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ABSTRACT. In this work, we study a model describing a syntrophic relationship of two microbial species with two input substrates, including both decay terms and inhibition of the first species by an excess of the second substrate. This model can be seen as a reduced and simplified version of the anaerobic digestion process. We give necessary and sufficient conditions on the operating parameters of the system (the dilution rate D and the input concentrations of the two substrates s_0^{in} and s_1^{in}) for the existence and stability of all equilibria. By means of operating diagrams, we describe the asymptotic behavior of the model with respect to the control parameters and we study the effect of the second input substrate.

RÉSUMÉ. Dans ce travail, on étudie un modèle décrivant une relation de syntrophie de deux espèces microbiennes avec deux substrats à l'entrée, incluant des termes de mortalité et l'inhibition de la première espèce par un excès du second substrat. Ce modèle est une version réduite et simplifiée du processus de la digestion anaérobie. On donne des conditions nécessaires et suffisantes sur les paramètres opératoires du système (le taux de dilution D et les concentrations à l'entrée des deux substrats s_0^{in} et s_1^{in}) pour l'existence et la stabilité des équilibres. En utilisant les diagrammes opératoires, on décrit le comportement asymptotique du modèle en fonction des paramètres de contrôle et on étudie l'effet du second substrat à l'entrée.

KEYWORDS : Microbial ecosystems, syntrophic relashionship, Mortality, Stability , Operating diagrams.

MOTS-CLÉS : Écosystème microbien, relation de syntrophie, mortalité, stabilité, diagrammes opératoires

1. Introduction

The anaerobic digestion (AD) is a natural process in which organic material is converted into biogas in an environment without oxygen by the action of a microbial ecosystem. It is used for the treatment of waste or wastewater and has the advantage of producing methane or hydrogen under appropriate conditions. To better understand and control this process, many models have been reported in the literature, cf. [2, 3, 4, 6]. In particular, a key biological step has been described as the syntrophic relationship between acid consumers (which produce hydrogen) and hydrogen consumer (which produce methane). Indeed, in degrading the hydrogen - which is inhibiting microbial growth rate - methanogens allow their coexistence with acid producers: this fragile equilibrium has been thoroughly studied in the past years.

In [6], a model of such a syntrophic relationship is studied. Using realistic parameters values, the authors have shown that the introduction of maintenance terms (equivalent to mortality terms in their study) does not destabilize the positive equilibrium of the system. This result has been made generic by Sari and Harmand (cf. [5]) in the sense they have shown that for a large class of kinetics and whatever the model parameters values, the stability of the equilibrium is maintained. However, in these studies, only one substrate input - the input substrate concentration in propionate - was considered. In reality, some hydrogen in produced by other reactions taking place in parallel of the main reactions considered in the model under interest. Thus, in the present study, we investigate the properties of the syntrophy model when a second input - the input substrate concentration in hydrogen - is considered.

2. The model

The two-step model reads:

$$\left\{\begin{array}{rcl}\dfrac{ds_0}{dt} & = & D(s_0^{in}-s_0)-\mu_0(s_0,s_1)x_0\\ \dfrac{dx_0}{dt} & = & -Dx_0+\mu_0(s_0,s_1)x_0-a_0x_0\\ \dfrac{ds_1}{dt} & = & D(s_1^{in}-s_1)+\mu_0(s_0,s_1)x_0-\mu_1(s_1)x_1\\ \dfrac{dx_1}{dt} & = & -Dx_1+\mu_1(s_1)x_1-a_1x_1\end{array}\right. \tag{1}$$

where s_0 and s_1 are the concentration substrates introduced, in the chemostat, with an input concentration s_0^{in} and s_1^{in} respectively, and at dilution rate D. This model includes the maintenance (or decay) terms a_0x_0 and a_1x_1. The functions $\mu_0(.,.)$ and $\mu_1(.)$ satisfy:

H1 For all s_0, $s_1>0$, $\mu_0\left(s_0,s_1\right)>0$, $\mu_0\left(0,s_1\right)=0$ and $\sup\limits_{s_0\geqslant 0}\mu_0(s_0,s_1)<+\infty$.

