



UNIVERSITÉ ABOU Bekr BELKAÏD-TLEMCEN  
FACULTÉ DES SCIENCES  
DÉPARTEMENT DE MATHÉMATIQUES  
LABORATOIRE D'ANALYSE NON LINÉAIRE &  
MATHÉMATIQUES APPLIQUÉES

Organisent

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Tendances dans les Applications Mathématiques  
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25-27 Février 2018



# Croissance et compétition des espèces microbiennes dans un chemostat

Tewfik Sari

Irstea, Montpellier

Réseau TREASURE

# Summary

## 1 Réseau TREASURE

Présentation du réseau

Livres

## 2 Competition of species in the chemostat

The chemostat

Maintenance

Operating diagram

Competitive exclusion Principle

## 3 Competition in the chemostat with an inhibitor

External inhibitor

Operating diagram

Internal inhibition

External lethal inhibitor

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# Le réseau TREASURE

TREASURE (pour **Treatment and Sustainable Reuse of Effluents in semiarid climates**) est un réseau de laboratoires de recherche et de chercheurs d'Europe du sud et d'Afrique du nord travaillant autour de questions touchant le traitement de l'eau, des déchets et leur valorisation par voie biologique.

- Ce réseau a été créé lors de l'Ecole-Symposium *Perturbations singulières en théorie du contrôle et en dynamique des populations*, qui s'est tenue à Tlemcen du 20-26/01/2006
- **Resp.** Jérôme Harmand, Directeur de Recherche, INRA
- **Sit web.** <https://www6.inra.fr/treasure/>
- 33 séminaires (Algérie, Maroc, Tunisie, France, Espagne)
- 14 thèses soutenues: Montpellier (1), Tunis (4), Tlemcen (4), Sidi Bel Abbes (1), cotutelle Montpellier-Tunis (2), cotutelle Montpellier-Tlemcen (2)
- 9 thèses en cours: Montpellier (5), Tunis (3), Kenitra (1)

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## CHEMOSTAT AND BIOPROCESSES SET



# Volume 1 The Chemostat

*Mathematical Theory  
of Microorganism Cultures*

Jérôme Harmand, Claude Lobry  
Alain Rapaport and Tewfik Sari

## COLLECTION GÉNIE DES PROCÉDÉS

Série Chémostat et bioprocédés



Volume 1

# Le chémostat

*théorie mathématique de  
la culture continue de micro-organismes*

Jérôme Harmand, Claude Lobry  
Alain Rapaport et Tewfik Sari

ISTE  
editions

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COLLECTION GÉNIE DES PROCÉDÉS

Série Chémostat et bioprocédés



Volume 2  
**La relation  
ressource-consommateur**  
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CHEMICAL ENGINEERING SERIES

CHEMOSTAT AND BIOPROCESSES SET



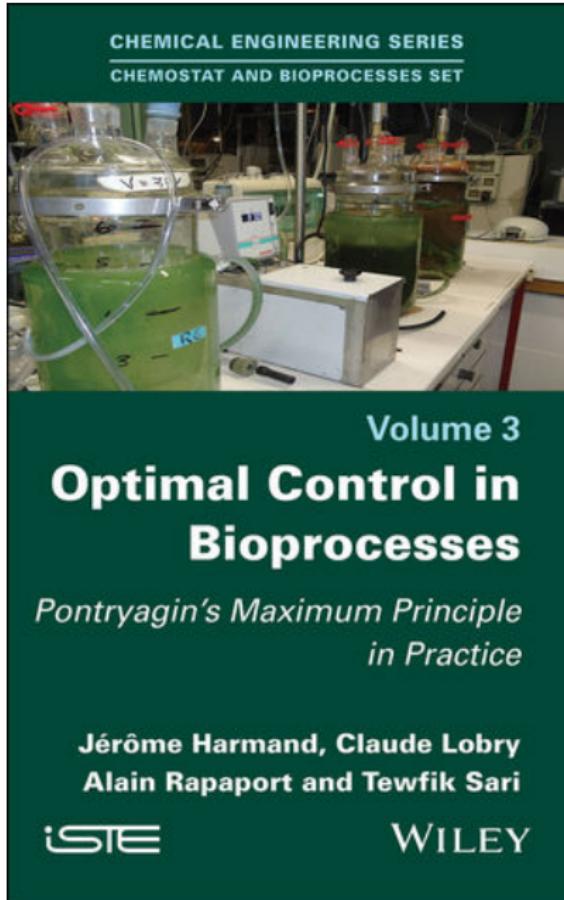
Volume 2  
**The Consumer–Resource  
Relationship**  
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Livres



