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GLOBAL ANALYSIS OF A MODEL OF COMPETITION IN CHEMOSTAT WITH INTERNAL INHIBITOR

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ABSTRACT. A model of two microbial species in a chemostat competing for a single resource in the presence of an internal inhibitor is considered. The model is a four-dimensional system of ordinary differential equations. Using general growth rate functions of the species, we give a complete analysis for the existence and local stability of all steady states. We describe the behavior of the system with respect to the operating parameters represented by the dilution rate and the input concentrations of the substrate. The operating diagram has the operating parameters as its coordinates and the various regions defined in it correspond to qualitatively different asymptotic behavior: washout, competitive exclusion of one species, coexistence of the species, bistability, multiplicity of positive steady states. This bifurcation diagram which determines the effect of the operating parameters, is very useful to understand the model from both the mathematical and biological points of view, and is often constructed in the mathematical and biological literature.

1. Introduction. The chemostat is an important laboratory apparatus used for the continuous culture of micro-organisms. Competition for single and multiple resources, evolution of resource acquisition, and competition among micro-organisms have been investigated in ecology and biology using chemostats [11, 21, 22, 28]. A detailed mathematical description of competition in the chemostat may be found in [10, 26].

The basic chemostat model predicts that coexistence of two or more microbial populations competing for a single non-reproducing nutrient is not possible. Only the species with the lowest ‘break-even’ concentration survives, this is the species which consumes less substrate to attain its steady state [13]. This result, known as the Competitive Exclusion Principle [9], was established under various hypotheses [4, 12, 24, 30]. The reader may consult [18, 20, 25] for a thorough account on the contributions of diverse authors.

This theoretical prediction has been corroborated by the experiences of Hansen and Hubell [8], but the biodiversity found in nature as well as in waste-water treatment processes and biological reactors are exceptions to this principle. Several authors [3, 5, 14, 15, 16, 19, 29], and recently [2, 6] studied the inhibition as a factor in the maintenance of the diversity of microbial ecosystems: Can the production

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of internal inhibitors or the introduction of external inhibitors induce the stable coexistence of competitors in a chemostat-like environment?

In this paper we consider the model introduced by De Freitas and Fredrickson [5]. In this model, two species $x$ and $y$ compete for a single limiting resource $S$ in presence of an internal inhibitor $p$, where both competitors produce a toxin that inhibits their growth rates. Let $S(t)$ denote the concentration of the substrate at time $t$; let $x(t)$, $y(t)$ denote the concentrations of the competitors and $p(t)$ is the concentration of the internal inhibitor. The model takes the form

$$
\begin{align*}
S' &= (S^0 - S)D - \mu_1(S,p)\frac{x}{\gamma_1} - \mu_2(S,p)\frac{y}{\gamma_2} \\
x' &= [\mu_1(S,p) - D]x \\
y' &= [\mu_2(S,p) - D]y \\
p' &= \alpha_1\mu_1(S,p)x + \alpha_2\mu_2(S,p)y - Dp
\end{align*}
$$

(1)

with initial condition $S(0) \geq 0$, $x(0) > 0$, $y(0) > 0$ and $p(0) \geq 0$. $S^0$ and $D$ denote, respectively, the concentration of the nutrient in the feed bottle and the dilution rate of the chemostat, all of which are assumed to be constant and are under the control of the experimenter. The parameters $\gamma_i > 0$, $i = 1, 2$, are the growth yield coefficients. The product $\alpha_i\gamma_i > 0$ is the yield of inhibitor by the $i$th population. The growth function $\mu_i(S,p)$, $i = 1, 2$ can depend not only on the substrate $S$ but also on the inhibitor concentration $p$. The function $\mu_i$ is assumed to be increasing in the variable $S$ and decreasing in the variable $p$. This model was considered by De Freitas and Fredrickson [5] when

$$
\mu_i(S,p) = \frac{m_iS}{(a_i + S)(1 + p/K_i)}, \quad i = 1, 2
$$

(2)

where $m_i$, $a_i$, $K_i$, $i = 1, 2$ are some positive constant parameters. Here, except the two variable operating (or control) parameters, which are the dilution rate $D$ and the inflowing substrate $S^0$, all the other parameters are biological parameters which depend on the organisms and substrate considered. The approach in [5] was to fix the biological parameters of the model, and discuss the behavior of the model with respect to the input concentrations of the limiting nutrient and the dilution rate, which are operating parameters of the model. By numerical computation, these authors established the ‘operating diagram’ of the model: six possible outcomes where shown, corresponding to six regions of the operating diagram, see [5], Fig. 1. Stability considerations were all local.

Hsu and Waltman [17] considered the case where $\alpha_2 = 0$ and the growth rate $\mu_1(S,p)$ depends only on the concentration of substrate $S$. These authors considered a particular situation where the growth functions are of the form

$$
\mu_1(S) = \frac{m_1S}{a_1 + S} \quad \text{and} \quad \mu_2(S,p) = \frac{m_2S}{a_2 + S}e^{-K_2p},
$$

(3)

The authors rescaled the biological and operating parameters of the model, creating a ‘standard’ environment in which the operating parameters are fixed to the value 1. This rescaling is often used in the mathematical literature on the chemostat [26]. The authors established global results and shown that system (3) has a unique positive equilibrium of coexistence, but which is unstable. However the operating diagram was not presented in [17].
The operating diagram has the operating parameters as its coordinates and the various regions defined in it correspond to qualitatively different dynamics. This bifurcation diagram which determines the effect of the operating parameters, that are controlled by the operator and which are the dilution rate and the input concentrations, is very useful to understand the model from both the mathematical and biological points of view, and is often constructed in the mathematical and biological literature [1, 7, 23].

It is more convenient to develop the theory for a general model. In this paper we extend [5, 17] by considering general growth functions and by describing the operating diagram. Using the concept of steady-state characteristic we present a geometric characterization of the existence of all equilibria of the model and their stability. We give a necessary and sufficient condition for the existence of a positive equilibrium, not only a sufficient condition as it is done in [5]. We show the existence of one or multiple positive locally exponentially stable equilibria. In the case of multiplicity, bistability can occur, for certain values of the operating parameters. We also extend [5] by describing theoretically the various regions of the operating diagram.

The organization of this paper is as follows. In Section 2, we present the assumptions on general model and some properties of its solutions. In Section 3, we discuss the existence and the local asymptotic stability of equilibria, and some global results. In Section 4, we present the operating diagrams. In Section 5, we consider examples and we give numerical simulations. A discussion follows in Section 6.

2. Assumptions on the model. We consider the general model (1) without restricting ourselves to the particular case where growth rates $\mu_i$ are of the form (2). We suppose only that $\mu_i$, $i = 1, 2$, in system (1) are $C^1$-functions satisfying the following conditions:

(H1) $\mu_i(0,p) = 0$ and $\mu_i(S,p) > 0$ for all $S > 0$ and $p \geq 0$.

(H2) $\frac{\partial \mu_i}{\partial S}(S,p) > 0$ and $\frac{\partial \mu_i}{\partial p}(S,p) < 0$ for all $S \geq 0$ and $p > 0$.

(H3) There is $\lambda_i > 0$ such that $\mu_i(\lambda_i,0) = D$.

(H1) means that the growth can take place if and only if the substrate is present. (H2) means that the growth rate of each species increases with the concentration of substrate and decreases with the inhibitor. (H3) means that in the absence of the inhibitor, the two species are not washed out. We have the following result:

Proposition 1. For non-negative initial conditions, all solutions of system (1) are bounded and remain non-negative for all $t > 0$. Moreover, the set

$$\Omega = \{(S,x,y,p) \in \mathbb{R}_+^4 : p = \alpha_1 x + \alpha_2 y, \quad S + x/\gamma_1 + y/\gamma_2 = S^0\}$$

is positively invariant and is a global attractor for system (1).

