Quantitave Analysis of a Chemostat Model with Allelopathy and Substrate Inhibition.

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Abstract

In this work, we consider a model of two microbial species in a chemostat in which one of the competitors can produce a toxin against the other competitor, and is itself inhibited by the substrate. The existence and stability conditions of all steady states of the reduced model in the plane are determined according to the operating parameters, it is well known that the model can have a unique positive equilibrium which is unstable as long as it exists. By including both monotone and non-monotone growth functions.This general model exhibits a rich behavior with the coexistence of two microbial species, the multi-stability, the occurrence of stable limit cycles through a super-critical Hopf bifurcations and the saddle-node bifurcations of limit cycles, the operating diagram describes the asymptotic behavior of this model by varying the operating parameters and illustrates the effect of the inhibition on the emergence of the coexistence region of the species.

1 Introduction

We consider the following model:

$$\begin{cases} S' = (S^0 - S)D - f(p)f_1(S)\dfrac{x}{\gamma_1} - f_2(S)\dfrac{y}{\gamma_2} \\ x' = [f(p)f_1(S) - D]x \\ y' = [(1-k)f_2(S) - D]y \\ p' = kf_2(S)y - Dp \end{cases} \quad (1.1)$$

In system (1.1), the parameter $0 \le k < 1$ represents the fraction of potential growth allocated to producing the toxin. The operating parameters $S^0 > 0$ and $D > 0$ denote, respectively, the input concentration of the nutrient and the dilution rate of the chemostat, all of which are assumed to be constant and are under the control of the experimenter; f_1 and f_2 are the growth functions of the competitors and γ_1, γ_2 the yield constants. The function f represents the degree of inhibition of p on the growth rate of x.

This model was considered by Hsu and Waltman [5] when

$$f_1(S) = \frac{m_1 S}{a_1 + S}, \quad f_2(S) = \frac{m_2 S}{a_2 + S}, \quad f(p) = e^{-\mu p}, \quad (1.2)$$

We consider the general model (1.1) without restricting ourselves to the special. We suppose only that f_i, $i = 1, 2$ and f, in system (1.1) are $\mathcal{C}^1$functions satisfying the following conditions:

H1: $f(0) = 0, f_1(+\infty) = m_1$ and $f_1'(S) > 0$ for all $S > 0$.

H2: $f_2(0) = 0$,$f_1(+\infty) = 0$ and there exists $S^m > 0$ such that $f_2'(S) > 0$ for $0 \le S \le S^m$ and $f_2'(S) > 0$ for $S > S^m$.

H3: $f(0) = 1$, $f(p) \ge 0$ and $f'(p) < 0$ for all $p \ge 0$, $\lim_{p \to +\infty} f(p) = 0$.

Proposition 1.1. for non-negative initial conditions, all solutions of system (1.1) are bounded and remain non-negative for all $t \ge 0$. Moreover,the set

$$\Omega = \left\{(S, x, y, p) \in \mathbb{R}^4_+ : yp = cy, \ c = k/(1-k), \ S + x + y + p = S^0\right\}$$

is positively invariant and is a global attractor for system (1.1).

To study the local asymptotic behavior of system (1.1) it is convenient to use change variable $\Sigma = S + x + y + p$ and $\Gamma = p - cy$ that reveal the cascade structure. Written in the variables (σ, Γ, x, y), system (1.1) becomes

$$\begin{cases} \Sigma' = -D(\Sigma - S^0) \\ \Gamma' = -D\Gamma \\ x' = [f(\Gamma + cy)f_1(\Sigma - \Gamma - x - (1+c)y) - D]x \\ y' = [(1-k)f_2(\Sigma - \Gamma - x - (1+c)y) - D]y. \end{cases} \quad (1.3)$$

Thus, the fourth-order system (1.3) can be reduced (for the local stability) to the two-dimensional system which is simply the projection on the plane (x, y),

$$\begin{cases} x' = [f(cy)f_1(S^0 - x - (1+c)y) - D]x \\ y' = [(1-k)f_2(S^0 - x - (1+c)y) - D]y \end{cases} \quad (1.4)$$

2 Existence of the equilibrium

Proposition 2.1. Assume that assumptions (H1),(H2) and (H3) hold. System (1.4) has at most six equilibrium:

