the solutions of the reduced system (3.1).

Recall that our model is a special case of the model considered by Daoud et al. [6] when neglecting the decay terms. In order to prove that the existence and stability results obtained in Theorem 1 agree with those in [6, Proposition 3.2 and Theorem 5.2], we first scale system (2.1) using the following change of variables and notations : $s_0 = p$, $s_0^{in} = p_{in}$, $x_0 = \frac{x_1}{\theta}$, $x_1 = \frac{x_2}{1-\theta}$, $s_1 = \frac{h}{1-\theta}$, $s_1^{in} = \frac{h_{in}}{1-\theta}$. The dimensionless system thus obtained is :

$$\begin{cases} \dot{s}_0 &= D(s_0^{in} - s_0) - \mu_0(s_0, s_1)x_0 \,, \\ \dot{x}_0 &= \mu_0(s_0, s_1)x_0 - Dx_0 \,, \\ \dot{s}_1 &= D(s_1^{in} - s_1) - \mu_1(s_1)x_1 + \mu_0(s_0, s_1)x_0 \,, \\ \dot{x}_1 &= \mu_1(s_1)x_1 - Dx_1 \,, \end{cases} \tag{4.2}$$

where $\mu_0(s_0, s_1) = \theta f_1(p, h)$ and $\mu_1(s_1) = f_2(h)$. This is exactly the model considered by Daoud et al. [6] when neglecting the decay terms.

In Table 2, we will give a comparison of existence and stability results with those of [6] using the notations of [6]. Firstly, note that the equilibrium points of system (2.1) given by E_0, E_1, E_2 and E^* are equivalent to those of [6] noted by $SS0$, $SS1$, $SS3$ and $SS2$, respectively.

Note that $s_0^{in} < F_0(D)$ (respectively, $s_0^{in} > F_0(D)$) in [6] is equivalent to $D_1 < D$ (respectively, $D_1 > D$) in our case. $s_0^{in} < F_2(D)$ (respectively, $s_0^{in} > F_2(D)$) in [6] is equivalent to $D_3 < D$ (respectively, $D_3 > D$) in our case. $F_1(D) < s_0^{in} + s_1^{in}$ (respectively, $F_1(D) > s_0^{in} + s_1^{in}$) in [6] is equivalent to $D < D_4$ (respectively, $D_4 < D$) in our case.

Table 2. Comparison of existence and stability results with those of [6].

	Existence and stability conditions	Equilibria	Stable	Unstable
Our case	$D < \min(D_1, D_2)$	E_0, E_1, E_2, E^*	E^*	E_0, E_1, E_2
In [6]	$D < \bar{D}, F_0(D) < s_0^{in}$	$SS0, SS1, SS3, SS2$	$SS2$	$SS0, SS1, SS3$
Our case	$D_2 < D < \min(D_1, D_4)$	E_0, E_1, E^*	E^*	E_0, E_1
In [6]	$\bar{D} < D, F_1(D) < s_0^{in} + s_1^{in}, F_0(D) < s_0^{in}$	$SS0, SS1, SS2$	$SS2$	$SS0, SS1$
Our case	$D_1 < D < \min(D_2, D_3)$	E_0, E_2, E^*	E^*	E_0, E_2
In [6]	$D < \bar{D}, F_2(D) < s_0^{in} < F_0(D)$	$SS0, SS3, SS2$	$SS2$	$SS0, SS3$
Our case	$D_4 < D < D_1$	E_0, E_1	E_1	E_0
In [6]	$\bar{D} < D, F_0(D) < s_0^{in} < F_1(D) - s_1^{in}$	$SS0, SS1$	$SS1$	$SS0$
Our case	$D_3 < D < D_2$	E_0, E_2	E_2	E_0
In [6]	$D < \bar{D}, s_0^{in} < F_2(D)$	$SS0, SS3$	$SS3$	$SS0$
Our case	$\max(D_1, D_2) < D$	E_0	E_0	
In [6]	$\bar{D} < D, s_0^{in} < F_0(D)$	$SS0$	$SS0$	

5. Optimal control problem via input concentration of hydrogen

Over the last few years, there is an increasing focus on alternative energy sources to reduce reliance on fossil fuels [13]. Fermentative biogas rich in either hydrogen or methane from organic wastes is widely considered as a clean and environmentally-friendly source of energy [14, 15], as it combines waste treatment and renewable energy production [16]. Further, it can be produced by several methods comprising biological and electrochemical processes. Bio-photolysis of water, photo fermentation, and dark fermentation have grown in popularity in bio-hydrogen production. Such interest is due to their low investment costs compared with photocatalytic, oxidation, and other chemical technologies [17]. Several studies were designed to assess the applicability of various modeling tools for representing hydrogen and methane co-production kinetics from food waste [18, 19]. The goal of this section, based on the considered model (2.1), is to propose an optimal strategy to maximise the size of both populations while minimising the input concentration of the hydrogen.