Proof. The invariance of $\mathbb{R}_+^4$ is guaranteed by the fact that:

$$S = 0 \implies S' = DS^0 > 0,$$

$$x = 0 \implies x' = 0,$$

$$y = 0 \implies y' = 0,$$

$$p = 0 \implies p' = \alpha_1 \mu_1(S,0)x + \alpha_2 \mu_2(S,0)y > 0.$$
Let $\Sigma = S + x/\gamma_1 + y/\gamma_2$. So, we have $\Sigma = -D(\Sigma - S^0)$, and thus the explicit solution,

$$S(t) + x(t)/\gamma_1 + y(t)/\gamma_2 = S^0 + (S(0) + x(0)/\gamma_1 + y(0)/\gamma_2 - S^0)e^{-Dt}. \quad (4)$$

Thus, we obtain

$$S(t) + x(t)/\gamma_1 + y(t)/\gamma_2 \leq \max\{S^0, S(0) + x(0)/\gamma_1 + y(0)/\gamma_2\} \quad \text{for all} \quad t \geq 0.$$ 

So $S(t)$, $x(t)$ and $y(t)$ are positively bounded. Let $\Gamma = p - \alpha_1 x - \alpha_2 y$, then $\Gamma' = -D\Gamma$, and thus the explicit solution,

$$p(t) - \alpha_1 x(t) - \alpha_2 y(t) = (p(0) - \alpha_1 x(0) - \alpha_2 y(0))e^{-Dt}. \quad (5)$$

One can write,

$$p(t) - \alpha_1 x(t) - \alpha_2 y(t) \leq p(0) - \alpha_1 x(0) - \alpha_2 y(0) \quad \text{for all} \quad t \geq 0.$$ 

So $p(t)$ is positively bounded. Therefore, the solutions of (1) are positively bounded and are defined for all $t \geq 0$. From (4) and (5), it can be deduced that the set $\Omega$ is positively invariant and is a global attractor for (1).

3. **Existence and local stability of equilibria.** Hereafter we use the following conditions and notations:

$$f_i(S) = \mu_i(S, 0) \quad \text{and} \quad g_i(p) = \mu_i(+\infty, p) \quad i = 1, 2.$$ 

The functions $f_i(\cdot)$, $i = 1, 2$ are strictly increasing and positive for all $S > 0$. When equations $f_1(S) = D$ and $f_2(S) = D$ have solutions, they are unique and then we define the break-even concentrations as:

$$\lambda_1 = f_1^{-1}(D) \quad \text{and} \quad \lambda_2 = f_2^{-1}(D). \quad (6)$$

Otherwise, we put $\lambda_1 = +\infty$ and $\lambda_2 = +\infty$. The functions $g_i(\cdot)$, $i = 1, 2$ are strictly decreasing and positive for all $p \geq 0$, and we have

$$g_i(0) = \mu_i(+\infty, 0) = f_i(+\infty) \quad i = 1, 2.$$ 

When equations $g_1(p) = D$ and $g_2(p) = D$ have solutions, they are unique and then we set

$$p_1^* = g_1^{-1}(D), \quad \text{and} \quad p_2^* = g_2^{-1}(D). \quad (7)$$

Otherwise, we put $p_1^* = +\infty$, $p_2^* = +\infty$.

3.1. **Existence of equilibria.** By the implicit function theorem, we show the following lemma

**Lemma 1.** Assume that $\lambda_i < D$ holds for $i = 1, 2$. The equation $\mu_i(S, p) - D = 0$ defines a smooth increasing function

$$F_i: [\lambda_i, +\infty) \rightarrow [0, g_i^{-1}(D)] \rightarrow F_i(S) = p \quad (8)$$

such that $F_i(\lambda_i) = 0$, and $\lim_{S \rightarrow +\infty} F_i(S) = g_i^{-1}(D)$.

**Proof.** Since the function $\mu_i$ is of class $C^1$ on $\mathbb{R}^+_1$, then according to the implicit function theorem, the equation $\mu_i(S, p) - D = 0$, defines a smooth increasing function $p = F_i(S)$ of class $C^1$ on $[\lambda_i, +\infty)$ with

$$F_i'(S) = \frac{-\partial \mu_i(S, F_i(S))}{\partial S}, \quad (9)$$

$$\frac{\partial \mu_i}{\partial p}(S, F_i(S))$$
Indeed, using (H2), we have $\frac{\partial \mu_1}{\partial S}(S,p) > 0$ and $\frac{\partial \mu_1}{\partial p}(S,p) < 0$, thus $F'_1(S) > 0$, which means that the function $F_1$ is increasing. Moreover, if $S = \lambda_1$, then

$$F_1(\lambda_1) = p \iff \mu_1(\lambda_1, p) - D = 0 \iff \mu_1(\lambda_1, p) = f_1(\lambda_1) \iff \mu_1(\lambda_1, p) = \mu_1(\lambda_1, 0) \iff p = 0.$$ 

If $S = +\infty$, then we have

$$F_1(+\infty) = p \iff \mu_1(+\infty, p) - D = 0 \iff g_1(p) = D \iff p = g_1^{-1}(D).$$

\[\square\]

The equilibria of (1) are the solutions of the nonlinear algebraic system

$$\begin{cases}
(S^0 - S)D = \mu_1(S,p)\frac{x}{\gamma_1} + \mu_2(S,p)\frac{y}{\gamma_2} \\
x[\mu_1(S,p) - D] = 0 \\
y[\mu_2(S,p) - D] = 0 \\
\alpha_1\mu_1(S,p)x + \alpha_2\mu_2(S,p)y = Dp
\end{cases} \quad (10)$$

- If $x = y = 0$, then from the first equation of (10), we have $S = S^0$, and the fourth equation we have $p = 0$. It’s the washout equilibrium $E_0(S^0, 0, 0, 0)$.

This equilibrium always exists.

- If $y = 0$ and $x > 0$, then from the second equation of (10), we have $\mu_1(S,p) = D$, and from the first equation, we get

$$x = \gamma_1(S^0 - S),$$

while the fourth equation gives us $p = \alpha_1 x$. Therefore,

$$p = L_1(S) := \alpha_1 \gamma_1(S^0 - S). \quad (12)$$

The function $L_1(S)$ is strictly decreasing, where $L_1(0) = \alpha_1 \gamma_1 S^0$ and $L_1(S^0) = 0$. Now, using Lemma 1, for all $S \geq 0$ and $p > 0$, the equation $\mu_1(S,p) - D = 0$ defines a smooth increasing function

$$p = F_1(S) \quad (13)$$

such that $F_1(\lambda_1) = 0$ and $\lim_{S \to \infty} F_1(S) = g_1^{-1}(D)$. The equilibria are the points of intersection of the graphs of functions

$$p = L_1(S) \quad \text{and} \quad p = F_1(S).$$

Since the function $L_1$ is strictly decreasing and the function $F_1$ is strictly increasing, then there exists a unique positive solution $S_1$ if $\lambda_1 < S^0$ and no solution if $\lambda_1 > S^0$ (see Fig.1). Replacing $S$ by $S_1$ in (11) and (12) we obtain $x_1 = \gamma_1(S^0 - S_1)$ and $p_1 = \alpha_1 \gamma_1(S^0 - S_1)$. Which is the extinction equilibrium of $y$,

$$E_1(S_1, x_1, 0, p_1).$$

- If $y \neq 0$ and $x = 0$, then from the third equation of (10), we have $\mu_2(S,p) = D$, and from the first equation, we get

$$y = \gamma_2(S^0 - S),$$

while the fourth equation gives us $p = \alpha_2 y$. Therefore,

$$p = L_2(S) := \alpha_2 \gamma_2(S^0 - S). \quad (15)$$
The function $L_2(S)$ is strictly decreasing, where $L_2(0) = \alpha_2 \gamma_2 S^0$ and $L_2(S^0) = 0$. Now, using Lemma 1, for all $S \geq 0$ and $p > 0$, the equation $\mu_2(S, p) - D = 0$ defines a smooth increasing function

$$p = F_2(S)$$

such that $F_2(\lambda_2) = 0$ and $\lim_{S \to \infty} F_2(S) = g_2^{-1}(D)$. The equilibria are the points of intersection of the graphs of functions

$$p = L_2(S)$$

and $p = F_2(S)$.

