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On a global stability of a two-step anaerobic digestion model

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Abstract

In this work, we consider a two-step anaerobic digestion model where two microorganisms mutually cooperate by producing a substrate for the other's growth. The model is a four-dimensional system of ordinary differential equations. Since the system is conservative by considering the same dilution rates, we show that the fourth-order model can be reduced to a second-order model. Using the nullcline method, we show that the system can have up to four steady states for a general class of growth rates and we analytically determine the necessary and sufficient conditions for their existence according to the operating parameters. Using the method of the vector field, we determine the necessary and sufficient conditions of local and global asymptotic stability of all steady states of the reduced model. Using Thieme's result, we show that the global asymptotic behavior of the solutions of the reduced model is the same as that of the complete system. For specific growth rates of Monod type, the numerical simulations illustrate our mathematical analysis.

Keywords

Anaerobic digestion; Chemostat; Global stability; Nullcline; Vector field.

I INTRODUCTION

Anaerobic digestion (AD) is a complex natural process in which organic matter is broken down into biogas and various by-products in an oxygen-free environment. Several mathematical models describe this process and are used to predict the production of biogas methane. The comprehensive Anaerobic Digestion Model (ADM1) is a model with a large number of state variables and parameters. The complexity of this model makes a qualitative analysis very difficult. A simple two-step AD model (called AM2) proposed by [2] provides satisfactory prediction of the AD process. Many papers in the literature have studied the AM2 model (see [3–7, 10, 12] and the reference therein).

In this work, we consider a reduced model of two-stage anaerobic digestion in a chemostat that was validated using parameter identification theory in Giovannini et al. [11]. Using informative data sets generated by ADM1 and Maximum Likelihood Principle Component Analysis (MLPCA), they propose the following macroscopic reaction scheme.

1. Acidogenesis, with a reaction rate $r_1 = \mu_1(\cdot)X_1$, such that $\mu_1(\cdot)$ is the specific growth rate of X_1 :



2. Methanogenesis, with a reaction rate $r_2 = \mu_2(\cdot)X_2$, such that $\mu_2(\cdot)$ is the specific growth rate of X_2 :



where $k_i, i = 1, \dots, 8$ represent the pseudo-stoichiometric coefficients.

The first microbial population X_1 converts organic matter S_1 into organic acids S_2 , methane CH_4 and hydrogen H_2 with a reaction rate r_1 . The products of the first reaction would then be used by the second population X_2 to produce methane with a reaction rate r_2 . The substrates S_1 and S_2 are introduced into the reactor with feed concentrations S_1^{in} and S_2^{in} , respectively, and a dilution rate D . These reactions are described by the following system of differential equations:

$$\begin{cases} \dot{S}_1 &= D(S_1^{in} - S_1) - k_1\mu_1(S_1)X_1 + k_2\mu_2(S_2)X_2, \\ \dot{X}_1 &= (\mu_1(S_1) - D_1)X_1, \\ \dot{S}_2 &= D(S_2^{in} - S_2) + k_3\mu_1(S_1)X_1 - k_4\mu_2(S_2)X_2, \\ \dot{X}_2 &= (\mu_2(S_2) - D_2)X_2, \end{cases} \quad (3)$$

where D_1 and D_2 are the removal rates of the first and second populations. The specific growth rates of $\mu_1(\cdot)$ acidogenes and $\mu_2(\cdot)$ methanogens are Monod-like.

Using a step-by-step parameter identification procedure to estimate the kinetic parameters, and parametric sensitivity analysis, Giovannini et al. [11] have validated the reduced two-step model (3). The most affected stoichiometric coefficient is k_2 which is associated to S_1 in the second reaction. It is small enough compared to other coefficients and it is relatively large uncertainty so that longer experiments with relatively rich excitation signals are necessary to extract the information about this coefficient k_2 . By eliminating this parameter, the direct validation results are quite satisfactory and the cross-validation results are perfectible. Indeed, the numerical results show the predictive capability of the low-dimensional model as compared to the original ADM1.

In the limit case when $k_2 = 0$, the two-step model (3) with a cascade of two biological reactions was introduced in [2]. In addition, this model was studied recently in [15],[13] by determining the best operating conditions which maximize the biogas production in the operating diagram according to the dilution rate and the substrate input concentrations.

Our aim of this work is to study the global behavior of model (3) by considering this coefficient k_2 is positive and small enough to understand the effect of the production of organic matter S_1 from S_2 in the second reaction. For a general class of growth rates and the same dilution rates, we determine theoretically the existence and local and global stability of all steady states. This study is original and has not been studied in the literature.

This paper is organized as follows. In section 2, we present the assumptions on the general model (4) and we show that the solutions of the ordinary differential equations remain positive and positively bounded for any positive initial condition. In section 3, we show that the fourth-order model can be reduced to a second-order model. In section 4, we determine the steady states of this reduced model and study their local and global stability according to the control parameters by giving necessary and sufficient conditions. In section 5, we illustrate the mathematical results demonstrated by numerical simulations. The conclusion is given in section 6. The proofs of all the results are presented in Appendix A.

