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On a Three Step Model of Anaerobic Digestion Including the Hydrolysis of Particulate Matter

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Abstract: In this work, we focus on the mathematical analysis of the model of chemostat with enzymatic degradation of a substrate (organic matter) that can partly be under a solid form Simeonov and Stoyanov (2003). The study of this 3-step model is derived from a smaller order sub-model since some variables can be decoupled from the others. We study the existence and the stability of equilibrium points of the sub-model considering both Monod or Haldane growth rates and distinct dilution rates. In the classical chemostat model with monotonic kinetics, it is well known that only one equilibrium point attracts all solutions and that bistability never occurs Smith and Waltman (1995). In the present study, although (i) only monotonic growth rates are considered and (ii) the concentrations of input substrate concentration is less than the break-even concentration, it is shown that the considered sub-model may exhibit bistability. Hence, the importance of hydrolysis in the appearance of positive equilibrium points and the bistability is pointed out. If a non monotonic growth rate is considered, depending on the input substrate concentration, it is shown that at most four positive equilibrium points exist. Furthermore, for any positive initial condition, the solution converges towards one of the positive equilibrium points for which the washout is unstable. Finally, we study the case where the growth rate is density-dependent, such as the Contois kinetics, which may be of interest if we consider that we work in a non homogeneous environment Lobry and Harmand (2006). Depending on the input substrate concentration, we show that the system can exhibit either a bistability or the global stability of the positive equilibrium point or of the washout.

Keywords: Enzymatic degradation, chemostat, models, growth rate, equilibrium, bistability.

1. INTRODUCTION

Anaerobic digestion is a biological process in which organic matter is transformed into methane and carbon dioxide (biogas) by microorganisms in the absence of oxygen. The search for models simple enough to be used for control design is of prior importance today to optimize fermentation processes and solve important problems such as the development of renewable energy from waste. Within the studies of microbiology, biochemistry and technology, the anaerobic digestion is generally considered as a three step process: hydrolysis and liquefaction of the large, insoluble organic molecules by extracellular enzymes, acid production by an acidogenic microbial consortium and a methane production stage realized by a methanogenic ecosystem. Several mathematical models describing these phenomena have been proposed in the literature. However, they are usually too complex to be used for control synthesis Simeonov and Stoyanov (2003); B. Benyahia and Harmand (2010a,b); Bastin and Dochain (1991). The chemical reactions of anaerobic digestion which converts the substrate into biomass is :

$$\begin{aligned} X_0 &\xrightarrow{r_0=\mu_0 X_0} k_0 S_1 \\ k_1 S_1 &\xrightarrow{r_1=\mu_1 X_1} X_1 + k_2 S_2 + CO_2 \\ k_3 S_2 &\xrightarrow{r_2=\mu_2 X_2} X_2 + CO_2 + CH_4 \end{aligned}$$

where $r_i = \mu_i X_i, i = 0 \cdots 2$, denotes the reaction rate, respectively, μ_0 is the specific growth rate of X_1 on X_0 and μ_i is the specific growth rate of X_i on S_i for $i = 1, 2$.

$k_i, i = 0 \dots 3$, denote the pseudo-stochiometric coefficients associated to the chemical reactions,

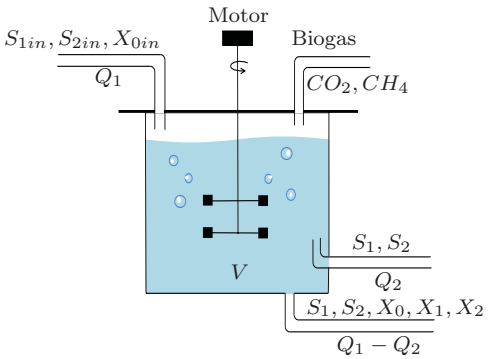

Fig. 1. Chemostat.

We consider a continuous culture, i.e the input flow rate Q_1 is equal to the output flow rate. For low concentrations of substrate, the biomass residence time is greater than the substrate one, then the output flow rate of biomass and substrate in the form macromolecules is $Q_1 - Q_2$. The three step model Simeonov and Stoyanov (2003) is :

$$\begin{cases} \dot{X}_0 &= DX_{0in} - \alpha D X_0 - \mu_0(X_0)X_1, \\ \dot{S}_1 &= D(S_{1in} - S_1) + k_0\mu_0(X_0)X_1 - k_1\mu_1(S_1)X_1, \\ \dot{X}_1 &= \Big(\mu_1(S_1) - \alpha D\Big)X_1, \\ \dot{S}_2 &= D(S_{2in} - S_2) + k_2\mu_1(S_1)X_1 - k_3\mu_2(S_2)X_2, \\ \dot{X}_2 &= \Big(\mu_2(S_2) - \alpha D\Big)X_2, \end{cases} \tag{1}$$

where

$$D = \frac{Q_1}{V} \quad \text{and} \quad \frac{Q_1 - Q_2}{V} = \alpha D.$$

D denotes the dilution rate of the chemostat and $\alpha \in [0, 1]$ represents the fraction of the biomass leaving the reactor. V denotes the volume of the bioreactor, $X_0(t)$ the concentration of the substrate in the form macromolecules at time t, with X_{0in} the concentration of the input nutriment. $S_j(t)$ denote the concentration of the substrates in the effluent, $j = 1, 2$, at time t; with S_{jin} the input substrate concentrations j. $X_i(t)$ denote the concentration of the ith population of microorganisms, $i = 1, 2$, at time t.