Since the function $L_2$ is strictly decreasing and the function $F_2$ is strictly increasing, then there exists a unique positive solution $S_2$ if $\lambda_2 < S^0$ and no solution if $\lambda_2 > S^0$ (see Fig.1). Replacing $S$ by $S_2$ in (14) and (15) we obtain $x_2 = \gamma_2(S^0 - S_2)$ and $p_2 = \alpha_2 \gamma_2(S^0 - S_2)$. Which is the extinction equilibrium of $x$,

$$E_2(S_2, 0, y_2, p_2).$$

We can state now the following result

**Proposition 2.** Assume that (H1), (H2) and (H3) are satisfied. System (1) has three boundary equilibrium:

- The washout equilibrium $E_0(S^0, 0, 0, 0)$, that always exists.
- The equilibrium $E_1(S_1, x_1, 0, p_1)$ of extinction of species $y$, It exists if and only if $\lambda_1 < S^0$, where $S_1$ is the solution of the equation

$$F_1(S) = L_1(S), \ x_1 = \gamma_1(S^0 - S_1), \ and \ p_1 = \alpha_1 \gamma_1(S^0 - S_1).$$

- The equilibrium $E_2(S_2, 0, y_2, p_2)$ of extinction of species $x$, It exists if and only if $\lambda_2 < S^0$, where $S_2$ is the solution of the equation

$$F_2(S) = L_2(S), \ y_2 = \gamma_2(S^0 - S_2), \ and \ p_2 = \alpha_2 \gamma_2(S^0 - S_2).$$

3.2. **Existence of the positive equilibrium.** A positive equilibrium $E_c$ is determined by the solutions of equations

$$\begin{cases} 
(S^0 - S)D = \mu_1(S, p) \frac{x}{\gamma_1} + \mu_2(S, p) \frac{y}{\gamma_2} \\
\mu_1(S, p) - D = 0 \\
\mu_2(S, p) - D = 0 \\
\alpha_1 \mu_1(S, p)x + \alpha_2 \mu_2(S, p)y = Dp
\end{cases}$$

Let us denote by $h_i$, $i = 1, 2$, the following functions of two variables:

$$h_1(S, p) := \mu_1(S, p) - D \quad \text{and} \quad h_2(S, p) := \mu_2(S, p) - D.$$ 

A positive equilibrium $E_c$ is given by the intersection of the graphs of functions $h_i$, $i = 1, 2$. Our aim is to show the following result:

**Proposition 3.** If $[F_1(S_1) - F_2(S_1)][F_1(S_2) - F_2(S_2)] < 0$, then there is at least one positive equilibrium $E_c(S_c, x_c, y_c, p_c)$ where $S_c$ is the solution of the equation

$$F_1(S) = F_2(S), \ p_c = F_1(S_c), \ x_c = \frac{\gamma_1 [p_c - L_2(S_c)]}{\gamma_1 \alpha_1 - \gamma_2 \alpha_2} \ and \ y_c = \frac{\gamma_2 [L_1(S_c) - p_c]}{\gamma_1 \alpha_1 - \gamma_2 \alpha_2}.$$ 

**Proof.** Without loss of generality, we assume in the first case $S_1 < S_2$. A positive equilibrium is given by the solutions of equations

$$h_1(S, p) = 0 \quad \text{and} \quad h_2(S, p) = 0.$$
according to Lemma 1, these equations define two functions \( p = F_1(S) \) and \( p = F_2(S) \) in \([S_1, S_2]\).

\[
F_1 : [S_1, S_2] \rightarrow [p_1, \bar{p}_1] \quad F_1(S) = p
\]

such that \( F_1(S_1) = p_1 \) and \( F_1(S_2) = \bar{p}_1 \).

\[
F_2 : [S_1, S_2] \rightarrow [\bar{p}_2, p_2] \quad F_2(S) = p
\]

such that \( F_2(S_2) = p_2 \) and \( F_2(S_1) = \bar{p}_2 \).

Thus, the positive equilibrium is given by the intersection of two isoclines corresponding to these functions (see Fig.1). For that we consider the function

\[
F(S) = F_1(S) - F_2(S).
\]

So, we have

\[
F(S_1) = F_1(S_1) - F_2(S_1) \quad \text{and} \quad F(S_2) = F_1(S_2) - F_2(S_2).
\]

According to the intermediate value theorem, there is at least one solution \( S_c \in [S_1, S_2] \) such that \( F_1(S_c) = F_2(S_c) = p_c \) if and only if

\[
[F_1(S_1) - F_2(S_1)][F_1(S_2) - F_2(S_2)] < 0. \quad (20)
\]

Thereafter, \( x_c \) and \( y_c \) are the solutions of the system

\[
\begin{align*}
x_c &= \frac{\gamma_1 [p_c - \gamma_2 \alpha_2 (S^0 - S_c)]}{\gamma_1 \alpha_1 - \gamma_2 \alpha_2} = \frac{\gamma_1 [p_c - L_2(S_c)]}{\gamma_1 \alpha_1 - \gamma_2 \alpha_2}, \quad (21) \\
y_c &= \frac{\gamma_2 [\gamma_1 \alpha_1 (S^0 - S_c) - p_c]}{\gamma_1 \alpha_1 - \gamma_2 \alpha_2} = \frac{\gamma_2 [L_1(S_c) - p_c]}{\gamma_1 \alpha_1 - \gamma_2 \alpha_2} \quad (22)
\end{align*}
\]

Now, using the fact that the functions \( L_i, \ i = 1, 2 \) defined by (12), (15), are decreasing, and the functions \( F_i, \ i = 1, 2 \) defined by (13), (16), are increasing, and as \( S_c \in [S_1, S_2] \) we get

\[
S_1 < S_c < S_2 \iff \begin{cases} L_1(S_c) < L_1(S_1) \text{ and } F_1(S_1) < F_1(S_c) \\ L_2(S_c) > L_2(S_2) \text{ and } F_2(S_2) > F_2(S_c) \end{cases} \iff \begin{cases} L_1(S_c) < p_c \\ L_2(S_c) > p_c \end{cases}
\]

and as \( S_1 < S_c < S_2 \), one can easily verify that \( \gamma_1 \alpha_1 < \gamma_2 \alpha_2 \).

\[
S_1 < S_c < S_2 \implies L_1(S_1) = F_1(S_1) < F_1(S_c) = F_2(S_c) < F_2(S_2) = L_2(S_2) \implies \gamma_1 \alpha_1 (S^0 - S_1) < \gamma_2 \alpha_2 (S^0 - S_2) \implies \gamma_1 \alpha_1 < \gamma_2 \alpha_2
\]

So, we deduce that

\[
x_c = \frac{\gamma_1 [p_c - L_2(S_c)]}{\gamma_1 \alpha_1 - \gamma_2 \alpha_2} > 0 \quad \text{and} \quad y_c = \frac{\gamma_2 [L_1(S_c) - p_c]}{\gamma_1 \alpha_1 - \gamma_2 \alpha_2} > 0.
\]

This ends the proof of the proposition. \( \square \)

**Remark 1.** The condition \([F_1(S_1) - F_2(S_1)][F_1(S_2) - F_2(S_2)] < 0\) of existence of the positive equilibrium \( E_c \) is not necessary, and if it exists the positive equilibrium is not always unique.
The fact that this sufficient condition of existence of the positive equilibrium is not necessary is illustrated by Fig. 2(a). The fact that the positive equilibrium is not unique, if it exists, is illustrated in Fig. 2(b).

