Modèles à trois étapes

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Séminaire du réseau Treasure
Le Hameau de l'Étoile

21 - 25 septembre 2015

La réalité ?

$$\frac{\mathrm{d}X_{\mathrm{ch}}}{\mathrm{d}t} = -DX_{\mathrm{ch}} + Y_{\mathrm{ch}} f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}} - k_{\mathrm{dec,ch}} X_{\mathrm{ch}}$$

$$\frac{\mathrm{d}X_{\mathrm{ph}}}{\mathrm{d}t} = -DX_{\mathrm{ph}} + Y_{\mathrm{ph}} f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ph}} - k_{\mathrm{dec,ph}} X_{\mathrm{ph}}$$

$$\frac{\mathrm{d}X_{\mathrm{H_2}}}{\mathrm{d}t} = -DX_{\mathrm{H_2}} + Y_{\mathrm{H_2}} f_2\left(S_{\mathrm{H_2}}\right) X_{\mathrm{H_2}} - k_{\mathrm{dec,H_2}} X_{\mathrm{H_2}}$$

$$\frac{\mathrm{d}S_{\mathrm{ch}}}{\mathrm{d}t} = D\left(S_{\mathrm{ch,in}} - S_{\mathrm{ch}}\right) - f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}}$$

$$\frac{\mathrm{d}S_{\mathrm{ph}}}{\mathrm{d}t} = D\left(S_{\mathrm{ph,in}} - S_{\mathrm{ph}}\right) + \frac{224}{208}\left(1 - Y_{\mathrm{ch}}\right) f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}} - f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ph}}$$

$$\frac{\mathrm{d}S_{\mathrm{H_2}}}{\mathrm{d}t} = \left(S_{\mathrm{H_2,in}} - S_{\mathrm{H_2}}\right) + \frac{32}{224}\left(1 - Y_{\mathrm{ph}}\right) f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ph}} - \frac{16}{208} f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}} - f_2\left(S_{\mathrm{H_2}}\right) X_{\mathrm{H_2}}$$

Chlorophenol degradation

- S_{ch} and X_{ch} are the chlorophenol substrate and biomass concentrations
- S_{ph} and X_{ph} those for phenol and $S_{\mathrm{H_2}}$ and $X_{\mathrm{H_2}}$ those for hydrogen
- Y_{ch}, Y_{ph} and Y_{H2} are the yield coefficients,
- $224/208\,(1 - Y_{\mathrm{ch}})$ represents the part of chlorophenol degraded to phenol,
- $32/224\,(1 - Y_{\mathrm{ph}})$ represents the part of phenol that is transformed to hydrogen

Growth functions take Monod form with hydrogen inhibition acting on the phenol degrader.

$$f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) = \frac{k_{m,\mathrm{ch}} S_{\mathrm{ch}}}{K_{S,ch} + S_{\mathrm{ch}}} \frac{S_{H_2}}{K_{S,\mathrm{H_2,c}} + S_{\mathrm{H_2}}}$$

$$f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H_2}}\right) = \frac{k_{m,\mathrm{ph}} S_{\mathrm{ph}}}{K_{S,\mathrm{ph}} + S_{\mathrm{ph}}} \frac{1}{1 + \frac{S_{\mathrm{H_2}}}{K_{i,\mathrm{H_2}}}}, \qquad f_2\left(S_{\mathrm{H_2}}\right) = \frac{k_{m,\mathrm{H_2}} S_{\mathrm{H_2}}}{K_{S,\mathrm{H_2}} + S_{\mathrm{H_2}}}$$

Wade et al. 2015

Plan du cours

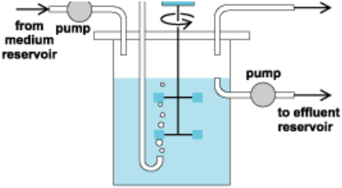
Plan du cours

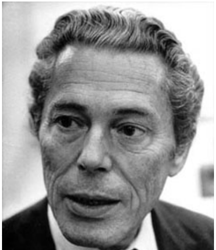
Chemostat

Chemostat : $S_1 \xrightarrow{\mu_1(\cdot)} X_1$

$$\begin{cases} \dot{S}_1 = D(S_1^{in} - S_1) - k_1\mu_1(S_1)X_1 \\ \dot{X}_1 = -DX_1 + \mu_1(S_1)X_1 \end{cases}$$

- S_1 : concentration of substrate
- X_1 : concentration of bacteria
- S_1^{in} : input concentration of substrate
- $D = Q/V$: Dilution rate
- k_1 : stoichiometric coefficient
- $\mu_1(\cdot)$: specific growth functions