II MATHEMATICAL MODEL AND ASSUMPTIONS

In this work, we study the model (3) where the removal rates D_1 and D_2 and the dilution rate D are equal, that is, $D = D_1 = D_2$. The model (3) can be reduced to the following model (see [14])

$$\begin{cases} \dot{s}_1 &= D(s_1^{in} - s_1) - f_1(s_1)x_1 + \omega f_2(s_2)x_2, \\ \dot{x}_1 &= (f_1(s_1) - D)x_1, \\ \dot{s}_2 &= D(s_2^{in} - s_2) + f_1(s_1)x_1 - f_2(s_2)x_2, \\ \dot{x}_2 &= (f_2(s_2) - D)x_2, \end{cases} \quad (4)$$

where

$$s_1 = S_1 \frac{k_3}{k_1}, \quad x_1 = k_3 X_1, \quad s_2 = S_2, \quad x_2 = k_4 X_2 \quad s_1^{in} = S_1^{in} \frac{k_3}{k_1} \quad \text{and} \quad s_2^{in} = S_2^{in}.$$

In what follows, we study model (4) using the following general assumption on the growth rates. For $i = 1, 2$ the function f_i belongs to $\mathcal{C}^1(\mathbb{R}_+)$ and satisfies:

(H1) $f_i(0) = 0$ and $f_i'(s_i) > 0$ for all $s_i > 0$.

(H2) $0 < \omega < 1$, where ω is defined by $\omega = \frac{k_3 k_2}{k_1 k_4}$.

Assumption (H1) means that the substrate is necessary for the growth of the two species. In addition, the growth rate of each species increases with the concentration of the substrate. Assumption (H2) is satisfied since, from the biological point of view, we can show that $k_1 > k_3 > 0$ and $k_4 > k_2 > 0$, using the two reaction schemes.

If the equation $f_i(s_i) = D$ has a solution, we note

$$\lambda_i(D) = f_i^{-1}(D), \quad i = 1, 2.$$

Otherwise, we write $\lambda_i(D) = +\infty$. To simplify the notation, we will denote in the sequence λ_i by $\lambda_i(D)$. The following result proves that model (4) preserves the biological significance where all solutions of the system are nonnegative and bounded for any nonnegative initial condition.

Proposition II.1:

For any nonnegative initial condition, the solution of system (4) exists for all nonnegative times, remains nonnegative and is positively bounded. In addition, the set

$$\Omega = \left\{ (s_1, x_1, s_2, x_2) \in \mathbb{R}_+^4 : s_1 + x_1 - \omega x_2 = s_1^{in} \quad \text{and} \quad s_2 + x_2 - x_1 = s_2^{in} \right\}$$

is positively invariant and is a global attractor for (4).

III REDUCED MODEL

In the following, we show that the fourth-order system (4) can be reduced to a second-order system using Thieme's results [1]. Consider (s_1, x_1, s_2, x_2) a solution of system (4). Let

$$z_1 = s_1 + x_1 - \omega x_2 \quad \text{and} \quad z_2 = s_2 + x_2 - x_1.$$

Thus, (z_1, x_1, z_2, x_2) is a solution of the following system

$$\begin{cases} \dot{z}_1 &= D(s_1^{in} - z_1), \\ \dot{x}_1 &= (f_1(z_1 - x_1 + \omega x_2) - D)x_1, \\ \dot{z}_2 &= D(s_2^{in} - z_2), \\ \dot{x}_2 &= (f_2(z_2 + x_1 - x_2) - D)x_2. \end{cases} \quad (5)$$

The solutions of the first and third equations of (5) are given by:

$$z_1(t) = s_1^{in} + (z_1(0) - s_1^{in})e^{-Dt} \quad \text{and} \quad z_2(t) = s_2^{in} + (z_2(0) - s_2^{in})e^{-Dt}.$$

Thus, $(x_1(t), x_2(t))$ is a solution of the following asymptotically autonomous system:

$$\begin{cases} \dot{x}_1 = (f_1(s_1^{in} + (z_1(0) - s_1^{in})e^{-Dt} - x_1 + \omega x_2) - D) x_1, \\ \dot{x}_2 = (f_2(s_2^{in} + (z_2(0) - s_2^{in})e^{-Dt} + x_1 - x_2) - D) x_2. \end{cases} \quad (6)$$

Then, system (6) converges to the next autonomous system:

$$\begin{cases} \dot{x}_1 = (f_1(s_1^{in} - x_1 + \omega x_2) - D) x_1, \\ \dot{x}_2 = (f_2(s_2^{in} + x_1 - x_2) - D) x_2. \end{cases} \quad (7)$$

In the section 4.3, we show that Thieme's results [1] apply and allow to deduce the asymptotic behavior of the solution of (4) from the asymptotic behavior of the autonomous system (7). This system is called the reduced model since it is simply the restriction of (4) to the set Ω . On the other hand, since s_1 and s_2 are positive then:

$$0 \leq x_1 \leq s_1^{in} + \omega x_2 \quad \text{and} \quad 0 \leq x_2 \leq s_2^{in} + x_1.$$

