A COMPETITION MODEL IN THE CHEMOSTAT WITH ALLELOPATHY AND SUBSTRATE INHIBITION

MOHAMED DELLAL\textsuperscript{a,c,*}, BACHIR BAR\textsuperscript{b,c} AND MUSTAPHA LAKRIB\textsuperscript{c}

\textsuperscript{a} Ibn Khaldoun University, 14000 Tiaret, Algeria
\textsuperscript{b} Ecole Normale Supérieure, 27000 Mostaganem, Algeria
\textsuperscript{c} LDM, Djillali Liabès University, 22000 Sidi Bel Abbès, Algeria

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Abstract. A model of two microbial species in a chemostat competing for a single resource is considered, where one of the competitors that produces a toxin, which is lethal to the other competitor (allelopathic inhibition), is itself inhibited by the substrate. Using general growth rate functions of the species, necessary and sufficient conditions of existence and local stability of all equilibria of the four-dimensional system are determined according to the operating parameters represented by the dilution rate and the input concentration of the substrate. With Michaelis-Menten or Monod growth functions, it is well known that the model can have a unique positive equilibrium which is unstable as long as it exists. If a non monotonic growth rate is considered (which is the case when there is substrate inhibition), it is shown that a new positive equilibrium point exists which can be stable according to the operating parameters of the system. We describe its operating diagram, which is the bifurcation diagram giving the behavior of the system with respect to the operating parameters. By means of this bifurcation diagram, we show that the general model presents a set of fifteen possible behaviors: washout, competitive exclusion of one species, coexistence, multi-stability, occurrence of stable limit cycles through a supercritical Hopf bifurcations, homoclinic bifurcations and flip bifurcation. This diagram is very useful to understand the model from both the mathematical and biological points of view.

1. Introduction. A fundamental result in ecology is the so called Gause’s Law, well-known also as the Competitive Exclusion Principle (CEP) \cite{11,14}. It asserts that in competition of two (or more) species for a single growth-limiting nutrient, generically at most one species can survive the competition. This was demonstrated using chemostat models \cite{13,15,17,26,29} under general hypotheses, in which the basic model for two species takes the form

\begin{equation}
\begin{aligned}
S' &= (S^0 - S)D - f_1(S) \frac{x}{S} - f_2(S) \frac{y}{S} \\
x' &= [f_1(S) - D]x \\
y' &= [f_2(S) - D]y
\end{aligned}
\end{equation}

where $S(t)$ denotes the concentration of the substrate at time $t$ and $x(t)$, $y(t)$ are the concentrations of the competitors at time $t$. The operating parameters $S^0 > 0$ and $D > 0$ denote, respectively, the input concentration of the nutrient and

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* Corresponding author: Mohamed Dellal.
the dilution rate of the chemostat, all of which are assumed to be constant and are under the control of the experimenter. The so-called functional responses \( f_i, \ i = 1, 2, \) represent the specific growth rates of the competitors and \( \gamma_i > 0, \ i = 1, 2, \) are the yield constants which can be chosen equal to one, without loss of generality.

Model (1) has been extensively studied in the literature, see for example Smith and Waltman [29]. Butler and Wolkowicz [4] have studied model (1) for a general class of response functions including monotonic and non-monotonic growth functions such as the Monod and Haldane laws.

However, the CEP contradicts the biodiversity found in nature as well as in wastewater treatment processes and biological reactors (see [16, 27]). Several mechanisms were proposed to explain this biodiversity, like flocculation [7, 12], and density-dependence [23], another one is the inhibition, which can be divided into two classes: - substrate induced inhibition (i.e., a nutrient which is essential at low concentrations may be inhibiting at higher concentrations [2], [15, Ch. 3, p. 80], [29, Ch. 2, p. 37]), which in mathematical terms means changing the functional response rather than adding an additional substance to the model, and - allelopathic inhibition which is the production of a chemical by one species that negatively impacts another species. For a discussion on the various models on inhibition and Allelopathy the reader is referred to the survey [21] and the references therein, see also [3, 5, 6, 8, 9, 24] for recent works.

One of the models introduced by Hsu and Waltman [19] is in which two species compete for a single limiting resource, where one of the competitors produces a toxin, which is lethal to the other competitor. Let \( p(t) \) denote the concentration of the internal inhibitor. The model takes the form

\[
\begin{align*}
S' &= (S^0 - S)D - f_1(S)x - f_2(S)y \\
x' &= [f_1(S) - D - \gamma p]x \\
y' &= [(1 - k)f_2(S) - D]y \\
p' &= k f_2(S)y - Dp.
\end{align*}
\]

In system (2), the inhibitor is called lethal since it acts on the death of the species \( x \) rather than on its growth. The parameter \( \gamma > 0 \) represents the lethal effect of the inhibitor \( p \) on \( x \). The parameter \( 0 \leq k < 1 \) represents the fraction of potential growth allocated to producing the toxin. This model was considered by Hsu and Waltman [19] when

\[
f_i(S) = \frac{m_i S}{a_i + S}, \quad i = 1, 2
\]

where \( m_i, a_i, \ i = 1, 2, \) are some positive constant parameters. These parameters are called biological parameters since they depend on the organisms and substrate considered. They are measurable in the laboratory. In contrast, the 'operating (or control) parameters' are the input concentration of the nutrient \( S^0 \) and the dilution rate \( D \) of the chemostat. These parameters are called operating parameters since they are under the control of the experimenter.

The complete mathematical analysis of (2), including some global results, was given in [19]. 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 [29]. The authors established global results and shown that system (2) has a unique positive equilibrium of coexistence, which is unstable.

Fergola et al. [8, 9] produced a model of the chemostat with Allelopathy and substrate inhibition, where the growth rate of the first competitor is Andrews.
In this approach, the inhibitor reduces the growth of the competitor rather than being lethal. The authors established global results. They gave conditions on the biological parameters for which the coexistence equilibrium becomes stable.

In this paper we consider model (2) where the species producing the toxin (i.e. $y$) is itself inhibited by the substrate, as noted before. This means that the function $f_2$ in (2) is no longer monotonous.

A useful contribution of the mathematical analysis of a chemostat model is to give to the engineers the operating diagram which is the bifurcation diagram for which the values of the biological parameters are fixed, and the behavior of the model is discussed with respect to the operating parameters. 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 concentration, is very useful to understand the model from both the mathematical and biological points of view, and is often constructed both in the biological literature [22, 25, 31] and the mathematical literature [1, 10, 28, 32]. The operating diagram was not presented in [19, 21]. Our study provides this important tool showing the behavior of model (2) according to the control parameters $D$ and $S^0$, when all biological parameters are fixed.

In this paper we extend [19, 21] by considering general growth functions, and substrate inhibition of the species which produces the toxin, and by describing the operating diagram. In [19], in the absence of substrate inhibition, at most one competitor can survive, while in our case, coexistence is possible. Our approach to handle the question of robustness with respect to parameter variations, is to present the computations for generic growth functions, rather than the specific functions (3), and to use the fact that the condition of stability of coexistence equilibrium point of the system is polynomial, of degree 2, with respect to the operating parameter $S^0$. The problem is then reduced to the determination of real valued function, which is built with the coefficients of this polynomial. This function depends only on the operating parameter $D$. Hence, by mathematical analysis, we can construct the operating diagram of the model.

The organization of this paper is as follows. In Section 2, we present the assumptions on general model. In Section 3, we present our main result which gives the conditions of existence and stability of the equilibrium points, explicitly with respect to the operating parameters, see Theorem 3.1, and we discuss the properties of the region of instability of the coexistence equilibrium, see Theorem 3.2. In Section 4, we present the operating diagrams. In Section 5, we consider examples and numerical simulations. Finally, we draw conclusions in the last Section 6. The mathematical proofs are given in Appendix A.

2. Assumptions on the model. In this paper, we consider the general model (2) without restricting ourselves to the particular cases for growth rates of the competitors. We suppose only that $f_i$, $i = 1, 2$, in system (2) are $C^1$-functions satisfying the following conditions, see Figure 1:

\begin{enumerate}
\item[(H1)] $f_1(0) = 0$, $f_1(+\infty) = m_1$ and $f_1'(S) > 0$ for all $S \geq 0$.
\item[(H2)] $f_2(0) = 0$, $f_2(+\infty) = 0$ and there exists $S_2^m > 0$ such that $f_2'(S) > 0$ for $0 \leq S < S_2^m$ and $f_2'(S) < 0$ for $S > S_2^m$.
\end{enumerate}
When equation \( f_1(S) = D \) has a solution, it is unique and then we define the break-even concentration as:

\[
\lambda_1 = f_1^{-1}(D).
\]

(4)

Otherwise, we put \( \lambda_1 = +\infty \).