- The washout equilibrium $E_0 = (0; 0)$, that always exists..
- The equilibrium $E_1 = (S^0 - \lambda, 0)$ of extinction of species y. E_1 exists if and only if $\lambda_1 < S^0$.
- The equilibrium $E_2^1 = (0, (S^0 - \lambda_2)(1-k))$ of extinction of species x. E_2^1 exists if and only if $\lambda_2 < S^0$.
- The equilibrium $E_2^2 = (0, (S^0 - \mu_2)(1-k))$ of extinction of species x. E_2^2 exists if and only if $\mu_2 < S^0$.
- The positive equilibrium $E_c^1 = (x_{c_1}, y_{c_1})$, where x_{c_1} and y_{c_1} are given by

$$y_{c_1} = \frac{1-k}{k} f^{-1}\left(\frac{D}{f_1(\lambda_2)}\right) \ \textit{and} \ x_{c_1} = S^0 - \lambda_2 - (1+c)y_{c_1}.$$

E_c^1 exists if and only if $\lambda_1 < S^0$ and $S^0 > F_1(D)$ with

$$F_1(D) = \lambda_2(D)\frac{1}{k}f^{-1}\left(\frac{D}{f_1(\lambda_2)}\right).$$

- The positive equilibrium $E_c^2 = (x_{c_2}, y_{c_2})$, where x_{c_2} and y_{c_2} are given by

$$y_{c_2} = \frac{1-k}{k} f^{-1}\left(\frac{D}{f_1(\mu_2)}\right) \ \textit{and} \ x_{c_2} = S^0 - \mu_2 - (1+c)y_{c_2}.$$

E_c^2 exists if and only if $\lambda_1 < S^0$ and $S^0 > F_2(D)$ with

$$F_2(D) = \mu_2(D)\frac{1}{k}f^{-1}\left(\frac{D}{f_1(\mu_2)}\right).$$

3 Local asymptotic stability of the equilibrium

In this section, we focus on the study of local asymptotic stability of each equilibrium of system (1.4). The local stability of the equilibrium points is then summarized in the following table:

Éq	Existence	stability condition
E_0	Always	$f_1(S^0) < D$ & $(1-K)f_2(S^0) < D$
E_1	$S^0 > \lambda_1(D)$	$(1-k)f_2(\lambda_1) < D$
E_2^1	$S^0 > \lambda_2(D)$	$S^0 > F_1(D)$
E_2^2	$S^0 > \mu_2(D)$	Unstable if it exists
E_c^1	$\lambda_1(D) < S^0$ & $S^0 > F_1(D)$	Unstable if it exists
E_c^2	$\lambda_1(D) < S^0$ & $S^0 > F_2(D)$	$F_3(D, S^0) > 0$

Table 1: Local stability of the equilibrium points

Curves Γ_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_2^1 exists
$\Gamma_3 = \{(D, S^0) : S^0 = \mu_2(D)\}$	Is the border to which E_2^2 exists
$\Gamma_4 = \{(D, S^0) : \lambda_1(D) = \lambda_2(D), \ S^0 > \lambda_1(D)\}$	IS border to which E_1 is stable and at the same E_c^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 unstable and at the same time E_c^2 exists
$\Gamma_6 = \{(D, S^0) : S^0 = F_1(D), S^0 > \lambda_2(D)\}$	Is the border to which E_2^1 is stable and at the same time E_c^1 exists
$\Gamma_7 = \{(D, S^0) : S^0 = F_2(D), S^0 > \mu_2(D)\}$	Is the border to which E_c^2 exists
$\Gamma_8 = \{(D, S^0) : S^0 = F_5(D)\}$	Is border to which E_c^2 is stable
$\Gamma_9 = \{(D, S^0) : \lambda_2(D) = \mu_2(D), S^0 > \lambda_2(D)\}$	Horizontal line $D = (1-k)f_2(S_2^m)$

Table 2: Definitions of the curves Γ_i, $i = 1...9$, in the operating diagram.

Théorème 3.1. (Hopf bifurcation). The positive equilibrium E_c^2 undergoes a simple Hopf bifurcation when crossing the curve $S^0 = F_5(D)$.

4 Operating diagram

The operating diagram describes the long-term behavior of the system as the operating parameters D and S^0 vary. The boundary curves Γ_i delimit regions in the (D, S^0) plane where bifurcations occur and the number or stability of steady states changes. These curves divide the plane into up to fifteen regions J_k, each defined by inequalities between $\lambda_1(D)$, $\lambda_2(D)$, $\mu_2(D)$, and $F_1(D)$. Notice that the curve of function $D = (1-k)f_2(S^0)$ is simply the union of the graphs of functions $S^0 = \lambda_2(D)$ and $S^0 = \mu_2(D)$, so