H2 For all $s_1>0$, $\mu_1\left(s_1\right)>0$, $\mu_1(0)=0$ and $m_1:=\sup\limits_{s_1\geqslant 0}\mu_1(s_1)<+\infty$.

H3 For all s_0, $s_1>0$, $\dfrac{\partial\mu_0}{\partial s_0}\left(s_0,s_1\right)>0$ and $\dfrac{\partial\mu_0}{\partial s_1}\left(s_0,s_1\right)<0$.

H4 For all $s_1>0$, $\dfrac{d\mu_1}{ds_1}\left(s_1\right)>0$.

For s_1 fixed, we denote: $m_0(s_1)=\sup_{s_0\geqslant 0}\mu_0(s_0,s_1)$. We assume that:

H5 For all $s_1 > 0$, $\dfrac{dm_0}{ds_1} < 0$.

We can prove that for every non-negative initial condition, the solution of (1) has non-negative components and is positively bounded and thus is defined for every positive t.

3. Steady state analysis and stability

A steady state of (1) is a solution of the following nonlinear algebraic system obtained by setting the right-hand sides of (1) equal to zero.

Since all state variables are concentrations, steady state $E = (s_0, x_0, s_1, x_1)$ exists if and only if all its components are non-negative.
From the second equation of (1) we deduce that: $x_0 = 0 \quad \text{or} \quad \mu_0(s_0, s_1) = D + a_0$, and from the fourth equation of (1) we deduce that: $x_1 = 0 \quad \text{or} \quad \mu_1(s_1) = D + a_1$.

For the description of the steady states, we need the following notations. Since the function $s_1 \mapsto \mu_1(s_1)$ is increasing, it has an inverse function $y \mapsto M_1(y)$, so that, for all $s_1 \geq 0$ and $y \in [0, m_1[$, $s_1 = M_1(y) \Longleftrightarrow y = \mu_1(s_1)$.
Let s_1 be fixed. Since the function $s_0 \mapsto \mu_0(s_0, s_1)$ is increasing, it has an inverse function $y \mapsto M_0(y, s_1)$, so that, for all $s_0, s_1 \geq 0$, and $y \in [0, m_0(s_1)[$,
$s_0 = M_0(y, s_1) \Longleftrightarrow y = \mu_0(s_0, s_1)$.

Thus, we can prove the following proposition:

Proposition 3.1. *Assume that* **H1–H4** *hold. Then, (1) has at most four steady states:*
_ $SS0 = \left(s_0^{in}, 0, s_1^{in}, 0\right)$. *It always exists.*
_ $SS1 = (s_{01}, x_{01}, s_{11}, 0)$, *where* s_{01} *is the solution of the equation:*
$\mu_0(s_{01}, (s_0^{in} + s_1^{in}) - s_{01}) = D + a_0$, $x_{01} = \frac{D}{D+a_0}(s_0^{in} - s_{01})$ *and* $s_{11} = (s_0^{in} + s_1^{in}) - s_{01}$.
It exists if and only if $s_0^{in} > M_0\left(D + a_0, s_1^{in}\right)$.
_ $SS2 = (s_{02}, x_{02}, s_{12}, x_{12})$, *where* $s_{02} = M_0\left(D + a_0, M_1(D + a_1)\right)$, $x_{02} = \frac{D}{D+a_0}\left(s_0^{in} - s_{02}\right)$,
$s_{12} = M_1(D + a_1)$ *and* $x_{12} = \frac{D}{D+a_1}\left((s_0^{in} + s_1^{in}) - s_{02} - s_{12}\right)$.
It exists if and only if $s_0^{in} > M_0\left(D + a_0, M_1(D + a_1)\right)$
and $s_0^{in} + s_1^{in} > M_0\left(D + a_0, M_1(D + a_1)\right) + M_1(D + a_1)$.
_ $SS3 = \left(s_0^{in}, 0, M_1(D + a_1), \frac{D}{D+a_1}\left(s_1^{in} - M_1(D + a_1)\right)\right)$.
It exists if and only if $s_1^{in} > M_1(D + a_1)$.

