STEADY-STATE ANALYSIS OF A SYNTROPHIC ASSOCIATION OF TWO SPECIES IN A CHEMOSTAT: THE EFFECT OF A NEW INPUT CONCENTRATION SUBSTRATE

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Y. Daoud [*], T. Sari [†], N. Abdellatif [‡] and J. Harmand [§]

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 discuss the existence and stability of all equilibria and we give necessary and sufficient conditions on the control parameters of the system (the dilution rate D and the input concentrations of the two substrates s_0^{in} and s_1^{in}). By means of operating diagrams, we describe the asymptotic behavior of the model with respect to the control parameters and we illustrate the effect of the second input substrate.
Keywords. Microbial ecosystems, syntrophic relashionship, Mortality, Stability , Operating diagrams.

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 and / or hydrogen. Anaerobic digestion is a four steps process including hydrolysis, acidogenesis, acetogenesis, and methanogenesis. In this paper, we are interested in a reduced anaerobic digestion model with two steps, the acetogenesis and the hydrogenetrophic methanogenesis, as shown in Figure 1. In the acetogenesis, the volatile fatty acids (VFA) are used by the acetogenic bacteria and converted into hydrogen (H_2). Then, the hydrogenotrophic methanogenic bacteria convert hydrogen to methane (CH_4). Formally, we then have the following biological reactions: one substrate s_0 is consumed by one microorganism x_0, to produce a product s_1. This product serves as the main limiting substrate for a second microorganism x_1 as schematically represented by the following reaction scheme:

$$s_0 \xrightarrow{\mu_0} x_0 + s_1, \qquad s_1 \xrightarrow{\mu_1} x_1$$

where μ_0 and μ_1 are the growth functions that may depend on both substrates.

Many authors were interested in such syntrophic relationship models. M. El Hajji and al., [2], have proposed a system of four ordinary differential equations describing a syntrophic relationship involving two populations of bacteria: the acetogens and the methanogens.

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They generalized the model proposed by R. Kreikenbohm and al., [3], by considering general kinetics and described the qualitative behavior of the trajectories. In this study, the authors assumed that the acetogenic bacteria is inhibited by the hydrogen that it produces during the acetogenic phase and neglected all species specific death rates. They demonstrated the existence of three equilibria and the global asymptotic stability of the positive equilibrium point, under general assumptions of monotonicity.

This last model has been revisited by T. Sari and al., [4]. In this paper, the authors assumed that there are two resources in the input influent and that for both populations, one resource is needed for growth and the other is inhibitory. This means in practice that acetogens are inhibited by an excess of hydrogen and methanogens by an excess of VFA. It is shown that the qualitative behavior of the system is then significantly modified.
In another paper of T.Sari and al., [5], based on the model proposed by A. Xu and al., [1], it was proved that introducing decay in the model preserves stability whatever its parameters values and for a wide range of kinetics.

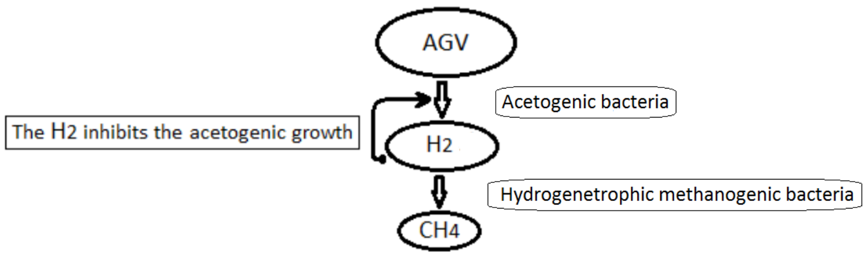

Figure 1: Two steps of anaerobic digestion

In the present paper, we modify slightly the model used in [5] by adding an input term on the equation describing the dynamic of hydrogen.

2 The model

We obtain the following model

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

Substrates s_0 and s_1 are 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 $s_0 > 0$ and $s_1 \geq 0$, $\mu_0(s_0, s_1) > 0$ and $\mu_0(0, s_1) = 0$.

H2 For all $s_1 > 0$, $\mu_1(S_1) > 0$ and $\mu_1(0) = 0$.

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

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

Hypothesis **H1** signifies that no growth can take place for species x_0 without the substrate s_0. Hypothesis **H2** means that the intermediate product s_1 is necessary for the growth of species x_1. Hypothesis **H3** means that the growth rate of species x_0 increases with the substrate s_0 but it is self-inhibited by the intermediate product s_1. Hypothesis **H4** means that the growth of species x_1 increases with intermediate product s_1 produced by species x_0. Note that this defines a syntrophic relationship between the two species.