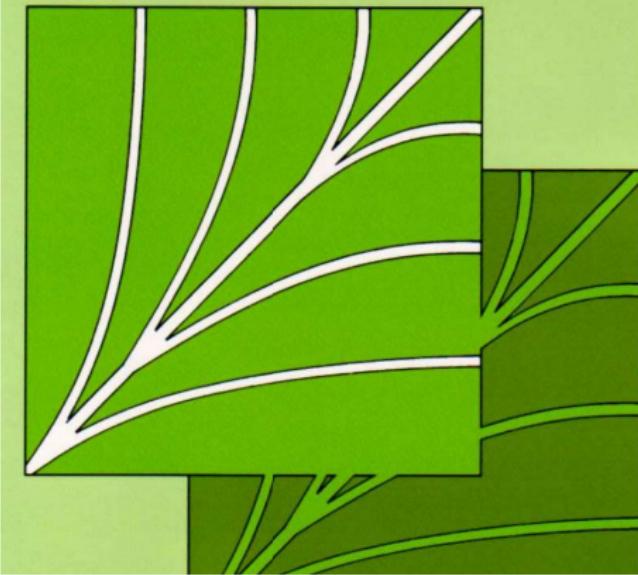
Hal L. Smith and Paul Waltman

Cambridge Studies in Mathematical Biology

# Livres

## The Theory of the Chemostat

## Dynamics of Microbial Competition



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External inhibitor

Operating diagram

Internal inhibition

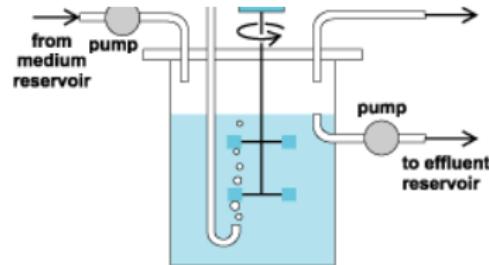
External lethal inhibitor



Chemostat:  $S \xrightarrow{\mu(\cdot)} X$

$$\begin{cases} \dot{S} = D(S^{in} - S) - \frac{1}{Y}\mu(S)X \\ \dot{X} = -DX + \mu(S)X \end{cases}$$

- $S$  : concentration of substrate
- $X$  : concentration of bacteria
- $S_{in}$  : input concentration of substrate
- $D = Q/V$  : Dilution rate
- $Y$  : yield
- $\mu(\cdot)$  : specific growth functions



## Steady states

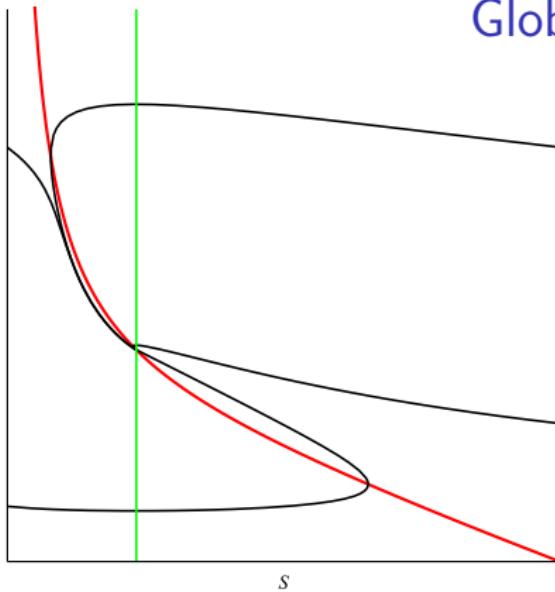
$$\begin{cases} \dot{S} = D(S_{in} - S) - \frac{1}{Y} \mu(S) X \\ \dot{X} = (\mu(S) - D) X \end{cases}$$

- $\mu(S)$  is increasing. Example: Monod function  $\mu(S) = \frac{\mu_{max}S}{K+S}$
- $E_0 = (S_{in}, 0)$  (washout) always exists
- $E_1 = (S^*, X^*)$  with  $\mu(S^*) = D$  and  $X^* = Y(S_{in} - S^*)$  which exists if and only if  $S_{in} > S^* \iff \mu(S_{in}) > D$

Steady-state	Existence condition	Stability condition
$E_0$	Always exists	$\mu(S_{in}) < D$
$E_1$	$\mu(S_{in}) > D$	Stable if it exists

The stability is global (in the positive cone)

## Global Stability



### Isoclines

- $\dot{S} = 0 \implies X = YD \frac{S_{in} - S}{\mu(S)}$  (in red on the figure)
- $\dot{X} = 0 \implies S = S^*$  (in green on the figure)