If \( D < (1-k)f_2(S_m^2) \), we denote \( \lambda_2(D) < \mu_2(D) \) the roots of equation \( (1-k)f_2(S) = D \). If \( D = (1-k)f_2(S_m^2) \), this equation has only one solution and we let \( \lambda_2(D) = \mu_2(D) \). If \( D > (1-k)f_2(S_m^2) \), this equation has no solution and we let \( \lambda_2(D) = +\infty \). We shall allow \( \mu_2 \) to be equal to \( +\infty \), and our results can then be applied for any monotonic growth rate. The popular Monod and Haldane growth functions are particular instances of such functions. Now, let us define the function \( g \) by

\[
g(S) = f_1(S) - D - \gamma k (S_0 - S), \text{ for } S \in (0,S_0).
\]

Using (H1), for all \( S \in (0,S_0) \) we have \( g'(S) > 0 \), \( g(0) = -D - \gamma k S_0 < 0 \) and \( g(S_0) = f_1(S_0) - D \). Therefore, when \( \lambda_1 < S_0 \), equation \( g(S) = 0 \) admits a unique solution that we denote \( \hat{\lambda}(D,S_0) \):

\[
g(\hat{\lambda}) = 0.
\]

(5)

Since \( g(\lambda_1) = -\gamma k (S_0 - \lambda_1) < 0 \) we have

\[
\lambda_1(D) < \hat{\lambda}(D,S_0).
\]

(6)

3. Existence and stability of equilibria.

3.1. Existence of equilibria. The steady states of (2) are the solutions of the set of equations

\[
\begin{align*}
0 &= (S^0 - S)D - f_1(S)x - f_2(S)y \\
0 &= [f_1(S) - D - \gamma p]x \\
0 &= [(1-k)f_2(S) - D]y \\
0 &= kf_2(S)y - Dp.
\end{align*}
\]

(7)

From the second equation of (7), it follows that

\[
x = 0 \quad \text{or} \quad f_1(S) - D - \gamma p = 0,
\]
and from the third equation of (7), we deduce that
\[ y = 0 \quad \text{or} \quad (1 - k)f_2(S) = D. \]

Therefore, besides the washout equilibrium \( E_0 = (S^0, 0, 0, 0) \) where both populations are extinct, that always exists, system (2) has the following types of equilibria:
- \( E_1: x > 0 \) and \( y = 0 \), where species \( y \) is extinct while species \( x \) survives.
- \( E_2: x = 0 \) and \( y > 0 \), where species \( x \) is extinct while species \( y \) survives.
- \( E_c: x > 0 \) and \( y > 0 \), where both species are maintained.

We show below that the equilibrium \( E_1 \) is unique if it exists and, generically, system (2) can have two equilibria \( E^1_2 \) and \( E^2_2 \) of type \( E_2 \) and two positive equilibria \( E^1_c \) and \( E^2_c \) of type \( E_c \).

The existence of equilibria of system (2) is stated by the following result:

**Proposition 1.** Assume that \((H1)\) and \((H2)\) are satisfied. System (2) has at most six equilibria:

- The washout equilibrium \( E_0 = (S^0, 0, 0, 0) \), that always exists.
- The boundary equilibrium \( E_1 = (\lambda_1, S^0 - \lambda_1, 0, 0) \) of extinction of species \( y \). This equilibrium exists if and only if \( \lambda_1 < S^0 \).
- The boundary equilibrium \( E^1_2 = (\lambda_2, 0, (S^0 - \lambda_2)(1 - k), (S^0 - \lambda_2)k) \) of extinction of species \( x \). This equilibrium exists if and only if \( \lambda_2 < S^0 \).
- The boundary equilibrium \( E^2_2 = (\mu_2, 0, (S^0 - \mu_2)(1 - k), (S^0 - \mu_2)k) \) of extinction of species \( x \). This equilibrium exists if and only if \( \mu_2 < S^0 \).
- The coexistence equilibrium \( E^1_c = (\lambda_2, x_{c_1}, y_{c_1}, p_{c_1}) \), where \( p_{c_1}, y_{c_1} \) and \( x_{c_1} \) are given by
  \[ p_{c_1} = \frac{f_1(\lambda_2) - D}{\gamma}, \quad y_{c_1} = \frac{1 - k}{k}p_{c_1}, \quad x_{c_1} = \frac{D}{f_1(\lambda_2)} \left( S^0 - \lambda_2 - \frac{y_{c_1}}{1 - k} \right). \]  
  This equilibrium exists if and only if \( \lambda_2(D) < S^0 \) and \( \lambda_1(D) < \lambda_2(D) < \lambda(D, S^0) \).
- The coexistence equilibrium \( E^2_c = (\mu_2, x_{c_2}, y_{c_2}, p_{c_2}) \), where \( p_{c_2}, y_{c_2} \) and \( x_{c_2} \) are given by
  \[ p_{c_2} = \frac{f_1(\mu_2) - D}{\gamma}, \quad y_{c_2} = \frac{1 - k}{k}p_{c_2}, \quad x_{c_2} = \frac{D}{f_1(\mu_2)} \left( S^0 - \mu_2 - \frac{y_{c_2}}{1 - k} \right). \]  
  This equilibrium exists if and only if \( \mu_2(D) < S^0 \) and \( \lambda_1(D) < \mu_2(D) < \lambda(D, S^0) \).

**Proof.** The proof is given in Appendix A.1. \( \square \)

### 3.2. Local asymptotic stability of equilibria.

The local asymptotic stability of equilibria of system (2) is determined by the sign of the real part of eigenvalues of the corresponding Jacobian matrix or by the Routh-Hurwitz criterion (in the case of \( E^2_c \)).

For the study of the stability of equilibria it is convenient to use the change of variable
\[ \Gamma = p - \frac{ky}{1 - k} \]
in system (2) that reveals the cascade structure of the system. Since \( \Gamma' = -D \Gamma \), system (2) may then be replaced by

\[
\begin{align*}
\Gamma' &= -D \Gamma \\
S' &= (S^0 - S)D - f_1(S)x - f_2(S)y \\
x' &= \left[ f_1(S) - D - \gamma \left( \Gamma + \frac{k}{1-k} y \right) \right] x \\
y' &= [(1-k)f_2(S) - D]y.
\end{align*}
\]

The Jacobian matrix for the linearization of system (10) at an equilibrium point \( E^* = (0, S^*, x^*, y^*) \) takes the triangular form

\[
J = \begin{bmatrix}
-D & 0 \\
A & M
\end{bmatrix},
\]

where \( M \) is the square matrix

\[
M = \begin{bmatrix}
m_{11} & m_{12} & m_{13} \\
m_{21} & m_{22} & m_{23} \\
m_{31} & 0 & m_{33}
\end{bmatrix},
\]

with

\[
m_{11} = -D - x^* f_1'(S^*) - y^* f_2'(S^*), \quad m_{12} = -f_1(S^*), \quad m_{13} = -f_2(S^*),
\]

\[
m_{21} = x^* f_1'(S^*), \quad m_{22} = f_1(S^*) - D - \frac{k\gamma}{1-k} y^*, \quad m_{23} = -\frac{k\gamma}{1-k} x^*
\]

\[
m_{31} = (1-k)y^* f_2'(S^*), \quad m_{33} = (1-k) f_2(S^*) - D.
\]

Therefore, the eigenvalues of \( J \) are \(-D\), together with the eigenvalues of matrix \( M \). Hence the equilibrium point \( E^* \) is LES (locally exponentially stable) if and only if the eigenvalues of \( M \) are of negative real parts. The local stability of equilibria of system (2) is given by the following result.

**Proposition 2.** Assume that (H1) and (H2) are satisfied. The stability of equilibria of system (2) is as follows:

- The equilibrium \( E_0 \) is LES if and only if \( f_1(S^0) < D \) and \( (1-k)f_2(S^0) < D \).
- The equilibrium \( E_1 \), if it exists, has at least three dimensional stable manifold and is LES if and only if \( (1-k)f_2(\lambda_1) < D \).
- The equilibrium \( E^1_2 \), if it exists, has at least three dimensional stable manifold and is LES if and only if \( \lambda_2(D) < \lambda(D, S^0) \).
- The equilibrium \( E^2_2 \) is unstable whenever it exists.
- The equilibrium \( E^1_3 \) is unstable whenever it exists.
- The equilibrium \( E^2_3 \), if it exists, is LES if and only if

\[
AB > C \quad \text{and} \quad A > 0
\]

where \( A, B \) and \( C > 0 \) are defined by:

\[
A = D + f_1'(\mu_2)x_{c_2} + f_2'(\mu_2)y_{c_2}, \quad B = f_1(\mu_2)f_1'(\mu_2)x_{c_2} + Df_2'(\mu_2)y_{c_2},
\]

\[
C = -\gamma k f_1'(\mu_2)f_2'(\mu_2)x_{c_2}y_{c_2}.
\]

**Proof.** The proof is given in Appendix A.2. \(\square\)

Suppose that \( \lambda_1 < S^0 \) and \( \lambda_2 < S^0 \) to make the problem interesting. The existence and stability conditions of the equilibria of (2) given by Propositions 1 and 2 depend on the relative positions of the real numbers \( \lambda_1, \lambda_2, \mu_2, \hat{\lambda} \) and of the
similarly. We have signs of \( AB - C \) and \( A \). We can distinguish eleven cases, according to the relative positions of these numbers. These cases are summarized in Table 1.

| Case | Condition | Equilibria and nature |
|------|-----------|-----------------------|
| \( \mu_2 > S^0 \) | \( \lambda_1 < \hat{\lambda} < \lambda_2 < \mu_2 \) | \( E_1 \) S U |
| \( \lambda_1 < \lambda_2 < \hat{\lambda} < \mu_2 \) | \( E_1 \) S S U |
| \( \lambda_2 < \hat{\lambda}_1 < \lambda < \mu_2 \) | U S |
| \( \mu_2 < S^0 \) | \( \lambda_1 < \lambda_2 < \mu_2 < \hat{\lambda} \) and \( AB > C \) and \( A > 0 \) | S S U U S |
| \( \lambda_1 < \lambda_2 < \mu_2 < \hat{\lambda} \) and \( AB < C \) or \( A < 0 \) | S S U U U |
| \( \lambda_2 < \lambda_1 < \mu_2 < \hat{\lambda} \) and \( AB > C \) and \( A > 0 \) | U S U S |
| \( \lambda_2 < \lambda_1 < \mu_2 < \hat{\lambda} \) and \( AB < C \) or \( A < 0 \) | U S U U |
| \( \lambda_2 < \mu_2 < \hat{\lambda}_1 < \hat{\lambda} \) | S S U |

Table 1. Existence and stability of equilibria of system (2) when \( \lambda_1 < S^0 \) and \( \lambda_2 < S^0 \). The letter S (resp. U) means stable (resp. unstable) and no letter means that the equilibrium does not exist.