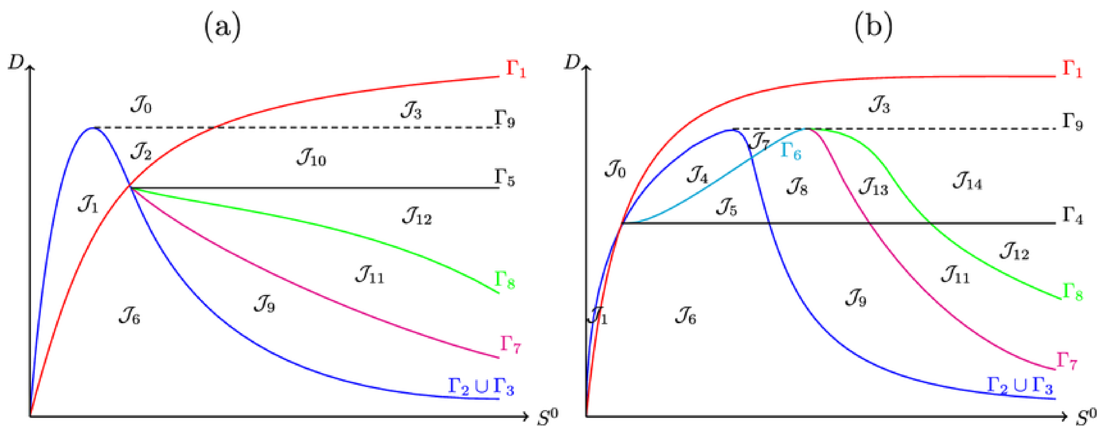
$$\Gamma_2 \cup \Gamma_3 = \{(D, S^0) : D = (1-k)f_2(S^0)\}.$$

the curves Γ_i, $i = 1...9$, separate the operating plane (D, S^0) into at most fifteen regions $\mathcal{J}_k$, $k = 0...14$, we have:

Regions	Definition
$\mathcal{J}_0$	$S^0 < \lambda_1(D)$ et $S^0 < \lambda_2(D)$
$\mathcal{J}_1$	$S^0 < \lambda_1(D)$ et $\lambda_2(D) < S^0 < \mu_2(D)$
$\mathcal{J}_2$	$S^0 < \lambda_1(D)$ et $S^0 > \mu_2(D)$
$\mathcal{J}_3$	$S^0 > \lambda_1(D)$ et $S^0 < \lambda_2(D)$
$\mathcal{J}_4$	$S^0 > \lambda_1(D)$, $\lambda_2(D) < S^0 < \mu_2(D)$ et $S^0 < F_1(D)$
$\mathcal{J}_5$	$S^0 > \lambda_1(D)$, $\lambda_2(D) < S^0 < \mu_2(D)$, $S^0 > F_1(D)$ et $\lambda_1(D) < \lambda_2(D)$
$\mathcal{J}_6$	$S^0 > \lambda_1(D)$, $\lambda_2(D) < S^0 < \mu_2(D)$, $S^0 > F_1(D)$ et $\lambda_2(D) < \lambda_1(D)$
$\mathcal{J}_7$	$S^0 > \lambda_1(D)$, $S^0 > \mu_2(D)$ et $S^0 < F_1(D)$
$\mathcal{J}_8$	$S^0 > \lambda_1(D)$, $S^0 > \mu_2(D)$, $F_1(D) < S^0 < F_2(D)$ et $\lambda_1(D) < \lambda_2(D)$
$\mathcal{J}_9$	$S^0 > \lambda_1(D)$, $S^0 > \mu_2(D)$, $F_1(D) < S^0 < F_2(D)$ et $\lambda_2(D) < \lambda_1(D)$
$\mathcal{J}_{10}$	$S^0 > \lambda_1(D)$, $S^0 > \mu_2(D)$ et $\lambda_1(D) > \mu_2(D)$
$\mathcal{J}_{11}$	$S^0 > \lambda_1(D)$, $S^0 > \mu_2(D)$, $S^0 > F_2(D)$, $S^0 < F_5(D)$ et $\lambda_2(D) < \lambda_1(D)$
$\mathcal{J}_{12}$	$S^0 > \lambda_1(D)$, $S^0 > \mu_2(D)$, $S^0 > F_2(D)$, $S^0 > F_5(D)$ et $\lambda_2(D) < \lambda_1(D)$
$\mathcal{J}_{13}$	$S^0 > \lambda_1(D)$, $S^0 > \mu_2(D)$, $S^0 > F_2(D)$, $S^0 < F_5(D)$ et $\lambda_1(D) < \lambda_2(D)$
$\mathcal{J}_{14}$	$S^0 > \lambda_1(D)$, $S^0 > \mu_2(D)$, $S^0 > F_2(D)$, $S^0 > F_5(D)$ et $\lambda_1(D) < \lambda_2(D)$

Table 3: Definitions of the regions $\mathcal{J}_k$, $k = 0...14$, in the operating diagram.