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Operating diagram

Internal inhibition

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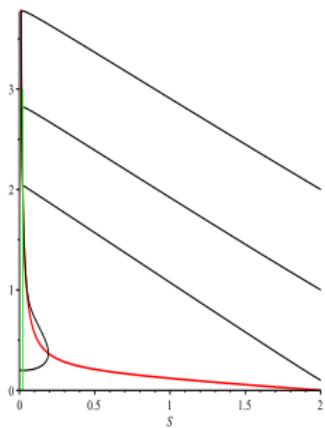
## Maintenance

$$\begin{cases} \dot{S} = D(S_{in} - S) - \mu(S) \frac{x}{Y} \\ \dot{x} = (\mu(S) - m - D)x \end{cases}$$

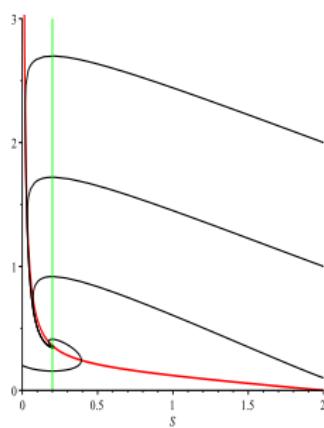
- $\mu(S)$  is increasing
- $\mu(S) = D + m \implies S = S^*$
- $x = x^* = \frac{YD}{D+m}(S_{in} - S^*)$
- The steady state  $E^* = (S^*, x^*)$  is stable (GAS) as long as it exists
- Oscillations may occur

Pirt, S. J. (1965). The Maintenance Energy of Bacteria in Growing Cultures. Proceedings of the Royal Society B: Biological Sciences, 163(991), 224–231

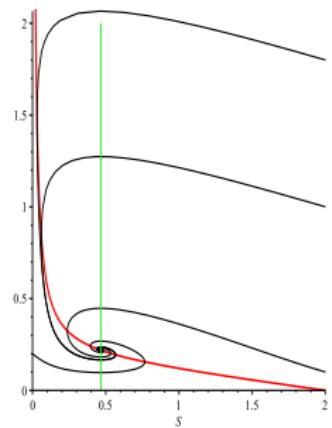
## Stables oscillations



$m = 0$



$m = 0.4$



$m = 0.6$

$$\begin{cases} \dot{S} = D(S_{in} - S) - \frac{S}{0.2+S}x \\ \dot{x} = \left( \frac{S}{0.2+S} - m - D \right)x \end{cases}$$

with  $D = 0.1$ ,  $S_{in} = 2$

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## Operating diagram

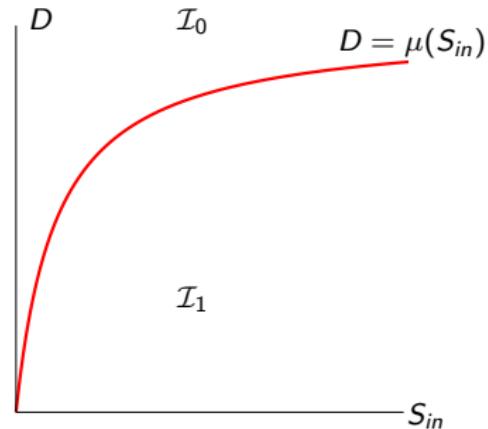
$$\begin{cases} \dot{S} = D(S_{in} - S) - k\mu(S)X \\ \dot{X} = -DX + \mu(S)X \end{cases}$$

Apart from the two operating (or control) parameters, which are the inflowing substrate  $S_{in}$  and the dilution rate  $D$ , that can vary, all others parameters ( $k$ , and parameters in  $\mu(S)$ ) have biological meaning and are fixed depending on the organisms and substrate considered.

The operating diagram describes the behaviour of the system with respect to the operating parameters

## Operating diagram: $\mu(S)$ increasing

region	$E_0$	$E_1$
$(S_{in}, D) \in \mathcal{I}_0$	S	
$(S_{in}, D) \in \mathcal{I}_1$	U	S



Steady-state	Existence condition	Stability condition
$E_0$	Always exists	$\mu(S_{in}) < D$
$E_1$	$\mu(S_{in}) > D$	Stable if it exists