In the particular case \( \mu_2 > S^0 \), the equilibria \( E_2 \) and \( E_2^c \) do not exist. Thus, we obtain the same result as in [19, 21]. The necessary and sufficient conditions of local stability of equilibria, obtained in Table of [19], are summarized in the first three lines of Table 1. The main change in the existence of equilibria of our model (2) compared to [19, 21] is the appearance of a second positive equilibrium, of type \( E_c \) and equilibrium of type \( E_2 \).

To emphasize the dependence of the equilibria of system (2) with respect to the operating parameters, we rewrite our previous results. Using the inverse functions \( \lambda_1 : I_1 \rightarrow \mathbb{R}^+, \lambda_2 : I_2 \rightarrow [0, S_1^m] \) and \( \mu_2 : I_2 \rightarrow [S_2^m, +\infty) \) where

\[
I_1 = [0, m_1) \quad \text{and} \quad I_2 = (0, (1 - K)f_2(S_2^m)]
\]

Note that \( y_{e_1} \) and \( y_{e_2} \) given by (8) and (9), respectively, are defined for \( D \in I_{e_1} \) and \( D \in I_{e_2} \), respectively, where

\[
I_{e_1} = \{ D \in I_1 \cap I_2 : \lambda_1(D) < \lambda_2(D) \}, \quad \quad (14)
\]

\[
I_{e_2} = \{ D \in I_1 \cap I_2 : \lambda_1(D) < \mu_2(D) \}.
\]

For simplicity we assume that equation \( f_1(S) = (1 - k)f_2(S) \) has at most one positive solution \( S = \overline{S} > 0 \). The case of multiple intersections can be treated similarly. We have

- \( I_{e_1} = \emptyset \) and \( I_{e_2} = \emptyset \) if \( f_1(S) < (1 - k)f_2(S) \) for all \( S > 0 \).
- \( I_{e_1} = (\overline{D}, (1 - k)f_2(S_2^m)] \) and \( I_{e_2} = (0, (1 - k)f_2(S_2^m)] \) if \( \overline{S} < S_2^m \), see Fig. 2(a).
- \( I_{e_1} = \emptyset \) and \( I_{e_2} = (0, \overline{D}) \) if \( S_2^m < \overline{S} \), see Figure 2(b).
\( I_{c_1} = I_{c_2} = (0, (1 - k)f_2(S_m^a)) \) if \( f_1(S) > (1 - k)f_2(S) \) for all \( S > 0 \).

![Graphs of \( f_1 \) (in red) and \((1 - k)f_2 \) (in blue) when equation \( f_1(S) = (1 - k)f_2(S) \) has a positive solution \( S = \bar{S} \) and graphical depiction of \( I_{c_1} \) and \( I_{c_2} \).](a): \( I_{c_1} = (\bar{D}, (1 - k)f_2(S_m^a)) \) and \( I_{c_2} = (0, (1 - k)f_2(S_m^a)) \). (b): \( I_{c_1} = \emptyset \) and \( I_{c_2} = (0, \bar{D}) \) where \( \bar{D} = f_1(\bar{S}) = f_2(\bar{S}) \). Intervals \( I_{c_1} \) and \( I_{c_2} \) are defined by (14).

Note that \( x_{c_1} \) and \( x_{c_2} \) given by (8) and (9), are defined for \( (D, S^0) \in J_{c_1} \) and \( (D, S^0) \in J_{c_2} \), respectively, where

\[
J_{c_1} = \left\{(D, S^0) \in I_{c_1} \times \mathbb{R}^+ : S^0 > \lambda_2(D) + \frac{1}{1 - k} \mu_2(D)\right\},
\]

\[
J_{c_2} = \left\{(D, S^0) \in I_{c_2} \times \mathbb{R}^+ : S^0 > \mu_2(D) + \frac{1}{1 - k} \mu_2(D)\right\},
\]

with \( I_{c_1} \) and \( I_{c_2} \) defined by (14).

3.3. Existence and stability of equilibria with respect to operating parameters. In what follows, our aim is to express the conditions of existence and stability of the equilibria in Proposition 2 with respect to the operating parameters \( D \) and \( S^0 \). For this purpose, we need the following definitions.

Let

\[
F_1(D) = \frac{1}{\gamma k} (f_1(\lambda_2(D)) - D) + \lambda_2(D), \quad F_2(D) = \frac{1}{\gamma k} (f_1(\mu_2(D)) - D) + \mu_2(D).
\]

If we assume that equation \( f_1(S) = (1 - k)f_2(S) \) has at most one positive solution \( S = \bar{S} > 0 \), then functions \( F_1 \) and \( F_2 \) are defined on \( I_{c_1} \) and \( I_{c_2} \), respectively, where \( I_{c_1} \) and \( I_{c_2} \) are defined by (14).

In case where \( \bar{S} < S_m^a \), functions \( F_1 \) and \( F_2 \) are defined and positive on \( I_{c_1} = (\bar{D}, (1 - k)f_2(S_m^a)) \) and \( I_{c_2} = (0, (1 - k)f_2(S_m^a)) \), respectively, with \( F_1(\bar{D}) = \bar{S}, \)

\( F_1((1 - k)f_2(S_m^a)) = F_2((1 - k)f_2(S_m^a)) = 0 \) and \( F_2 \) tends to infinity as \( D \) tends to 0 (see Figure 3(a)). Moreover, function \( F_2 \) is decreasing.

In case where \( \bar{S} > S_m^a \), function \( F_1 \) is not defined since \( \lambda_1(D) > \lambda_2(D) \) for all \( D \), and function \( F_2 \) is defined and positive on \( I_{c_2} = (0, \bar{D}) \), with \( F_2(\bar{D}) = \bar{S} \) and \( F_2 \) tends to infinity as \( D \) tends to 0 (see Figure 3(b)).

We have the following result.

**Lemma 1.** The following equivalences hold:

\[ x_{c_1}(D, S^0) > 0 \iff \lambda_2(D) < \lambda(D, S^0) \iff S^0 > F_1(D) \]
Using hypothesis (H2), the condition (1 − k)f2(λ1)<D of stability of E1 in Proposition 2 is equivalent to λ1(D) < λ2(D) or λ1(D) > μ2(D). Using Lemma 1, the condition λ2(D) < λ(D, S0) of stability of E2 in Proposition 2 is equivalent to S0 < F1(D).

Let us consider now the existence and stability of E_1^c and E_2^c. Using Lemma 1, we see that the condition μ2(D) < λ(D, S0) of existence of E_2 in Proposition 1 is equivalent to S0 < F_2(D). Finally, taking into account (17), the condition of stability of E_2^c in Proposition 2 is equivalent to A(D, S0) > 0 and F_3(S0, D) > 0.
3.4. Necessary and sufficient conditions for instability of $E^2_c$. We give now the necessary and sufficient conditions on the operating parameters $D$ and $S^0$ such that the positive equilibrium $E^2_c$ is unstable. That is we discuss the sign of $F_3(D, S^0)$ and $A(D, S^0)$. We have

$$A = D + f'_1(\mu_2)x_{c_2} + f'_2(\mu_2)y_{c_2}. \quad (18)$$

Notice that, since $f'_1(\mu_2) > 0$, we have $A < 0$ if and only if $x_{c_2} < x_0(D) = -(D + f'_2(\mu_2)y_{c_2})/f'_1(\mu_2)$ where $x_0(D)$ is the positive real root of $A$. The root $x_0(D)$ is positive if and only if $D + f'_2(\mu_2)y_{c_2}(D) < 0$.