Let us consider an optimal strategy using a time-varying control function $h_{in}(t)$ expressing the input concentration of hydrogen. Assume that f_1 and f_2 are globally Lipschitz with an upper bounds $\bar{f_1} = \sup_{p,h>0} f_1(p,h)$ and $\bar{f_2} = \sup_{h>0} f_2(h)$, and Lipschitz constants L_1 and L_2, respectively. For finite final time T, the control set $\mathbf{P_{ad}}$ is

$$\mathbf{P_{ad}} = \{h_{in}(t) : 0 \le h_{in}^{\min} \le h_{in}(t) \le h_{in}^{\max},\ 0 \le t \le T,\ h_{in}(t) \text{ is Lebesgue measurable}\}.$$

The goal is to find the control $h_{in}(t)$ and the associated state variables $x_1(t)$, $x_2(t)$, $p(t)$ and $h(t)$ to minimize the following objective functional:

$$J(h_{in}) = \int_0^T \Big(-\alpha_1 x_1(t) - \alpha_2 x_2(t) + \frac{\alpha_3}{2} h_{in}^2(t) \Big)\, dt.$$

By choosing appropriate positive balancing constants, α_1, α_2 and α_3, the goal is to maximize the size of the two populations while minimizing the cost of the control. One can show by standard results that an optimal control and corresponding optimal states exist [20]. For $\varphi = (x_1, x_2, p, h)^t$, the model (2.1) can be written as follows

$$\dot{\varphi} = A\varphi + F(\varphi) = G(\varphi) \tag{5.1}$$

where $A = \begin{pmatrix} -D & 0 & 0 & 0 \\ 0 & -D & 0 & 0 \\ 0 & 0 & -D & 0 \\ 0 & 0 & 0 & -D \end{pmatrix}$ and $F(\varphi) = \begin{pmatrix} \theta f_1(p,h)x_1 \\ f_2(h)x_2 \\ Dp_{in} - f_1(p,h)x_1 \\ Dh_{in} + (1-\theta)f_1(p,h)x_1 - f_2(h)x_2 \end{pmatrix}$.

Proposition 2. *G is a uniformly Lipschitz continuous function.*

Proof. F is a uniformly Lipschitz continuous function since

$$\begin{aligned}
\left\|F(\varphi') - F(\varphi)\right\|_1 &= \left|\theta f_1(p',h')x_1' - \theta f_1(p,h)x_1\right| + \left|f_2(h')x_2' - f_2(h)x_2\right| + \left| - f_1(p',h')x_1' + f_1(p,h)x_1\right| \\
&\quad + \left|(1-\theta)f_1(p',h')x_1' - f_2(h')x_2' - (1-\theta)f_1(p,h)x_1 + f_2(h)x_2\right| \\
&\le \theta\left|f_1(p',h')x_1' - f_1(p,h)x_1\right| + \left|f_2(h')x_2' - f_2(h)x_2\right| + \left|f_1(p',h')x_1' - f_1(p,h)x_1\right| \\
&\quad + (1-\theta)\left|f_1(p',h')x_1' - f_1(p,h)x_1\right| + \left|f_2(h')x_2' - f_2(h)x_2\right| \\
&= 2\left|f_1(p',h')x_1' - f_1(p,h)x_1\right| + 2\left|f_2(h')x_2' - f_2(h)x_2\right| \\
&= 2\left|f_1(p',h')x_1' - f_1(p',h')x_1 + f_1(p',h')x_1 - f_1(p,h)x_1\right| \\
&\quad + 2\left|f_2(h')x_2' - f_2(h')x_2 + f_2(h')x_2 - f_2(h)x_2\right| \\
&\le 2f_1(p',h')|x_1' - x_1| + 2x_1\left|f_1(p',h') - f_1(p,h)\right| + 2f_2(h')|x_2' - x_2| + 2x_2\left|f_2(h') - f_2(h)\right| \\
&\le 2\bar{f}_1|x_1' - x_1| + 2\theta p_{in}L_1\|(p',h') - (p,h)\|_1 + 2\bar{f}_2|x_2' - x_2| + 2((1-\theta)p_{in} + h_{in})L_2|h' - h| \\
&\le M\left\|\varphi_1 - \varphi_2\right\|_1
\end{aligned}$$

where $M = 2\max(\bar{f}_1, \theta p_{in}L_1, \bar{f}_2, ((1-\theta)p_{in} + h_{in})L_2)$. Since $\left\|A\varphi_1 - A\varphi_2\right\|_1 \le D\left\|\varphi_1 - \varphi_2\right\|_1$, therefore $\left\|G(\varphi_1) - G(\varphi_2)\right\|_1 \le K\left\|\varphi_1 - \varphi_2\right\|_1$ with $K = \max(M, D)$, and therefore G is a uniformly Lipschitz continuous function.