Figure 1: operating diagrams in the plane (S^0, D) .



Régions	$\mathcal{J}_0$	$\mathcal{J}_1$	$\mathcal{J}_2$	$\mathcal{J}_3$	$\mathcal{J}_4$	$\mathcal{J}_5$	$\mathcal{J}_6$	$\mathcal{J}_7$	$\mathcal{J}_8$	$\mathcal{J}_9$	$\mathcal{J}_{10}$	$\mathcal{J}_{11}$	$\mathcal{J}_{12}$	$\mathcal{J}_{13}$	$\mathcal{J}_{14}$
E_0	S	U	S	U	U	U	U	U	U	U	U	U	U	U	U
E_1				S	S	S	U	S	S	U	S	U	U	S	S
E_2^1		S	S		U	S	S	U	S	S	S	S	S	S	S
E_2^2			U					U	U	U	U	U	U	U	U
E_c^1						U			U					U	U
E_c^2												U	S	U	S

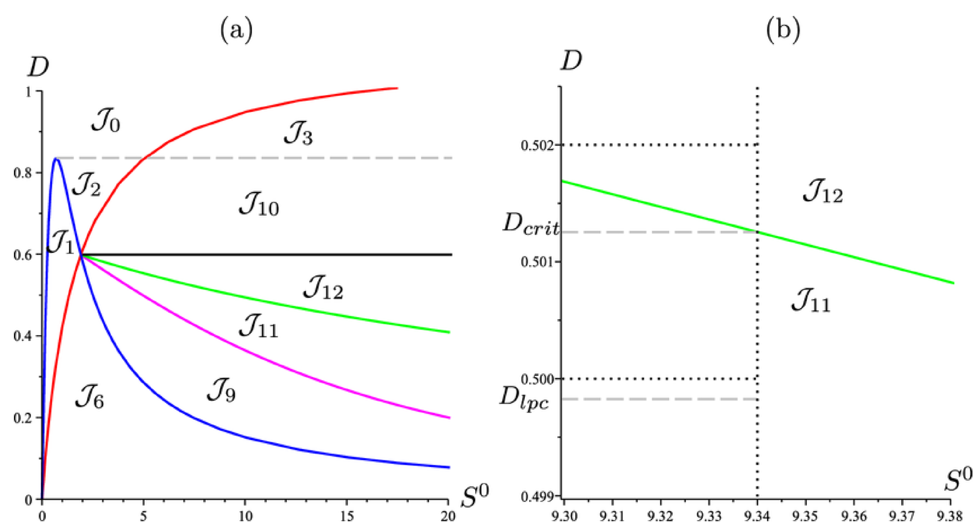
Table 4: Existence and stability of equilibria in the regions of the operating diagram.

4.1 Illustrative Examples

we consider model (1.4) with f, f_1 and f_2 given par 1.2 and the values of the biological parameters: $m_1 = 1$, $a_1 = 1.6$, $m_2 = 4$, $a_2 = 1.0$, $K = 0.5$, $k = 0.2$, $\mu = 0.6$.

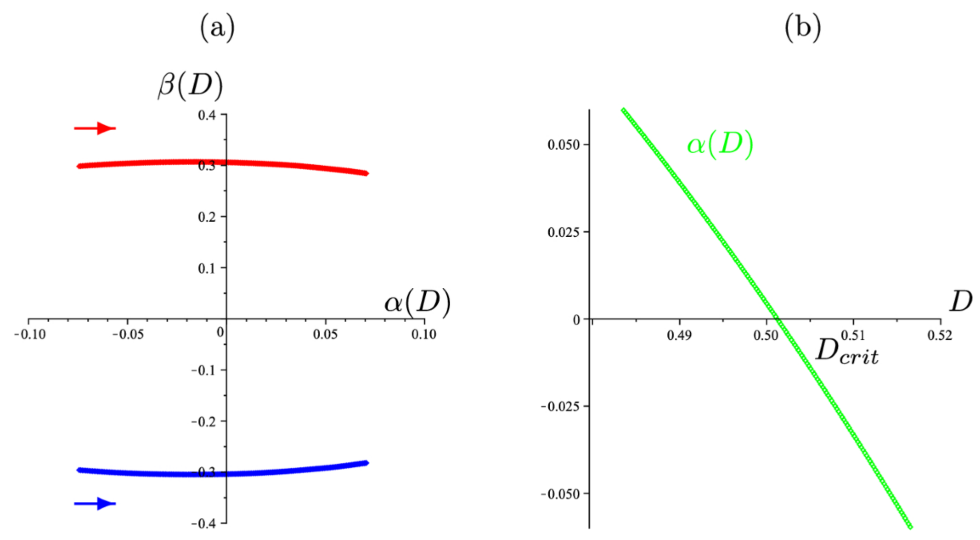
In order to show that the positive steady state E_c^2 can change stability through a Hopf bifurcation with emergence limit cycle by the passage the region.