We define the subsets $I_3$, $I_4$ and $I_5$ by:

$$I_3 = \{ D \in I_{c_2} : D + f'_2(\mu_2)y_{c_2}(D) < 0 \}, \quad I_4 = \{ D \in I_{c_2} : D + f'_2(\mu_2)y_{c_2}(D) > 0 \},$$

$$I_5 = \{ D \in I_{c_2} : D + f'_2(\mu_2)y_{c_2}(D) = 0 \},$$

where $I_{c_2}$ is defined by (14). We define the following function

$$F_6(D) = \frac{1}{D} f_1(\mu_2(D))x_0(D) + F_2(D), \quad D \in I_3 \cup I_5, \quad (20)$$

where $F_2(D)$ is given by (16). Notice that $F_2(D) < F_6(D)$ for $D \in I_3$ and equality holds for $D \in I_5$.

**Remark 1.** If $D \in I_4 \cup I_5$, that is $D + f'_2(\mu_2)y_{c_2}(D) \geq 0$, then $A(D, S^0) > 0$.

**Lemma 2.** Suppose that equilibrium $E^2_c$ exists and $D \in I_3$. Then we have

- $A(D, S^0) < 0 \iff S^0 < F_6(D)$.
- If $S^0 < F_6(D)$ then $E^2_c$ is unstable.

**Proof.** The proof is given in Appendix A.4.

We study the sign of $F_3$. We have

$$F_3 = a_2 x_{c_2}^2 + a_1 x_{c_2} + a_0, \quad (21)$$

where coefficients $a_2 = a_2(D)$, $a_1 = a_1(D)$ and $a_0 = a_0(D)$ are given by

$$a_2 = (f'_1(\mu_2))^2 f_1(\mu_2), \quad a_0 = D f'_2(\mu_2)y_{c_2}[D + f'_2(\mu_2)y_{c_2}],$$

$$a_1 = f'_1(\mu_2)f_1(\mu_2)[D + f'_2(\mu_2)y_{c_2}] + D f'_1(\mu_2)f'_2(\mu_2)y_{c_2} + \gamma k f_1(\mu_2)f'_2(\mu_2)y_{c_2}. \quad (22)$$

Hence, $F_3$ given by (21) appears as a second order polynomial in $x_{c_2}$ whose coefficients are depending only on $D$ and not on $S^0$. Let $\Delta = \Delta(D)$ be the discriminant of $F_3$:

$$\Delta = a_1^2 - 4a_0 a_2. \quad (23)$$

**Lemma 3.** Depending on the value $D$ we have the following:

- If $D \in I_3$, then $a_0(D) > 0$, $a_1(D) < 0$ and $\Delta(D) > 0$.
- If $D \in I_4$, then $a_0(D) < 0$ and $\Delta(D) > 0$.
- If $D \in I_5$, then $a_0(D) = 0$ and $\Delta(D) > 0$.

**Proof.** The proof is given in Appendix A.5.

According to Lemma 3, we have $\Delta > 0$. The roots of $F_3 = 0$ are $x_1(D)$ and $x_2(D)$. Their product is equal to $\frac{a_0}{a_2}$ which is positive (resp. negative) if $D \in I_3$ (resp. $D \in I_4$). Therefore, the roots exist and are positive (resp. of opposite signs) if and only if $D \in I_3$ (resp. $D \in I_4$). It is easy to see that when $D \in I_5$ then one root is positive and the other is zero. Notice that, since $a_2 > 0$, we have $F_3 < 0$ if
and only if \( \max(0, x_1(D)) < x_{c_2} < x_2(D) \) where \( x_1(D) \) and \( x_2(D) \) are the real roots of \( F_3 \):

\[
x_1(D) = \frac{-a_1 - \sqrt{\Delta}}{2a_2} \quad \text{and} \quad x_2(D) = \frac{-a_1 + \sqrt{\Delta}}{2a_2}.
\]

We define the following functions

\[
F_4(D) = \frac{1}{\gamma} f_1(\mu_2(D)) \max(0, x_1(D)) + F_2(D),
\]

\[
F_5(D) = \frac{1}{\gamma} f_1(\mu_2(D)) x_2(D) + F_2(D),
\]

where \( F_2(D) \) is given by (16) and \( x_1(D), x_2(D) \) are given by (24). Notice first that \( F_2(D) < F_3(D) \) for \( 0 < D < f_2(S^m_2) \) and equality holds for \( D = f_2(S^m_2) \). Notice also that \( F_2(D) < F_4(D) \) for \( D \in I_3 \) and equality holds for \( D \in I_4 \cup I_5 \). For the study of the relative position to the graphs of functions \( F_4, F_5 \) and \( F_6 \) in the subset \( I_3 \) we use the following facts. Since \( A(x_0(D)) = 0 \), from \( F_3 = AB - C \) we deduce that

\[
F_3(x_0(D)) = -C(x_0(D)) = \gamma k f_1(\mu_2) f_2'(\mu_2) y_{c_2} x_0(D) < 0.
\]

Therefore, from \( F_3(0) = a_0 > 0 \) for \( D \in I_3 \) and \( F_3(+\infty) = +\infty \), one deduces that the polynomial \( F_3 \) has two positive real roots

\[
x_1(D) \in (0, x_0(D)) \quad \text{and} \quad x_2(D) \in (x_0(D), +\infty), \text{ see Figure 4.}
\]

Thus

\[
F_4(D) < F_6(D) < F_5(D) \quad \text{for all} \quad D \in I_3.
\]

\[\text{Figure 4. The graphs of } F_3(x_{c_2}) \text{ and } A(x_{c_2}), \text{ showing the relative positions of the roots } x_i = x_i(D), i = 0, 2, \text{ of } F_3(x_{c_2}) \text{ with respect to the root } x_0 = x_0(D) \text{ of } A(x_{c_2}), \text{ when } D \in I_3.\]

We can now determine the sign of \( F_3 \), that is the stability of \( E^2_{c_2} \), as stated in the following result.

**Theorem 3.2.** Assume that the positive equilibrium \( E^2_{c_2} \) exists, that is, the subset \( I_{c_2} \) given by (14) is non empty and \( S^0 > F_2(D) \). Then \( E^2_{c} \) is unstable if and only if the following condition is satisfied by the operating parameters \( D \) and \( S^0 \):

\[
F_2(D) < S^0 < F_5(D),
\]

where \( F_2(D) \) and \( F_5(D) \) are given by (16) and (25), respectively.
Proof. The proof is given in Appendix A.6.

Using ideas in [30], in the following result we prove that when $E_c^2$ is destabilized, it does so only through a Hopf bifurcation.

**Theorem 3.3** (Hopf bifurcation). For $D \in I_{c_2}$, $E_c^2$ undergoes a Hopf bifurcation when crossing the curve $S^0 = F_2(D)$.

**Proof.** The proof is given in Appendix A.7.

---

4. Operating diagram. Our aim now is to describe the operating diagram of system (2). The boundaries of the regions in the operating diagram are locations where bifurcations occur. In order to construct this operating diagram one must compute these boundaries. Using Theorem 3.1, these boundaries are the following curves of the $(D,S^0)$-plane, where curves $\Gamma_i$, $i = 1...9$, are defined by Table 3.

| The curve $\Gamma_i$, $i = 1...9$ | Boundary |
|----------------------------------|----------|
| $\Gamma_1 = \{(D,S^0) : S^0 = \lambda_1(D)\}$ | is the border to which $E_1$ exists |
| $\Gamma_2 = \{(D,S^0) : S^0 = \lambda_2(D)\}$ | is the border to which $E_1^1$ exists |
| $\Gamma_3 = \{(D,S^0) : S^0 = \mu_2(D)\}$ | is the border to which $E_2$ exists |
| $\Gamma_4 = \{(D,S^0) : \lambda_1(D) = \lambda_2(D), S^0 > \lambda_1(D)\}$ | is the border to which $E_1$ is stable and at the same time $E_1^1$ exists |
| $\Gamma_5 = \{(D,S^0) : \lambda_1(D) = \mu_2(D), S^0 > \lambda_1(D)\}$ | is the border to which $E_1$ is stable and at the same time $E_2$ exists |
| $\Gamma_6 = \{(D,S^0) : F_1(D), S^0 > \lambda_2(D)\}$ | is the border to which $E_1$ is stable and at the same time $E_1^1$ exists |
| $\Gamma_7 = \{(D,S^0) : F_2(D), S^0 > \mu_2(D)\}$ | is the border to which $E_2$ exists |
| $\Gamma_8 = \{(D,S^0) : F_3(D)\}$ | is the border to which $E_2$ is stable |
| $\Gamma_9 = \{(D,S^0) : \lambda_2(D) = \mu_2(D), S^0 > \lambda_2(D)\}$ | Horizontal line $D = (1-k)f_2(S_c^m)$ |

**Table 3.** Boundaries of the regions in the operating diagram.

**Remark 2.** Notice that the curve of function $D = f_2(S^0)$ is simply the union of the graphs of functions $S^0 = \lambda_2(D)$ and $S^0 = \mu_2(D)$, so

$$\Gamma_2 \cup \Gamma_3 = \{(D,S^0) : D = f_2(S^0)\}.$$

Notice that $\lambda_2(D) < \mu_2(D)$ for $0 < D < f_2(S_c^m)$ and equality holds for $D = f_2(S_c^m)$. Similarly $F_1(D) < F_2(D)$ for $0 < D < f_2(S_c^m)$ and equality holds for $D = f_2(S_c^m)$. Therefore, the curves $\Gamma_i$, $i = 1...9$, separate the operating plane $(D,S^0)$ into at most fifteen regions, as illustrated by Figure 5, labeled $J_k$, $k = 0...14$, and defined in Table 4. These regions of the operating parameters plane $(D,S^0)$ correspond to different behaviors of system (2). From Table 2, we deduce the following result.