According to the principle of conservation of matter within the reaction scheme we have

$$\int_{t_1}^{t_2} \mu_0(X_0)X_1 V d\tau \geqslant \int_{t_1}^{t_2} k_0\mu_0(X_0)X_1 V d\tau \quad \text{i.e} \quad 1 \geqslant k_0,$$

which means that, the quantity of X_0 degraded is greater than or equal to the quantity of S_1 produced. Similarly, we have

$$k_1 \geqslant 1 + k_2 \quad \text{and} \quad k_3 \geqslant 1$$

which means that, the quantity of S_1 degraded is greater than or equal to the quantity of X_1 and S_2 produced. The quantity of S_2 degraded is greater than or equal to the quantity of X_2 produced.

In the following, we focus on the study of the sub-model given by the first three equations of system (1), the last two equations being decoupled since the first three equations are independent of variables X_2 and S_2. Thus, we study the existence and stability of equilibrium points of the following sub-model :

$$\begin{cases} \dot{X}_0 = D(X_{0in} - \alpha X_0) - \mu_0(X_0)X_1, \\ \dot{S}_1 = D(S_{1in} - S_1) + k_0\mu_0(X_0)X_1 - k_1\mu_1(S_1)X_1, \\ \dot{X}_1 = \Big[\mu_1(S_1) - \alpha D\Big]X_1. \end{cases} \tag{2}$$

First, we establish the following result :

Proposition 1.1.

(1) For any non-negative initial condition, the solutions of system (2) stay positive at any time and are bounded when $t \to +\infty$.

(2) The set

$$\Omega = \{(X_0, S_1, X_1) \in \mathbb{R}_+^3 : Z = k_0X_0 + S_1 + k_1X_1 \leqslant \max\big(Z(0), \tfrac{S_{in}}{\alpha D}\big)\}$$

is positively invariant and attractor of all solutions of (2), with $S_{in} = D(k_0X_{0in} + S_{1in})$.

2. STUDY OF THE SUB-MODEL

The washout equilibrium $E_0 = \big(\frac{X_{0in}}{\alpha}, S_{1in}, 0\big)$, always exists. To look for positive equilibria, we consider the function

$$\xi(X_0) = \frac{D(X_{0in} - \alpha X_0)}{\mu_0(X_0)}.$$

We assume that

H0: The function $\mu_0(\cdot)$ is increasing, $\mu_0(0) = 0$ and $\mu_0''(X_0) \leqslant 0$ for all $X_0 \in \big]0, \frac{X_{0in}}{\alpha}\big[$.

Lemma 2.1. Under assumption **H0**, the function $\xi(\cdot)$ vanishes on $\frac{X_{0in}}{\alpha}$, is decreasing and convex.

In the case where the function $\mu_0(\cdot)$ is linear or of Monod type, the assumption **H0** is satisfied.

2.1 Study of the sub-model with monotonic growth rate $\mu_1(\cdot)$

In this section, we study the existence of equilibrium points of system (2) under the following assumption

H1: $\mu_1(0) = 0$ and $\mu_1'(S_1) > 0$ for all $S_1 \geqslant 0$.

H2: The equation $\mu_1(S_1) = \alpha D$ has a finite solution $\lambda_1 = \mu_1^{-1}(\alpha D)$.

Let Δ the line of equation :

$$X_1 = \delta(X_0) = \frac{1}{k_1\alpha}\Big[(S_{1in} - \lambda_1) + k_0(X_{0in} - \alpha X_0)\Big].$$

Lemma 2.2. The equation $\xi'(X_0) = -\frac{k_0}{k_1}$ has a unique solution $\bar{X}_0 \in \big]0, \frac{X_{0in}}{\alpha}\big[$ if and only if

$$\xi'\left(\frac{X_{0in}}{\alpha}\right) > -\frac{k_0}{k_1}.$$

Moreover,

$$\xi'\left(\frac{X_{0in}}{\alpha}\right) > -\frac{k_0}{k_1} \iff k_0\mu_0\left(\frac{X_{0in}}{\alpha}\right) > k_1\alpha D.$$

If $\xi'\big(\frac{X_{0in}}{\alpha}\big) > -\frac{k_0}{k_1}$, the intersection of the line Δ with the curve of the function ξ, has at most two points. Let us denote by $E_1^* = (X_0^*, \lambda_1, X_1^*)$ and $E_1^{**} = (X_0^{**}, \lambda_1, X_1^{**})$ (see Fig. 2). By Lemma 2.2, there exists a unique solution $\bar{X}_0 \in \big]0, \frac{X_{0in}}{\alpha}\big[$ of equation $\xi'(X_0) = -\frac{k_0}{k_1}$. Thus, there is a

limit value X_1^{Min} for which the curve ξ is tangent to the line Δ and who satisfied

$$X_1^{Min} = \bar{X}_1 + \frac{k_0}{k_1}\bar{X}_0$$

with $\bar{E}_1 = (\bar{X}_0, \lambda_1, \bar{X}_1)$ an equilibrium of (2) (see case 4 of the Fig. 3). At this limite value X_1^{Min}, we associate S_{1in}^{Min} which satisfied

$$X_1^{Min} = \delta(0) = \frac{1}{k_1\alpha}\Big[(S_{1in}^{Min} - \lambda_1) + k_0 X_{0in}\Big].$$

In the generic case where $S_{1in}^{Min} > 0$, we have shown the following result :

Proposition 2.1.