Thus, system (7) is defined on the set:

$$M = \{(x_1, x_2) \in \mathbb{R}_+^2 : 0 \leq x_1 \leq s_1^{in} + \omega x_2 \quad \text{and} \quad 0 \leq x_2 \leq s_2^{in} + x_1\}. \quad (8)$$

Fig. 1 (a) describes the domain M in the case where $0 < \omega < 1$ in the plane (x_1, x_2) . In the limiting case where $\omega = 1$, Fig. 1 (b) shows that the two lines Δ_1^M and Δ_2^M are parallel. Note that the equations of the lines Δ_1^M and Δ_2^M are defined by:

$$\Delta_1^M : x_2 = \frac{x_1 - s_1^{in}}{\omega} \quad \text{and} \quad \Delta_2^M : x_2 = s_2^{in} + x_1.$$

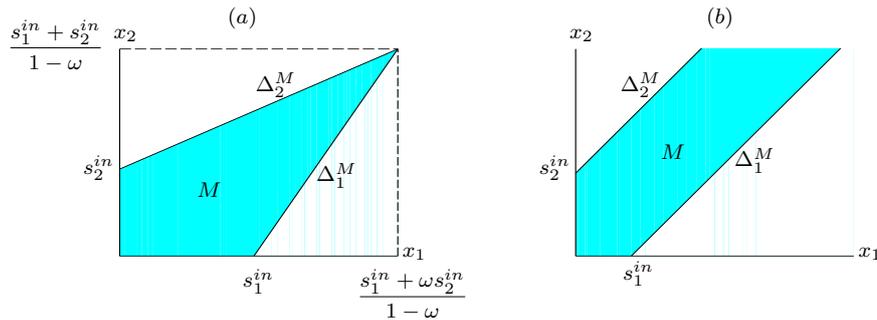


Figure 1: The set M : (a) the case where $0 < \omega < 1$, (b) the case where $\omega = 1$

IV STUDY OF THE REDUCED MODEL

In this section, we are interested in the study of the reduced system (7) in M (see Fig. 1) using the nullcline method (voir [8, 9]).

4.1 Existence of the steady states

In the following, we study the existence and uniqueness of the steady states of system (7) under the assumptions (H1) and (H2). The steady states of (7) are the intersection points of the nullclines in M .

Definition 1:

We call nullcline of x_1 of system (7) and denote by $\dot{x}_1 = 0$, the set of points where

$$(f_1(s_1^{in} - x_1 + \omega x_2) - D) x_1 = 0.$$

Similarly, the nullcline of x_2 : $\dot{x}_2 = 0$, is the set of points where

$$(f_2(s_2^{in} + x_1 - x_2) - D) x_2 = 0.$$

Remark 1:

From the hypothesis (H1), we easily determine the nullclines of system (7):

$$\begin{aligned} \dot{x}_1 = 0 &\iff x_1 = 0 \quad \text{or} \quad s_1^{in} - x_1 + \omega x_2 = \lambda_1, \\ \dot{x}_2 = 0 &\iff x_2 = 0 \quad \text{or} \quad s_2^{in} + x_1 - x_2 = \lambda_2. \end{aligned}$$

Thus, the nullclines are given by the two axes and the following two lines:

$$\Delta_1 : x_2 = \frac{x_1 - s_1^{in} + \lambda_1}{\omega} \quad \text{and} \quad \Delta_2 : x_2 = x_1 + s_2^{in} - \lambda_2. \quad (9)$$

Proposition IV.1:

Assume that hypotheses (H1) and (H2) hold. Then, the six steady states of (7) are given in Table 1. The conditions of their existence and local stability are given in Table 2. Note that the existence condition of \mathcal{E}^* is given by

$$s_1^{in} + s_2^{in} > \lambda_1 + \lambda_2 \quad \text{and} \quad s_1^{in} + \omega s_2^{in} > \lambda_1 + \omega \lambda_2. \quad (10)$$

Table 1: Steady states of (7).

	x_1, x_2 components
\mathcal{E}_0	$x_1 = 0, x_2 = 0$
\mathcal{E}_1	$x_1 = s_1^{in} - \lambda_1, x_2 = 0$
\mathcal{E}_2	$x_1 = 0, x_2 = s_2^{in} - \lambda_2$
\mathcal{E}^*	$x_1 = \frac{s_1^{in} + \omega s_2^{in} - \lambda_1 - \omega \lambda_2}{1 - \omega}, x_2 = \frac{s_1^{in} + s_2^{in} - \lambda_1 - \lambda_2}{1 - \omega}$

Corollary 1:

Table 3 determines the necessary conditions of local exponential stability of all steady state according to the operating parameters, where six cases can be distinguished.

Table 2: Necessary and sufficient conditions of existence and local stability of steady states of model (7).

	Existence condition	Stability condition
\mathcal{E}_0	always exists	$s_1^{in} < \lambda_1$ and $s_2^{in} < \lambda_2$
\mathcal{E}_1	$s_1^{in} > \lambda_1$	$s_1^{in} + s_2^{in} < \lambda_1 + \lambda_2$
\mathcal{E}_2	$s_2^{in} > \lambda_2$	$s_1^{in} + \omega s_2^{in} < \lambda_1 + \omega \lambda_2$
\mathcal{E}^*	(10)	LES whenever it exists

Table 3: Existence and local stability of the steady states of system (7) according to the position of s_1^{in} with respect to λ_1 and of s_2^{in} with respect to λ_2 : The absence of a letter means that steady state does not exist.