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Maintenance

Operating diagram

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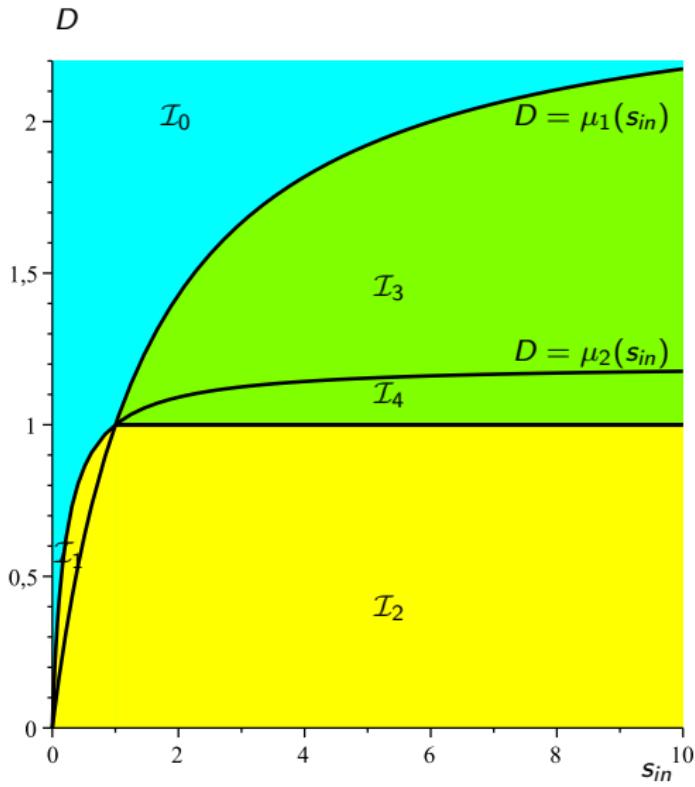
External lethal inhibitor

## Competition of two species

$$\begin{cases} S' = D(S_{in} - S) - \mu_1(S)x_1 - \mu_2(S)x_2 \\ x'_1 = (\mu_1(S) - D)x_1 \\ x'_2 = (\mu_2(S) - D)x_2 \end{cases}$$

- Break-even concentrations :  $\lambda_i = \mu_i^{-1}(D)$
- $E_0 = (S = S_{in}, x_1 = 0, x_2 = 0)$
- $E_1 = (S = \lambda_1, x_1 = S_{in} - \lambda_1, x_2 = 0)$
- $E_2 = (S = \lambda_2, x_1 = 0, x_2 = S_{in} - \lambda_2)$
- If  $\lambda_1 < \lambda_2$  then  $E_1$  is stable (GAS).
- At equilibrium, only one species can survive (Competitive Exclusion Principle)
- The result is true for  $n > 2$  competing species

# Operating diagram



region	$E_0$	$E_1$	$E_2$
$(s_{in}, D) \in \mathcal{I}_0$	S		
$(s_{in}, D) \in \mathcal{I}_1$	U		S
$(s_{in}, D) \in \mathcal{I}_2$	U	U	S
$(s_{in}, D) \in \mathcal{I}_3$	U	S	
$(s_{in}, D) \in \mathcal{I}_4$	U	S	U

## Different removal rates

$$\begin{cases} S' = D(S_{in} - S) - \mu_1(S)x_1 - \mu_2(S)x_2 \\ x'_1 = (\mu_1(S) - D_1)x_1 \\ x'_2 = (\mu_2(S) - D_2)x_2 \end{cases}$$

$$D_i = \alpha_i D + m_i, \quad i = 1, 2, \quad (0 \leq \alpha_i \leq 1, \quad m_i \geq 0)$$

- Break-even concentrations :  $\lambda_i = \mu_i^{-1}(D_i)$
- $E_0 = (S = S_{in}, x_1 = 0, x_2 = 0)$
- $E_1 = (S = \lambda_1, x_1 = \frac{D}{D_1}(S_{in} - \lambda_1), x_2 = 0)$
- $E_2 = (S = \lambda_2, x_1 = 0, x_2 = \frac{D}{D_1}(S_{in} - \lambda_2))$
- If  $\lambda_1 < \lambda_2$  then  $E_1$  is stable and  $E_2$  is unstable.
- Open problem : LAS  $\Rightarrow$  GAS ?
- If  $\mu_i(S) = \frac{m_i}{K_i + S}$  are Monod then  $E_1$  is GAS (Hsu 1978)

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# External inhibitor

Joint work with Dellal and Lakrib

PhD of Mohammed Dellal coadvised with Mustapha Lakrib  
(February, 28, 2019, Sidi Bel Abbes, Algeria)

R. E. Lenski and S. Hattingh (1986)

S. B. Hsu and P. Waltman (1991)

H. L. Smith and P. Waltman (1995)

S. B. Hsu and P. Waltman (2004)

M. Dellal, M. Lakrib and T. S. (2018)



The operating diagram of a model of two competitors in a chemostat with an external inhibitor

Mohamed Dellal<sup>a,b</sup>, Mustapha Lakrib<sup>b</sup>, Tewfik Sari<sup>c,d</sup>

<sup>a</sup> Université Ibn Khaldoun, Tizi Ouzou, Algeria

<sup>b</sup> Laboratoire de Mathématiques, Université Djillali Liabes, Sétif 19000, Algeria