Matrice de Petersen–Gujer

- Le modèle

$$\begin{aligned} \dot{S} &= D(S_{in} - S) \quad -\mu(S)\frac{X}{Y} \\ \dot{X} &= -DX \quad +\mu(S)X \end{aligned}$$

- est représenté schématiquement par la matrice

	Components $\rightarrow i$	1	2	Rates
j	Process $\downarrow$	S	X	
1	Uptake of S	$-\frac{1}{Y}$	1	$\mu(S)X$

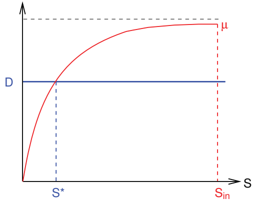
Plan du cours

Chemostat : Stabilité des équilibres

Détermination des équilibres

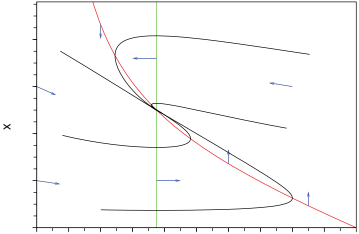
$$\dot{s} = -\mu(s)x + D(s_{in} - s) \qquad \dot{x} = \mu(s)x - Dx \Rightarrow \boxed{\begin{array}{c} x^\star = 0 \\ s^\star = s_{in} \end{array}} \text{ or } \boxed{\begin{array}{c} \mu(s^\star) = D \\ x^\star = s_{in} - s^\star \end{array}}$$

lessivage — équilibre positif

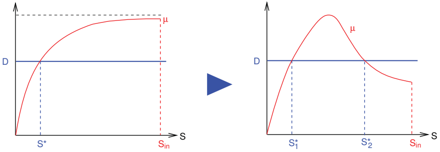


Portrait de phase

$$\dot{s} = -\mu(s)x + D(s_{in} - s)$$
$$\dot{x} = \mu(s)x - Dx$$



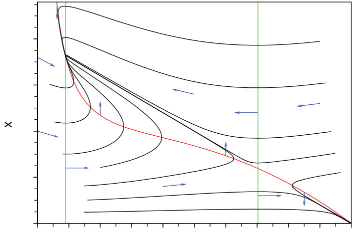
Détermination des équilibres



croissance monotone — croissance non monotone

Portrait de phase

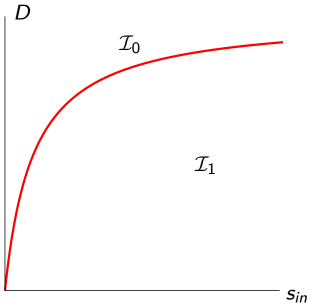
$$\dot{s} = -\mu(s)x + D(s_{in} - s)$$
$$\dot{x} = \mu(s)x - Dx$$

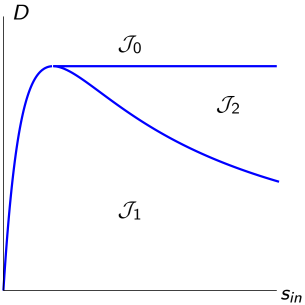


Chemostat : Diagramme opératoire

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 have biological meaning and are fixed depending on the organisms and substrate considered

Diagramme opératoire





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

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

Plan du cours

Mixed culture :

$$S_1 \xrightarrow{\mu_1(\cdot)} X_1 + S_2, \quad S_2 \xrightarrow{\mu_2(\cdot)} X_2$$

$$\left\{ \begin{array}{rclcl} \dot{S}_1 & = & D(S_1^{in} - S_1) & - & k_1\mu_1(\cdot)X_1 \\ \dot{X}_1 & = & -DX_1 & + & \mu_1(\cdot)X_1 \\ \dot{S}_2 & = & -DS_2 & + & k_3\mu_1(\cdot)X_1 - k_2\mu_2(\cdot)X_2 \\ \dot{X}_2 & = & -DX_2 & + & \mu_2(\cdot)X_2 \end{array} \right.$$

- S_1, S_2 : concentrations of substrate and product
- X_1, X_2 : concentrations of bacteria
- S_1^{in} : input concentration of substrate
- D : Dilution rate
- k_1, k_2, k_3 : steochiometric coefficients (inverses of yields)
- $\mu_1(\cdot)$, $\mu_2(\cdot)$: specific growth functions

Plan du cours

Chemostat
Modèle à deux étapes
Commensalisme

État d'animaux ou de végétaux vivant associés à d'autres espèces et profitant de leurs aliments sans leur porter préjudice.
http ://www.cnrtl.fr/definition/commensalisme