- If $\lambda_1 \leqslant S_{1in}$, there exists a unique positive equilibrium $E_1^* = (X_0^*, \lambda_1, X_1^*)$.
- If $S_1^{Min} < S_{1in} < \lambda_1$, there exist two positive equilibria E_1^* et E_1^{**}.
- If $S_{1in} = S_1^{Min}$, there exists a unique positive equilibrium $\bar{E}_1 = (\bar{X}_0, \lambda_1, \bar{X}_1)$.
- If $S_{1in} < S_1^{Min}$, there is no positive equilibrium.

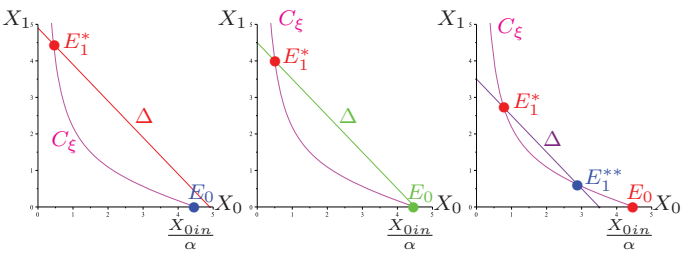

Fig. 2. Case 1: $\lambda_1 < S_{1in} = 5.5$, case 2: $S_{1in} = 4.5 = \lambda_1$, case 3: $S_1^{Min} < S_{1in} = 2 < \lambda_1$.

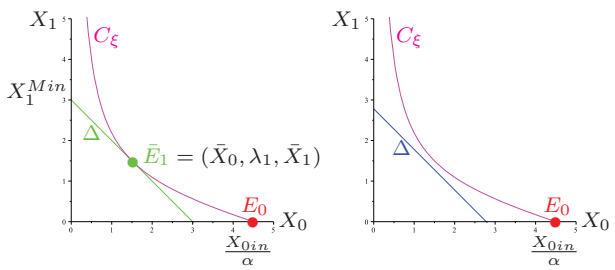

Fig. 3. Case 4: $S_{1in} = 0.75 = S_1^{Min}$, case 5: $S_{1in} = 0.2 < S_1^{Min}$.

In the following, we show the asymptotic behavior of equilibrium points. We choose the red color for Locally Asymptotically Stable (LAS) equilibrium, the green color for saddle node equilibrium and blue color for unstable equilibrium.

Proposition 2.2.

- E_0 is LAS if and only if $\mu_1(S_{1in}) < \alpha D$.
- If E_1^* exists, then it is LAS (stable node).
- If E_1^{**} exists, then it is unstable (saddle point).

Proof. At washout $E_0 = (\frac{X_{0in}}{\alpha}, S_{1in}, 0)$, the Jacobian matrix of (2) is

$$\mathbf{J_0} = \begin{bmatrix} -\alpha D & 0 & -\mu_0(\frac{X_{0in}}{\alpha}) \\ 0 & -D & k_0\mu_0(\frac{X_{0in}}{\alpha}) - k_1\mu_1(S_{1in}) \\ 0 & 0 & \mu_1(S_{1in}) - \alpha D \end{bmatrix}$$

The eigenvalues are $-\alpha D, -D$ and $\mu_1(S_{1in}) - \alpha D$. Then, the equilibrium E_0 is LAS if and only if $\mu_1(S_{1in}) < \alpha D$.

At a positive equilibrium $E_1^* = (X_0^*, \lambda_1, X_1^*)$, the Jacobian matrix is

$$\mathbf{J_1} = \begin{bmatrix} -m_{11} & 0 & -m_{13} \\ m_{21} & -m_{22} & \theta \\ 0 & m_{32} & 0 \end{bmatrix}$$

where

$$m_{11} = \alpha D + \mu_0'(X_0^*)X_1^*, \quad m_{13} = \mu_0(X_0^*),$$
$$m_{21} = k_0\mu_0'(X_0^*)X_1^*, \quad m_{22} = D + k_1\mu_1'(\lambda_1)X_1^*,$$
$$\theta = k_0\mu_0(X_0^*) - k_1\alpha D, \quad m_{32} = \mu_1'(\lambda_1)X_1^*,$$

with $m_{11}, m_{13}, m_{21}, m_{22}$ and m_{32} are positive. The characteristic polynomial of J_1 is given by

$$P_{J_1}(\lambda) = a_0\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$$

with

$$a_0 = -1, \quad a_1 = -(m_{11} + m_{22}), \quad a_2 = -m_{11}m_{22} + \theta m_{32},$$
$$a_3 = -m_{32}(m_{21}m_{13} - \theta m_{11}).$$