With respect to [5], a new steady state SS3 exists. Notice that, if $s_1^{in} = 0$ the condition $\mu_1(s_1^{in}) > a_1$ is not satisfied and SS3 does not exist. In the next section, we analyse local stability of the steady states.

The stability of the steady states is given by the sign of the real part of eigenvalues of the Jacobian matrix or by the Routh-Hurwitz criteria (in the case of $SS2$). In the following, we use the abreviations LES for locally exponentially stable.

Proposition 3.2. *Assume that assumptions* **H1–H4** *hold. Then, the local stability of steady states of (1) is given by:*
_ $SS0$ *is LES if and only if* $s_1^{in} < M_1(D + a_1)$ *and* $s_0^{in} < M_0\left(D + a_0, s_1^{in}\right)$.
_ $SS1$ *is LES if and only if* $s_0^{in} + s_1^{in} < M_0\left(D + a_0, M_1(D + a_1)\right) + M_1(D + a_1)$.
_ $SS2$ *is LES if it exists.*
_ $SS3$ *is LES if and only if* $s_0^{in} < M_0\left(D + a_0, M_1(D + a_1)\right)$.

4. Operating diagram

The operating diagram shows how the system behaves when we vary the three operating parameters s_0^{in}, s_1^{in} and D. These diagrams are specially useful for the operators, to estimate in particular, for a given a triplet s_0^{in}, s_1^{in} and D, the margin of stability they have, with respect to a region of the space where the washing out of at least one biomass is stable.

Since we have three parameters, we have to fix one of them. In [1], we fixed s_1^{in} and we gave the operating diagram in the plane (s_0^{in}, D). Here, we fix s_0^{in} and we give the operating diagram in the plane (s_1^{in}, D), since s_1^{in} is the new input substrate in model (1). We need to define the functions F_i, $i = 1, 2$:

$$\begin{array}{rcl} F_1(D) & = & M_1(D + a_1) + M_0(D + a_0, M_1(D + a_1)) \\ F_2(D) & = & M_0(D + a_0, M_1(D + a_1)) \end{array} \tag{2}$$

For s_0 fixed, the function $s_1 \mapsto \mu_0(s_0, s_1)$ is decreasing. Thus, it has a decreasing inverse function $z \mapsto M_2(s_0, z)$, so that, for all $s_0, s_1 \geq 0$, and $z \in [0, \sup \mu_0(s_0, \cdot)[$,
$s_1 = M_2(s_0, z) \Longleftrightarrow z = \mu_0(s_0, s_1)$.
We define the function: $F_3(D) = M_2\left(s_0^{in}, D + a_0\right)$.

Let $\bar{D}_1$, if it exists, the largest solution of $F_2(D) = s_0^{in}$, $\bar{D}_2 = min(m_1 - a_1, D_2)$ and $\bar{D}_3$ the solution of $F_3(D) = 0$, if it exists.
It is useful to state the next properties on the functions F_i, $i = 1, 2, 3$.

Lemma 4.1. *We assume that $\bar{D}_2 > 0$. Then, we have*
• *If $D > \bar{D}_1$ then $F_3(D) < F_1(D) - F_2(D) < F_1(D) - s_0^{in}$.*
• *If $D < \bar{D}_1$ and $\bar{D}_1 > 0$ then $F_1(D) - s_0^{in} < F_1(D) - F_2(D) < F_3(D)$.*
Moreover, the three curves of functions $F_1 - F_2$, $F_1 - s_0^{in}$ and F_3 intersect at $D = \bar{D}_1$ satisfying $\bar{D}_3 > \bar{D}_1$.

From Prop 3.1 and Prop 3.2, we have to distinguish three cases as given in Theorem 4.1.