Commensalism

'Two populations of microorganisms which grow in a mixed culture and interact in such a way that one population (the commensal population) depends for its growth on the other population and thus benefits from the interaction while the other population (the host) is not affected by the growth of the commensal population constitutes an example of commensalism.'

$$\mu_1(\cdot) = \mu_1(S_1), \quad \mu_2(\cdot) = \mu_2(S_2)$$

are monotone increasing (Monod) or can exhibit a maximum if the growth is inhibited at high substrate concentrations (Haldane)

$$\begin{cases} \dot{S}_1 = D(S_1^{in} - S_1) - k_3\mu_1(S_1)X_1 \\ \dot{X}_1 = -DX_1 + \mu_1(S_1)X_1 \\ \dot{S}_2 = -DS_2 + k_1\mu_1(S_1)X_1 - k_2\mu_2(S_2)X_2 \\ \dot{X}_2 = -DX_2 + \mu_2(S_2)X_2 \end{cases}$$

Stephanopoulos 1981

Commensalism

$$
\begin{cases}
\dot{S}_1 = D(S_1^{in} - S_1) - k_3\mu_1(S_1)X_1 \\
\dot{X}_1 = -DX_1 + \mu_1(S_1)X_1 \\
\dot{S}_2 = -DS_2 + k_1\mu_1(S_1)X_1 - k_2\mu_2(S_2)X_2 \\
\dot{X}_2 = -DX_2 + \mu_2(S_2)X_2
\end{cases}
$$

- Solve the first and second equations for S_1, X_1
- Use this result is the remaining equations to find S_2, X_2
- Consequently S_1 and X_1 are the same in pure and mixed culture experiments
- In contrast to this, synthrophic associations exhibit a mutual dependance of the two members of the food chain

Reilly 1974, Stephanopoulos 1981,
Bernard et al. 2001, Benyahia et al. 2012

Plan du cours

Chemostat
Modèle à deux étapes
Commensalisme : Modèle AM2

Modèle AM2

$$\begin{cases} \dot{S}_1 = D(S_1^{in} - S_1) - k_3\mu_1(S_1)X_1 \\ \dot{X}_1 = -\alpha D X_1 + \mu_1(S_1)X_1 \\ \dot{S}_2 = D(S_2^{in} - S_2) + k_1\mu_1(S_1)X_1 - k_2\mu_2(S_2)X_2 \\ \dot{X}_2 = -\alpha D X_2 + \mu_2(S_2)X_2 \end{cases}$$

$$\mu_1(S_1) = \frac{m_1 S_1}{K_1 + S_1}, \quad \mu_2(S_2) = \frac{m_2 S_2}{K_2 + S_2 + S_2^2/K_i}$$

$$\begin{cases} 0 = D(S_1^{in} - S_1) - k_3\mu_1(S_1)X_1 & (6) \\ 0 = (\mu_1(S_1) - \alpha D)\, X_1 & (7) \\ 0 = D(S_2^{in} - S_2) + k_1\mu_1(S_1)X_1 - k_2\mu_2(S_2)X_2 & (8) \\ 0 = (\mu_2(S_2) - \alpha D)\, X_2 & (9) \end{cases}$$

Bernard et al. 2001, Benyahia et al. 2012

Matrice de Petersen–Gujer

$$
\begin{aligned}
\dot{S}_1 &= D(S_{1in} - S_1) & -k_1 \mu_1(S_1) X_1 \\
\dot{X}_1 &= -DX_1 & +\mu_1(S_1) X_1 \\
\dot{S}_2 &= D(S_{2in} - S_2) & +k_2 \mu_1(S_1) X_1 - k_3 \mu_2(S_2) X_2 \\
\dot{X}_2 &= -DX_2 & +\mu_2(S_2) X_2
\end{aligned}
$$

	Components $\rightarrow i$	1	2	3	4	Rates
j	Process $\downarrow$	S_1	S_2	X_1	X_2	
1	Acidogenesis	$-k_1$	k_2	1	0	$\mu_1(S_1)X_1$
2	Methanogenesis	0	$-k_3$	0	1	$\mu_2(S_2)X_2$

$$
\mu_1(S_1) = \frac{\mu_{1max} S_1}{K_1 + S_1} \qquad \mu_2(S) = \frac{\mu_{2max} S_2}{K_2 + S_2 + S_2^2 / K_i}
$$

Chemostat
Modèle à deux étapes
Commensalisme
Syntrophie

syntrophe, adj.[En parlant d'une souche de bactéries ou de champignons] Qui n'est capable de se développer sur un milieu nutritif minimal que quand elle est associée à une autre (d'apr. Méd. Biol. t. 3 1972).
syntrophie, subst. fém. Aptitude de deux cellules ou de deux souches bactériennes à être syntrophes (d'apr. Méd. Biol. t. 3 1972).
http ://www.cnrtl.fr/definition/syntrophie