According to the Routh-Hurwitz criterion, E_1^* is LAS if and only if

$$\begin{cases} a_i < 0, & i = 0 \cdots 3 \\ a_1a_2 - a_0a_3 > 0. \end{cases}$$

We have

$$a_2 = \Big[k_0\mu_0(X_0^*) - k_1\alpha D - k_1\mu_0'(X_0^*)X_1^*\Big]\mu_1'(\lambda_1)X_1^*$$
$$- \Big[D\mu_0'(X_0^*)X_1^* + \alpha D\Big(D + k_1\mu_1'(\lambda_1)X_1^*\Big)\Big].$$

Since

$$\xi'(X_0^*) + \frac{k_0}{k_1} = \frac{-k_1\alpha D - k_1\mu_0'(X_0^*)X_1^* + k_0\mu_0(X_0^*)}{k_1\mu_0(X_0^*)}$$

then we deduce

$$a_2 = \Big[\xi'(X_0^*) + \tfrac{k_0}{k_1}\Big]k_1\mu_0(X_0^*)\mu_1'(\lambda_1)X_1^*$$
$$- \Big[D\mu_0'(X_0^*)X_1^* + \alpha D\Big(D + k_1\mu_1'(\lambda_1)X_1^*\Big)\Big]$$

therefore, if $\xi'(X_0^*) < -\frac{k_0}{k_1}$, then $a_2 < 0$. Moreover

$$a_3 = m_{32}\alpha D[k_0\mu_0(X_0^*) - k_1\alpha D - k_1\mu_0'(X_0^*)X_1^*]$$
$$= m_{32}\alpha D\Big[\xi'(X_0^*) + \tfrac{k_0}{k_1}\Big]k_1\mu_0(X_0^*)$$

is negative if and only if $\xi'(X_0^*) < -\frac{k_0}{k_1}$. Finally

$$a_1a_2 - a_0a_3 = -\Big[\xi'(X_0^*) + \tfrac{k_0}{k_1}\Big]k_1\mu_0(X_0^*)\mu_0'(X_0^*)\mu_1'(\lambda_1)X_1^{*2}$$
$$+ P$$

where

$$P = Dm_{11}^2 + \Big((\alpha D)^2 + \alpha D\mu_0'(X_0^*)X_1^*\Big)k_1\mu_1'(\lambda_1)X_1^* - m_{22}a_2$$

is positive if $\xi'(X_0^*) < -\frac{k_0}{k_1}$. Since E_1^* satisfies $\xi'(X_0^*) < -\frac{k_0}{k_1}$, then it is LAS and E_1^{**} satisfies $\xi'(X_0^{**}) > -\frac{k_0}{k_1}$, then it is unstable.

The simulations shown in Fig. 4 where obtained for the following Monod functions

$$\mu_0(X_0) = \frac{2.5X_0}{1.5 + X_0} \quad \text{and} \quad \mu_1(S) = \frac{2S}{1.5 + S}$$

and the following values of the parameters

$$X_{0in} = 3, \quad D = 1, \quad \alpha = 0.75, \quad k_0 = 1 \quad \text{and} \quad k_1 = 1.2$$

The value of the break-even concentration is $\lambda_1 = 0.9$. We illustrate the case of bistability for $S_{1in} = 0.7$ such as

$$\xi'\Big(\frac{X_{0in}}{\alpha}\Big) = -0.412 > -0.833 = -\frac{k_0}{k_1}.$$

In this case, the equation $\xi(X_0) = \delta(X_0)$ admits two solutions (see Fig. 4 on the left) and the system (2) has a washout equilibrium

$$E_0 = (4, 0.5, 0)$$

and two positive equilibria

$$E_1^* = (1.201, 0.9, 1.887), \quad E_1^{**} = (2.808, 0.9, 0.548).$$

The Fig. 4 in the middle shows the convergence to the positive equilibrium E_1^* for the initial condition

$$X_0(0) = 4.5, \quad S_1(0) = 2 \quad \text{and} \quad X_1(0) = 0.368$$

and the washout for the initial condition (see Fig. 4 on the right)

$$X_0(0) = 4.5, \quad S_1(0) = 2 \quad \text{and} \quad X_1(0) = 0.367$$

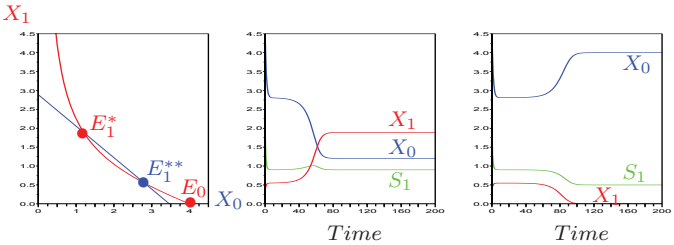

Fig. 4. Existence of two positive equilibria and bistability for $S_{1in} < \lambda_1$.

2.2 Study of the sub-model with non-monotonic growth rate $\mu_1(\cdot)$

In the following, we study the existence of equilibrium points of system (2) under the following assumption

H3: The function $\mu_1(\cdot)$ is non monotonic and is such that the equation $\mu_1(S_1) = \alpha D$ admits two solutions λ_1 and λ_2 with $\lambda_1 < \lambda_2$.