Therefore, system (5.1) admits a unique solution. Let's apply Pontryagin's Maximum Principle [20–22] in order to obtain necessary conditions for the optimal strategy. The Hamiltonian is

$$\begin{aligned}
H &= -\alpha_1 x_1 - \alpha_2 x_2 + \frac{\alpha_3}{2}h_{in}^2 + \lambda_1\dot{x}_1 + \lambda_2\dot{x}_2 + \lambda_3\dot{p} + \lambda_4\dot{h} \\
&= -\alpha_1 x_1 - \alpha_2 x_2 + \frac{\alpha_3}{2}h_{in}^2 + \lambda_1((\theta f_1(p,h) - D)x_1) + \lambda_2((f_2(h) - D)x_2) \\
&\quad + \lambda_3(D(p_{in} - p) - f_1(p,h)x_1) + \lambda_4(D(h_{in} - h) + (1-\theta)f_1(p,h)x_1 - f_2(h)x_2).
\end{aligned} \tag{5.2}$$

For a given optimal control h^*_{in}, there exist adjoint functions $\lambda_1, \lambda_2, \lambda_3$ and λ_4 corresponding to the states x_1, x_2, p and h, such that:

$$\begin{cases} \dot{\lambda}_1 &= -\dfrac{\partial H}{\partial x_1} = \alpha_1 - \lambda_1(\theta f_1(p,h) - D) + \lambda_3 f_1(p,h) - \lambda_4(1-\theta) f_1(p,h), \\ \dot{\lambda}_2 &= -\dfrac{\partial H}{\partial x_2} = \alpha_2 - \lambda_2(f_2(h) - D) + \lambda_4 f_2(h), \\ \dot{\lambda}_3 &= -\dfrac{\partial H}{\partial p} = -\lambda_1\theta\dfrac{\partial f_1}{\partial p}(p,h)x_1 - \lambda_3\left(-D - \dfrac{\partial f_1}{\partial p}(p,h)x_1\right) - \lambda_4(1-\theta)\dfrac{\partial f_1}{\partial p}(p,h)x_1, \\ \dot{\lambda}_4 &= -\dfrac{\partial H}{\partial h} = -\lambda_1\dfrac{\partial f_1}{\partial h}(p,h)x_1 - \lambda_2 f_2'(h)x_2 + \lambda_3\dfrac{\partial f_1}{\partial h}(p,h)x_1 - \lambda_4\left(-D + (1-\theta)\dfrac{\partial f_1}{\partial h}(p,h)x_1 - f_2'(h)x_2\right), \end{cases} \tag{5.3}$$

where $\lambda_1(T) = 0$, $\lambda_2(T) = 0$, $\lambda_3(T) = 0$ and $\lambda_4(T) = 0$ are the transversality conditions.

The Hamiltonian is minimized with respect to the control variable at h^*_{in}. Since the Hamiltonian is quadratic in the control, its derivative is, then, given by $\dfrac{\partial H}{\partial h_{in}} = \alpha_3 h_{in} + \lambda_4 D$. Therefore, $\dfrac{\partial H}{\partial h_{in}} = 0$ admits the solution $h_{in}(t) = -\dfrac{D\lambda_4}{\alpha_3}$ provided that $\alpha_3 \neq 0$ and $h^{\min}_{in} \leq -\dfrac{D\lambda_4}{\alpha_3} \leq h^{\max}_{in}$. To summarize, the control characterization is:

$$\begin{cases} \text{if } \dfrac{\partial H}{\partial h_{in}} < 0 \text{ at } t, \text{ then } h_{in}(t) = h^{\max}_{in}, \\ \text{if } \dfrac{\partial H}{\partial h_{in}} > 0 \text{ at } t, \text{ then } h_{in}(t) = h^{\min}_{in}, \\ \text{if } \dfrac{\partial H}{\partial h_{in}} = 0 \text{ at } t, \text{ then } h_{in}(t) = -\dfrac{D\lambda_4}{\alpha_3}. \end{cases}$$

6. Numerical results and conclusions

We performed numerical results on a system that uses Monod functions to express growth rates taking into account of the hydrogen inhibition of species 1 growth: $f_1(p,h) = \dfrac{\bar{f}_1 p}{(k_1 + p)(1 + mh)}$ and $f_2(h) = \dfrac{\bar{f}_2 h}{(k_2 + h)}$, where k_1, k_2 and m are constants. f_1 and f_2 are globally Lipschitz and continuous on $\mathbb{R}_+$ with Lipschitz constants $\bar{f}_1/k_1$ and $\bar{f}_2/k_2$, respectively. One can readily check that the functions f_1 and f_2 satisfy Assumptions **A1–A3**.

6.1. Numerical results for the direct problem

Note that the numerical simulations presented here are done for the non-reduced system (2.1), and not for the reduced one. Let $k_1 = k_2 = 2$ and $m = 1$ $\bar{f}_1 = 9$ $\bar{f}_2 = 4$, $\theta = 0.6$, $p_{in} = 4$ and $h_{in} = 2$, then $D_1 = f_1(p_{in}, h_{in}) = 1.2$ and $D_2 = f_2(h_{in}) = 2$. In Figure 3, if $D = 0.8$, which satisfies $D < \min(D_3 = 2.4, D_4 = 2.28)$, the trajectories filling the whole domain are converging to the equilibrium E^* whence the persistence of both species. In Figure 4, if $D = 1.8$, which satisfies $D_3 = 1.37 < D < D_2 = 2$, the trajectories filling the whole domain are converging to the equilibrium E_2, from where the persistence of species 2 and the extinction of species 1 are seen. In Figure 5, if $D = 2.5$, which satisfies

$\max(D_1, D_2) < D$, the trajectories filling the whole domain are converging to the equilibrium E_0 from where the extinction of both species.