Syntrophy

$$\begin{cases} \dot{S}_1 = D(S_1^{in} - S_1) - k_3\mu_1(S_1, S_2)X_1 \\ \dot{X}_1 = \mu_1(S_1, S_2)X_1 - DX_1 \\ \dot{S}_2 = k_1\mu_1(S_1, S_2)X_1 - DS_2 - k_2\mu_2(S_2)X_2 \\ \dot{X}_2 = \mu_2(S_2)X_2 - DX_2 \end{cases}$$

- The first organism is inhibited by high concentrations of the product S_2
- Therefore, the extent to which the substrate S_1 is degraded by the organism X_1 depends on the efficienty of the removal of the product S_2 by the bacteria X_2
- Bistability cannot occur

Wilkinson et al. 1974, Kreikenbohm & Bohl 1986, Burchard 1994, El Hajji et al. 2011, Harvey et al. 2014

Syntrophic associations

- El Hajji et al. 2011 : General functions satisfying

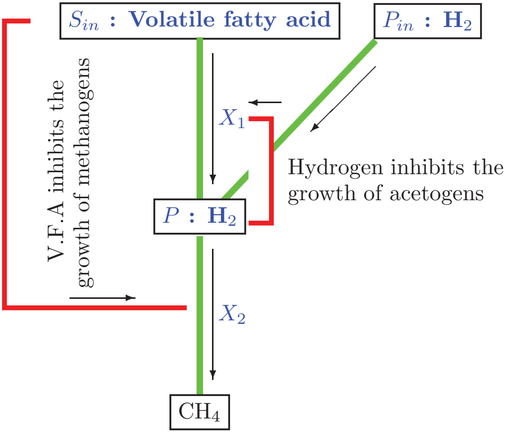
$$\frac{\partial \mu_1}{\partial S_1} > 0, \quad \frac{\partial \mu_1}{\partial S_2} < 0, \quad \frac{d\mu_2}{dS_2} > 0$$

- The system has not a cascade structure : the determination of steady states is more delicate.

$$\begin{cases} 0 &= D(S_1^{in} - S_1) - k_3\mu_1(S_1, S_2)X_1 \\ 0 &= \mu_1(S_1, S_2)X_1 - DX_1 \\ 0 &= k_1\mu_1(S_1, S_2)X_1 - DS_2 - k_2\mu_2(S_2)X_2 \\ 0 &= \mu_2(S_2)X_2 - DX_2 \end{cases}$$

Plan du cours

Anaerobic Digestion



Inhibition of X_2 by S_1

$$\begin{cases} \dot{S}_1 = D(S_1^{in} - S_1) - k_3\mu_1(S_1, S_2)X_1 \\ \dot{X}_1 = \mu_1(S_1, S_2)X_1 - DX_1 \\ \dot{S}_2 = k_1\mu_1(S_1, S_2)X_1 + D(S_2^{in} - S_2) - k_2\mu_2(S_1, S_2)X_2 \\ \dot{X}_2 = \mu_2(S_1, S_2)X_2 - DX_2 \end{cases}$$

- The first organism is inhibited by high concentrations of the product S_2
- The second organism is inhibited by high concentrations of the substrate S_1
- If $\frac{\partial \mu_1}{\partial S_1} > 0$ and $\frac{\partial \mu_1}{\partial S_2} < 0$ and $\frac{\partial \mu_2}{\partial S_1} < 0$ and $\frac{\partial \mu_2}{\partial S_2} > 0$ a stable coexistence steady state can occur. Also bistability can occur.

Kreikenbohm & Bohl 1988, Sari et al. 2012

Rescaling

$$s_1 = \frac{k_1}{k_3} S_1,\ x_1 = k_1 X_1,\ s_2 = S_2,\ x_2 = k_2 X_2,\ s_1^{in} = \frac{k_1}{k_3} S_1^{in},\ s_2^{in} = S_2^{in}\ .$$

$$\left\{ \begin{array}{rcl} \dot{s}_1 & = & D(s_1^{in} - s_1) - f_1(s_1, s_2)x_1 \\ \dot{x}_1 & = & f_1(s_1, s_2)x_1 - Dx_1 \\ \dot{s}_2 & = & D(s_2^{in} - s_2) - f_2(s_1, s_2)x_2 + f_1(s_1, s_2)x_1 \\ \dot{x}_2 & = & f_2(s_1, s_2)x_2 - Dx_2 \end{array} \right.$$

where

$$f_1(s_1, s_2) = \mu_1 \left(\frac{k_3}{k_1} s_1, s_2 \right) \quad f_2(s_1, s_2) = \mu_2 \left(\frac{k_3}{k_1} s_1, s_2 \right)$$