Proposition 2.1. *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

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

$$D(s_0^{in} - s_0) - \mu_0(s_0, s_1)x_0 = 0 \quad (2)$$

$$-Dx_0 + \mu_0(s_0, s_1)x_0 - a_0x_0 = 0 \quad (3)$$

$$D(s_1^{in} - s_1) + \mu_0(s_0, s_1)x_0 - \mu_1(s_1)x_1 = 0 \quad (4)$$

$$-Dx_1 + \mu_1(s_1)x_1 - a_1x_1 = 0 \quad (5)$$

A steady-state $E = (s_0, x_0, s_1, x_1)$ exists if and only if all its components are non-negative. From equation (3) we deduce that:

$$x_0 = 0 \quad \text{or} \quad \mu_0(s_0, s_1) = D + a_0$$

and from equation (5) we deduce that:

$$x_1 = 0 \quad \text{or} \quad \mu_1(s_1) = D + a_1$$

We obtain the four equilibria:
SS0: $x_0 = 0$, $x_1 = 0$ where both species are washed out.
SS1: $x_0 > 0$, $x_1 = 0$, where species x_1 is washed out while x_0 survives.
SS2: $x_0 > 0$, $x_1 > 0$, where both species survive.
SS3: $x_0 = 0$, $x_1 > 0$, where species x_0 is washed out while x_1 survives.

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 $y \in [0, \sup \mu_1(\cdot)[$

$$s_1 = M_1(y) \Longleftrightarrow y = \mu_1(s_1)$$

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 $y \in [0, \sup \mu_0(\cdot, s_1)[$

$$s_0 = M_0(y, s_1) \Longleftrightarrow y = \mu_0(s_0, s_1)$$

Proposition 3.1. *Assume that assumptions* **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 eventually exists.
In the next section, we analyse the steady-state local stability.

4 Stability analysis

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 4.1. *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* $s_0^{in} < M_0\left(D + a_0, M_1(D + a_1)\right)$.

□

We define the functions:

$$\begin{array}{rcl} F_0(D) & = & M_0\left(D + a_0, s_1^{in}\right) \\ F_1(D) & = & M_1(D + a_1) + M_0(D + a_0, M_1(D + a_1)) \\ F_2(D) & = & M_0(D + a_0, M_1(D + a_1)) \end{array} \tag{6}$$

Notice that

$$s_1^{in} < M_1(D + a_1) \iff D > \mu_1(s_1^{in}) - a_1$$

The results are summarized in Table 1.

Steady-state	Existence condition	Stability condition
SS0	Always exists	$s_0^{in} < F_0(D)$ and $D > \mu_1(s_1^{in}) - a_1$
SS1	$s_0^{in} > F_0(D)$	$s_0^{in} + s_1^{in} < F_1(D)$
SS2	$s_0^{in} + s_1^{in} > F_1(D)$ and $s_0^{in} > F_2(D)$	Always Stable
SS3	$\mu_1(s_1^{in}) > a_1$ and $D < \mu_1(s_1^{in}) - a_1$	$s_0^{in} < F_2(D)$

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

If $s_1^{in} = 0$ the condition $\mu_1(s_1^{in}) > a_1$ is not satisfied and SS3 does not exist.

Because of lack of space, we give only a sketch of the proof: For SSi, $i = 0, 1$ and 3, the Jacobian of the system is analytically obtained and its eigenvalues are determined explicitely. Conditions of them to be negative (reported in the last column of Table 1) are directly obtained from these analytical computations. For SS2, we use the Routh-Hurwitz criterion adapted from [5].

5 Operating diagram

The operating diagram shows how the system behaves when we vary the three control parameters s_0^{in}, s_1^{in} and D. Let $F_0(D)$, $F_1(D)$ and $F_2(D)$ be the functions defined by (6). We define the curve γ_{20} of equation $s_0^{in} = F_0(D)$, the curve γ_{10} of equation $s_0^{in} = F_1(D) - s_1^{in}$ and the curve γ_{00} of equation $s_0^{in} = F_2(D)$. We denote $\overline{D} = \mu_1(s_1^{in}) - a_1$, see Table 1.
These curves with the line $D = \overline{D}$ separate the operating plane (s_0^{in}, D) in at most six regions as shown in Fig. 4, labelled $\mathcal{R}^1, \cdots, \mathcal{R}^6$. The results of Proposition 4.1 are summarized in the next theorem which shows the existence and local stability of the steady-states SS0, $\cdots$, SS3 in the regions $\mathcal{R}^1, \cdots, \mathcal{R}^6$ of the operating diagram, for a given s_1^{in}.