**Proposition 3.** Assume that (H1) and (H2) are satisfied. The existence and stability properties of equilibria of system (2) are given in Table 5, where the regions $J_k$, $k = 0...14$, are defined in Table 4.

Let us describe the behavior in the regions of the operating diagram.

When $\bar{S} < S_c^m$, the operating diagram is divided into at most nine regions, as shown in Figure 5(a). The region $J_0$ corresponds to the washout equilibrium $E_0$. 



Table 4. Definitions of the regions $I_k$, $k = 0...14$, in the operating diagrams in Figures 5, 6 and 11.

| Region | Definition |
|--------|------------|
| $J_0$  | $S^0 < \lambda_1(D)$ and $S^0 < \lambda_2(D)$ |
| $J_1$  | $S^0 < \lambda_1(D)$ and $\lambda_2(D) < S^0 < \mu_2(D)$ |
| $J_2$  | $S^0 < \lambda_1(D)$ and $S^0 > \mu_2(D)$ |
| $J_3$  | $S^0 > \lambda_1(D)$ and $S^0 < \lambda_2(D)$ |
| $J_4$  | $S^0 > \lambda_1(D)$, $\lambda_2(D) < S^0 < \mu_2(D)$ and $S^0 < F_1(D)$ |
| $J_5$  | $S^0 > \lambda_1(D), \lambda_2(D) < S^0 < \mu_2(D), S^0 > F_1(D)$ and $\lambda_1(D) < \lambda_2(D)$ |
| $J_6$  | $S^0 > \lambda_1(D), \lambda_2(D) < S^0 < \mu_2(D), S^0 > F_1(D)$ and $\lambda_2(D) < \lambda_1(D)$ |
| $J_7$  | $S^0 > \lambda_1(D), S^0 > \mu_2(D)$ and $S^0 < F_1(D)$ |
| $J_8$  | $S^0 > \lambda_1(D), S^0 > \mu_2(D), F_1(D) < S^0 < F_2(D)$ and $\lambda_1(D) < \lambda_2(D)$ |
| $J_9$  | $S^0 > \lambda_1(D), S^0 > \mu_2(D), F_1(D) < S^0 < F_2(D)$ and $\lambda_2(D) < \lambda_1(D)$ |
| $J_{10}$ | $S^0 > \lambda_1(D), S^0 > \mu_2(D)$ and $\lambda_1(D) > \mu_2(D)$ |
| $J_{11}$ | $S^0 > \lambda_1(D), S^0 > \mu_2(D), S^0 > F_2(D), S^0 < F_3(D)$ and $\lambda_2(D) < \lambda_1(D)$ |
| $J_{12}$ | $S^0 > \lambda_1(D), S^0 > \mu_2(D), S^0 > F_2(D), S^0 > F_3(D)$ and $\lambda_2(D) < \lambda_1(D)$ |
| $J_{13}$ | $S^0 > \lambda_1(D), S^0 > \mu_2(D), S^0 > F_2(D), S^0 < F_3(D)$ and $\lambda_1(D) < \lambda_2(D)$ |
| $J_{14}$ | $S^0 > \lambda_1(D), S^0 > \mu_2(D), S^0 > F_2(D), S^0 > F_3(D)$ and $\lambda_1(D) < \lambda_2(D)$ |

Figure 5. Illustrative operating diagrams corresponding to cases (a) and (b) in Figure 2. The curves $\Gamma_i$, $i = 0\cdots9$, defined in Table 3, separate the operating plane $(D, S^0)$ into fifteen regions labeled $I_k, k = 0..14$. The existence and stability of equilibria $E_0$, $E_1$, $E_2^j$ and $E_3^j$ in the regions $J_0$, $J_1,\ldots,J_{14}$ of these diagrams are shown by Table 5.

which is LES. The region $J_2$ corresponds to the bi-stability of $E_0$ and $E_2^1$ while $E_2^2$ is unstable. The region $J_3$ corresponds to the case where equilibrium $E_1$ of exclusion of species $y$ is LES. The region $J_1 \cup J_6 \cup J_9$ corresponds to the case where equilibrium $E^1_1$ of exclusion of species $x$ is LES. The region $J_{10}$ corresponds to the bi-stability of $E_1$ and $E_2^1$ while $E_0$ and $E_2^2$ are unstable. The region $J_{12}$ corresponds to the bi-stability of $E_2^2$ and $E_2^2$ while $E_0$, $E_1$ and $E_2^2$ are unstable. Additionally, by Theorem 3.3, the curve $\Gamma_8$ (boundary between $J_{12}$ and $J_{11}$) corresponds to a Hopf bifurcation.
Table 5. Existence and stability of equilibria in the regions of the operating diagrams in Figures 5, 6 and 11.

When $\mathcal{S} > S^m_{14}$, the operating diagram in Figure 5(b) is divided into at most thirteen regions. Figure 5(b) shows that regions $J_0$, $J_1$, $J_3$, $J_6$, $J_9$, $J_{11}$ and $J_{12}$ are identical to those of the operating diagram in Figure 5(a) when $\mathcal{S} < S^m_{11}$. The operating diagram in Figure 5(b) shows the occurrence of six other regions $J_4$, $J_5$, $J_7$, $J_8$, $J_{13}$ and $J_{14}$, and the disappearance of two regions $J_2$ and $J_{10}$. The region $J_5 \cup J_8 \cup J_{13}$ corresponds to the bi-stability of $E_1$ and $E_{12}$. The region $J_4 \cup J_5 \cup J_{14}$ corresponds to the case where equilibrium $E_1$ of exclusion of species $y$ is LES. The region $J_{14}$ corresponds to the tri-stability of $E_1$, $E_2$ and $E_c$ while $E_0$, $E_2$ and $E_c$ are unstable. We claim that as we cross the boundary between regions $J_{14}$ and $J_{13}$, we observe a Hopf bifurcation and, in $J_{13}$, close to the boundary with $J_{14}$, a limit cycle appears.

5. Numerical simulations. In the following examples we consider the functions $f_1$ and $f_2$ given by

$$f_1(S) = \frac{m_1 S}{K_1 + S} \quad \text{and} \quad f_2(S) = \frac{m_2 S}{K_2 + S + S^2/K_3}, \quad (27)$$

and the biological parameters given below.

| Case | $m_1$ | $m_2$ | $K_1$ | $K_2$ | $K_3$ | $k$ | $\gamma$ | Figs |
|------|-------|-------|-------|-------|-------|-----|---------|------|
| 1    | 1.0   | 4.0   | 1.0   | 1.0   | 0.5   | 0.2 | 0.3     | 6, 7, 8, 9, 10 |
| 2    | 1.5   | 2.7   | 1.0   | 1.0   | 0.08  | 0.2 | 0.3     | 11, 12, 14, 15 |

Table 6. Biological parameters values used in the numerical computations shown in the figures.

Let us consider the biological parameters given in Table 6, Case 1, and plot the associated operating diagram in Figure 6.

Let us also consider $S^0 = 15$ and change $D$ from top to bottom, to obtain the following behavior.

5.1. Bi-stability and Hopf bifurcation of $E_c^2$. When we change the value of $D$ from $J_{10}$ to $J_{12}$, then $E_c^2$ appears and is stable, and in this region we have bi-stability between $E_c^2$ and $E_2$ (see Table 5). This is illustrated in Figure 8(a). If we transition to the region $J_{11}$ (by decreasing $D$), then $E_c^2$ is destabilized when crossing the curve $\Gamma_8$ (the green curve), which according to Theorem 3.3 gives rise to a limit cycle through a Hopf bifurcation (see [20]). Indeed, the Jacobian matrix
of the system at $E^2_0$ has two negative eigenvalues and one pair of complex-conjugate eigenvalues

$$\lambda_j(D) = \alpha(D) \pm i\beta(D), \quad j = 1, 2.$$ 

Decreasing the operating parameter $D$, this pair crosses the imaginary axis at the critical value $D = D_{crit} = F^{-1}_5(S^0 = 15) \approx 0.521403$ from negative half plane to positive half plane (see Figure 7), that is, it becomes purely imaginary for $D_{crit}$ such that $\alpha(D_{crit}) = 0$, with $\beta(D_{crit}) \neq 0$. The transversality condition

$$\frac{d\alpha}{dD}(D_{crit}) \neq 0$$

is clearly satisfied (this is obvious from Figure 7(b)). The bifurcation is super-critical since a unique stable limit cycle (see Figure 8(b)) bifurcates from the equilibrium $E^2_0$ (the first Lyapunov coefficient was calculated using Matcont and is negative $l_1(D_{crit}) \approx -0.00125$).