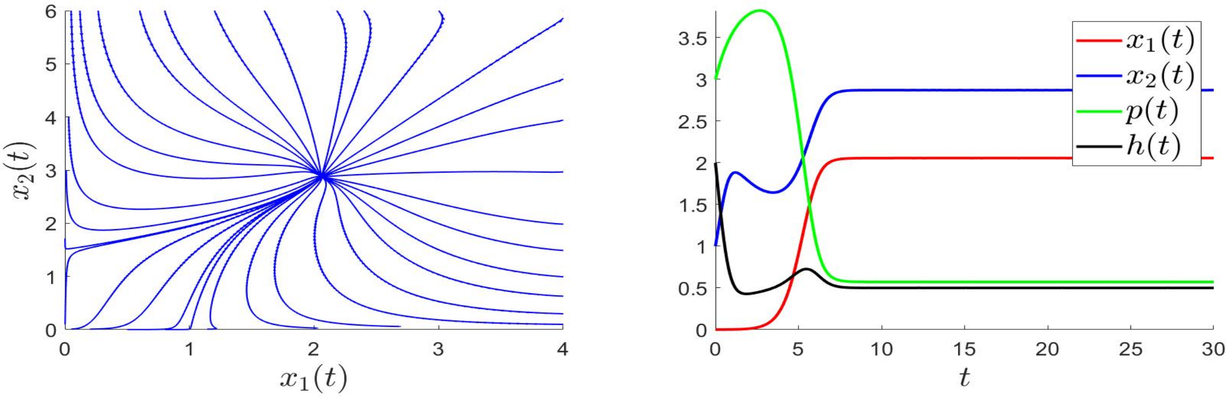

Figure 3. $x_1 - x_2$ behaviour for $D = 0.8 < \min(D_3 = 2.4, D_4 = 2.28)$. The trajectories of system (2.1) converge asymptotically to E^*.

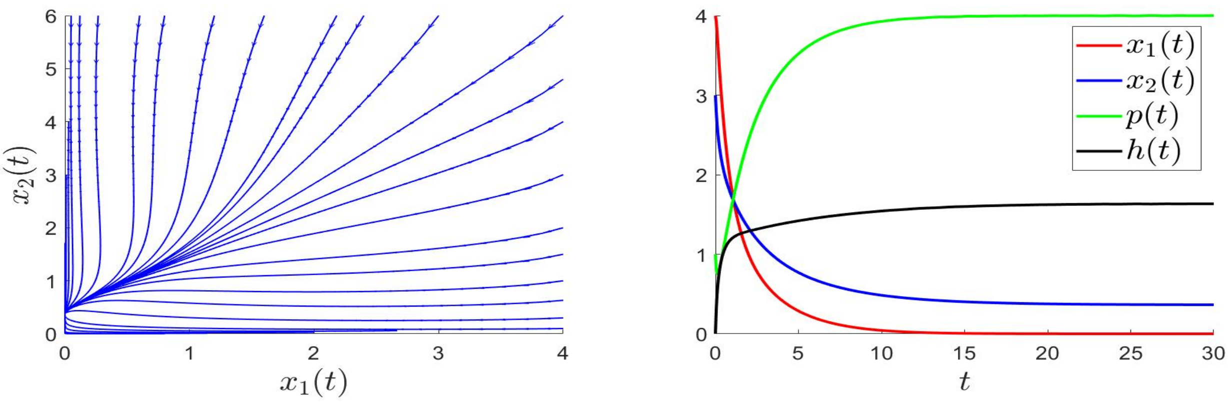

Figure 4. $x_1 - x_2$ behaviour for $D_3 = 1.37 < D = 1.8 < D_2 = 2$. The trajectories of system (2.1) converge asymptotically to E_2.

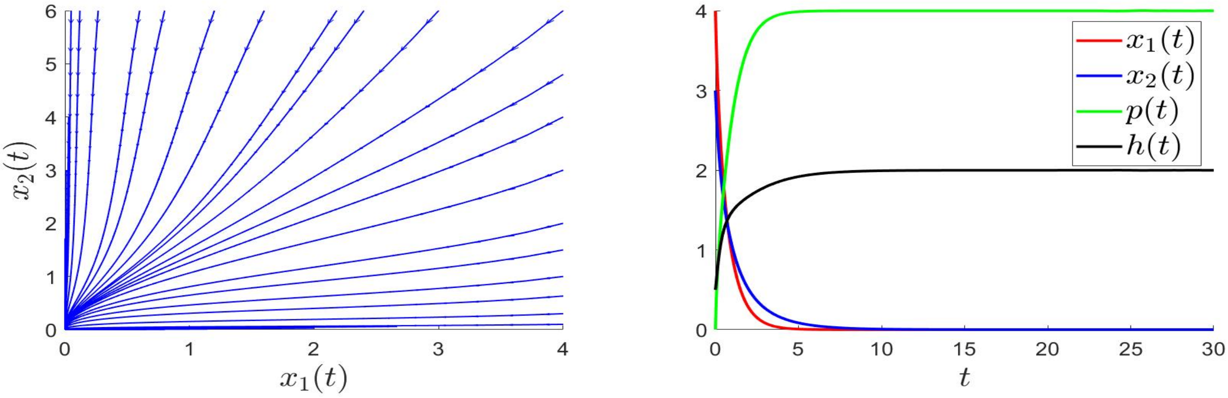

Figure 5. $x_1 - x_2$ behaviour for $\max(D_1 = 1.2, D_2 = 2) < D = 2.5$. The trajectories of system (2.1) converge asymptotically to E_0.