If $\mu_1(s_1^{in}) < a_1$ then we have always $F_0(D) < F_1(D) - s_1^{in}$, if$\mu_1(s_1^{in}) > a_1$ and $D > \overline{D}$ then we have always $F_0(D) < F_1(D) - s_1^{in}$ and if $\mu_1(s_1^{in}) > a_1$ and $D < \overline{D}$ then we have always $F_2(D) < F_0(D)$.

Theorem 5.1. *The existence and stability properties of the system (1), in the plane (s_0^{in}, D), are summarised in the following tables:*

Condition	Region	SS0	SS1	SS2	SS3
$s_0^{in} < F_0(D)$	$(s_0^{in}, D) \in \mathcal{R}^1$	S			
$F_0(D) < s_0^{in} < F_1(D) - s_1^{in}$	$(s_0^{in}, D) \in \mathcal{R}^2$	U	S		
$F_1(D) - s_1^{in} < s_0^{in}$	$(s_0^{in}, D) \in \mathcal{R}^3$	U	U	S	

Table 2: The cases $\mu_1(s_1^{in}) < a_1$

Condition	Region	SS0	SS1	SS2	SS3
$D > \overline{D}$ & $s_0^{in} < F_0(D)$	$(s_0^{in}, D) \in \mathcal{R}^1$	S			
$D > \overline{D}$ & $F_0(D) < s_0^{in} < F_1(D) - s_1^{in}$	$(s_0^{in}, D) \in \mathcal{R}^2$	U	S		
$D > \overline{D}$ & $F_1(D) - s_1^{in} < s_0^{in}$	$(s_0^{in}, D) \in \mathcal{R}^3$	U	U	S	
$D < \overline{D}$ & $s_0^{in} > F_0(D)$	$(s_0^{in}, D) \in \mathcal{R}^4$	U	U	S	U
$D < \overline{D}$ & $F_2(D) < s_0^{in} < F_0(D)$	$(s_0^{in}, D) \in \mathcal{R}^5$	U		S	U
$D < \overline{D}$ & $s_0^{in} < F_2(D)$	$(s_0^{in}, D) \in \mathcal{R}^6$	U			S

Table 3: The cases $\mu_1(s_1^{in}) > a_1$

The letter S (resp. U) means that the corresponding equilibrium is LES (resp. unstable). The absence of letter means that the equilibrium does not exist.

□

These results are essentially the same then those presented in Table 1. Notice that Table 2 is identical to the Table 2 of [5], it corresponds to the case where the concentration s_1^{in} is small or equal to zero. Table 3 emerges due the presence of s_1^{in}, it appears three new regions of existence of equilibrium SS3. Moreover, in the regions R^i, $i = 1, \cdots, 6$, there is only one steady-state stable and all other equilibria are unstable or not even exist.

6 Simulations

The stability regions of steady-states are given by the operating diagram in the plane (s_0^{in}, D) in Figure 2, 3, 4 and 5, for different values of s_1^{in}. For the simulations, we use the following growth functions:

$$\mu_0\left(s_0,s_1\right)=\frac{m_0s_0}{K_0+s_0}\frac{1}{1+s_1/K_i},\quad \mu_1\left(s_1\right)=\frac{m_1s_1}{K_1+s_1}$$

For the operating diagrams in Figure 2, 3, 4 and 5, we use the parameters given in Table 4.

Parameters	Units	Nominal Value
m_0	d^{-1}	0.52
K_0	$\mathrm{kg\,COD/m^3}$	0.124
m_1	d^{-1}	2.10
K_1	$\mathrm{kg\,COD/m^3}$	0.25
K_i	$\mathrm{kg\,COD/m^3}$	0.035
a_0	d^{-1}	0.02
a_1	d^{-1}	0.02

Table 4: Nominal parameters values.