Reduction to the plane

$$\begin{cases} \dot{s}_1 &= D(s_1^{in} - s_1) - f_1(s_1, s_2)x_1 \\ \dot{x}_1 &= f_1(s_1, s_2)x_1 - Dx_1 \\ \dot{s}_2 &= D(s_2^{in} - s_2) - f_2(s_1, s_2)x_2 + f_1(s_1, s_2)x_1 \\ \dot{x}_2 &= f_2(s_1, s_2)x_2 - Dx_2 \end{cases}$$

Notice that

$$\dot{z}_1 = D(s_1^{in} - z_1), \qquad z_1 = s_1 + x_1$$

$$\dot{z}_2 = D(s_2^{in} - z_2), \qquad z_2 = s_2 + x_2 - x_1$$

Thus

$$s_1(t) + x_1(t) \to s_1^{in}, \quad s_2(t) + x_2(t) - x_1(t) \to s_2^{in}$$

We can restrict the study to the positive invariant attractor

$$\Omega = \left\{ (s_1, x_1, s_2, x_2) \in \mathbb{R}_+^4 : \; s_1 + x_1 = s_1^{in}, \quad s_2 + x_2 - x_1 = s_2^{in} \right\}$$

Plan du cours

ADM1 : Propionate degradation

$$
\left\{
\begin{array}{rcl}
\frac{dS_{pro}}{dt} & = & D\left(S_{pro,in} - S_{pro}\right) - f_0\left(S_{pro}, S_{H2}\right) X_{pro} \\
\frac{dX_{pro}}{dt} & = & -DX_{pro} + Y_{pro} f_0\left(S_{pro}, S_{H2}\right) X_{pro} - k_{dec,pro} X_{pro} \\
\frac{dS_{H2}}{dt} & = & -DS_{H2} + 0.43\left(1 - Y_{pro}\right) f_0\left(S_{pro}, S_{H2}\right) X_{pro} - f_1\left(S_{H2}\right) X_{H2} \\
\frac{dX_{H2}}{dt} & = & -DX_{H2} + Y_{H2} f_1\left(S_{H2}\right) X_{H2} - k_{dec,H2} X_{H2}
\end{array}
\right.
$$

- S_{pro} and X_{pro} are propionate substrate and biomass concentrations, S_{H2} and X_{H2} are those for hydrogen
- Y_{pro} and Y_{H2} are the Yield coefficients and $0.43\left(1 - Y_{pro}\right)$ represents the part which goes to hydrogen substrate

$$
f_0\left(S_{pro}, S_{H2}\right) = \frac{k_{m,pro} S_{pro}}{K_{s,pro} + S_{pro}} \frac{1}{1 + \frac{S_{H2}}{K_{I,H2}}}, \quad f_1\left(S_{H2}\right) = \frac{k_{m,H2} S_{H2}}{K_{s,H2} + S_{H2}}
$$

Xu et al. 2011

Maintenance does not affect the stability

$$\begin{cases} \dfrac{dS_{pro}}{dt} = & D\left(S_{pro,in} - S_{pro}\right) - f_0\left(S_{pro}, S_{H2}\right) X_{pro} \\ \dfrac{dX_{pro}}{dt} = & -DX_{pro} + Y_{pro} f_0\left(S_{pro}, S_{H2}\right) X_{pro} - k_{dec,pro} X_{pro} \\ \dfrac{dS_{H2}}{dt} = & -DS_{H2} + 0.43\left(1 - Y_{pro}\right) f_0\left(S_{pro}, S_{H2}\right) X_{pro} - f_1\left(S_{H2}\right) X_{H2} \\ \dfrac{dX_{H2}}{dt} = & -DX_{H2} + Y_{H2} f_1\left(S_{H2}\right) X_{H2} - k_{dec,H2} X_{H2} \end{cases}$$

- Xu et al. 2011 : For ADM1 consensus parameter values, the positive steady state is stable as long as it exists (numerical verification)
- Sari & Harmand 2014 : for all values of the parameters the positive steady state is stable as long as it exists

Xu et al. 2011, Sari & Harmand 2014

Change of notation

$$\begin{cases} \dot{S}_0 &= D(S_0^{in} - S_0) - f_0(S_0, S_1)X_0 \\ \dot{X}_0 &= Y_0 f_0(S_0, S_1)X_0 - DX_0 - a_0 X_0 \\ \dot{S}_1 &= Y_2 f_0(S_0, S_1)X_0 - DS_1 - f_1(S_1)X_1 \\ \dot{X}_1 &= Y_1 f_1(S_1)X_1 - DX_1 - a_1 X_1 \end{cases}$$