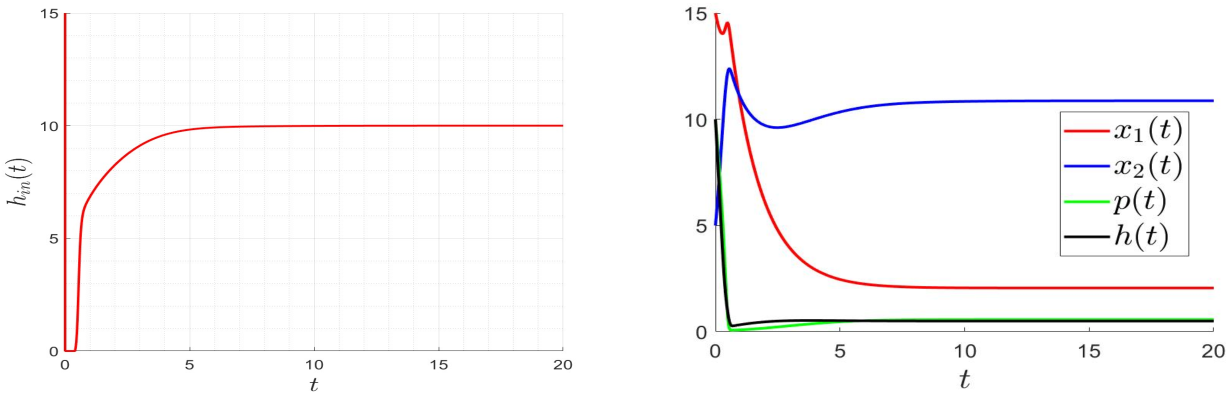

Figure 6. Dynamics of the states (right) and the cost (left) where the balancing constants are given by $\alpha_1 = 10, \alpha_2 = 10, \alpha_3 = 1$ for a final time $T = 20$. The functional value J is about -1847 and the final value of the state variable (x_1, x_2, p, h) is about $(2.06, 10.87, 0, 0)$.

6.2. Numerical results for the optimal strategy

An improved Gauss-Seidel implicit finite-difference method was used for the state system and a first-order backward-difference was used for the adjoint system (see Appendix A). The used parameters values are the same as for the first case of the direct problem (2.1), where we have coexistence of both species and are given by: $k_1 = k_2 = 2$ and $m = 1$ $\bar{f}_1 = 9$ $\bar{f}_2 = 4$, $\theta = 0.6$, $D = 0.8$, $p_{in} = 4$, and h_{in} is a variable such that the initial condition $h_{in}(0) = 15$ and with bounds $h_{in}^{\min} = 0$ and $h_{in}^{\max} = 20$. We plot, in Figures 6–9, the behaviours of h_{in} (left), $x_1(t), x_2(t), p(t)$ and $h(t)$ (right) with respect to time for different values of α_1, α_2 and α_3 which clearly influenced both the control and the behaviour of the solution. It can be seen that the control values are not the same for the different simulations and the same thing for the state variables. In particular, a periodic behavior can be seen in Figure 8.

The three balancing constants α_1, α_2 and α_3 are the weighted states and the weighted cost associated with the use of the states $x_1(t)$ and $x_2(t)$ and the control h_{in}, respectively. The main idea developed here