Case	Condition 1	Condition 2	\mathcal{E}_0	\mathcal{E}_1	\mathcal{E}_2	\mathcal{E}^*
1	$s_1^{in} < \lambda_1$ $s_2^{in} < \lambda_2$	(10) is not verified	LES			
2	$s_1^{in} > \lambda_1$ $s_2^{in} < \lambda_2$	$s_1^{in} + s_2^{in} < \lambda_1 + \lambda_2$	I	LES		
3	$s_1^{in} < \lambda_1$ $s_2^{in} > \lambda_2$	$s_1^{in} + \omega s_2^{in} < \lambda_1 + \omega \lambda_2$	I		LES	
4	$s_1^{in} > \lambda_1$ $s_2^{in} > \lambda_2$		I	I	I	LES
5	$s_1^{in} > \lambda_1$ $s_2^{in} < \lambda_2$	(10) is verified	I	I		LES
6	$s_1^{in} < \lambda_1$ $s_2^{in} > \lambda_2$		I		I	LES

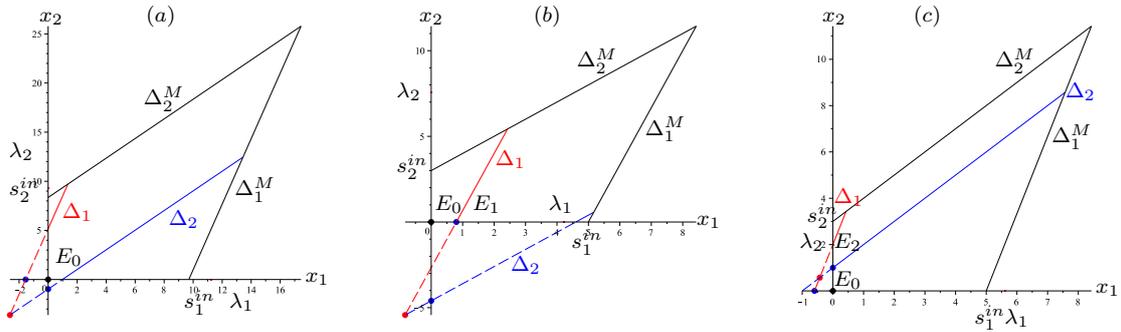


Figure 2: Nullclines Δ_1 and Δ_2 : (a) case 1 (b) case 2 (c) case 3 of Table 3.

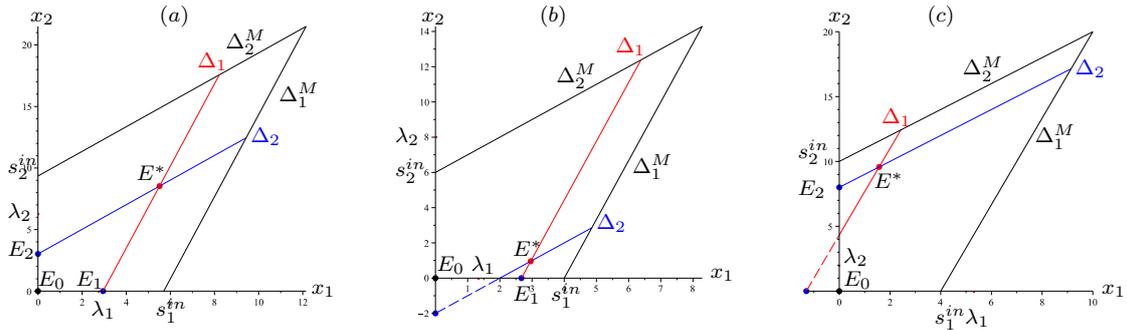


Figure 3: Nullclines Δ_1 and Δ_2 : (a) case 4 (b) case 5 (c) case 6 of Table 3.

4.2 Global stability of the reduced model

In this section, we study the global stability of the steady states by the nullcline and vector field methods used in [9]. In the following, we use the abbreviation GAS for Globally Asymptotically Stable. Note that in the following figures, we choose the red color for stable steady state and the blue color for unstable steady state.

Proposition IV.2:

Under the assumptions (H1) and (H2), the conditions of existence and global stability of the steady state of system (7) are given in Table 4.

Table 4: Existence and global asymptotic stability of the steady states of system (7) according to the operating parameters D , s_1^{in} et s_2^{in} .

	Existence condition	Global stability condition
\mathcal{E}_0	always exists	$s_1^{in} \leq \lambda_1$ and $s_2^{in} \leq \lambda_2$
\mathcal{E}_1	$s_1^{in} > \lambda_1$	$s_1^{in} + s_2^{in} \leq \lambda_1 + \lambda_2$
\mathcal{E}_2	$s_2^{in} > \lambda_2$	$s_1^{in} + \omega s_2^{in} \leq \lambda_1 + \omega \lambda_2$
\mathcal{E}^*	(10)	LES whenever it exists

From Corollary 1 and Table 4, we summarize the existence and global stability in Table 5 according to the position of s_1^{in} with respect to λ_1 and s_2^{in} with respect to λ_2 .