- Maintenance does not affect the stability of the food chain, for general growth function

$$\frac{\partial f_0}{\partial S_0} > 0, \quad \frac{\partial f_0}{\partial S_1} < 0, \quad \frac{df_1}{dS_1} > 0$$

Sari & Harmand 2014

Rescaling

$$s_0 = Y_2 S_0, \;\; x_0 = \frac{Y_2}{Y_0} X_0, \;\; s_1 = S_1, \;\; x_1 = \frac{1}{Y_1} X_1, \;\; s_0^{in} = Y_2 S_0^{in}$$

$$\left\{ \begin{array}{lcl} \frac{ds_0}{dt} & = & D(s_0^{in} - s_0) - \mu_0(s_0, s_1) x_0 \\ \frac{dx_0}{dt} & = & -D x_0 + \mu_0(s_0, s_1) x_0 - a_0 x_0 \\ \frac{ds_1}{dt} & = & -D s_1 + \mu_0(s_0, s_1) x_0 - \mu_1(s_1) x_1 \\ \frac{dx_1}{dt} & = & -D x_1 + \mu_1(s_1) x_1 - a_1 x_1 \end{array} \right.$$

where

$$\mu_0(s_0, s_1) = Y_0 f_0 \left(\frac{1}{Y_2} s_0, s_1 \right), \quad \mu_1(s_1) = Y_1 f_1(s_1)$$

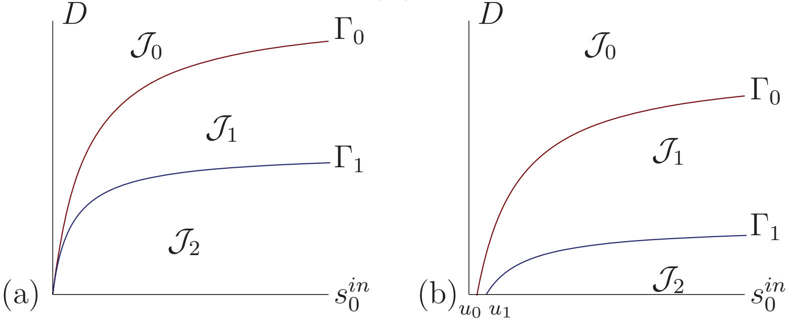
Steady states

$$
\begin{cases}
\frac{ds_0}{dt} & = & D(s_0^{in} - s_0) - \mu_0(s_0, s_1)x_0 \\
\frac{dx_0}{dt} & = & -Dx_0 + \mu_0(s_0, s_1)x_0 - a_0 x_0 \\
\frac{ds_1}{dt} & = & -Ds_1 + \mu_0(s_0, s_1)x_0 - \mu_1(s_1)x_1 \\
\frac{dx_1}{dt} & = & -Dx_1 + \mu_1(s_1)x_1 - a_1 x_1
\end{cases}
$$

- SS0 : $x_0 = 0$, $x_1 = 0$ where both species are washed out.
- SS1 : $x_0 > 0$, $x_1 = 0$, where species x_1 is washed out while x_0 survives.
- SS2 : $x_0 > 0$, $x_1 > 0$, where both species survives.

Xu et al. 2011, Sari & Harmand 2014

Operating diagram without (a) and with (b) maintenance effects



Region	SS0	SS1	SS2
$(s_0^{in}, D) \in \mathcal{J}_0$	S		
$(s_0^{in}, D) \in \mathcal{J}_1$	U	S	
$(s_0^{in}, D) \in \mathcal{J}_2$	U	U	S

Plan du cours

Chlorophenol degradation

$$\frac{\mathrm{d}X_{\mathrm{ch}}}{\mathrm{d}t} = -DX_{\mathrm{ch}} + Y_{\mathrm{ch}} f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}} - k_{\mathrm{dec,ch}} X_{\mathrm{ch}}$$

$$\frac{\mathrm{d}X_{\mathrm{ph}}}{\mathrm{d}t} = -DX_{\mathrm{ph}} + Y_{\mathrm{ph}} f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ph}} - k_{\mathrm{dec,ph}} X_{\mathrm{ph}}$$

$$\frac{\mathrm{d}X_{\mathrm{H_2}}}{\mathrm{d}t} = -DX_{\mathrm{H_2}} + Y_{\mathrm{H_2}} f_2\left(S_{\mathrm{H_2}}\right) X_{\mathrm{H_2}} - k_{\mathrm{dec,H_2}} X_{\mathrm{H_2}}$$