Let Δ_i the line of equation :

$$X_1 = \delta_i(X_0) = \frac{1}{k_1\alpha}\Big[(S_{1in}-\lambda_i)+k_0(X_{0in}-\alpha X_0)\Big], \; i = 1, 2.$$

The positive equilibrium $E_i^* = (X_{0i}^*, \lambda_i, X_{1i}^*)$ of system (2) is a solution of the equation

$$X_{1i}^* = \delta_i(X_{0i}^*) = \xi(X_{0i}^*), \qquad i = 1, 2.$$

When the intersection of the curve ξ and the line Δ_i is formed by two points, let us denote them by $E_i^* = (X_{0i}^*, \lambda_i, X_{1i}^*)$ if $\xi'(X_{0i}^*) < -\frac{k_0}{k_1}$ and by $E_i^{**} = (X_{0i}^{**}, \lambda_i, X_{1i}^{**})$, otherwise (see Fig. 5 and Fig. 6). In the case $\xi'\left(\frac{X_{0in}}{\alpha}\right) > -\frac{k_0}{k_1}$, there exists a unique solution $\bar{X}_0 \in \left]0, \frac{X_{0in}}{\alpha}\right[$ of the equation $\xi'(X_0) = -\frac{k_0}{k_1}$. As the two lines Δ_1 and Δ_2 are parallel, then there exists for $i = 1, 2$ a limit value X_1^{Min} for which the curve of ξ is tangent to the line Δ_i and which satisfies

$$X_1^{Min} = \bar{X}_1 + \frac{k_0}{k_1}\bar{X}_0$$

with $\bar{E}_i = (\bar{X}_0, \lambda_i, \bar{X}_1)$ an equilibrium of (2) for $i = 1, 2$. At this limit value X_1^{Min}, we associate S_{1i}^{Min} such that

$$X_1^{Min} = \delta(0) = \frac{1}{k_1\alpha}[S_{1i}^{Min} - \lambda_i + k_0 X_{0in}].$$

In the generic case where $S_{1i}^{Min} > 0$ for $i = 1, 2$, the cases $S_{12}^{Min} < \lambda_1$ and $S_{12}^{Min} > \lambda_1$ have to be distinguished. When $S_{12}^{Min} < \lambda_1$, we have shown the following result :

Proposition 2.3.

- If $S_{1in} \geqslant \lambda_2 > \lambda_1$, there exist two positive equilibrium E_i^*, $i = 1, 2$.
- If $\lambda_1 \leqslant S_{1in} < \lambda_2$, there exist three positive equilibrium E_i^* and E_2^{**}.
- If $S_{12}^{Min} < S_{1in} < \lambda_1$, there exist four positive equilibrium E_i^* and E_i^{**}.
- If $S_{12}^{Min} = S_{1in}$, there exist three positive equilibrium E_1^*, E_1^{**} and $\bar{E}_2$.
- If $S_{11}^{Min} < S_{1in} < S_{12}^{Min}$, there exist two positive equilibrium E_1^* and E_1^{**}.
- If $S_{11}^{Min} = S_{1in}$, there exists a unique positive equilibrium $\bar{E}_1$.
- If $S_{1in} < S_{11}^{Min}$, there is no positive equilibrium.

In the case where $S_{12}^{Min} > \lambda_1$, we can prove, similarly, that if $S_{1in} \geqslant S_{11}^{Min}$, we have one, two, three or four positive equilibria, depending on the position of S_{1in}.

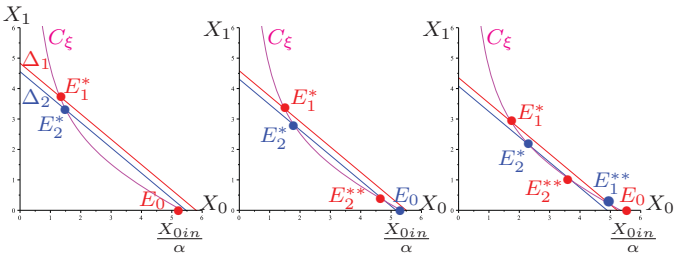

Fig. 5. Case 1: $S_{1in} = 8 > \lambda_2 = 7$, case 2: $\lambda_1 = 4.5 < S_{1in} = 5.75 < \lambda_2$, case 3: $S_{12}^{Min} < S_{1in} = 3.7 < \lambda_1$.

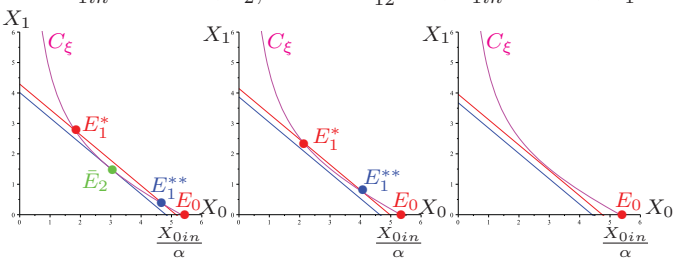

Fig. 6. Case 4: $S_{1in} = 3.125 = S_{12}^{Min}$, case 5: $S_{11}^{Min} = 0.62 < S_{1in} = 1.8 < S_{12}^{Min}$, case 6: $S_{1in} = 0.1 < S_{11}^{Min}$.