Theorem 4.1. *The existence and stability properties of the system (1), in the plane (s_1^{in}, D), are given in the following tables:*

Condition	Region	SS0	SS3
$s_1^{in} < F_1(D) - F_2(D)$	$(s_1^{in}, D) \in J^2$	S	
$F_1(D) - F_2(D) < s_1^{in}$	$(s_1^{in}, D) \in J^3$	U	S

Table 1. *The cases $\bar{D}_1 < 0$, $\bar{D}_3 < 0$ and $0 < D < \bar{D}_2$*

Condition	Region	SS0	SS1	SS3
$s_1^{in} < F_3(D)$	$(s_1^{in}, D) \in J^1$	U	S	
$F_3(D) < s_1^{in} < F_1(D) - F_2(D)$	$(s_1^{in}, D) \in J^2$	S		
$F_1(D) - F_2(D) < s_1^{in}$	$(s_1^{in}, D) \in J^3$	U		S

Table 2. *The cases $\bar{D}_1 < 0$, $\bar{D}_3 > 0$ and $0 < D < \bar{D}_2$*

	Conditions	Region	SS0	SS1	SS2	SS3
	$s_1^{in} < F_3(D)$	$(s_1^{in}, D) \in J^1$	U	S		
$\bar{D}_1 < D$	$F_3(D) < s_1^{in} < F_1(D) - F_2(D)$	$(s_1^{in}, D) \in J^2$	S			
	$F_1(D) - F_2(D) < s_1^{in}$	$(s_1^{in}, D) \in J^3$	U			S
	$F_3(D) < s_1^{in}$	$(s_1^{in}, D) \in J^4$	U		S	U
$D < \bar{D}_1$	$F_1(D) - F_2(D) < s_1^{in} < F_3(D)$	$(s_1^{in}, D) \in J^5$	U	U	S	U
	$F_1(D) - s_0^{in} < s_1^{in} < F_1(D) - F_2(D)$	$(s_1^{in}, D) \in J^6$	U	U	S	
	$s_1^{in} < F_1(D) - s_0^{in}$	$(s_1^{in}, D) \in J^7$	U	S		

Table 3. *The cases* $\bar{D}_1 > 0$, $\bar{D}_3 > 0$ *and* $0 < D < \bar{D}_2$

We define by Γ_0 the curve of the function $s_1^{in} = F_1(D) - s_0^{in}$, Γ_1 the curve of the function $s_1^{in} = F_1(D) - F_2(D)$ and Γ_2 the curve of the function $s_1^{in} = F_3(D)$. These curves with the line $D = \bar{D}_1$ separate the operating plane (s_1^{in}, D) in at most seven regions as shown in Fig. 3.

5. Simulations

For the simulations, we use the following growth functions:

$$\mu_0\left(s_0, s_1\right) = \frac{m_0 s_0}{K_0 + s_0} \frac{1}{1 + s_1/K_i}, \quad \mu_1\left(s_1\right) = \frac{m_1 s_1}{K_1 + s_1}$$

For the operating diagrams in Figure 1 and 2, we use the parameters of Table 3 of [5] and obtained from Table 1 of [6].

Figure 1 and Figure 2 illustrate the operating diagram for different values of s_0^{in}.