5.2. Occurrence of a homoclinic bifurcation. As we move down in $J_{11}$ (keeping $S^0 = 15$ fixed), we have bi-stability of $E^2_0$ and a limit cycle which is born out of Hopf bifurcation. The limit cycle gets larger (see Figure 9(a)) until the value $D = D_{hom} \approx 0.5081029$ (see Figure 6(b)) is reached where it disappears (see Figure 9(b)) via a homoclinic bifurcation when it collides with a homoclinic orbit to the saddle point $E_1$.

The limit cycle in Figure 9(a) seems to approach saddle points $E^2_0$ and $E_0$, which may suggests a heteroclinic bifurcation (if the limit cycle collides with a heteroclinic cycle connecting $E_0$, $E_1$ and $E^2_0$), so to exclude the possibility of the cycle bifurcation being heteroclinic. We plot the one parameter bifurcation diagram in Figure 10, which shows that at $D \approx D_{hom}$ the limit cycle touches $E_1$ but does not approach $E_0$ (see Figure 10(a)), and it does not approach $E^2_0$ (see Figure 10(b)).

5.3. Tri-stability. According to Table 5, region $J_{14}$ corresponds to the tri-stability of the coexistence equilibrium $E^2_0$, the $y$ species-free equilibrium $E_1$ and the $x$ species-free equilibrium $E^3_0$. For that we consider the biological parameters in Table 6, Case 2. The associated operating diagram is in Figure 11.
Figure 7. Hopf bifurcation. Biological values are in Table 6, Case 1, and $S^0 = 15$. (a): Variation of a pair of complex-conjugate eigenvalues. (b): The real part of the eigenvalues showing that its change of stability at $D = D_{\text{crit}} \approx 0.521403$ indicating a Hopf bifurcation.

Figure 8. (a): $(S^0, D) = (15, 0.53) \in J_{12}$. In this case we have bi-stability of $E^2_c$ and $E^1_c$. (b): $(S^0, D) = (15, 0.51) \in J_{11}$. In this case $E^2_c$ loses its stability through a super-critical Hopf bifurcation (see Figure 7) creating a stable limit cycle. We use the color codes; Green: initial conditions, Red: local attractors and Blue: unstable equilibria.

When $(D, S^0) = (0.26, 3.5)$, this corresponds to region $J_{14}$. In this case there is a tri-stability of equilibria $E^2_c$, $E^1_c$ and $E_1$ (see Figure 12(a)). Moving to region $J_{13}$ (by decreasing $D$ for example. We take $(D, S^0) = (0.25785, 3.5)$ makes $E^2_c$
Figure 9. Homoclinic bifurcation (a): \((S^0, D) = (15, 0.508105)\). After the Hopf bifurcation, the limit cycle gets larger. (b): \((S^0, D) = (15, 0.50)\). The limit cycle loses its stability (through homoclinic bifurcation) and the only attractor remaining is \(E_1\). We use the color codes, Green: initial conditions, Red: local attractors and Blue: unstable equilibria.

Figure 10. One parameter bifurcation diagram for the homoclinic bifurcation. We plot the projections of the \(\omega\)-limit set in variables \(\{S, y\}\) for \(D \in [0.5, 0.53]\), which reveals the emergence of limit cycle through a Hopf bifurcation and its disappearance through a homoclinic bifurcation. Solid line is for stable fixed point (dashed when unstable). H: Hopf bifurcation.

unstable through a super-critical Hopf bifurcation. Hence we get a tri-stability of equilibria \(E_2^1\), \(E_1\) and a limit cycle (see Figure 12(b)).

5.4. Saddle-node bifurcation. The transition from the region \(J_3\) to one of the regions \(J_8, J_{13}, J_{14}\) by crossing the curve \(\Gamma_9\), generates the appearance of equilibria \(E_2^1\), and \(E_2^2\) through a saddle-node bifurcation, also the transition from the region \(J_3\) to one of the regions \(J_{13}, J_{14}\), two other equilibria appear \((E_1^1, E_2^2)\) through a saddle-node bifurcation.
Figure 11. (a): Operating diagram corresponding to Table 6, Case 2. (b): A zoom of the operating diagram near regions $J_{13}$ and $J_{14}$.

Figure 12. Tri-stability (a): $(D, S^0) = (0.26, 3.5) \in J_{14}$ (see Figure 11(b)). In this case there is tri-stability of equilibria $E^c_2$, $E^1_2$ and $E_1$. (b): $(D, S^0) = (0.25785, 3.5) \in J_{13}$ (see Figure 11(b)). Tri-stability of equilibria $E^1_2$, $E_1$ and a stable limit cycle.

In Figure 13, we plot the one parameter bifurcation of $S$ in function of $D$ (we fix $S^0 = 5$) for equilibria $E^1_2$ and $E^2_2$ (see Figure 13(a)), and for equilibria $E^1_c$ and $E^2_c$ (see Figure 13(b)). We notice also in Figure 13(b) the appearance of a stable limit cycle (when $E^2_c$ undergoes a super-critical Hopf bifurcation). The limit cycle then undergoes a flip bifurcation (period doubling) which we will discuss in the next subsection.

5.5. Period doubling. Another kind of bifurcations of limit cycles that system (2) exhibits is the flip bifurcation (or period doubling). This bifurcation is associated with the appearance of multiplier $\mu = -1$ (see [20] for more details). In Figure
Figure 13. One parameter bifurcation diagram. Biological values are in Table 6 case 2, and $S^0 = 5$. (a): Saddle node bifurcation of $E^1_2$ and $E^2_2$. (b): Saddle node bifurcation of $E^1_c$ and $E^2_c$. Solid line is for stable fixed point; dashed when unstable. H: Hopf bifurcation. LP: Limit Point (Saddle-node). PD: Period Doubling.

We plot bifurcation diagrams related to period doubling. Figure 14(a) is a one parameter bifurcation diagram where we fix $S^0 = 5$ and plot the projection of the limit cycle on the $(S,x)$-space as a function of $D$. Figure 14(b) is a two parameters flip bifurcation diagram which shows that when we fix $S^0 = 5$, then we obtain two period doubling points $D_1 = 0.24705$ and $D_2 = 0.24841$. We plot the limit cycle in the cases $(D, S^0) = (0.24845, 5)$ and $(D, S^0) = (0.24835, 5)$ in Figure 15.

Figure 14. Bifurcation diagrams of the limit cycle. (a) Continuation of the limit cycle (we fix $S^0 = 5$ and plot the projection of the limit cycle on the $(S,x)$ space as a function of $D$). (b) Two parameter bifurcation of the limit cycle, the curves (in blue) correspond to the period doubling (flip bifurcation). Matcont was used to produce both of the diagrams. PD: Period Doubling, LPC: Limit Point Cycle.
6. Conclusion. In this work, we have extended model (2) of a competition in a chemostat in presence of internal inhibitor presented in [19], by considering the case when the species producing the inhibitor is itself inhibited by the substrate and considering general growth functions. Our mathematical analysis of the model has revealed several possible behaviors. Theorem 3.1 provides a complete theoretical description of the outcome of competition.

In contrast with the model with substrate inhibition (see [15, page. 84]), model (2) studied in [19] does have a positive equilibrium which is unstable when it exists, and thus coexistence is not possible (at least not as a steady state). In this paper we have considered the combination of allelopathy (producing a toxin) and substrate inhibition, and we showed that the coexistence is possible either as a steady state or sustained oscillations, even more surprising was the very rich dynamics including multi-stability (bi-stability and tri-stability), Hopf, homoclinic and flip bifurcations.

In order to make the results useful for engineers, we gave a description of the outcome of competition with respect to the operating parameters, knowing that the study of bifurcations according to the operating parameters $D$ and $S^0$ is the most meaningful one for the laboratory model, since one can easily vary these parameters.

Since the condition of instability is polynomials in the operating parameters $D$ and $S^0$ as shown in Section 3.4, we reduced the problem of exploring all the two dimensional set of operating parameters to the determination of real valued function of only one variable, the dilution rate $D$ (see Theorem 3.2). This problem is easily solved numerically.

By using the operating diagram, we showed how the system behaves when we vary the operating parameters. In the operating diagrams shown in Figures 5, 6 and 11, curves $\Gamma_i$, $i = 1..9$, partition the positive $(S^0, D)$-plane to regions $J_i$, $i = 0..14$, of existence and stability of different equilibria, among which regions $J_i$, $i = 11..14$, present most interesting (possibility of coexistence) and rich dynamics. In region $J_{12}$, all equilibria (except for $E^1_c$) exist and we have bi-stability of $E^1_c$ and $E^2_c$. As we move to region $J_{11}$, $E^2_c$ is destabilized, creating a limit cycle through a Hopf bifurcation when crossing curve $\Gamma_8$ (see Theorem 3.3) leading to bi-stability of a
limit cycle and equilibrium $E^1_2$. Then the limit cycle may lose its stability through a homoclinic bifurcation (see Subsection 5.2) when it collides with a homoclinic orbit of equilibrium $E_1$. In region $J_{14}$, all equilibria exist and we have tri-stability of $E_1$, $E^1_2$ and $E^2_2$, which means that choosing the operating parameters $D, S^0$ in this region, a variety of behaviors are possible. Now, if we cross $J_8$ to region $J_{13}$, we obtain tri-stability of $E_1$, $E^1_2$ and a limit cycle (borne out of Hopf bifurcation of equilibrium $E^2_2$). If we decrease $D$ (keeping $S^0$ fixed), the limit cycle exhibits a flip bifurcation (period doubling).