We study now the local stability properties of the equilibria. For E_0, E_1^* and E_1^{**}, we have the same results as in Proposition 2.2. Moreover, we can prove :

Proposition 2.4.

- If E_2^* exists, then it is unstable.
- If E_2^{**} exists and $D + k_1\mu_1'(\lambda_2)X_{12}^{**} > 0$, then it is LAS.

Proof. The Jacobian of the system (2) at E_2^* is

$$\mathbf{J_2} = \begin{bmatrix} -m_{11} & 0 & -m_{13} \\ m_{21} & \beta & \theta \\ 0 & -m_{32} & 0 \end{bmatrix}$$

where

$$m_{11} = \alpha D + \mu_0'(X_{02}^*)X_{12}^*, \quad m_{13} = \mu_0(X_{02}^*),$$
$$m_{21} = k_0\mu_0'(X_{02}^*)X_{12}^*, \quad \beta = -\big(D + k_1\mu_1'(\lambda_2)X_{12}^*\big),$$
$$\theta = k_0\mu_0(X_{02}^*) - k_1\alpha D, \quad m_{32} = -\mu_1'(\lambda_2)X_{12}^*,$$

with m_{11}, m_{13}, m_{21} and m_{32} are positive. The characteristic polynomial of J_2 is given by

$$P_{J_2}(\lambda) = a_0\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$$

with

$$a_0 = -1, \quad a_1 = \beta - m_{11}, \quad a_2 = m_{11}\beta - \theta m_{32},$$
$$a_3 = m_{32}(m_{21}m_{13} - \theta m_{11}).$$

We have

$$a_2 = \Big[\xi'(X_{02}^*) + \tfrac{k_0}{k_1}\Big] k_1\mu_0(X_{02}^*)\mu_1'(\lambda_2)X_{12}^*$$
$$- \Big[D\mu_0'(X_{02}^*)X_{12}^* + \alpha D\Big(D + k_1\mu_1'(\lambda_2)X_{12}^*\Big)\Big].$$

If $D + k_1\mu_1'(\lambda_2)X_{12}^* > 0$ and $\xi'(X_{02}^*) > -\frac{k_0}{k_1}$, then $a_2 < 0$. It is easy to check that

$$a_3 = -m_{32}\alpha D\Big[\xi'(X_{02}^*) + \frac{k_0}{k_1}\Big] k_1\mu_0(X_{02}^*)$$

who is negative if and only $\xi'(X_{02}^*) > -\frac{k_0}{k_1}$. Thus, E_2^* is unstable. One can readily check that

$$a_1a_2 - a_0a_3 = m_{11}\beta^2 - m_{11}^2\beta + m_{32}(m_{21}m_{13} - \theta\beta)$$

and

$$\theta X_{12}^{**} = k_0\mu_0(X_{02}^{**})X_{12}^{**} - k_1\mu_1(\lambda_2)X_{12}^{**} = -D(S_{1in} - \lambda_2).$$

If E_2^{**} exists then $S_{1in} < \lambda_2$, thus $\theta > 0$. We conclude that according to the Routh-Hurwitz criterion, if E_2^{**} exists and

$$D + k_1\mu_1'(\lambda_2)X_{12}^{**} > 0,$$

then it is LAS.

3. STUDY OF CONTOIS MODEL

In this section we study the case where the growth rate $\mu_0(.)$ depends on X_0 and also on X_1. Models with such growth rates may be of interest if we consider that we work in a non homogeneous environment Lobry and Harmand (2006). The Contois function is an exemple of these growth rates. We consider the model

$$\begin{cases} \dot{X}_0 = D(X_{0in} - \alpha X_0) - \mu_0(X_0, X_1)X_1, \\ \dot{S}_1 = D(S_{1in} - S_1) + k_0\mu_0(X_0, X_1)X_1 - k_1\mu_1(S_1)X_1, \\ \dot{X}_1 = \Big[\mu_1(S_1) - \alpha D\Big]X_1. \end{cases} \tag{3}$$

Let us denote by

$$f(X_0, X_1) = \mu_0(X_0, X_1)X_1 - D(X_{0in} - \alpha X_0).$$

We assume that

H4: $\mu_0(0, X_1) = 0$ and $\mu_0(0, X_1) > 0$ for all $X_0 > 0$ and all $X_1 \geqslant 0$.

H5: $\dfrac{\partial \mu_0}{\partial X_0} > 0$ and $\dfrac{\partial \mu_0}{\partial X_1} < 0$ for all $X_0 > 0$ and all $X_1 \geqslant 0$.

H6: $\mu_1(0) = 0, \mu_1'(S_1) > 0$ for all $S_1 \geqslant 0$ and the equation $\mu_1(S_1) = \alpha D$ has a unique solution λ_1.