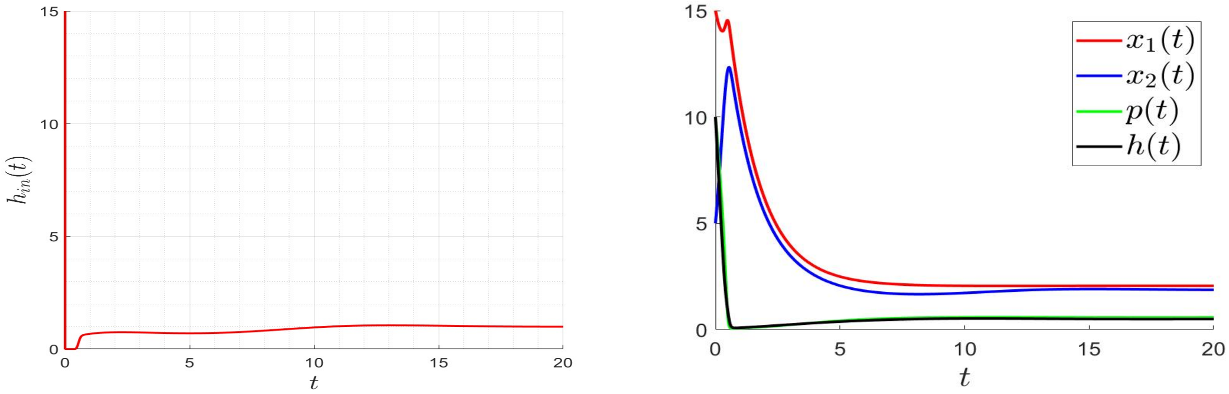

Figure 7. Dynamics of the states (right) and the cost (left) where the balancing constants are given by $\alpha_1 = 1, \alpha_2 = 1, \alpha_3 = 1$ for a final time $T = 20$. The functional value J is about -110.16 and the final value of the state variable (x_1, x_2, p, h) is about $(2.06, 1.87, 0.57, 0.498)$.

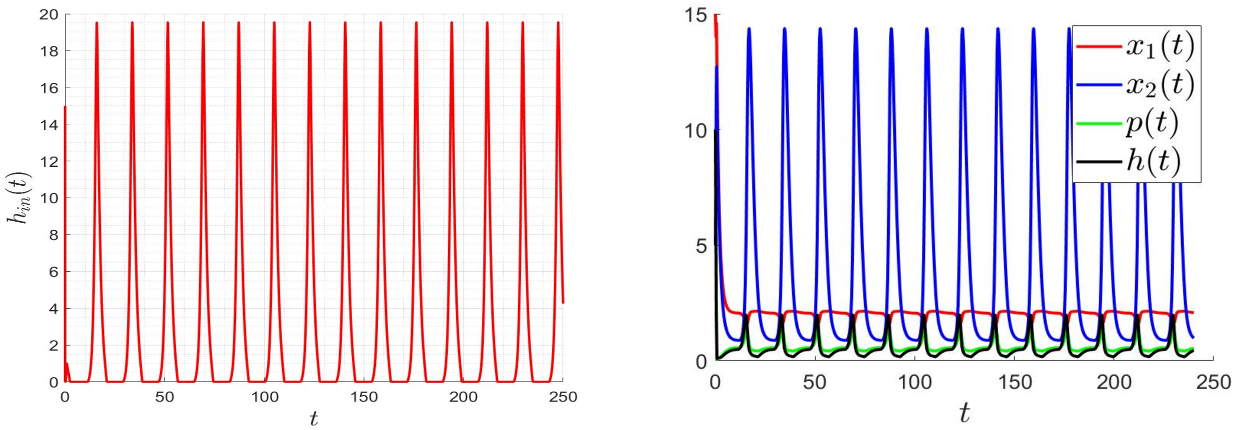

Figure 8. Dynamics of the states (right) and the cost (left) where the balancing constants are given by $\alpha_1 = 10, \alpha_2 = 1, \alpha_3 = 1$ for a final time $T = 250$. The functional value J is about -1742.1.

is the optimal control in order to search among the available strategies, and to the most efficiency in increasing the biomass inside the reactor while optimizing the cost (input concentration of hydrogen). In conclusion, observing the figures, a biologist has the choice to choose the best strategy leading to his priorities. For example, one can choose which biomass to increase more, or both of them by acting on the values of α_1, α_2 and α_3. For example, by comparing the final value of x_2, which is equal to 10.87 for $\alpha_2 = 10$ (Figures 6 and 9), and about 1.87 for $\alpha_2 = 1$ (Figure 7), we can deduce that the α_2-value affects the x_2-final value by the intermediate of h_{in}, which depends indirectly on α_2-value.

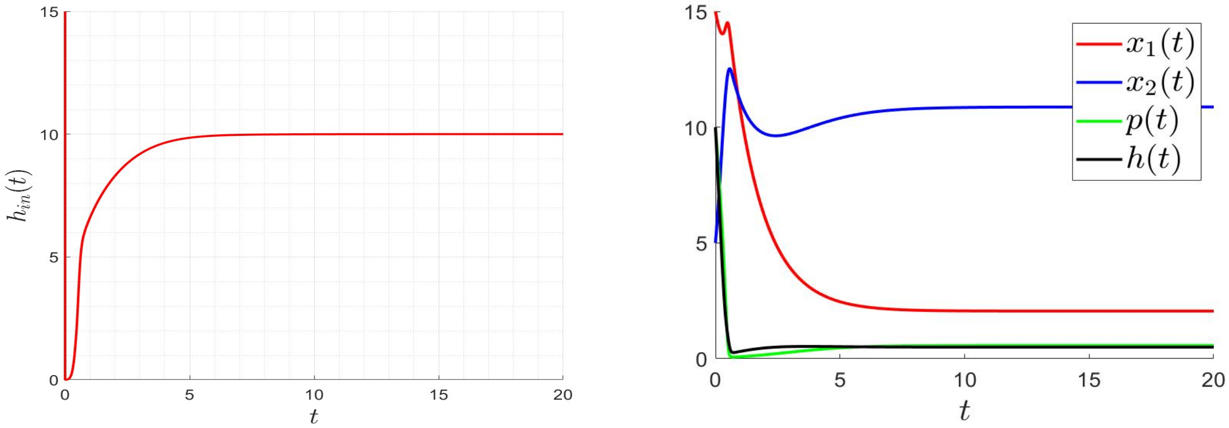

Figure 9. Dynamics of the states (right) and the cost (left) where the balancing constants are given by $\alpha_1 = 1, \alpha_2 = 10, \alpha_3 = 1$ for a final time $T = 20$. The functional value J is about -1274.6 and the final value of the state variable (x_1, x_2, p, h) is about $(2.06, 10.87, 0, 57, 0.5)$.