Table 5: Existence and global stability of the steady states of system (7) according to the six cases of the Table 3: The absence of a letter means that the steady state does not exist.

Case	Condition 1	Condition 2	\mathcal{E}_0	\mathcal{E}_1	\mathcal{E}_2	\mathcal{E}^*
1	$s_1^{in} \leq \lambda_1$ $s_2^{in} \leq \lambda_2$		GAS			
2	$s_1^{in} > \lambda_1$ $s_2^{in} \leq \lambda_2$	(10) is not verified	I	GAS		
3	$s_1^{in} \leq \lambda_1$ $s_2^{in} > \lambda_2$		I		GAS	
4	$s_1^{in} > \lambda_1$ $s_2^{in} > \lambda_2$		I	I	I	GAS
5	$s_1^{in} > \lambda_1$ $s_2^{in} \leq \lambda_2$	(10) is verified	I	I		GAS
6	$s_1^{in} \leq \lambda_1$ $s_2^{in} > \lambda_2$		I		I	GAS

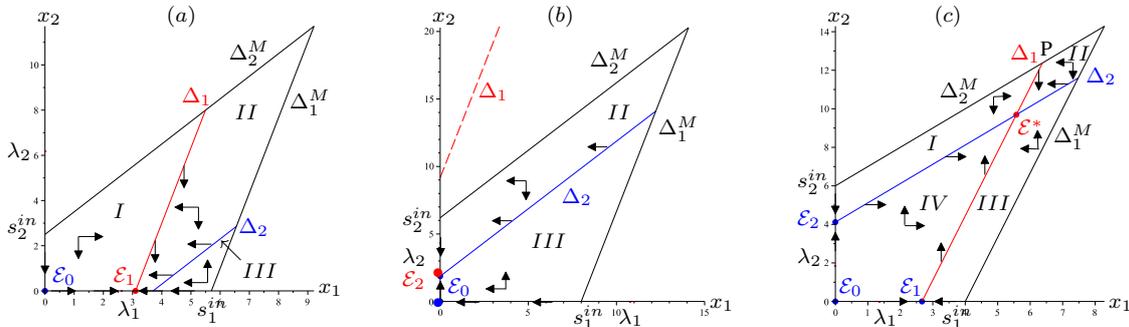


Figure 4: Global stability of the steady states of (7): (a) case 2 of table 5, where \mathcal{E}_0 is GAS, (b) case 3 of table 5, where \mathcal{E}_1 is GAS, (c) case 4 of table 5, where \mathcal{E}^* is GAS.

4.3 Global behavior

In the following, we study the full two-stage model (4) under the assumptions (H1) and (H2). To each steady state $\mathcal{E} = (x_1, x_2)$ of system (7) corresponds an steady state

$$\mathcal{F} = (s_1, x_1, s_2, x_2)$$

where (x_1, x_2) are the components of the steady state \mathcal{E} and (s_1, s_2) are defined by:

$$s_1 = \omega x_2 - x_1 + s_1^{in} \quad \text{and} \quad s_2 = s_2^{in} + x_1 - x_2.$$

This construction allows us to obtain the steady state \mathcal{F}_0 , \mathcal{F}_1 , \mathcal{F}_2 and \mathcal{F}^* from the steady state \mathcal{E}_0 , \mathcal{E}_1 , \mathcal{E}_2 and \mathcal{E}^* .

Proposition IV.3:

The steady state of system (4) are given in the Table 6 :

Table 6: Steady states of (4).

	s_1, s_2 components	x_1, x_2 components
\mathcal{F}_0	$s_1 = s_1^{in}, s_2 = s_2^{in}$	$x_1 = 0, x_2 = 0$
\mathcal{F}_1	$s_1 = \lambda_1, s_2 = s_1^{in} + s_2^{in} - \lambda_1$	$x_1 = s_1^{in} - \lambda_1, x_2 = 0$
\mathcal{F}_2	$s_1 = s_1^{in} + \omega(s_2^{in} - \lambda_2), s_2 = \lambda_2$	$x_1 = 0, x_2 = s_2^{in} - \lambda_2$
\mathcal{F}^*	$s_1 = \lambda_1, s_2 = \lambda_2$	$x_1 = \frac{s_1^{in} + \omega s_2^{in} - \lambda_1 - \omega \lambda_2}{1 - \omega}$ $x_2 = \frac{s_1^{in} + s_2^{in} - \lambda_1 - \lambda_2}{1 - \omega}$

Lemma IV.1:

Consider system (7). Let $(x_1(t), x_2(t))$ be a trajectory of positive initial condition $(x_1(0), x_2(0))$, the limit set of this trajectory is non-empty and does not contain any periodic orbit.

Corollary 2:

The global asymptotic behavior of the complete system (4) is the same as that of the reduced system (7).

Proposition IV.4:

Under the assumptions (H1) and (H2), the conditions of existence and global stability of the steady state of system (4) are given in Table 7.