Using similar arguments to those from Proposition 3, we show the following result:

**Proposition 4.** A positive equilibrium $E_0(S_c, x_c, y_c, p_c)$ of (1) exists if and only if the graphs of functions $F_1$ and $F_2$ have a positive intersection between the lines $L_1$ and $L_2$, that is, $(S_c, p_c)$ is a positive solution of equations

$$p = F_1(S_c) \quad \text{and} \quad p = F_2(S_c) \quad \text{with} \quad \min(S_1, S_2) < S_c < \max(S_1, S_2).$$

(23)

$x_c, y_c$ are given by (21), (22), respectively.
3.3. Local asymptotic stability of equilibria. For the study of the stability of each equilibrium point of dynamics (1), it is convenient to use the change of variable

$$\Sigma = S^0 - S - x/\gamma_1 - y/\gamma_2$$

in system (1) that reveals the cascade structure of the system. Since $$\Sigma = -D\Sigma$$, the system (1) may then be replaced by

$$\begin{align*}
\Sigma' &= -D\Sigma \\
x' &= \left[\mu_1(S^0 - \Sigma - x/\gamma_1 - y/\gamma_2, p) - D\right]x \\
y' &= \left[\mu_2(S^0 - \Sigma - x/\gamma_1 - y/\gamma_2, p) - D\right]y \\
p' &= \alpha_1\mu_1(S^0 - \Sigma - x/\gamma_1 - y/\gamma_2, p)x + \alpha_2\mu_2(S^0 - \Sigma - x/\gamma_1 - y/\gamma_2, p)y - Dp
\end{align*}$$

(24)

Now we make the change of variable $$\Gamma = p - \alpha_1 x - \alpha_2 y$$ in (24). Since $$\Gamma' = -D\Gamma$$, the system (24) may then be replaced by

$$\begin{align*}
\Gamma' &= -D\Gamma \\
\Sigma' &= -D\Sigma \\
x' &= \left[\mu_1(S^0 - \Sigma - x/\gamma_1 - y/\gamma_2, \Gamma + \alpha_1 x + \alpha_2 y) - D\right]x \\
y' &= \left[\mu_2(S^0 - \Sigma - x/\gamma_1 - y/\gamma_2, \Gamma + \alpha_1 x + \alpha_2 y) - D\right]y
\end{align*}$$

(25)

The Jacobian matrix for the linearization of (25) at an equilibrium point $$E^* = (0, 0, x^*, y^*)$$ takes the triangular form

$$J = \begin{bmatrix}
-D & 0 & 0 \\
0 & -D & 0 \\
A & B & M
\end{bmatrix}$$

where $$M$$ is the square matrix

$$M = \begin{bmatrix}
m_{11} & m_{12} \\
m_{21} & m_{22}
\end{bmatrix},$$

(26)

with

$$m_{11} = \left(-\frac{1}{\gamma_1} \frac{\partial \mu_1}{\partial S} + \alpha_1 \frac{\partial \mu_1}{\partial p}\right) x^* + \mu_1(S^0 - x^*/\gamma_1 - y^*/\gamma_2, \alpha_1 x^* + \alpha_2 y^*) - D,$$

$$m_{12} = \left(-\frac{1}{\gamma_2} \frac{\partial \mu_1}{\partial S} + \alpha_2 \frac{\partial \mu_1}{\partial p}\right) x^*, \quad m_{21} = \left(-\frac{1}{\gamma_1} \frac{\partial \mu_2}{\partial S} + \alpha_1 \frac{\partial \mu_2}{\partial p}\right) y^*,$$

$$m_{22} = \left(-\frac{1}{\gamma_2} \frac{\partial \mu_2}{\partial S} + \alpha_2 \frac{\partial \mu_2}{\partial p}\right) y^* + \mu_2(S^0 - x^*/\gamma_1 - y^*/\gamma_2, \alpha_1 x^* + \alpha_2 y^*) - D.$$

Therefore, $$J$$ has a double eigenvalue $$-D$$, together with the eigenvalues of matrix $$M$$. Hence the equilibrium point $$E^*$$ is locally exponentially stable (LES) if and only if the eigenvalues of $$M$$ are of negative real parts. The local stability of equilibria of system (25) is given by the following result.

**Proposition 5.** Assume that (H1), (H2) and (H3) are satisfied. The stability of equilibria of (1) is as follows:

- The equilibrium $$E_0$$ is LES if and only if $$\lambda_1 > S^0$$ and $$\lambda_2 > S^0$$.
- The equilibrium $$E_1$$, if it exists, has at least three dimensional stable manifold and is LES if and only if $$F_1(S_1) > F_2(S_1)$$.
- The equilibrium $$E_2$$, if it exists, has at least three dimensional stable manifold and is LES if and only if $$F_2(S_2) > F_1(S_2)$$.
- The equilibrium $$E_c$$, if it exists, is LES if and only if

$$\left(\alpha_1\gamma_1 - \alpha_2\gamma_2\right)|F_2'(S_c) - F_1'(S_c)| > 0.$$  

(27)
The following table summarizes all the results on the existence and the local stability of the equilibria of (1),

| Equilibria | Existence | Local exponential stability |
|------------|-----------|----------------------------|
| $E_0$      | Always    | $\lambda_1 > S^0$ and $\lambda_2 > S^0$ |
| $E_1$      | $\lambda_1 < S^0$ | $F_1(S_1) > F_2(S_1)$ |
| $E_2$      | $\lambda_2 < S^0$ | $F_2(S_2) > F_1(S_2)$ |
| $E_c$      | (23) has a solution $\left(\alpha_1 \gamma_1 - \alpha_2 \gamma_2\right) [F_2'(S_c) - F_1'(S_c)] > 0$ |

Table 1. Existence and local asymptotic stability of equilibria of system (1).

In the following, without loss of generality, we suppose that $S_1 < S_2$, we study the local stability of the points of equilibrium of the system (1), according to the number $n$ of solutions of the equation $F_1(S) = F_2(S)$ for $S_1 < S < S_2$. We restrict our attention to the generic situation, where all intersections are transversal. Note by $E_c^i$ the positive equilibria for $i = 1, 2, ..., n$.

**Proposition 6.** Assume that $S_1 < S_2$, we distinguish the two following cases:
1) $F_1(S_1) > F_2(S_1)$, in this case, $E_1$ is stable and $E_0$ is unstable. Moreover,
- If $n = 2p$, $p \in \mathbb{N}^*$, then $E_2$ is unstable
- If $n = 2p + 1$, $p \in \mathbb{N}$, then $E_c^{2p+1}$ is unstable and $E_2$ is stable
  where $E_c^{2i-1}$ is unstable and $E_c^{2i}$ is stable for $1 \leq i \leq p$.
2) $F_1(S_1) < F_2(S_1)$, in this case, $E_1$ and $E_0$ are unstable. Moreover,
- If $n = 2p$, $p \in \mathbb{N}^*$, then $E_2$ is stable
- If $n = 2p + 1$, $p \in \mathbb{N}$, then $E_c^{2p+1}$ is stable and $E_2$ is unstable
  where $E_c^{2i-1}$ is stable and $E_c^{2i}$ is unstable for $1 \leq i \leq p$.