In this model we have considered the substrate inhibition on the species producing an allelopathic agent (toxin). One can also consider the model where one species is under double inhibition from a toxin and the substrate. This will be treated in a future work.

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Appendix A. Proofs.

A.1. Proof of Proposition 1. Equilibria of (2) are the solutions of the set of equations (7).

- At equilibrium $E_0$, one has $x = 0$ and $y = 0$. From the first and last equations of (7), it follows that $S = S^0$ and $p = 0$. Thus, the washout equilibrium $E_0 = (S^0, 0, 0, 0)$ always exists.
- The components $S = S_1$, $x = x_1$ and $p = p_1$ of the boundary equilibrium $E_1$ are the solutions of (7) with $x > 0$ and $y = 0$; that is $p_1 = 0$ and

\[(S^0 - S_1)D = f_1(S_1)x_1 \quad (S^0 - S_1)p_1 = D. \quad \]

Therefore, from (29) we have $S_1 = \lambda_1$, where $\lambda_1$ is given by (4). Then, using (28) we deduce that $x_1 = S^0 - \lambda_1$. This equilibrium exists if and only if $x_1 > 0$; that is $\lambda_1 < S^0$.
- The components $S = S_2$, $y = y_2$ and $p = p_2$ of the boundary equilibrium $E_2$ are the solutions of (7) with $x = 0$ and $y > 0$; that is

\[(S^0 - S_2)D = f_2(S_2)y_2 \quad (1 - k)f_2(S_2) = D \quad k f_2(S_2)y_2 = Dp_2. \quad \]

From hypothesis (H2), equation (31) has two positive solutions $\lambda_2$ and $\mu_2$ (with $\lambda_2 < \mu_2$) or no solution and we then put $\lambda_2 = +\infty$ and $\mu_2 = +\infty$. Using (30), we deduce that

\[y^1_2 = (S^0 - \lambda_2)(1 - k) \quad \text{and} \quad y^2_2 = (S^0 - \mu_2)(1 - k). \quad \]

As a consequence of equations (31), (32) and (33), we have

\[p^1_2 = k(S^0 - \lambda_2) \quad \text{and} \quad p^2_2 = k(S^0 - \mu_2). \quad \]

Thus, one can conclude that equilibrium $E^1_2$ exists if and only if $y^1_2 > 0$ and $p^1_2 > 0$; that is $\lambda_2 < S^0$, and $E^2_2$ exists if and only if $y^2_2 > 0$ and $p^2_2 > 0$; that is $\mu_2 < S^0$.
- The components of $E_c = (S_c, x_c, y_c, p_c)$, a positive equilibrium of (2), are the
solutions of (7) with \( x > 0 \) and \( y > 0 \). Hence, \((1 - k)f_2(S_c) = D\); that is \( S_{c_1} = \lambda_2 \) and \( S_{c_2} = \mu_2 \), and for \( j = 1, 2 \)
\[
(S^0 - S_{c_j})D = f_1(S_{c_j})x_{c_j} + f_2(S_{c_j})y_{c_j} 
\]
\[
f_1(S_{c_j}) - D = \gamma p_{c_j} 
\]
\[
kf_2(S_{c_j})y_{c_j} = Dp_{c_j}. 
\]
From (36) we have \( p_{c_j} = \frac{1}{\gamma}(f_1(S_{c_j}) - D) \), from (37) we have \( y_{c_j} = \frac{1 - k}{\gamma}(f_1(S_{c_j}) - D) \) and from (35) we have \( x_{c_j} = \frac{D}{f_1(S_{c_j})} \left( S^0 - S_{c_j} - \frac{1}{1 - k}y_{c_j} \right) \).

Therefore \( p_{c_j}, y_{c_j} \) and \( x_{c_j} \) are given by (8) and (9). Hence, a positive equilibrium \( E^j_c, j = 1, 2, \) of system (2), if it exists, is unique.

Let us study conditions of existence of \( E^j_c \). We first note that
\[
f_1(S_{c_j})x_{c_j} + \frac{D}{1 - k}y_{c_j} = D(S^0 - S_{c_j}) > 0 \iff S_{c_j} < S^0 \iff \lambda_2 < S^0 \text{ and } \mu_2 < S^0. 
\]

Moreover, we have
\[
y_{c_j} > 0 \iff f_1(S_{c_j}) > D \iff S_{c_j} > \lambda_1, \tag{39}
\]
\[
x_{c_j} > 0 \iff S^0 - S_{c_j} - \frac{1}{1 - k}y_{c_j} > 0 \iff f_1(S_{c_j}) < D + \gamma k(S^0 - S_{c_j}). \tag{40}
\]
\[
\iff g(S_{c_j}) < 0 \iff S_{c_j} < \hat{\lambda}. \tag{41}
\]
Taking into account (38), from (39) and (41), we conclude finally that \( E^j_c \) exists if and only if \( S_{c_j}(D) < S^0 \) and \( \lambda_1(D) < S_{c_j}(D) < \hat{\lambda}(D, S^0) \).

A.2. Proof of Proposition 2. • At washout equilibrium \( E_0 \), the matrix \( M \) defined by (11) is
\[
M_0 = \begin{bmatrix} -D & -f_1(S^0) & -f_2(S^0) \\ 0 & f_1(S^0) - D & 0 \\ 0 & 0 & (1 - k)f_2(S^0) - D \end{bmatrix}. 
\]

The eigenvalues of \( M_0 \) are: \(-D, f_1(S^0) - D \) and \((1 - k)f_2(S^0) - D\). Then, equilibrium \( E_0 \) is LES if and only if \( f_1(S^0) < D \) and \((1 - k)f_2(S^0) - D < D\).

• Suppose that equilibrium \( E_1 \) exists; that is \( \lambda_1 < S^0 \). At \( E_1 \) the matrix \( M \) defined by (11) is
\[
M_1 = \begin{bmatrix} -D - (S^0 - \lambda_1)f'_1(\lambda_1) & -D & -f_2(\lambda_1) \\ 0 & (S^0 - \lambda_1)f'_1(\lambda_1) & 0 \\ 0 & 0 & (1 - k)f_2(\lambda_1) - D \end{bmatrix}, 
\]

The eigenvalues of \( M_1 \) are: \(-D, -(S^0 - \lambda_1)f'_1(\lambda_1) < 0 \) and \((1 - k)f_2(\lambda_1) - D \). Since \( E_1 \) has three negative eigenvalues, it has at least three-dimensional stable manifold. Moreover, \( E_1 \) is LES if and only if \((1 - k)f_2(\lambda_1) < D \), or equivalently, \( \lambda_1 < \lambda_2 \) or \( \lambda_1 > \mu_2 \).

• Suppose that equilibria \( E^j_2, j = 1, 2, \) exist; that is \( \lambda_2 < S^0 \) and \( \mu_2 < S^0 \). At \( E^j_2 \) the matrix \( M \) defined by (11) is
\[
M_2 = \begin{bmatrix} -D - y^j_2f'_2(S^j_2) & -f_1(S^j_2) & -D \\ 0 & f_1(S^j_2) - D - \frac{k\gamma}{1 - k}y^j_2 & 0 \\ (1 - k)y^j_2f'_2(S^j_2) & 0 & 0 \end{bmatrix}, 
\]
Then, \( f_1(S^2) - D - \frac{k\gamma}{1-k} y_2^2 \) is an eigenvalue of \( M_2 \). The two other eigenvalues of \( M_2 \) are the eigenvalues of matrix

\[
A = \begin{bmatrix}
-D - \frac{k\gamma}{1-k} y_2^2 & -D \\
(1-k) y_2^2 & 0
\end{bmatrix}.
\]

At \( E_2^1 \), we have \( \det(A) > 0 \) and \( tr(A) < 0 \) since \( f_2'(S_2^2) = f_2'(\lambda_2) > 0 \). Thus, the two eigenvalues of \( A \) have negative real parts. Therefore, \( E_2^1 \) is LES if and only if \( f_1(\lambda_2) < D + \gamma k(S^0 - \lambda_2) \), or equivalently, \( \lambda_2 < \hat{\lambda} \).

At \( E_2^2 \), we have \( \det(A) < 0 \) since \( f_2'(S_2^2) = f_2'(\mu_2) < 0 \). Thus, the two eigenvalues of \( A \) have opposite signs. Consequently, \( E_2^2 \) is unstable.

- At \( E_c^1 \), the matrix \( M \) defined by (11) takes the form

\[
M_c = \begin{bmatrix}
m_{11} & m_{12} & m_{13} \\
m_{21} & 0 & m_{23} \\
m_{31} & 0 & 0
\end{bmatrix},
\]

where

\[
m_{11} = -D - x_{c_1} f_1'(S_{c_1}) - y_{c_1} f_2'(S_{c_1}), \quad m_{12} = -f_1(S_{c_1}), \quad m_{13} = -\frac{D}{1-k},
\]

\[
m_{21} = x_{c_1} f_1'(S_{c_1}), \quad m_{23} = -\frac{k\gamma}{1-k} x_{c_1}, \quad m_{31} = (1-k) y_{c_1} f_2'(S_{c_1}).
\]

At \( E_c^1 \), we have \( \det(M_c) = m_{11} m_{23} m_{31} > 0 \) because \( f_2'(S_{c_1}) = f_2'(\lambda_2) > 0 \). Thus, \( E_c^1 \) is unstable. Since \( tr(M_c) = m_{11} < 0 \), \( E_c^1 \) is unstable with a two-dimensional stable manifold.