H7: $\dfrac{\partial f}{\partial X_1}(X_0, X_1) = \mu_0(X_0, X_1) + \dfrac{\partial \mu_0}{\partial X_1}X_1 > 0$ for all $X_0 > 0$ and all $X_1 \geqslant 0$.

H8: There exist $a \in]0, \frac{X_{0in}}{\alpha}[$ such that

$$\lim_{\substack{X_0 \to a \\ X_1 \to +\infty}} f(X_0, X_1) = 0.$$

We consider, now, the existence of positive equilibria. We first prove :

Lemma 3.1. Assume that **H4-H8** hold. The equation $f(X_0, X_1) = 0$ defines a decreasing function

$$F : \Big]a, \tfrac{X_{0in}}{\alpha}\Big] \longrightarrow \mathbb{R}_+$$
$$X_0 \longrightarrow F(X_0) = X_1$$

where $0 < a < \frac{X_{0in}}{\alpha}$ and such that

$$\lim_{X_0 \to a} F(X_0) = +\infty, \quad F\Big(\frac{X_{0in}}{\alpha}\Big) = 0 \quad \text{and} \quad F'(X_0) < 0.$$

Then we state the following result :

Proposition 3.1.

- For $S_{1in} > \lambda_1$, if $F''(X_0) > 0$ for all $X_0 \in \Big]a, \frac{X_{0in}}{\alpha}\Big]$, then there exists a unique positive equilibrium. If $F''(X_0)$ changes sign for $X_0 \in \Big]a, \frac{X_{0in}}{\alpha}\Big]$, then there exists at least one positive equilibrium. Generically one has an odd number of positive equilibria (see Fig. 7).
- For $S_{1in} < \lambda_1$, if $F''(X_0) > 0$ for all $X_0 \in \Big]a, \frac{X_{0in}}{\alpha}\Big]$, then there exist at most two positive equilibria. If $F''(X_0)$ changes sign for $X_0 \in \Big]a, \frac{X_{0in}}{\alpha}\Big]$, then the system has generically no positive equilibria or an even number of positive equilibria (see Fig. 8).

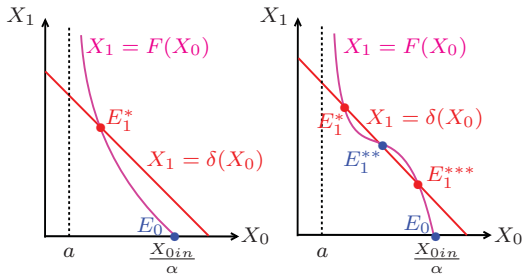

Fig. 7. Null-clines $X_1 = F(X_0)$ and $X_1 = \delta(X_0)$ for $S_{1in} > \lambda_1$. On the left, $F(\cdot)$ concave. On the right, $F''(\cdot)$ changes sign.

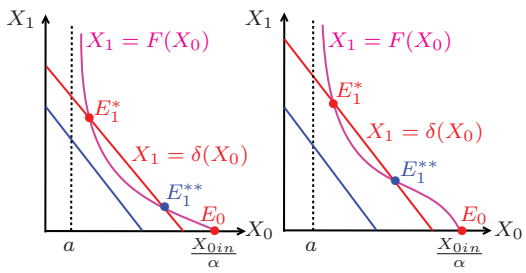

Fig. 8. Null-clines $X_1 = F(X_0)$ and $X_1 = \delta(X_0)$ for $S_{1in} < \lambda_1$. On the left, $F(\cdot)$ concave. On the right, $F''(\cdot)$ changes sign.

Example We consider the following function of Contois

$$\mu_0(X_0, X_1) = \frac{m_0X_0}{X_0 + a_0X_1}$$

where $m_0 > 0$ and $a_0 > 0$. We have

$$\frac{\partial f}{\partial X_1}(X_0, X_1) = \frac{m_0X_0^2}{(X_0 + a_0X_1)^2} > 0$$

thus Assumption **H7** is satisfied. Moreover,

$$\lim_{X_1 \to +\infty} f(X_0, X_1) = 0$$

$$\Longrightarrow \quad X_0 = \frac{DX_{0in}}{\frac{m_0}{a_0} + \alpha D} = a$$

where $0 < a < \frac{X_{0in}}{\alpha}$. Therefore, there exists $a \in]0, \frac{X_{0in}}{\alpha}[$ such that $\lim_{\substack{X_0 \to a \\ X_1 \to +\infty}} f(X_0, X_1) = 0$ i.e, $\lim_{X_0 \to a} F(X_0) = +\infty$. By the implicit function theorem, we have

$$F'(X_0) = -\frac{m_0 a_0 X_1^2 + \alpha D(X_0 + a_0 X_1)^2}{m_0 X_0^2} < 0$$

and

$$F''(X_0) = \frac{2a_0 a_0 X_1 \Big[m_0 X_1 + \alpha D(X_0 + a_0 X_1)\Big]}{m_0 X_0^3} > 0.$$

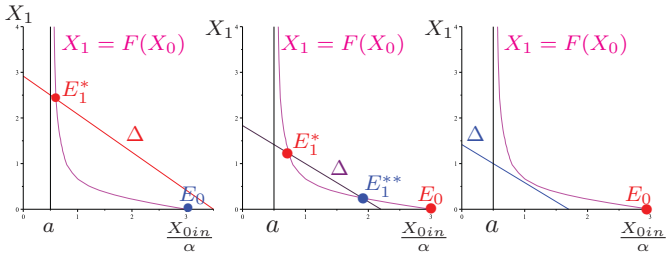

Fig. 9. Cas 1: $S_{1in} = 2 > \lambda_1 = 1.5$, cas 2: $S_{1in} = 0.7 < \lambda_1$, cas 3: $S_{1in} = 0.2$.