**Proof.** Assume that in the first case that $F_1(S_1) > F_2(S_1)$, according to Lemma 5, we have $E_1$ is stable and $E_0$ is unstable. We now assume that the equation $F_1(S) = F_2(S)$ admits $n = 2p + 1$ solutions $S_j^i$, $j = 1, 2, ..., n$. As the intersections are transversal (see Fig. 3), then for each $1 \leq i \leq p$ we have:

$$F_1'(S_c^{2i+1}) < F_2'(S_c^{2i+1}), \quad F_1'(S_c^{2i}) > F_2'(S_c^{2i}), \quad \text{and} \quad F_1'(S_c^1) < F_2'(S_c^1).$$

By Lemma 5, we deduce that the equilibria $E_c^{2i+1}$ are unstable and the equilibria $E_c^{2i}$ are stable.

If $n = 2p$, then $F_1(S_2) > F_2(S_2)$, that is, the equilibrium $E_2$ is unstable. If $n = 2p + 1$, then $F_1(S_2) < F_2(S_2)$ and the equilibrium $E_2$ is stable. Similarly, the second case could be checked easily. \qed

### 3.4. Global asymptotic stability of the positive equilibrium.

The aim of this section is to study the global asymptotic stability of the positive equilibrium of (1) when it exists and is unique.

Let $\Sigma = S + x/\gamma_1 + y/\gamma_2$ and $\Gamma = p - \alpha_1 x - \alpha_2 y$, by Proposition 1, for non-negative initial conditions, all solutions of system (1) are bounded. Moreover, the set $\Omega$ attracts all the trajectories. Using (5) and (4), system (1) is equivalent to non-autonomous system of two differential equations

$$\begin{align*}
  x' &= \left[\mu_1(\Sigma(t) - x/\gamma_1 - y/\gamma_2, \Gamma(t) + \alpha_1 x + \alpha_2 y) - D\right] x \\
  y' &= \left[\mu_2(\Sigma(t) - x/\gamma_1 - y/\gamma_2, \Gamma(t) + \alpha_1 x + \alpha_2 y) - D\right] y
\end{align*}$$
This is an asymptotically autonomous differential system which converges to the autonomous system

\[
\begin{align*}
  x' &= \mu_1(S^0 - x/y_1 - y_2, \alpha_1 x + \alpha_2 y) - Dx \\
  y' &= \mu_2(S^0 - x/y_1 - y_2, \alpha_1 x + \alpha_2 y) - Dy
\end{align*}
\]  

(28)

The system (28) is defined on the set $$\Delta = \{(x, y) \in \mathbb{R}^2_+: x/y_1 + y/y_2 \leq S^0\}$$. The set $$\Delta$$ is bounded and positively invariant, that is, system (28) is dissipative. Notice that the equilibria of (28)

\[
E_0 = (0, 0), \quad E_1 = (x_1, 0), \quad E_2 = (0, y_2), \quad E_c = (x_c, y_c)
\]

correspond to the equilibria of (1), respectively,

\[
E_0(S^0, 0, 0, 0), \quad E_1(S_1, x_1, 0, p_1), \quad E_2(S_2, 0, y_2, p_2), \quad E_c(S_c, x_c, y_c, p_c)
\]

where $$x_1 = \gamma_1(S^0 - S_1)$$, $$y_2 = \gamma_2(S^0 - S_2)$$ and $$x_c, y_c$$ are given by (21), (22), respectively.

By Proposition 5 the study of phase portrait of (28) on $$\Delta$$, shows that there are only stable nodes, unstable nodes and saddle points. For any initial condition on the $$x$$ axis [resp. $$y$$ axis], the solution cannot converge to $$E_2$$ [resp. $$E_1$$] since $$E_0$$ is an unstable node. Hence, there is no trajectory joining two saddle points. Thus, according to Thieme [27], we thereof deduce the asymptotic behavior of the solution of (1) from the asymptotic behavior of the autonomous system (28) which is called the reduced model.

The following lemma shows that the system (28) cannot have periodic orbits inside $$\Delta$$.

**Lemma 2.** The system (28) has no periodic orbit inside $$\Delta$$.

**Proof.** By the change of variable $$\xi_1 = \ln(x)$$ and $$\xi_2 = \ln(y)$$, whose derivatives with respect to time $$\xi'_1 = x'/x$$ and $$\xi'_2 = y'/y$$, respectively. We then obtain the following system:

\[
\begin{align*}
  \xi'_1 &= k_1(\xi_1, \xi_2) := \mu_1(S^0 - e^{\xi_1}/\gamma_1 - e^{\xi_2}/\gamma_2, \alpha_1 e^{\xi_1} + \alpha_2 e^{\xi_2}) - D \\
  \xi'_2 &= k_2(\xi_1, \xi_2) := \mu_2(S^0 - e^{\xi_1}/\gamma_1 - e^{\xi_2}/\gamma_2, \alpha_1 e^{\xi_1} + \alpha_2 e^{\xi_2}) - D
\end{align*}
\]  

(29)
We have
\[ \frac{\partial k_1}{\partial \xi_1} + \frac{\partial k_2}{\partial \xi_2} = -\frac{e^{\xi_1}}{\gamma_1} \frac{\partial \mu_1}{\partial S} + \alpha_1 e^{\xi_1} \frac{\partial \mu_1}{\partial \gamma_2} + \frac{e^{\xi_2}}{\gamma_2} \frac{\partial \mu_2}{\partial S} + \alpha_2 e^{\xi_2} \frac{\partial \mu_2}{\partial \gamma_2} < 0, \]
according to the Dulac criterion, we deduce that the system (29) has no periodic trajectory. Therefore (28) has no periodic orbit in \( \Delta \).

**Theorem 3.1.** Assume that the equation \( F_1(S) = F_2(S) \) has a unique solution \( S_c \), such that \( S_1 < S_c < S_2 \). If \( F_1(S_1) < F_2(S_1) \), then the positive equilibrium \( E_c \) is globally asymptotically stable with respect to solutions with positive initial conditions.

**Proof.** The conditions of existence and stability of \( E_0, E_1, E_2 \) and \( E_c \) are those of \( E_0, E_1, E_2 \) and \( E_c \), respectively, given in Table 1. So, if \( F_1(S_1) < F_2(S_1) \), then from Proposition 6, the equilibria \( E_0, E_1, E_2 \) are unstable, the equilibrium \( E_c \) is stable. To prove the theorem it remains only to show that it is a global attractor.

We have \( x/\gamma_1 + y/\gamma_2 \leq \max(S^0, x(0)/\gamma_1 + y(0)/\gamma_2) \) for all \((x, y) \in \mathbb{R}_+^2 \), then for any non-negative initial condition, the solutions of the system (29) are positively bounded and consequently the \( \omega \)-limit sets are compact non-empty. Using Poincaré-Bendixon Theorem, these limit sets are either equilibrium points or periodic orbits or polycycles. According to Lemma 2, we cannot have in the set \( \omega \)-limit a periodic orbit.