$$\frac{\mathrm{d}S_{\mathrm{ch}}}{\mathrm{d}t} = D\left(S_{\mathrm{ch,in}} - S_{\mathrm{ch}}\right) - f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}}$$

$$\frac{\mathrm{d}S_{\mathrm{ph}}}{\mathrm{d}t} = D\left(S_{\mathrm{ph,in}} - S_{\mathrm{ph}}\right) + \frac{224}{208}\left(1 - Y_{\mathrm{ch}}\right) f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}} - f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ph}}$$

$$\frac{\mathrm{d}S_{\mathrm{H_2}}}{\mathrm{d}t} = \left(S_{\mathrm{H_2,in}} - S_{\mathrm{H_2}}\right) + \frac{32}{224}\left(1 - Y_{\mathrm{ph}}\right) f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ph}} - \frac{16}{208} f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H_2}}\right) X_{\mathrm{ch}} - f_2\left(S_{\mathrm{H_2}}\right) X_{\mathrm{H_2}}$$

Chlorophenol degradation

- S_{ch} and X_{ch} are the chlorophenol substrate and biomass concentrations
- S_{ph} and X_{ph} those for phenol and S_{H_2} and X_{H_2} those for hydrogen
- Y_{ch}, Y_{ph} and Y_{H2} are the yield coefficients,
- $224/208\,(1-Y_{\mathrm{ch}})$ represents the part of chlorophenol degraded to phenol,
- $32/224\,(1-Y_{\mathrm{ph}})$ represents the part of phenol that is transformed to hydrogen

Growth functions take Monod form with hydrogen inhibition acting on the phenol degrader.

$$f_0\left(S_{\mathrm{ch}}, S_{\mathrm{H}_2}\right) = \frac{k_{m,\mathrm{ch}} S_{\mathrm{ch}}}{K_{S,ch}+S_{\mathrm{ch}}} \frac{S_{H_2}}{K_{S,\mathrm{H}_2,\mathrm{c}}+S_{\mathrm{H}_2}}$$

$$f_1\left(S_{\mathrm{ph}}, S_{\mathrm{H}_2}\right) = \frac{k_{m,\mathrm{ph}} S_{\mathrm{ph}}}{K_{S,\mathrm{ph}}+S_{\mathrm{ph}}} \frac{1}{1+\frac{S_{\mathrm{H}_2}}{K_{i,\mathrm{H}_2}}}, \qquad f_2\left(S_{\mathrm{H}_2}\right) = \frac{k_{m,\mathrm{H}_2} S_{\mathrm{H}_2}}{K_{S,\mathrm{H}_2}+S_{\mathrm{H}_2}}$$

Wade et al. 2015, Sari et Wade 2015

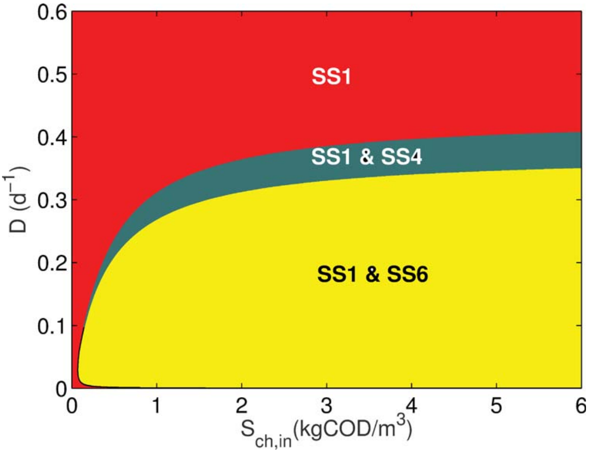


FIG. 2. Steady–state diagram for operational parameters D and $S_{\mathrm{ch,in}}$ in the three-tier chlorophenol model ($S_{\mathrm{ph,in}} = S_{\mathrm{H_2,in}} = 0$).

The system has 3 steady states SS1, SS4 and SS6. The diagram indicates the stable steady states

Wade et al. 2015

Change of notations and resacling

$$\frac{\mathrm{d}X_0}{\mathrm{d}t} = -DX_0 + Y_0 f_0(S_0, S_2) X_0 - a_0 X_0$$
$$\frac{\mathrm{d}X_1}{\mathrm{d}t} = -DX_1 + Y_1 f_1(S_1, S_2) X_1 - a_1 X_1$$
$$\frac{\mathrm{d}X_2}{\mathrm{d}t} = -DX_2 + Y_2 f_2(S_2) X_2 - a_2 X_2$$
$$\frac{\mathrm{d}S_0}{\mathrm{d}t} = D\left(S_0^{\mathrm{in}} - S_0\right) - f_0(S_0, S_2) X_0$$
$$\frac{\mathrm{d}S_1}{\mathrm{d}t} = D\left(S_1^{\mathrm{in}} - S_1\right) + Y_3 f_0(S_0, S_2) X_0 - f_1(S_1, S_2) X_1$$
$$\frac{\mathrm{d}S_2}{\mathrm{d}t} = D\left(S_2^{\mathrm{in}} - S_2\right) + Y_4 f_1(S_1, S_2) X_1 - Y_5 f_0(S_0, S_2) X_0 - f_2(S_2) X_2$$