Figure 2: operating diagrams with biological parameters.



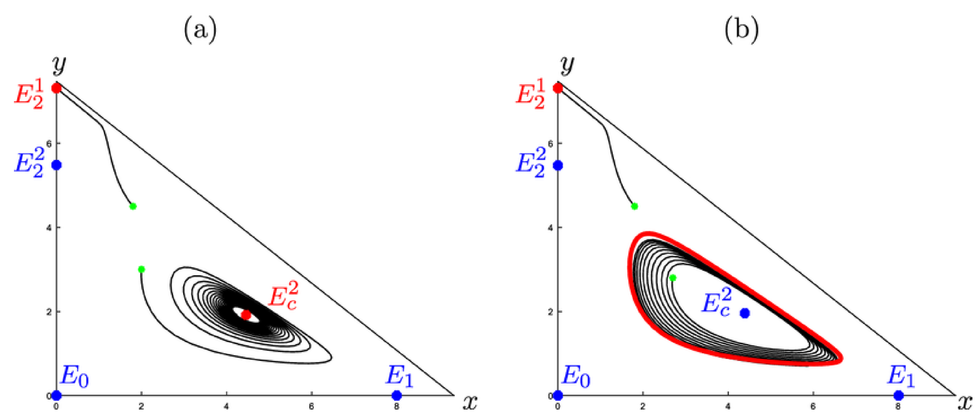
5 Bifurcation

Figure 3: Super-critical Hopf bufurcation.



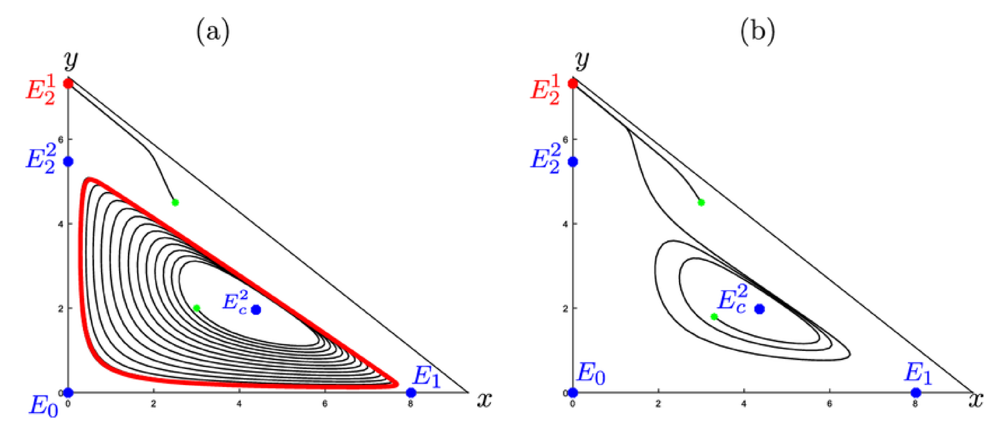
5.1 Bi-stability

Figure 4: E_c^2 loses its stability through a super- critical Hopf bifurcation.



5.2 Saddle-node bifurcation of limit cycles

Figure 5: Limit point of cycles bifurcation.



6 Conclusion

In this paper, we have extended the mathematical analysis of the model (1.1) of a competition in a chemostat in presence of internal inhibitor, assuming inhibited growth for species producing the toxin. Under general growth functions, we give, in a first step, a complete analysis for the existence and stability of all equilibria according to the control parameters. System (1.1) can have up to six types of equilibria: the washout equilibrium which always exists, two positive equilibrium of coexistence and three other equilibria corresponding to the extinction of one species.

The study demonstrates that coexistence of a system can occur as a steady state or sustained oscillations, with rich dynamics including multi-stability, Hopf, and saddle-node of limit cycles bifurcations. Analytical analysis of operating diagrams is crucial for determining system behavior based on substrate concentration and dilution rate. The results obtained show that substrate inhibition mechanism leads to coexistence, and could lead to the occurrence of limit cycles with coexistence of species under certain conditions. The numerical simulations illustrate the mathematical results demonstrated in the case where the growth rates are of Monod and Haldane-type.

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