We show now that the \( \omega \)-limit set (It will be denoted by \( \omega \)) cannot contain any point of the axes \( x = 0 \) or \( y = 0 \). The stable manifold of \( E_0 \) is the origin \((0, 0)\). The stable manifolds of \( E_1 \) and \( E_2 \) are the \( x \)-axis and \( y \)-axis, respectively. Since the initial condition of the solution \((x(t), y(t))\) does not belong to any of these stable manifolds, then \( \omega \) cannot be any of the three equilibria. Moreover, \( \omega \) cannot contain any of these equilibria by the Butler-McGehee theorem [10, Lemma A1]. It cannot contain \( E_0 \) since it is a repeller. Suppose then that \( E_1 \in \omega \) [resp. \( E_2 \in \omega \)]. As it has been shown that \( \omega \neq \{E_1\} \) [resp. \( \omega \neq \{E_2\} \)], then it must also contain an entire orbit different from \( E_1 \) [resp. \( E_2 \)] belonging to the \( x \)-axis [resp. \( y \)-axis]. There are only two possible orbits; one is unbounded, thus it cannot be included in the compact set \( \omega \), and the other has \( \alpha \)-limit set \( E_0 \), thus it cannot contain \( E_0 \) since it is a reseller. Therefore, \( E_1 \) [resp. \( E_2 \)] cannot be included in \( \omega \). Now, if \( \omega \) contains a point of the \( x \)-axis or \( y \)-axis then, by the invariance of \( \omega \), it must contain one of the equilibria \( E_0, E_1, E_2 \) or an unbounded orbit, thus it cannot be included in the compact set \( \omega \). Since none of these alternatives are possible, then \( \omega \) cannot contain any point of the axes \( x = 0 \) or \( y = 0 \). If it does not contain the point \( E_c \), then, according to the PoincaréBendixson theorem, solutions converge toward a cycle, and according to Lemma 2, this system cannot have a periodic orbit inside \( \Delta \). Therefore, it contains the point \( E_c \). It is equal to it because \( E_c \) is LES. This shows that \( E_c \) is GAS. Finally, applying the result of Thieme [27] and concluding that \( E_c \) is a globally asymptotically stable equilibrium point for the system (1). \( \square \)

4. **Operating diagrams.** The operating diagram has the operating parameters \( D \) and \( S^0 \) as its coordinates and the various regions defined in it correspond to qualitatively different dynamics. This bifurcation diagram which determines the effect of the operating parameters, that are controlled by the operator and which are the dilution rate and the the inflowing substrate, is very useful to understand the model from both the mathematical and biological points of view. We assume
that the functions \( \mu_i, \ i = 1, 2 \) are fixed. The following change of dependent variables

\[
\hat{x} = \frac{x}{\gamma_1}, \quad \hat{y} = \frac{y}{\gamma_2},
\]

which reduces (1) to

\[
\begin{align*}
S' &= (S^0 - S)D - \mu_1(S,p)\hat{x} - \mu_2(S,p)\hat{y} \\
\hat{x}' &= [\mu_1(S,p) - D])\hat{x} \\
\hat{y}' &= [\mu_2(S,p) - D])\hat{y} \\
p' &= \hat{\alpha}_1\mu_1(S,p)\hat{x} + \hat{\alpha}_2\mu_2(S,p)\hat{y} - Dp
\end{align*}
\]

(30)

where \( \hat{\alpha}_1 = \alpha_1\gamma_1 \) and \( \hat{\alpha}_2 = \alpha_2\gamma_2 \). Therefore, without loss of generality we can assume that the yields in (1) are equal to 1 \( (\gamma_1 = \gamma_2 = 1) \). So, we consider the system

\[
\begin{align*}
S' &= (S^0 - S)D - \mu_1(S,p)x - \mu_2(S,p)y \\
x' &= [\mu_1(S,p) - D])x \\
y' &= [\mu_2(S,p) - D])y \\
p' &= \alpha_1\mu_1(S,p)x + \alpha_2\mu_2(S,p)y - Dp
\end{align*}
\]

(31)

Our aim now is to describe operating diagram. The operating diagram shows how the system behaves when we vary the two control parameters \( D \) and \( S^0 \) in the system (31).

Let \( \Gamma_i \) be the curve of equation \( S^0 = \lambda_i(D), \ i = 1, 2 \),

\[ \Gamma_i = \{ (D, S^0) : S^0 = \lambda_i(D) \}. \]

(32)

According to Table 1, the curve \( \Gamma_1 \) is the border to which \( E_1 \) exists (the blue curve in Figs. 5 and 6), the curve \( \Gamma_2 \) is the border to which \( E_2 \) exists (the black curve in Figs. 5 and 6).

Recall that \( S_i, \ i = 1, 2 \) are defined as the solutions of \( F_i(S,D) = L_i(S,S^0) \), \( i = 1, 2 \), respectively. Therefore, \( S_i, \ i = 1, 2 \) depend on the operating parameters \( D \) and \( S^0 \). We note them by \( S_i(D,S^0), \ i = 1, 2 \). We define the sets

\[
\begin{align*}
\Gamma_1^i &= \{ (D, S^0) : F_1(S_1(D,S^0), D) = F_2(S_1(D,S^0), D) \}, \\
\Gamma_2^i &= \{ (D, S^0) : F_1(S_2(D,S^0), D) = F_2(S_2(D,S^0), D) \},
\end{align*}
\]

(33)

which are curves in the generic case. If the curves \( \Gamma_i, \ i = 1, 2 \) intersect in a point \( (D_*, S_0^*) \) of the plane, then one has

\[
\mu_1(S_0^*, 0) = \mu_2(S_0^*, 0) = D_*,
\]

(34)

using Lemma 1, equation (34) can be written as follows

\[
F_1(S_0^*, D_*) = F_2(S_0^*, D_*) = 0
\]

(35)

From (35), we deduce that

\[
F_1(S_1(D_*, S_0^*), D_*) = F_2(S_1(D_*, S_0^*), D_*)
\]

\[
F_1(S_2(D_*, S_0^*), D_*) = F_2(S_2(D_*, S_0^*), D_*)
\]

Therefore, the point \( (D_*, S_0^*) \) belongs to the sets \( \Gamma_i^i, \ i = 1, 2 \). Hence, if \( \Gamma_i, \ i = 1, 2 \) intersect in a point of the plan \( (D, S^0) \), then the curves \( \Gamma_i^i \) intersect in the same point.

The curves \( \Gamma_1^i \) and \( \Gamma_2^i \) are the boundaries for which \( E_1 \) and \( E_2 \) unstable and at the same time \( E_c \) exists and unstable (the red and green curves in Figs. 5 and 6, respectively).
5. Illustrative examples. In this section, we consider the model (31) with \( \mu_i, i = 1, 2 \) given by (2). Let us show the usefulness of our results on the construction of the operating diagram corresponding to various set of biological parameters encountered in the literature, in particular those considered in [5], see Cases (a) and (b), in Table 2.

We consider also set of biological parameters which are not taken from the existing literature, and are chosen due to their interesting properties, see Case (c), in Table 2.