Table 7: Existence and global (asymptotic) stability of the steady states of system (4) according to the operating parameters D , s_1^{in} et s_2^{in} .

	Existence condition	Global stability condition
\mathcal{F}_0	always exists	$s_1^{in} \leq \lambda_1$ and $s_2^{in} \leq \lambda_2$
\mathcal{F}_1	$s_1^{in} > \lambda_1$	$s_1^{in} + s_2^{in} \leq \lambda_1 + \lambda_2$
\mathcal{F}_2	$s_2^{in} > \lambda_2$	$s_1^{in} + \omega s_2^{in} \leq \lambda_1 + \omega \lambda_2$
\mathcal{F}^*	(10)	LES whenever it exists

V NUMERICAL SIMULATIONS

In this section, we consider system (7). Recall that the existence and stability of the steady states are summarized in Table 5. In order to illustrate the results of the section 4.2, we perform the simulations for Monod type growth rates which are defined by

$$f_1(s_1) = \frac{m_1 s_1}{s_1 + k_1} \quad \text{and} \quad f_2(s_2) = \frac{m_2 s_2}{s_2 + k_2}, \quad (11)$$

where m_1, m_2 denote the maximum growth rates; k_1, k_2 denote the Michaelis-Menten constants. The parameter values are provided in Table 8. Moreover, we consider that the inflowing concentrations of the second substrate in the chemostat s_2^{in} is equal to 1.2.

Table 8: Parameter values used for (7) when f_1 and f_2 are given by (11).

Paramètre	m_1	k_1	m_2	k_2
Valeur	5.62	2.61	2.48	2.46

First, we choose $(D, s_1^{in}) = (2.4, 0.4)$. Thus,

$$s_1^{in} < \lambda_1 \approx 2.091 \quad \text{and} \quad s_2^{in} < \lambda_2 \approx 73.80.$$

In this case, the figure 5 (a) illustrates the global convergence towards the unique steady state $\mathcal{E}_0 = (0, 0)$ which is GAS inside M . Figure 5 (b) shows the global convergence to $\mathcal{E}_1 \approx (0.770, 0)$ which is GAS inside M when $(D, s_1^{in}) = (1.8, 2)$ means,

$$s_1^{in} > \lambda_1 \approx 1.22 \quad \text{and} \quad s_2^{in} < \lambda_2 \approx 6.51.$$

Similarly, we choose $(D, s_1^{in}) = (0.7, 0.1)$ so that

$$s_1^{in} < \lambda_1 \approx 0.371 \quad \text{and} \quad s_2^{in} > \lambda_2 \approx 0.967.$$

In this case, the figure 6 (a) illustrates the global convergence to $\mathcal{E}_2 \approx (0, 0.232)$ which is GAS inside M . Figure 6 (b) illustrates the global convergence to $\mathcal{E}^* \approx (3.446, 3.861)$ which is GAS inside M when $(D, s_1^{in}) = (0.6, 2.6)$ means,

$$s_1^{in} > \lambda_1 \approx 0.311 \quad \text{and} \quad s_2^{in} > \lambda_2 \approx 0.785.$$

While $\mathcal{E}_1 \approx (2.288, 0)$, $\mathcal{E}_2 \approx (0, 0.414)$ and \mathcal{E}_0 are unstable.

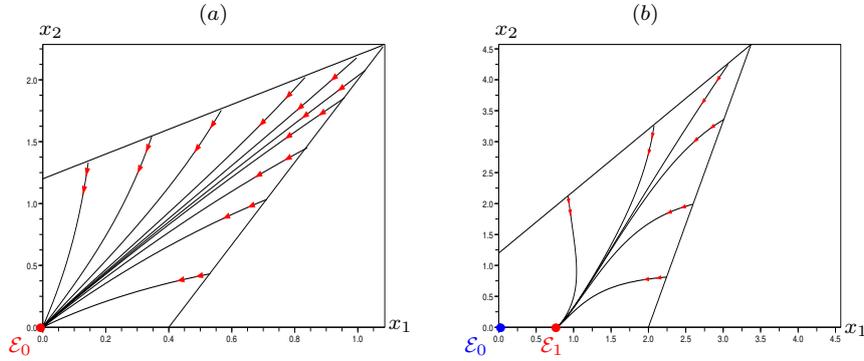


Figure 5: Phase portraits of system (7): (a) Global convergence to \mathcal{E}_0 . (b) Global convergence to \mathcal{E}_1 .