The stability results we obtain in this case are given by :

Proposition 3.2.

- The washout equilibrium E_0 is LAS if and only if $\mu_1(S_{1in}) < \alpha D$.
- If the positive equilibrium E_1^* exists, then it is LAS (stable node).
- If the positive equilibrium E_1^{**} exists, then it is unstable (saddle point).

Proof. At washout $E_0 = (\frac{X_{0in}}{\alpha}, S_{1in}, 0)$, the Jacobian matrix is

$$\mathbf{J_0} = \begin{bmatrix} -\alpha D & 0 & -\mu_0\left(\frac{X_{0in}}{\alpha}, 0\right) \\ 0 & -D & k_0\mu_0\left(\frac{X_{0in}}{\alpha}, 0\right) - k_1\mu_1(S_{1in}) \\ 0 & 0 & \mu_1(S_{1in}) - \alpha D \end{bmatrix}$$

The eigenvalues are $-\alpha D, -D$ and $\mu_1(S_{1in}) - \alpha D$. Then, the equilibrium E_0 is LAS if and only if $\mu_1(S_{1in}) < \alpha D$.

At a positive equilibrium $E_1^* = (X_0^*, \lambda_1, X_1^*)$, the Jacobian matrix is

$$\mathbf{J_1} = \begin{bmatrix} -m_{11} & 0 & -m_{13} \\ m_{21} & -m_{22} & \theta \\ 0 & m_{32} & 0 \end{bmatrix}$$

where

$$m_{11} = \alpha D + \frac{\partial \mu_0}{\partial X_0} X_1^*, \quad m_{13} = \mu_0(X_0^*, X_1^*) + \frac{\partial \mu_0}{\partial X_1} X_1^*,$$

$$m_{21} = k_0 \frac{\partial \mu_0}{\partial X_0} X_1^*, \quad m_{22} = D + k_1 \mu_1'(\lambda_1) X_1^*,$$

$$\theta = k_0 \frac{\partial \mu_0}{\partial X_1} X_1^* + k_0 \mu_0(X_0^*, X_1^*) - k_1 \alpha D, \quad m_{32} = \mu_1'(\lambda_1) X_1^*,$$

with $m_{11}, m_{13}, m_{21}, m_{22}$ and m_{32} are positive. The characteristic polynomial of J_1 is given by

$$P_{J_1}(\lambda) = a_0\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$$

with

$$a_0 = -1, \quad a_1 = -(m_{11} + m_{22}), \quad a_2 = -m_{11}m_{22} + \theta m_{32},$$
$$a_3 = -m_{32}(m_{21}m_{13} - \theta m_{11}).$$

One can easily check that

$$a_2 = \left[F'(X_0^*) + \frac{k_0}{k_1}\right] k_1 \frac{\partial f}{\partial X_1} \mu_1'(\lambda_1) X_1^* - \left(D \frac{\partial \mu_0}{\partial X_0} X_1^* + \alpha D m_{22}\right).$$

Therefore, if $F'(X_0^*) < -\frac{k_0}{k_1}$, then $a_2 < 0$. One can also check that

$$a_3 = m_{32}\alpha D \left[F'(X_0^*) + \frac{k_0}{k_1}\right] k_1 \frac{\partial f}{\partial X_1}$$

is negative if and only if $F'(X_0^*) < -\frac{k_0}{k_1}$. So, E_1^{**} is unstable. Finally

$$a_1 a_2 - a_0 a_3 = -\left[F'(X_0^*) + \frac{k_0}{k_1}\right] k_1 \frac{\partial f}{\partial X_1} \frac{\partial \mu_0}{\partial X_0} \mu_1'(\lambda_1) X_1^{*2} + P$$

where

$$P = D m_{11}^2 + \left[(\alpha D)^2 + \alpha D \frac{\partial \mu_0}{\partial X_0} X_1^*\right] k_1 \mu_1'(\lambda_1) X_1^* - m_{22} a_2$$

is positive if $F'(X_0^*) < -\frac{k_0}{k_1}$. Since E_1^* satisfy $\xi'(X_0^*) < -\frac{k_0}{k_1}$, then according to the Routh-Hurwitz criterion, it is LAS.

4. CONCLUSION

In this work, we have analyzed a model of the chemostat with enzymatic degradation of a substrate that can partly be under a solid form. The sub-model studied with monotonic growth rates may exhibit a bi-stable behavior, while it may only occur in the classical chemostat model when the growth rate is non monotonic. We also studied the case where the growth rate is density-dependent. Depending on the input substrate concentration, it was shown that the system can exhibit either a bistability or the global stability of the positive equilibrium point or of the washout.

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