The inverse functions $M_1(.)$ and $M_0(., s_1)$ of the functions $\mu_1(.)$ and $\mu_0(., s_1)$ can be calculated explicitly: we have

$$y\in[0,m_1[\mapsto M_1(y)=\frac{K_1y}{m_1-y},$$

$$y\in\left[0,\frac{m_0}{1+s_1/K_i}\right[\mapsto M_0(y,s_1)=\frac{K_0y}{\frac{m_0}{1+s_1/K_i}-y}$$

The functions $F_0(D)$, $F_1(D)$ and $F_2(D)$ are given explicitly by

$$\begin{aligned}
F_0(D) &= \frac{K_0(D+a_0)(1+\frac{s_1^{in}}{K_i})}{m_0-(D+a_0)(1+\frac{s_1^{in}}{K_i})}\\
F_1\left(D\right) &= \frac{K_1(D+a_1)}{m_1-(D+a_1)}+\frac{K_0(D+a_0)(1+\frac{M_1(D+a_1)}{K_i})}{m_0-(D+a_0)(1+\frac{M_1(D+a_1)}{K_i})}\\
F_2\left(D\right) &= \frac{K_0(D+a_0)(1+\frac{M_1(D+a_1)}{K_i})}{m_0-(D+a_0)(1+\frac{M_1(D+a_1)}{K_i})}
\end{aligned} \tag{7}$$

F_0 is defined if

$$D<\frac{m_0-a_0(1+\frac{s_1^{in}}{K_i})}{1+\frac{s_1^{in}}{K_i}}$$

and

$$\frac{(m_0-a_0)K_i}{a_0}\geq s_1^{in}$$

.

F_1 and F_2 are defined if

$$D<m_1-a_1$$

and

$$(K_i-K_1)D^2+((K_i-K_1)(a_0+a_1)-K_i(m_1+m_0))D+((m_0-a_0)K_i(m_1-a_1)-a_0a_1K_1)>0$$

.

Figures 2, 3, 4 and 5 illustrate the operating diagrams for increasing values of s_1^{in}. When s_1^{in} is small, namely $s_1^{in} = 0.005$, the most important regions are the regions $\mathcal{R}^i$, $i = 1, 2, 3$, (see Fig. 2). These regions correspond to those obtained in the case $s_1^{in} = 0$, see (Fig. 1 of [5]). Increasing s_1^{in} leads to the emergence of the existence region of equilibrium SS3 $\mathcal{R}^i$, $i = 4, 5, 6$ and to the reduction of the region $\mathcal{R}^2$ and $\mathcal{R}^3$, (see Fig. 3 and 4). Thus, the input concentration of the second species leads to the emergence of a new region related to the new equilibrium SS3 and to changes in the size of the existence and stability regions of the other equilibria.