VI CONCLUSION

This work is devoted to the mathematical study of a two-stage anaerobic digestion model (4) in a chemostat where, the first microbial population x_1 transforms the organic matter s_1 into organic acids s_2 , methane CH_4 and hydrogen H_2 . The products of the first reaction would then be used by the second population x_2 to produce methane. Using Thieme's results, the asymptotic behavior of the solution of system (4) in dimension four is deduced from the asymptotic behavior of the reduced two-dimensional system (7). We have proved that the system can admit at most four steady states noted \mathcal{F}_0 , \mathcal{F}_1 , \mathcal{F}_2 and \mathcal{F}^* which represent respectively the washout, the extinction of second species, the extinction of first species and the coexistence of two populations. When the coexistence steady state exists in the positive half-plane, the other steady

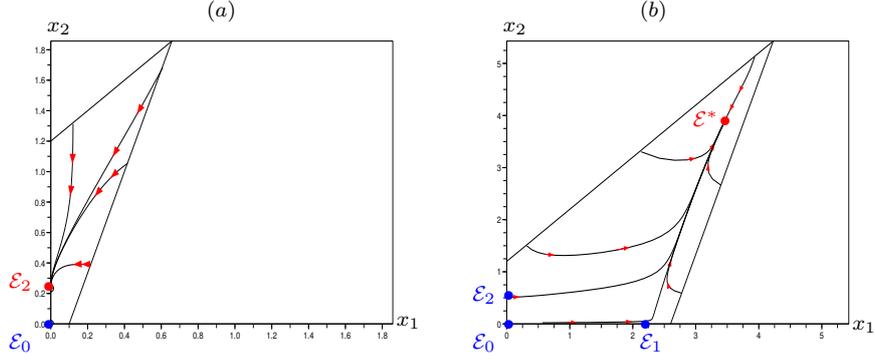


Figure 6: Phase portraits of system (7): (a) Global convergence to \mathcal{E}_2 . (b) Global convergence to \mathcal{E}^* .

states appear unstable. Then, we analyzed the local asymptotic behavior of all steady states by determining their necessary and sufficient conditions as a function of the operating parameters. Using the nullcline method [9], we were able to determine the necessary and sufficient conditions of the global asymptotic stability of each steady-state. This system does not exhibit bistability, i.e., the asymptotic behavior of this process does not depend on the initial condition. Finally, numerical simulations demonstrate the mathematical results and validate the theoretical results. In this work, we have done the mathematical analysis of the model (4) in the particular case $D = D_1 = D_2$. However, several questions remain open such as the effect of mortality or maintenance as well as substrate inhibition on the behavior of this anaerobic digestion model.

A PROOFS

Proof of Proposition IV.1. The steady states of system (7) are given by the solutions of the following two equations:

$$\begin{cases} (f_1(s_1^{in} - x_1 + \omega x_2) - D)x_1 = 0 \\ (f_2(s_2^{in} + x_1 - x_2) - D)x_2 = 0. \end{cases} \quad (12)$$

We can easily verify the existence of the steady state $\mathcal{E}_0 = (0, 0)$.

For \mathcal{E}_1 , we have $x_1 > 0$ and $x_2 = 0$. From the first equation of (12), we have $f_1(s_1^{in} - x_1) = D$. From the assumption (H1), we obtain

$$s_1^{in} - \bar{x}_1 = \lambda_1 \iff \bar{x}_1 = s_1^{in} - \lambda_1.$$

Hence, \bar{x}_1 is strictly positive if and only if $s_1^{in} > \lambda_1$. Similarly, for \mathcal{E}_2 , we have $x_1 = 0$ and $x_2 > 0$. From the second equation of (12), we have $f_2(s_2^{in} - x_2) = D$. From the assumption (H1), we obtain

$$s_2^{in} - \bar{x}_2 = \lambda_2 \iff \bar{x}_2 = s_2^{in} - \lambda_2.$$

Hence, \bar{x}_2 is strictly positive if and only if $s_2^{in} > \lambda_2$. For \mathcal{E}^* , we have $x_1 > 0$ and $x_2 > 0$. According to (12), we have

$$\begin{cases} f_1(s_1^{in} - x_1 + \omega x_2) = D, \\ f_2(s_2^{in} + x_1 - x_2) = D. \end{cases} \iff \begin{cases} s_1^{in} - x_1 + \omega x_2 = \lambda_1, \\ s_2^{in} + x_1 - x_2 = \lambda_2. \end{cases} \quad (13)$$

Note that, the interior M° of M is defined by:

$$M^\circ = \{(x_1, x_2) \in \mathbb{R}_+^2 : 0 < x_1 < s_1^{in} + \omega x_2 \text{ and } 0 < x_2 < s_2^{in} + x_1\}. \quad (14)$$

Thus, the strictly positive steady state \mathcal{E}^* is given by the intersection of the lines Δ_1 and Δ_2 in M° defined by (14). From (13), we can write the components of $\mathcal{E}^* = (x_1^*, x_2^*)$ as follows:

$$x_1^* = \frac{s_1^{in} + \omega s_2^{in} - \lambda_1 - \omega \lambda_2}{1 - \omega} \quad \text{and} \quad x_2^* = \frac{s_1^{in} + s_2^{in} - \lambda_1 - \lambda_2}{1 - \omega},$$

where x_1^* and x_2^* are strictly positive if and only if condition (10) is verified. ■

Proof of Corollary 1.

- For case 2 of the table 3, we have \mathcal{E}_1 is LES if and only if, $s_1^{in} > \lambda_1$ and $s_1^{in} + s_2^{in} < \lambda_1 + \lambda_2$. Then, $s_1^{in} > \lambda_1$, $s_2^{in} < \lambda_2$ and $s_1^{in} + s_2^{in} < \lambda_1 + \lambda_2$.
- For case 3 of the table 3, we have \mathcal{E}_2 is LES if and only if, $s_2^{in} > \lambda_2$ and $s_1^{in} + \omega s_2^{in} < \lambda_1 + \omega \lambda_2$. Then, $s_1^{in} < \lambda_1$, $s_2^{in} > \lambda_2$ and $s_1^{in} + \omega s_2^{in} < \lambda_1 + \omega \lambda_2$.