<sup>c,d</sup> IRST, Paris, Montpellier SupAgro, University of Montpellier, Montpellier, France

## External inhibition

$$\begin{cases} S' = (S^0 - S)D - f(p)f_1(S)x - f_2(S)y \\ x' = [f(p)f_1(S) - D]x \\ y' = [f_2(S) - D]y \\ p' = (p^0 - p)D - g(p)y \end{cases}$$

- One species is sensitive and the other is resistant.
- The sensitive species has the lowest break-even concentration and wins the competition in absence of the inhibitor
- The presence of the inhibitor allows the coexistence of both species
- The resistant species is able to remove the inhibitor from the environment

The inhibitor is not removed:  $g(p) = 0$

$$\begin{cases} S' &= (S^0 - S)D - f(p)f_1(S)x - f_2(S)y \\ x' &= [f(p)f_1(S) - D]x \\ y' &= [f_2(S) - D]y \\ p' &= (p^0 - p)D \end{cases}$$

$p(t)$  tends to  $p^0$  and the system is reduced to

$$\begin{cases} S' &= (S^0 - S)D - f(p^0)f_1(S)x - f_2(S)y \\ x' &= [f(p^0)f_1(S) - D]x \\ y' &= [f_2(S) - D]y \end{cases}$$

- $E_0 = (S^0, 0, 0, p^0)$
- $E_1 = (\lambda^+, S^0 - \lambda^+, 0, p^0)$  where  $f_1(\lambda^+) = \frac{D}{f(p^0)}$
- $E_2 = (\lambda_2, 0, S^0 - \lambda_2, p^0)$  where  $f_2(\lambda_2) = D$

if  $\lambda^+ < \lambda_2$ ,  $E_1$  is Stable and  $E_2$  is unstable  
if  $\lambda^+ > \lambda_2$ ,  $E_2$  is Stable and  $E_1$  is unstable

## The inhibitor is removed

$$\begin{cases} S' = (S^0 - S)D - f(p)f_1(S)x - f_2(S)y \\ x' = [f(p)f_1(S) - D]x \\ y' = [f_2(S) - D]y \\ p' = (p^0 - p)D - g(p)y \end{cases}$$

- $E_0 = (S^0, 0, 0, p^0)$ .
- $E_1 = (\lambda^+, S^0 - \lambda^+, 0, p^0)$
- $E_2 = (\lambda_2, 0, S^0 - \lambda_2, p^*)$
- $E_c = (\lambda_2, x_c, y_c, p_c)$

$$f_1(\lambda^+) = \frac{D}{f(p^0)}, \quad f_2(\lambda_2) = D, \quad W(p^*) = S^0 - \lambda_2$$

$$f(p_c) = \frac{D}{f_1(\lambda_2)}, \quad y_c = W(p_c), \quad x_c(D) = S^0 - \lambda_2 - y_c$$

with

$$W(p) = \frac{D(p^0 - p)}{g(p)}$$

## Existence and stability

$$\begin{cases} S' = (S^0 - S)D - f(p)f_1(S)x - f_2(S)y \\ x' = [f(p)f_1(S) - D]x \\ y' = [f_2(S) - D]y \\ p' = (p^0 - p)D - g(p)y \end{cases}$$

	Existence	Stability
$E_0$	Always	$\min(\lambda^+, \lambda_2) > S^0$
$E_1$	$\lambda^+ < S^0$	$\lambda^+ < \lambda_2$
$E_2$	$\lambda_2 < S^0$	$\lambda_2 < \lambda^-$
$E_c$	$\lambda^- < \lambda_2 < \min(\lambda^+, S^0)$	$(A + B)(A + B + C)C > BEF$

$$f_1(\lambda^-) = \frac{D}{f(p^*)}, \quad f_1(\lambda^+) = \frac{D}{f(p^0)}, \quad f_2(\lambda_2) = D$$

$$A = f(p_c)f'_1(\lambda_2)x_c, \quad B = f'_2(\lambda_2)y_c, \quad C = 1 + g'(p_c)y_c$$