7. Conclusions

In this work, we proposed a simplified model of a phenol- mineralising two-tiered microbial 'food web', where the growth rates are general smooth functions. Our study considers the phenol and hydrogen as input matters. More precisely, we have proposed a mathematical model involving a syntrophic relationship of two bacteria. For one of the populations, one resource is needed for its growth, and the other is inhibitory for the other population growth. One of the populations produces, as a by-product, the resource that is inhibitory to itself but needed for growth by the other population. Extending the model studied in [3], it is considered that there is hydrogen influent at the input.

Our first aim was the theoretical analysis of the two-tiered model by providing a complete study on the existence and local stability of all steady states. Our mathematical analysis of the model has revealed several possible asymptotic behaviours. Due to some conservative relations, the proposed model was reduced to a two-dimensional system. In fact, since the solutions of the proposed model (2.1) converge exponentially into the invariant set Ω, and since we aim to study the asymptotic behavior of the system (2.1), we studied the asymptotic behavior of the restriction of (2.1) on Ω. We provided a complete theoretical description of the existence and stability of the steady states, according to the operating parameters and the growth rates of species. Therefore, thanks to Thieme's results [12], we drew conclusions on the asymptotic behavior of the main system (2.1). We finished by proposing an optimal strategy to maximise the size of both species through a time-varying control function, $h_{in}(t)$, expressing the input concentration of hydrogen. Thus we constructed an objective function for the optimal control problem. We discussed the existence of the optimal control using the Pontryagin's maximum principle, and then derived the first order necessary conditions for the optimal control through constructing the Hamiltonian. We give some numerical simulations validating the obtained results for both, the behavior of the solution and also for the proposed optimal strategy. As can be seen in Figures 6, 7 and 9, the values of the three balancing constants α_1, α_2 and α_3 can affect the final values of the state variables.

Acknowledgements

This Project was funded by the Deanship of Scientific Research (DSR) at King Abdulaziz University (KAU), Jeddah, Saudi Arabia, under grant no. (G: 279-130-1443). The authors, therefore, acknowledge, with thanks, DSR's technical and financial support.

We are also grateful to the unknown referees for many constructive suggestions, which helped to improve the presentation of the paper.

Conflict of interest

We declare that there are no conflicts of interest.

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Appendix

A. Applied numerical scheme

Consider the subdivision $[0,T] = \bigcup_{n=0}^{N-1}[t_n, t_{n+1}]$, $t_n = n\ dt$, $dt = T/N$. Define x_1^n, x_2^n, p^n, h^n, λ_1^n, λ_2^n, λ_3^n, λ_4^n and h_{in}^n be an approximation of $x_1(t), x_2(t), p(t), h(t)$, $\lambda_1(t)$, $\lambda_2(t), \lambda_3(t), \lambda_4(t)$ and the control $h_{in}(t)$ at the time t_n. We applied an improved Gauss-Seidel implicit finite-difference method for he state system and a first-order backward-difference for the adjoint system (see [23–26] for other applications).

$$
\left\{
\begin{array}{lcl}
\dfrac{x_1^{n+1}-x_1^n}{dt} &=& (\theta f_1(p^n,h^n)-D)\,x_1^{n+1},\\
\dfrac{x_2^{n+1}-x_2^n}{dt} &=& (f_2(h^n)-D)\,x_2^{n+1},\\
\dfrac{p^{n+1}-p^n}{dt} &=& D(p_{in}-p^{n+1})-\dfrac{\bar{f}_1 p^{n+1}x_1^{n+1}}{(k_1+p^n)(1+mh^n)},\\
\dfrac{h^{n+1}-h^n}{dt} &=& D(h_{in}^n-h^{n+1})+(1-\theta)f_1(p^{n+1},h^n)x_1^{n+1}-\dfrac{\bar{f}_2 h^{n+1}x_2^{n+1}}{(k_2+h^n)},\\
\dfrac{\lambda_1^{N-n}-\lambda_1^{N-n-1}}{dt} &=& \alpha_1-\lambda_1^{N-n-1}\left(\theta f_1(p^{n+1},h^{n+1})-D\right)+\lambda_3^{N-n}f_1(p^{n+1},h^{n+1})-\lambda_4^{N-n}(1-\theta)f_1(p^{n+1},h^{n+1}),\\
\dfrac{\lambda_2^{N-n}-\lambda_2^{N-n-1}}{dt} &=& \alpha_2-\lambda_2^{N-n-1}\left(f_2(h^{n+1})-D\right)+\lambda_4^{N-n}f_2(h^{n+1}),\\
\dfrac{\lambda_3^{N-n}-\lambda_3^{N-n-1}}{dt} &=& -\lambda_1^{N-n-1}\theta\dfrac{\partial f_1}{\partial p}(p^{n+1},h^{n+1})x_1^{n+1}-\lambda_3^{N-n-1}\left(-D-\dfrac{\partial f_1}{\partial p}(p^{n+1},h^{n+1})x_1^{n+1}\right)\\
&& -\lambda_4^{N-n}(1-\theta)\dfrac{\partial f_1}{\partial p}(p^{n+1},h^{n+1})x_1^{n+1},\\
\dfrac{\lambda_4^{N-n}-\lambda_4^{N-n-1}}{dt} &=& -\lambda_1^{N-n-1}\dfrac{\partial f_1}{\partial h}(p^{n+1},h^{n+1})x_1^{n+1}-\lambda_2^{N-n-1}f_2'(h^{n+1})x_2^{n+1}+\lambda_3^{N-n-1}\dfrac{\partial f_1}{\partial h}(p^{n+1},h^{n+1})x_1^{n+1}\\
&& -\lambda_4^{N-n-1}\left(-D+(1-\theta)\dfrac{\partial f_1}{\partial h}(p^{n+1},h^{n+1})x_1^{n+1}-f_2'(h^{n+1})x_2^{n+1}\right).
\end{array}
\right.
$$