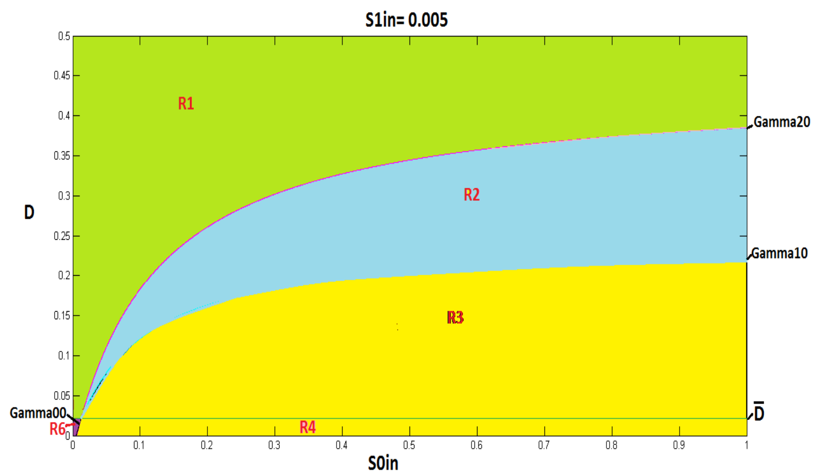

Figure 2: Operating diagram of the model (1) for $s_1^{in} = 0.005$

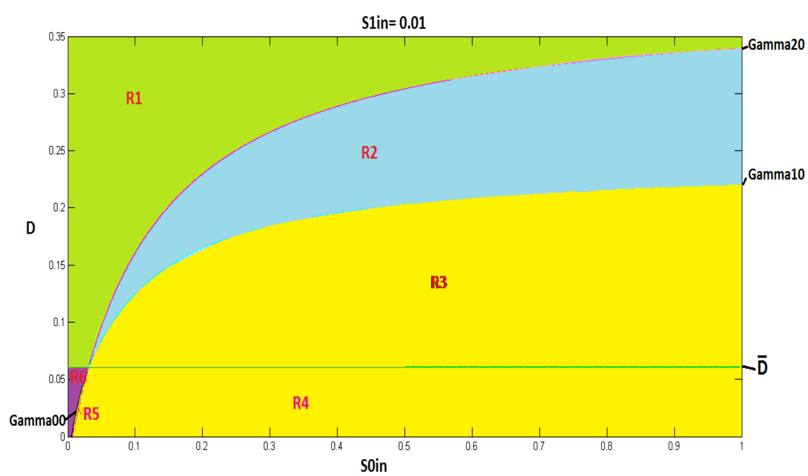

Figure 3: Operating diagram of the model (1) for $s_1^{in} = 0.01$

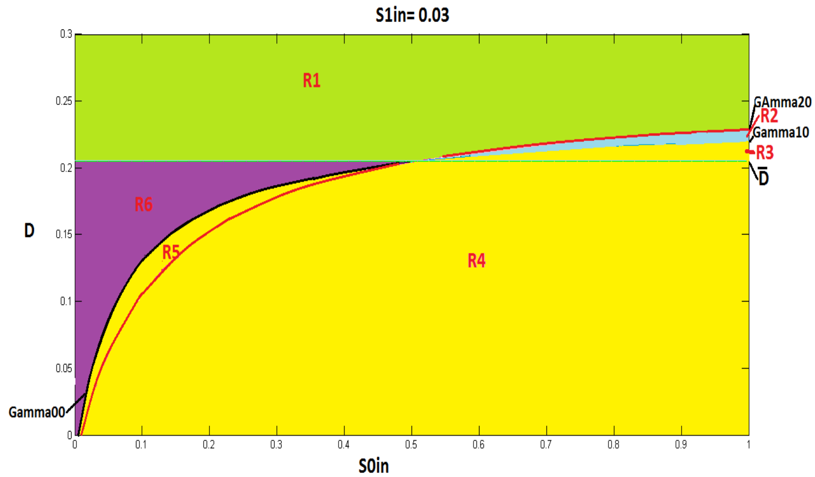

Figure 4: Operating diagram of the model (1) for $s_1^{in} = 0.03$

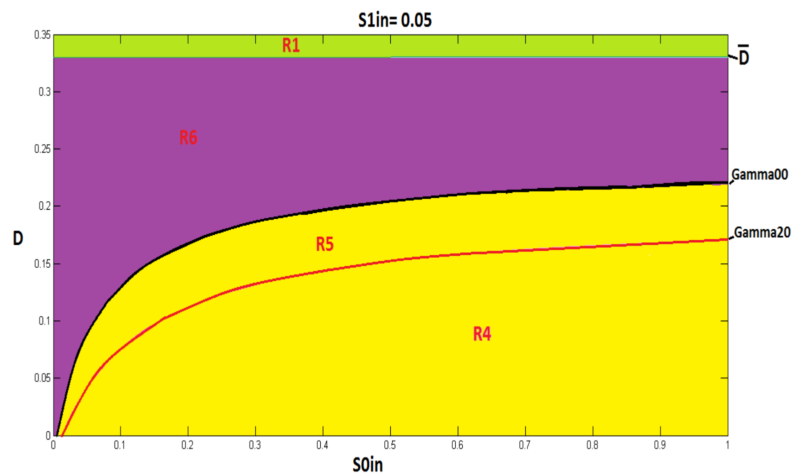

Figure 5: Operating diagram of the model (1) for $s_1^{in} = 0.05$

Discussion:
Including s_1^{in} in the model changes slightly the operating diagram of [5]. When s_1^{in} increases, $\bar{D}$ increases (it may be verified that $\frac{d\bar{D}}{ds_1^{in}} > 0$). The stability region of SS2 under the curve γ_{00} remains the same (γ_{00} does not depend to s_1^{in}). On the other side, the stability region R^6 of SS3, which corresponds to the extinction of the first species, increases in size.

The last operating diagrams were obtained by fixing s_1^{in} and varying the control parameters D and s_0^{in}, it would be interesting to fix s_0^{in} and to describe the existence and the asymptotic behavior of the equilibria by operating diagrams in the plane (s_1^{in}, D). Note that we performed only the local stability of the equilibria in this paper. The global stability is under investigation. Another interesting question, which is the object of a future work, is to consider the effect of an inhibition on the second species which can be modeled by a growth function $\mu_1(\cdot)$ of Haldane type, for instance.

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