$$E = g(p_c), \quad F = -f'(p_c)f_1(\lambda_2)x_c,$$

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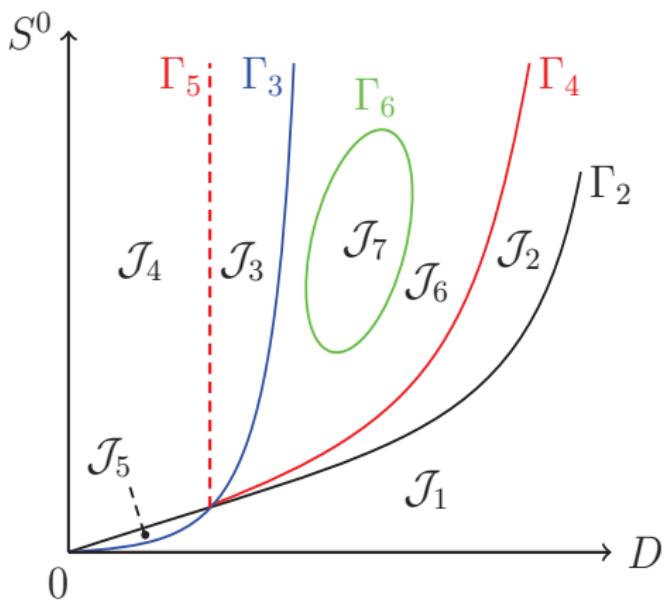
External inhibitor

Operating diagram

Internal inhibition

External lethal inhibitor

# Operating diagram



Regions	$E_0$	$E_1$	$E_2$	$E_c$
$\mathcal{J}_1$	S			
$\mathcal{J}_2$	U		S	
$\mathcal{J}_3$	U	U	U	S
$\mathcal{J}_4$	U	S	U	
$\mathcal{J}_5$	U	S		
$\mathcal{J}_6$		U	U	S
$\mathcal{J}_7$	U	U	U	

## Application

$$\begin{cases} S' &= D(S^0 - S) - f(p)f_1(S)x - f_2(S)y \\ x' &= [f(p)f_1(S) - D]x \\ y' &= [f_2(S) - D]y \\ p' &= D(p^0 - p) - g(p)y \end{cases}$$

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

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$$\mu = 5 \quad m_1 = 5 \quad a_1 = 0.5 \quad m_2 = 6 \quad a_2 = 3.5 \quad \delta = 50 \quad K = 0.1$$

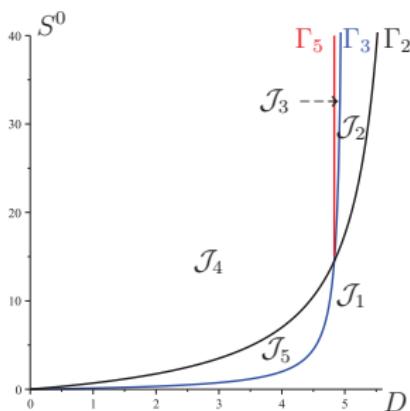
S. B. Hsu and P. Waltman (1991, 2004).

Studied the stability of steady states,

Noticed that the positive steady state  $E_c$  can be unstable

Showed that for  $S^0 = 1$ ,  $p^0 = 1$  and  $D = 1$ , it is unstable.

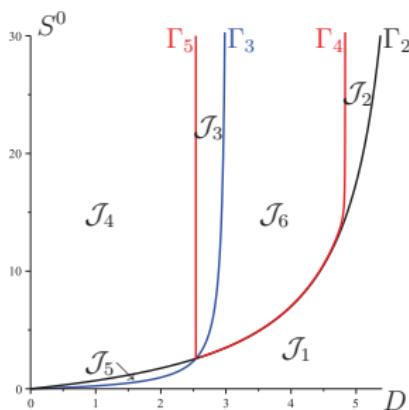
# Operating diagram: $p^0 = 0$



Regions	$E_0$	$E_1$	$E_2$
$\mathcal{J}_1$	S		
$\mathcal{J}_2$	U		S
$\mathcal{J}_3$	U	U	S
$\mathcal{J}_4$	U	S	U
$\mathcal{J}_5$	U	S	

TABLE 5. Existence and stability of equilibria in the regions of the operating diagram of Figure 6.

# Operating diagram: $p^0 = 0.1$



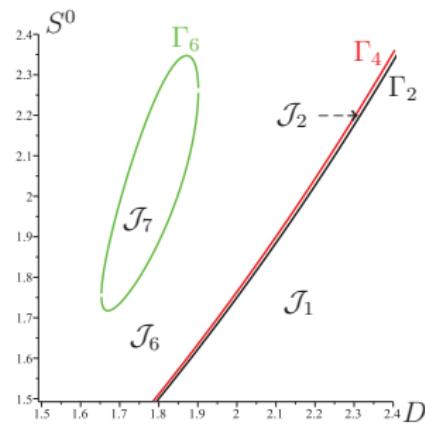
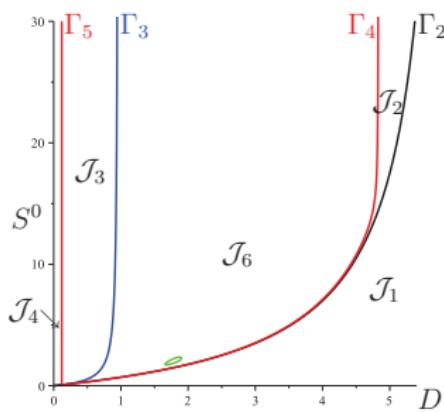
Regions	$E_0$	$E_1$	$E_2$	$E_c$
$\mathcal{J}_1$	S			
$\mathcal{J}_2$	U		S	
$\mathcal{J}_3$	U	U	U	S
$\mathcal{J}_4$	U	S	U	
$\mathcal{J}_5$	U	S		
$\mathcal{J}_6$	U		U	S

TABLE 6. Existence and stability of equilibria in the regions of the operating diagram of Figure 7.