We restrict our attention to (31) where \( \mu_i, i = 1, 2 \) are given by (2). In this case, the functions \( \lambda_1(D) \) and \( \lambda_2(D) \) defined by (6) are given explicitly:

\[
\lambda_1(D) = \frac{a_1 D}{m_1 - D} \quad \text{and} \quad \lambda_2(D) = \frac{a_2 D}{m_2 - D}.
\]

The expressions of functions \( F_i, i = 1, 2 \) and \( L_i, i = 1, 2 \) defined by (13), (16), (12) and (15), respectively, can be calculated explicitly:

\[
F_i(S, D) = \frac{K_i[(m_i - D)S - a_i D]}{D(a_i + S)} \quad \text{and} \quad L_i(S, S^0) = \alpha_i(S^0 - S), \quad i = 1, 2.
\]

On the other hand, the solutions \( S_i(D, S^0), i = 1, 2 \) of equations \( F_i(S_i, D) = L_i(S_i, S^0), i = 1, 2 \) which are used in \( E_i, i = 1, 2 \), respectively, are simply the positive solutions of the quadratic equations:

\[
K_i[(m_i - D)S_i - a_i D] = \alpha_i D(S^0 - S)(a_i + S_i), \quad i = 1, 2.
\]

The solution \( S_i(D) \) of the equation \( F_1(S_c, D) = F_2(S_c, D) \) which is used in \( E_c \) is simply the positive solution of the quadratic equation:

\[
K_1 D(a_2 + S_c)[(m_1 - D)S_c - a_1 D] = K_2 D(a_1 + S_c)[(m_2 - D)S_c - a_2 D].
\]

Note that the equation (39) can not have more than two solutions.

If we assume that equation \( F_1(S_c, D) = F_2(S_c, D) \) has at most two positive solutions \( S_1^c(D) \) and \( S_2^c(D) \) as in the preceding case, then \( \Gamma_i^c \) [resp. \( \Gamma_2^c \)] given by (33) is simply the union of the graphs of functions \( S_1(D, S^0) = S_1^c(D) \) and \( S_1(D, S^0) = S_2^c(D) \) [resp. \( S_2(D, S^0) = S_1^c(D) \) and \( S_2(D, S^0) = S_2^c(D) \)], see Fig.4.

![Illustrative graph of \( \Gamma_i^c \), \( i = 1, 2 \) defined by (33), showing the relative positions of the roots \( S_1^c(D) \) and \( S_2^c(D) \) of (39) with respect to the root \( S_i(D,S^0) \) of (38). Region I: \( S_i < S_1^c < S_2^c \); region II: \( S_1^c < S_2^c < S_i \); region III: \( S_1^c < S_i < S_2^c \).](image-url)
5.1. Operating diagram: the curves $\Gamma_1^c$ and $\Gamma_2^c$ do not intersect. This case corresponds to the parameter values used by [5] given in Table 2(a,b). In this case, the curves $\Gamma_1^c$ and $\Gamma_2^c$ do not intersect. Notice that $\Gamma_1^c$ and $\Gamma_2^c$ are simply the graphs of functions $S_1(D, S^0) = S_2^c(D)$ and $S_2(D, S^0) = S_2^c(D)$, respectively. We see from Table 1 that the curve $\Gamma_1$ and $\Gamma_2$ of the operating diagram, given by (32) are the border to which $E_1$ and $E_2$ exist, respectively. Beside these curves, we plot also on the operating diagram of Fig. 5, the curves $\Gamma_1^c$ and $\Gamma_2^c$. According to Proposition 5, these curves separate the region of existence of $E_c$ into two subregions labelled $J_6$ and $J_7$, such that $E_c$ is stable in $J_6$ (see Fig. 5(a)), and unstable in $J_7$ (see Fig. 5(b)). In the region $J_7$, the system exhibits bistability of $E_1$ and $E_2$. Therefore, the curves $\Gamma_i$ and $\Gamma_i^c$, $i = 1, 2$ separate the operating plane $(D, S^0)$ into at most seven regions, as illustrated by Fig. 5, labelled $J_1$, $J_2$, $J_3$, $J_4$, $J_5$, $J_6$ and $J_7$. Some of these regions may be empty as shown on Fig. 5. The region $J_6$ is empty in case (a) and the region $J_7$ is empty in case (b). The operating diagram is illustrated in Fig. 5 (Our diagram is similar to the diagram in [5], Fig. 1). From Table 1, we deduce the following result:

**Proposition 7.** The results are summarised in Table 3, which shows the existence and local stability of the equilibria $E_0$, $E_1$, $E_2$ and $E_c$ in the regions of the operating diagram in Fig. 5.

| Region | The relative positions of $S_i$ and $S^c_i$ | $E_0$ | $E_1$ | $E_2$ | $E^c_i$ | $E^c_2$ |
|--------|----------------------------------|------|------|------|-------|-------|
| $(S^0, D) \in J_1$ | $S_1$ and $S_2$ do not exist | S | | | | |
| $(S^0, D) \in J_2$ | $S_1$ does not exist | U | S | | | |
| $(S^0, D) \in J_3$ | $S_1^c < S_i < S^c_i$, $i = 1, 2$ ** | U | U | S | | |
| $(S^0, D) \in J_4$ | $S_1^c < S_i < S^c_i$, $i = 1, 2$ | U | S | U | | |
| $(S^0, D) \in J_5$ | $S_2$ does not exist | U | S | | | |
| $(S^0, D) \in J_6$ | $S_1^c < S_2 < S^c_2 < S_1$ | U | U | U | S | |
| $(S^0, D) \in J_7$ | $S_1^c < S_2 < S^c_2 < S_2$ | U | S | S | U | |

** When $S_1^c$ and $S_2^c$ do not exist, the condition reduces to $S_i$, $i = 1, 2$ exist.

Table 3. Existence and stability of equilibria in the regions of the operating diagrams of Fig. 5, when the curves $\Gamma_i^c$ do not intersect. The letter S (resp. U) means stable (resp. unstable) and empty if that equilibrium does not exist.

| Table 2. Parameter values used in Section 5 where $\mu_i$ are given by (2). |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Parameters | $m_1$ | $m_2$ | $a_1$ | $a_2$ | $K_1$ | $K_2$ | $\alpha_1$ | $\alpha_2$ | Figures |
| Units | $h^{-1}$ | $h^{-1}$ | $gl^{-1}$ | $gl^{-1}$ | $gl^{-1}$ | $gl^{-1}$ | | | |
| Case (a) | 1.0 | 2.0 | 0.01 | 0.04 | 0.01 | 0.006 | 0.1 | 4.0 | 5(a) |
| Case (b) | 1.0 | 2.0 | 0.01 | 0.04 | 0.01 | 0.006 | 4.0 | 0.1 | 5(b) |
| Case (c) | 2.0 | 9.0 | 0.006 | 0.04 | 0.005 | 0.001 | 0.005 | 0.4 | 6(a), 7 |
| Case (d) | 2.0 | 9.0 | 0.006 | 0.04 | 0.005 | 0.001 | 0.4 | 0.005 | 6(b) |
5.2. Operating diagram: the curves $\Gamma^c_1$ and $\Gamma^c_2$ intersect. This case corresponds to the parameter values given in Table 2(c,d). In this case, the curves $\Gamma^c_1$ and $\Gamma^c_2$ intersect. When $D < 1.1769$, equation (39) has exactly two solutions denoted by $S_1^c(D)$ and $S_2^c(D)$, corresponding to two equilibria $E_1^c$ and $E_2^c$, respectively. Notice that $\Gamma^c_1$ [resp. $\Gamma^c_2$] is simply the union of the graphs of functions $S_1(D,S^0) = S_1^c(D)$ and $S_1(D,S^0) = S_2^c(D)$ [resp. $S_2(D,S^0) = S_1^c(D)$ and $S_2(D,S^0) = S_2^c(D)$].

We plot also on the operating diagram of Fig. 6, the horizontal line $\Gamma_3$ defined by

$$\Gamma_3 = \{(D,S^0) : D \approx 1.1769, S^0 > 0.0207\},$$

where $(S^0 \approx 0.0207, D \approx 1.1769)$ are maximum point of the curve $\Gamma^c_2$ of Fig. 6(a) [resp. $\Gamma^c_1$ of Fig. 6(b)].