Therefore we apply the following algorithm using MATLAB software.

Algorithm 1: Optimal control resolution

1: $x_1^0 \leftarrow x_1(0), x_2^0 \leftarrow x_2(0), p^0 \leftarrow p(0), h^0 \leftarrow h(0), \lambda_1^N \leftarrow 0, \lambda_2^N \leftarrow 0, \lambda_3^N \leftarrow 0, \lambda_4^N \leftarrow 0, h_{in}^0 \leftarrow h_{in}(0),$

2: **for** $n = 0$ to $N-1$ **do**

$$
\left|
\begin{array}{l}
x_1^{n+1} \leftarrow \dfrac{x_1^n}{1 - dt(\theta f_1(p^n, h^n) - D)}, \\
x_2^{n+1} \leftarrow \dfrac{x_2^n}{1 - dt(f_2(h^n) - D)}, \\
p^{n+1} \leftarrow \dfrac{p^n + dtDp_{in}}{1 + dt\left(D + \dfrac{\bar{f}_1 x_1^{n+1}}{(k_1 + p^n)(1 + mh^n)}\right)}, \\
h^{n+1} \leftarrow \dfrac{h^n + dtDh_{in}^n + dt(1-\theta) f_1(p^{n+1}, h^n) x_1^{n+1}}{1 + dt\left(D + \dfrac{\bar{f}_2 x_2^{n+1}}{(k_2 + h^n)}\right)}, \\
\lambda_1^{N-n-1} \leftarrow \dfrac{\lambda_1^{N-n} - dt\left(\alpha_1 + \lambda_3^{N-n} f_1(p^{n+1}, h^{n+1}) - \lambda_4^{N-n}(1-\theta) f_1(p^{n+1}, h^{n+1})\right)}{1 - dt\left(\theta f_1(p^{n+1}, h^{n+1}) - D\right)}, \\
\lambda_2^{N-n-1} \leftarrow \dfrac{\lambda_2^{N-n} - dt\left(\alpha_2 + \lambda_4^{N-n} f_2(h^{n+1})\right)}{1 - dt\left(f_2(h^{n+1}) - D\right)}, \\
\lambda_3^{N-n-1} \leftarrow \dfrac{\lambda_3^{N-n} + dt\left(\lambda_1^{N-n-1}\theta \dfrac{\partial f_1}{\partial p}(p^{n+1}, h^{n+1}) x_1^{n+1} + \lambda_4^{N-n}(1-\theta)\dfrac{\partial f_1}{\partial p}(p^{n+1}, h^{n+1}) x_1^{n+1}\right)}{1 + dt\left(D + \dfrac{\partial f_1}{\partial p}(p^{n+1}, h^{n+1}) x_1^{n+1}\right)}, \\
\lambda_4^{N-n-1} \leftarrow \dfrac{\lambda_4^{N-n} + dt\left(\lambda_1^{N-n-1}\dfrac{\partial f_1}{\partial h}(p^{n+1}, h^{n+1}) x_1^{n+1} + \lambda_2^{N-n-1} f_2'(h^{n+1}) x_2^{n+1} - \lambda_3^{N-n-1}\dfrac{\partial f_1}{\partial h}(p^{n+1}, h^{n+1}) x_1^{n+1}\right)}{1 + dt\left(D - (1-\theta)\dfrac{\partial f_1}{\partial h}(p^{n+1}, h^{n+1}) x_1^{n+1} + f_2'(h^{n+1}) x_2^{n+1}\right)}, \\
h_{in}^{n+1} \leftarrow \max\left(\min\left(-\dfrac{D}{\alpha_3}\lambda_4^{N-n-1}, h_{in}^{\max}\right), h_{in}^{\min}\right).
\end{array}
\right.
$$

end