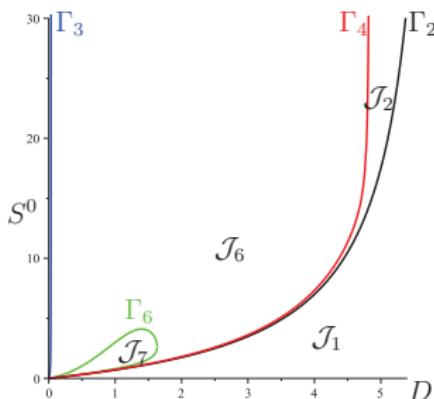
Regions	$E_0$	$E_1$	$E_2$	$E_c$
$\mathcal{J}_1$	S			
$\mathcal{J}_2$	U		S	
$\mathcal{J}_3$	U	U	U	S
$\mathcal{J}_4$	U	S	U	U
$\mathcal{J}_6$	U		U	S
$\mathcal{J}_7$	U		U	U

Operating diagram:  $p^0 = 0.33$

TABLE 7. Existence and stability of equilibria in the regions of the operating diagram of Figure 8.



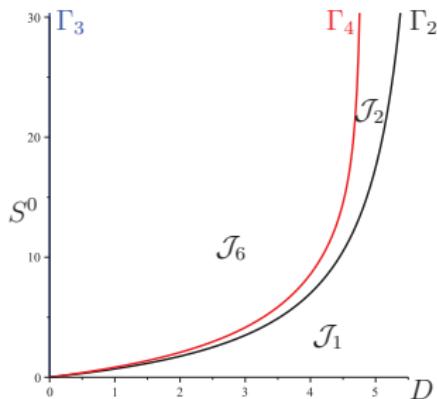
# Operating diagram: $p^0 = 1$



Regions	$E_0$	$E_1$	$E_2$	$E_c$
$J_1$	S			
$J_2$	U		S	
$J_3$	U	U	U	S
$J_6$	U		U	S
$J_7$	U	U	U	U

TABLE 8. Existence and stability of equilibria in the regions of the operating diagram of Figure 9.