At \( E_c^2 \), the characteristic polynomial of \( M_c \) is given by

\[
\lambda^3 + A \lambda^2 + B \lambda + C = 0,
\]

with

\[
a = D + f_1'(\mu_2) x_{c_2} + f_2'(\mu_2) y_{c_2}, \quad b = f_1(\mu_2) f_1'(\mu_2) x_{c_2} + D f_2'(\mu_2) y_{c_2} \quad \text{and} \quad c = -\gamma k f_1(\mu_2) f_2'(\mu_2) x_{c_2} y_{c_2}.
\]

Since \( f_2'(\mu_2) < 0 \), we have \( C > 0 \) and by the Routh-Hurwitz criterion, \( E_c \) is LES if and only if \( A > 0 \) and \( AB > C \), that is to say (12) holds.

\[\square\]

A.3. **Proof of Lemma 1.** Using (5), (8) and the definition (16), we have

\[
x_{c_1}(D, S^0) > 0 \iff S^0 > \lambda_2(D) + \frac{1}{1-k} y_{c_1}(D)
\]

\[
\iff f_1(\lambda_2(D)) < D + \gamma k(S^0 - \lambda_2(D))
\]

\[
\iff \lambda_2(D) < \hat{\lambda}(D, S^0)
\]

\[
\iff S^0 > F_1(D).
\]

Similarly, the second case could be checked easily. \[\square\]

A.4. **Proof of Lemma 2.** Using definitions (9) and (16) of \( y_{c_2} \) and \( y_{c_2}^2 \), respectively, one has

\[
F_2(D) = \frac{1}{1-k} y_{c_2}(D) + \mu_2(D).
\]  (42)
On the other hand, using (9), (18) and (20), we have
\[
S^0 < F_6(D) \iff S^0 < \frac{f_1(\mu_2(D))}{D} x_0(D) + F_2(D) \iff S^0 < \frac{f_1(\mu_2(D))}{D} x_0(D) + \frac{y_{c_2}}{1 - \mu} + \mu_2(D)
\]
\[
\iff \frac{D}{f_1(\mu_2)} \left( S^0 - \mu_2 - \frac{y_{c_2}}{1 - \mu} \right) < x_0(D) \iff x_{c_2}(D, S^0) < x_0(D)
\]
\[
\iff x_{c_2}(D, S^0) < \frac{-1}{f_1(\mu_2)} (D + f'_2(\mu_2)y_{c_2}) \iff A(D, S^0) < 0.
\]
Therefore, equilibrium \( E^0_c \) is unstable as long as it exists with \( S^0 < F_6(D) \), since condition \( A > 0 \) of the Routh–Hurwitz criterion (12) is unfulfilled.

A.5. **Proof of Lemma 3.** Let \( D \in I_3 \); that is \( D + f'_2(\mu_2)y_{c_2}(D) < 0 \). Using definition (22) of \( a_0(D) \) and \( a_1(D) \), one sees that \( a_0 > 0 \) and \( a_1 < 0 \). Now, from (22), \( a_1(D) \) can be written as follows:
\[
a_1 = c_1 + c_2 + c_3,
\]
where \( c_1 = f'_1(\mu_2)f_1(\mu_2)[D + f'_2(\mu_2)y_{c_2}] < 0 \), \( c_2 = Df'_1(\mu_2)f'_2(\mu_2)y_{c_2} < 0 \) and \( c_3 = \gamma k_f f_1(\mu_2)f'_2(\mu_2)y_{c_2} < 0 \).
By using expressions (22) of \( a_0(D) \) and \( a_2(D) \), it follows that
\[
a_0a_2 = D(f'_1(\mu_2))^2 f_1(\mu_2)f'_2(\mu_2)y_{c_2}[D + f'_2(\mu_2)y_{c_2}] = c_1c_2,
\]
so that, by using the fact that \( c_i < 0 \), \( i = 1, 3 \), we obtain
\[
\Delta = a_1^2 - 4a_0a_2 = c_1^2 + c_2^2 + c_3^2 + 2c_1c_2 + 2c_1c_3 + 2c_2c_3 - 4a_0a_2
\]
\[
= c_1^2 + c_2^2 + c_3^2 + 2c_1c_3 + 2c_2c_3 - 2c_1c_2
\]
\[
= (c_1 - c_2)^2 + c_3^2 + 2c_1c_3 + 2c_2c_3 > 0.
\]
Let \( D \in I_4 \); that is \( D + f'_2(\mu_2)y_{c_2}(D) > 0 \). Thus, \( a_0(D) < 0 \) and from expression (23) of \( \Delta \) one has \( \Delta(D) > 0 \). If \( D \in I_5 \); that is \( D + f'_2(\mu_2)y_{c_2}(D) = 0 \), then \( a_0(D) = 0 \) and from (23) one has \( \Delta(D) = (a_1(D))^2 > 0 \).

A.6. **Proof of Theorem 3.2.** Suppose that equilibrium \( E^0_c \) exists; that is \( D \in I_{c_2} \) and \( S^0 > F_2(D) \). The roots \( x_1(D) \) and \( x_2(D) \) of \( F_3 \), given by (24), exist and are positive or of opposite signs. \( F_3 < 0 \) if and only if \( x_{c_2} \) is between the roots; that is,
\[
\max(0, x_1(D)) < x_{c_2} < x_2(D).
\]
Using (9) and (42) we have \( x_{c_2} = \frac{D}{f_1(\mu_2(D))}(S^0 - F_2(D)) \). Therefore, (43) is equivalent to
\[
F_4(D) < S^0 < F_5(D),
\]
where \( F_4(D) \) and \( F_5(D) \) are defined by (25).
• If \( D \in I_4 \cup I_5 \) then \( A(D, S^0) > 0 \) for all operating parameters \( D \) and \( S^0 \) (see Remark 1). Therefore, \( E^0_c \) is unstable if and only if \( F_3 < 0 \), or equivalently, \( F_4(D) = F_2(D) < S^0 < F_5(D) \).
• If \( D \in I_3 \), using Lemma 2 we have: \( A(D, S^0) < 0 \) if and only if
\[
S^0 < F_6(D).
\]
Taking into account (26), from (44) and (45), we conclude finally that \( E^0_c \) is unstable if and only if \( S^0 < F_6(D) \).
A.7. **Proof of Theorem 3.3.** To prove the occurrence of the Hopf bifurcation (see [20]), let us consider the characteristic polynomial at $E_2^c$ which takes the form

$$F(\lambda) = (\lambda + D)(\lambda^3 + A\lambda^2 + B\lambda + C) = (\lambda + D)P(\lambda).$$

Since $D > 0$, then one eigenvalue is $\lambda_1 = -D$ which is negative, and the fact that $C > 0$ implies the existence of another negative eigenvalue $\lambda_3$ (because $P(0) = C > 0$, and $\lim_{\lambda \to -\infty} \lambda P(\lambda) = -\infty$), and because $D, C \neq 0$, $F$ cannot have $\lambda = 0$ as a root. The preceding argument shows that the only way that $E_2^c$ is destabilized is for the two complex conjugate eigenvalues $\lambda_j(D) = \alpha(D) \pm i\beta(D), j = 1, 2$, to cross the imaginary axis (because of the continuity of coefficients of $P$ with respect to the parameters), which is the case when

$$F_3(D, S^0) = AB - C = 0, \quad \text{i.e.} \quad S^0 = F_5(D).$$

Actually, in that case we have

$$P(\lambda) = \lambda^3 + A\lambda^2 + B\lambda + C = \lambda^3 + A\lambda^2 + B\lambda + AB = (\lambda + A)(\lambda^2 + B).$$

Hence the polynomial $P$ has a simple pair of purely imaginary eigenvalues $\pm i\sqrt{B}$ and the negative real value $-A$.

To have a Hopf bifurcation we need the transversality condition to be verified, i.e. the derivative of the real part of the eigenvalue with respect to the bifurcation parameter evaluated at the critical value when the real parts are zero is non-zero. For that we need to guarantee that the derivative of $F_3$ with respect to $S^0$ is not equal to zero when $F_3(D, S^0) = 0$ (see [30]).

As $F_3(D, S^0) = a_2 x_{c_2}^2 + a_1 x_{c_2} + a_0$, where only $x_{c_2}$ is depending on $S^0$ (strictly increasing in $S^0$), it suffices to show that $x_{c_2}$ is not a local minimum of the polynomial with the coefficients $a_i, i = 0..2$, which is the case since $\Delta > 0$ when $D \in I_{c_2}$ (see Lemma 3).

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E-mail address: dellal.m48@univ-tiaret.dz
E-mail address: bachir.bar1@gmail.com
E-mail address: m.lakrib@univ-sba.dz