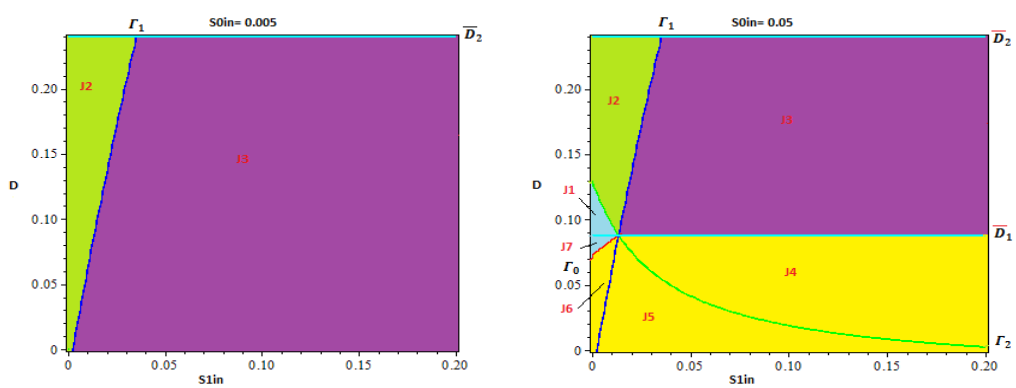
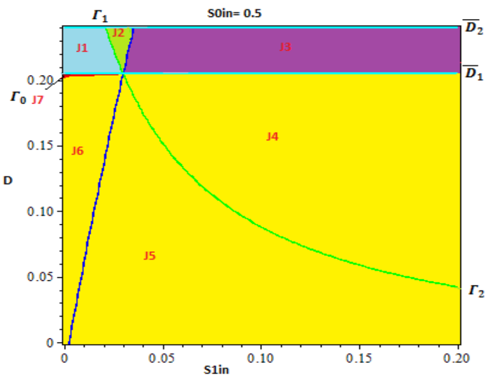


Figure 1. *Operating diagram of (1) for* $s_0^{in} = 0.005$ *at left and for* $s_0^{in} = 0.05$ *at right*

When s_0^{in} increases, $\bar{D}_1$ increases and new regions $J_4, \cdots, J_6$ appear under $\bar{D}_1$ and Γ_0. This regions correspond to the stability region of the coexistence steady state $SS2$.



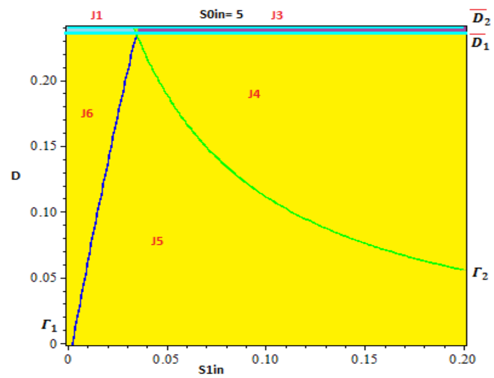


Figure 2. *Operating diagram of (1) for $s_0^{in} = 0.5$ at left and for $s_0^{in} = 5$ at right*

Conclusion

We have analyzed the model of [5] considering a new input s_{1in}. We have highlighted the existence of a new equilibrium point corresponding to the washing out of the first species and the existence of the second one. In all cases, we have shown that, whatever the region of space considered, there exists only one LES steady state. These diagrams can be useful to interpret experimental results. J_4, J_5 and J_6 are the regions of stability of the coexistence steady-state.

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6. References

[1] Y. DAOUD, N. ABDELLATIF, T. SARI, J. HARMAND, " Steady state analysis of a syntrophic association of two species in a chemostat: The effect of a new input concentration subsrate ", *Fourth international conference on complex dynamical systems in life sciences: Modeling and analysis, Agadir 26-28 October 2016, Morocco*.

[2] M. EL HAJJI, F. MAZENC, J. HARMAND, "A mathematical study of a syntrophic relationship of a model of anaerobic digestion process", *Math. Biosci. Eng*, vol. 7, num. 641-656, 2010.

[3] R. KREIKENBOHM, E. BOHL, "A mathematical model of syntrophic cocultures in the chemostat", *FEMS Microbiol. Ecol.*, vol. 38, num. 131-140, 1986.

[4] T. SARI, M. EL HAJJI, J. HARMAND, "The mathematical analysis of a syntrophic relationship between two microbial species in a chemostat", *Math. Bio. Eng*, vol. 9, num. 627-645, 2012.

[5] T. SARI, J. HARMAND, "A model of a syntrophic relationship between two microbial species in a chemostat including maintenance", *Math. Biosci. Eng*, vol. 275, num. 1-9, 2016.

[6] A. XU, J. DOLFING, T.P. CURTIS, G. MONTAGUE, E. MARTIN, "Maintenance affects the stability of a two-tiered microbial 'food chain"', *J. Theoret. Biol.*, vol. 276, num. 35-41, 2011.