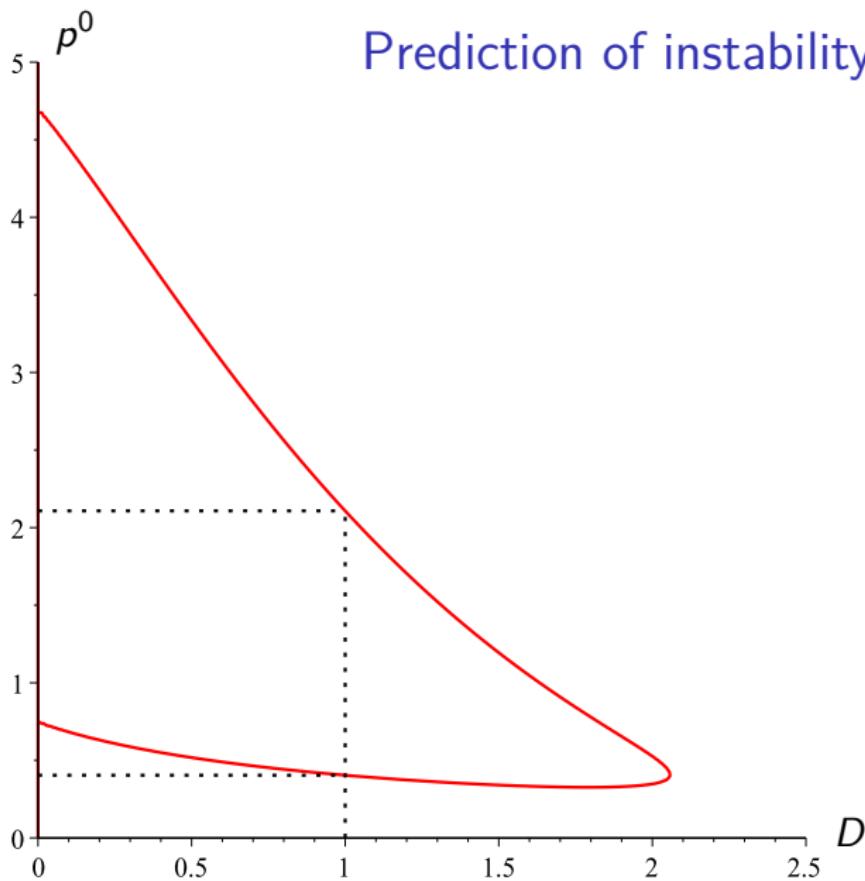
# Operating diagram: $p^0 = 4.72$



Regions	$E_0$	$E_1$	$E_2$	$E_c$
$\mathcal{J}_1$	S			
$\mathcal{J}_2$	U		S	
$\mathcal{J}_3$	U	U	U	S
$\mathcal{J}_6$	U	U	U	S

TABLE 9. Existence and stability of equilibria in the regions of the operating diagram of Figure 10.

## Prediction of instability of $E_c$



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**Internal inhibition**

External lethal inhibitor

## Internal inhibitor

$$\begin{cases} S' = (S^0 - S)D - f_1(S, p)\frac{x_1}{\gamma_1} - f_2(S, p)\frac{x_2}{\gamma_2} \\ x'_1 = [f_1(S, p) - D]x_1 \\ x'_2 = [f_2(S, p) - D]x_2 \\ p' = \alpha_1 f_1(S, p)x_1 + \alpha_2 f_2(S, p)x_2 - Dp \end{cases}$$

- The species are sensitive to the product.
- The presence of the inhibitor allows the coexistence of both species

PhD of Mohamed Dellal coadvised with Mustapha Lakrib  
(February, 28, 2019, Sidi Bel Abbès, Algeria)  
M. Dellal (Poster, TAMTAM2019)

M.J. De Freitas, A.G. Fredrickson (1978)

S. B. Hsu and P. Waltman (2004)

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## ① Réseau TREASURE

Présentation du réseau

Livres

## ② Competition of species in the chemostat

The chemostat

Maintenance

Operating diagram

Competitive exclusion Principle

## ③ Competition in the chemostat with an inhibitor

External inhibitor

Operating diagram

Internal inhibition

External lethal inhibitor

## External lethal inhibition

$$\begin{cases} S' = (S^0 - S)D - f_1(S)x - f_2(S)y \\ x' = [f_1(S) - D - \gamma p]x \\ y' = [f_2(S) - D]y \\ p' = (p^0 - p)D - g(p)y \end{cases}$$

- One species is sensitive and the other is resistant.
- The sensitive species has the lowest break-even concentration and wins the competition in absence of the inhibitor
- The presence of the inhibitor allows the coexistence of both species
- The resistant species is able to remove the inhibitor from the environment

The inhibitor is not removed:  $g(p) = 0$

$$\begin{cases} S' &= (S^0 - S)D - f_1(S)x - f_2(S)y \\ x' &= [f_1(S) - D - \gamma p]x \\ y' &= [f_2(S) - D]y \\ p' &= (p^0 - p)D \end{cases}$$

$p(t)$  tends to  $p^0$  and the system is reduced to

$$\begin{cases} S' &= (S^0 - S)D - f_1(S)x - f_2(S)y \\ x' &= [f_1(S) - D - \gamma p^0]x \\ y' &= [f_2(S) - D]y \end{cases}$$

- $E_0 = (S^0, 0, 0, p^0)$
- $E_1 = \left(\lambda^+, \frac{D}{D + \gamma p^0} (S^0 - \lambda^+), 0, p^0\right)$  where  $f_1(\lambda^+) = D + \gamma p^0$
- $E_2 = (\lambda_2, 0, S^0 - \lambda_2, p^0)$  where  $f_2(\lambda_2) = D$

if  $\lambda^+ < \lambda_2$ ,  $E_1$  is Stable and  $E_2$  is unstable  
if  $\lambda^+ > \lambda_2$ ,  $E_2$  is Stable and  $E_1$  is unstable

The inhibitor is removed

$$\begin{cases} S' = (S^0 - S)D - f_1(S)x - f_2(S)y \\ x' = [f_1(S) - D - \gamma p]x \\ y' = [f_2(S) - D]y \\ p' = (p^0 - p)D - g(p)y \end{cases}$$

- $E_0 = (S^0, 0, 0, p^0)$ .
- $E_1 = \left(\lambda^+, \frac{D}{D+\gamma p^0} (S^0 - \lambda^+), 0, p^0\right)$
- $E_2 = (\lambda_2, 0, S^0 - \lambda_2, p^*)$
- $E_c = (\lambda_2, x_c, y_c, p_c)$

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B. Bar and T. S. (TAMTAM2019)

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S. B. Hsu and P. Waltman (2004)

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Merci pour votre attention



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