Therefore, the curves $\Gamma_i$, $i = 1, 3$ and $\Gamma^c_i$, $i = 1, 2$ separate the operating plane $(D,S^0)$ into at most eleven regions, as illustrated by Fig. 6, labelled $J_i$, , $i = 1.5$ and $J^a_i$, $i = 6.8$ and $J^b_i$, $i = 6.8$. The operating diagram is illustrated in Fig. 6. From Table 1, we deduce the following result:

**Proposition 8.** The results are summarised in Table 4, which shows the existence and local stability of the equilibria $E_0$, $E_1$, $E_2$, $E_1^c$ and $E_2^c$ in the regions of the operating diagram in Fig. 6.

In order to illustrate and validate the results of this section, we perform the simulations for the same biological parameter values that were considered for the plot of operating diagram in Fig. 6(a).

Fig. 7(a) shows the bi-stability of $E_1 \approx (0.094, 0)$ and $E_2 \approx (0, 0.014)$ which are LES while $E_1^c \approx (0.023, 0.013)$ and $E_0 = (0, 0)$ are unstable when

$$(S^0, D) = (0.1, 0.9) \in J^a_7$$

or whenever $S_1^c < S_1 < S_2^c < S_2$. 

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**Figure 5.** The operating diagram of the system (1) where $\mu_i$ are given by (2) and the curves $\Gamma_i^c$ do not intersect. (a): The occurrence of the bistability region $J_7$, where the coexistence region $J_6$ does not exist. (b): The occurrence of the coexistence region $J_6$. The biological parameters used to construct Figs. 5(a,b) are exactly the same except that the values of $\alpha_i$ have been inverted.
**Table 4.** Existence and stability of equilibria in the regions of the operating diagrams of Fig. 6, when the curves \( \Gamma^c_i \) intersect.

| Region | The relative positions of \( S_i \) and \( S^c_i \) | \( E_0 \) | \( E_1 \) | \( E_2 \) | \( E^c_1 \) | \( E^c_2 \) |
|--------|-----------------------------------------|--------|--------|--------|--------|--------|
| \((S^0, D) \in J_1\) | \( S_1 \) and \( S_2 \) do not exist | S |     |     |     |     |
| \((S^0, D) \in J_2\) | \( S_1 \) does not exist | U | S |     |     |
| \((S^0, D) \in J_3\) | \( S_i < S^1_i < S^2_i, i = 1, 2 \)** | U | U | S |     |
| \((S^0, D) \in J_4\) | \( S^c_i < S_i < S^2_i, i = 1, 2 \) | U | S | U |     |
| \((S^0, D) \in J_5\) | \( S_2 \) does not exist | U | S |     |     |
| \((S^0, D) \in J_6^a\) | \( S_1 < S^1_i < S_2 < S^2_i \) | U | U | S | S |
| \((S^0, D) \in J_6^b\) | \( S_1 < S^1_i < S^2_i < S^2_i \) | U | S | S | U |
| \((S^0, D) \in J_7^a\) | \( S_2 < S^1_i < S^2_i < S^2_i \) | U | S | U | S |
| \((S^0, D) \in J_7^b\) | \( S_2 < S^1_i < S^2_i < S^2_i \) | U | S | U | S |

**When \( S^1_i \) and \( S^2_i \) do not exist, the condition reduces to \( S_i, i = 1, 2 \) exist.**

**Table 5.** Parameter values of \( S_i \) and \( S^c_i \) used in Fig. 7.

| \((S^0, D)\) | Regions | \( S_1 \) | \( S_2 \) | \( S^c_1 \) | \( S^c_2 \) | Figures |
|-------------|---------|--------|--------|--------|--------|--------|
| \((0.1, 0.9)\) | \( J_2^a \) | 0.006  | 0.085  | 0.005  | 0.064  | 7(a)   |
| \((0.05, 1.15)\) | \( J_2^b \) | 0.009  | 0.042  | 0.012  | 0.025  | 7(b)   |
| \((0.02, 1.15)\) | \( J_2^a \) | 0.008  | 0.017  | 0.012  | 0.025  | 7(c)   |

Here \( E_1 \) and \( E_2 \) are both stable and \( E^c_1 \) is a saddle point whose separatrix separates the phase plane into the basins of attraction of \( E_1 \) and \( E_2 \).
Fig. 7(b) shows the bi-stability of \( E_2 \approx (0,0.008) \) and \( E_1^c \approx (0.036,0.002) \) which are LES while \( E_2^c \approx (0.02,0.005) \), \( E_1 \approx (0.041,0) \) and \( E_0 \) are unstable when
\[
(S^0, D) = (0.05,1.15) \in \mathcal{J}_8^a \text{ or whenever } S_1 < S_1^c < S_2^c < S_2.
\]
Here \( E_1 \) and \( E_2^c \) are both stable and \( E_1^c \) is a saddle point whose separatrix separates the phase plane into the basins of attraction of \( E_1 \) and \( E_2^c \).

In this case, Fig. 7(c) shows the coexistence of the two species and the global convergence to the unique positive equilibrium \( E_1^c \approx (0.006,0.002) \) when
\[
(S^0, D) = (0.02,1.15) \in \mathcal{J}_6^a \text{ or whenever } S_1 < S_1^c < S_2 < S_2^c.
\]
In each case, the parameter values of \( S_i, i = 1,2 \) and \( S_i^c, i = 1,2 \) is given in Table 5, where the equilibria in green are stable, the blue ones are unstable.

![Figure 7](image)

**Figure 7.** The trajectories of the reduced model (28) where \((S^0, D)\) are chosen in regions of Fig. 6(a). (a): Bistability of \( E_1 \) and \( E_2 \) when \((S^0, D) = (0.1,0.9) \in \mathcal{J}_7^a\). (b): Bistability of \( E_1^c \) and \( E_2 \) when \((S^0, D) = (0.05,1.15) \in \mathcal{J}_8^a\). (c): Global stability of \( E_1^c \) when \((S^0, D) = (0.02,1.15) \in \mathcal{J}_6^a\).

6. **Conclusion.** In this work we have extended the model (1) with (2) of competition in the chemostat with an internal inhibitor proposed by [5] by considering the model (1) with general growth rate functions of competitors, the functions are assumed to be increasing in the substrate \( S \) and decreasing in inhibitor \( p \), it also includes the model considered in [16] when only one of the competitors produces an inhibitor which inhibits the other specie (i.e (1) together with (3)).

We give the conditions of existence and local stability of all corresponding steady states of (1). We define the functions \( L_1, F_1, L_2, \) and \( F_2 \), and the numbers \( S_1, S_2 \), and illustrate the relative positions of the different equilibria geometrically (see Figs.1, 2, and 3), Props.3 and 4 give sufficient and necessary conditions for the existence of the positive equilibria, specifically our mathematical analysis of the model has revealed the possibility of multiple positive steady states, we show that the system may exhibit bistability, which could occur in the classic chemostat model only when the growth rate is non-monotonic [10]. By reducing the model (1) to planer model (28), and using Dulac’s criterion, we show the nonexistence of periodic orbits for the system, and due to Thieme’s results [27], the global asymptotic stability of the positive steady state of (1) when it’s unique is obtained.

The operating diagrams show the effect of the control parameter \( S^0 \) and \( D \) on the asymptotic behavior of the system, to have the coexistence of the two microbial
species in the process, the operating parameters values should be chosen in the region $J_6$ which is more preferable because we have a globally asymptotically stable equilibrium, whereas $J_8$ there is bistability between coexistence and exclusion of the first species. Furthermore, the operating diagrams show that the system can have a unique steady state of washout $J_1$, or exclusion of one of two species ($J_i$, $i = 2, 5$), or bistability between exclusion of the first species and the second species $J_7$.

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