■

Proof of Proposition IV.2. We consider the case $s_1^{in} + s_2^{in} > \lambda_1 + \lambda_2$ and $s_1^{in} + \omega s_2^{in} > \lambda_1 + \omega \lambda_2$. We place ourselves in the generic case where $s_1^{in} > \lambda_1$ and $s_2^{in} > \lambda_2$, that is to say the case 4 of the Table 3 where the steady states \mathcal{E}_1 and \mathcal{E}_2 exist and are unstable (see Fig. 4 (c)). Since the lines Δ_1 and Δ_2 intersect inside M , then the nullclines define four regions where the signs of \dot{x}_1 and \dot{x}_2 are constant in each region noted by:

$$\begin{aligned} I : \dot{x}_1 > 0, \dot{x}_2 < 0, \quad II : \dot{x}_1 < 0, \dot{x}_2 < 0, \\ III : \dot{x}_1 < 0, \dot{x}_2 > 0, \quad IV : \dot{x}_1 > 0, \dot{x}_2 > 0. \end{aligned}$$

Indeed, for any $(x_1, x_2) \in IV$, we have

$$\frac{x_1 - s_1^{in} + \lambda_1}{\omega} < x_2 < x_1 + s_2^{in} - \lambda_2 \iff \dot{x}_1 > 0 \text{ et } \dot{x}_2 > 0.$$

In the same way, we will determine the signs of \dot{x}_1 and \dot{x}_2 in the regions I , II and III .

Let a trajectory of (7) originate from a point inside the region IV .

- It cannot exit along the interval $] \mathcal{E}_1, \mathcal{E}^* [$ since at a point in this interval the velocity vector is vertical and directed upwards so is strictly entering in IV .
- For the same reason it cannot go out along the interval $] \mathcal{E}_2, \mathcal{E}^* [$.
- it cannot neither leave along the interval $] \mathcal{E}_0, \mathcal{E}_1 [$, nor through the interval $] \mathcal{E}_0, \mathcal{E}_2 [$ since these are trajectories.
- The trajectory cannot go out it tends to a continuous steady state in IV it can only be the steady state \mathcal{E}^* , because in IV , the functions $x_1(t)$ and $x_2(t)$ are strictly increasing.

Similarly, a trajectory from a point inside the region II tends to the steady state \mathcal{E}^* . Let us now consider a trajectory originating from a point inside the region I .

- Either, it leaves the region I and then it can only be according to $] \mathcal{E}_2, \mathcal{E}^* [$ or $] \mathcal{E}^*, P [$. Thus, it enters the region IV or II and then it tends towards the steady state \mathcal{E}^* .
- Either, it remains in the region I and then it tends to an steady state located in I , it cannot be \mathcal{E}_2 because the function $x_1(t)$ is strictly increasing in I , it is thus \mathcal{E}^* .

In a similar way, a trajectory coming from a point inside III can tend directly to \mathcal{E}^* or enter the region IV or II .

■

Proof of Lemma IV.1. By making the change of variable $\xi_i = \ln(x_i)$, $i = 1, 2$, so the derivatives with respect to time are $\dot{x}_i = \frac{\dot{x}_i}{x_i}$, $i = 1, 2$, system (7) becomes:

$$\begin{cases} \dot{\xi}_1 &= f_1(s_1^{in} - e^{\xi_1} + \omega e^{\xi_2}) - D \\ \dot{\xi}_2 &= f_2(s_2^{in} + e^{\xi_1} - e^{\xi_2}) - D. \end{cases} \quad (15)$$

The divergence of the vector field $G(\xi_1, \xi_2) = \begin{bmatrix} f_1(s_1^{in} - e^{\xi_1} + \omega e^{\xi_2}) - D \\ f_2(s_2^{in} + e^{\xi_1} - e^{\xi_2}) - D \end{bmatrix}$ is:

$$\mathbf{div} G = \frac{df_1}{d\xi_1} + \frac{df_2}{d\xi_2} = -e^{\xi_1} f_1'(s_1^{in} - e^{\xi_1} + \omega e^{\xi_2}) - e^{\xi_2} f_2'(s_2^{in} + e^{\xi_1} - e^{\xi_2}) < 0,$$

then according to the Bendixon–Dulac criterion, we cannot have in the limit set a periodic orbit or a polycycle. ■

Proof of Corollary 2. Let $(x_1(t), x_2(t))$ be a trajectory contained in M . Hence for any positive initial condition, the solutions of system (7) are positively bounded and consequently the limit sets are compact and non empty. According to the Poincaré-Bendixson theorem, these limit sets are either steady states or periodic orbits or polycycles. Using Lemma IV.1, we obtain that the set omega limit is steady states. Then according to Thieme's convergence theorem [1], the asymptotic behavior of the solution of (4) is the same as that of (7). ■

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