Rescaling

$$x_0 = \frac{Y_3 Y_4}{Y_0} X_0, \quad x_1 = \frac{Y_4}{Y_1} X_1, \quad x_2 = \frac{1}{Y_2} X_1$$
$$s_0 = Y_3 Y_4 S_0, \quad s_1 = Y_4 S_1, \quad s_2 = S_2$$

Rescaling

$$\frac{\mathrm{d}x_0}{\mathrm{d}t} = -Dx_0 + \mu_0(s_0, s_2)\, x_0 - a_0 x_0$$

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = -Dx_1 + \mu_1(s_1, s_2)\, x_1 - a_1 x_1$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = -Dx_2 + \mu_2(s_2)\, x_2 - a_2 x_2$$

$$\frac{\mathrm{d}s_0}{\mathrm{d}t} = D\left(s_0^{\mathrm{in}} - s_0\right) - \mu_0(s_0, s_2)\, x_0$$

$$\frac{\mathrm{d}s_1}{\mathrm{d}t} = D\left(s_1^{\mathrm{in}} - s_1\right) + \mu_0(s_0, s_2)\, x_0 - \mu_1(s_1, s_2)\, x_1$$

$$\frac{\mathrm{d}s_2}{\mathrm{d}t} = D\left(s_2^{\mathrm{in}} - s_2\right) + \mu_1(s_1, s_2)\, x_1 - \omega\mu_0(s_0, s_2)\, x_0 - \mu_2(s_2)\, x_2$$

$$\mu_0(s_0, s_2) = \frac{m_0 s_0}{K_0 + s_0}\frac{s_2}{L_0 + s_2}, \quad \mu_1(s_1, s_2) = \frac{m_1 s_1}{K_1 + s_1}\frac{1}{1 + s_2/K_i},$$

$$\mu_2(s_2) = \frac{m_2 s_2}{K_2 + s_2}, \quad \omega = \frac{Y_5}{Y_3 Y_4} = \frac{1}{2(1 - Y_0)(1 - Y_1)}$$

General growth functions

We assume only that the growth functions are positive and satisfy

- H1 $\mu_0(s_0, s_2) < +\infty$, $\mu_0(0, s_2) = 0$, $\mu_0(s_0, 0) = 0$.
- H2 $\mu_1(s_1, s_2) < +\infty$, $\mu_1(0, s_2) = 0$.
- H3 $0 < \mu_2(s_2) < +\infty$, $\mu_2(0) = 0$.
- H4 $\frac{\partial \mu_0}{\partial s_0}(s_0, s_2) > 0$, $\frac{\partial \mu_0}{\partial s_2}(s_0, s_2) > 0$.
- H5 $\frac{\partial \mu_1}{\partial s_1}(s_1, s_2) > 0$,, $\frac{\partial \mu_1}{\partial s_2}(s_1, s_2) < 0$.
- H6 $\frac{d\mu_2}{ds_2}(s_2) > 0$.
- H7 $s_2 \mapsto \mu_0(+\infty, s_2)$ is monotonically increasing
- H8 $s_2 \mapsto \mu_1(+\infty, s_2)$ is monotonically decreasing.

These properties are satisfied by

$\mu_0(s_0, s_2) = \frac{m_0 s_0}{K_0 + s_0} \frac{s_2}{L_0 + s_2}$

$\mu_1(s_1, s_2) = \frac{m_1 s_1}{K_1 + s_1} \frac{1}{1 + s_2/K_i}$

$\mu_2(s_2) = \frac{m_2 s_2}{K_2 + s_2}$

Steady-states when $s_1^{\text{in}} = s_2^{\text{in}} = 0$

$$[\mu_0(s_0, s_2) - D - a_0]\, x_0 = 0 \qquad (1)$$

$$[\mu_1(s_1, s_2) - D - a_1]\, x_1 = 0 \qquad (2)$$

$$[\mu_2(s_2) - D - a_2]\, x_2 = 0 \qquad (3)$$

$$D\left(s_0^{\text{in}} - s_0\right) - \mu_0(s_0, s_2)\, x_0 = 0 \qquad (4)$$

$$-Ds_1 + \mu_0(s_0, s_2)\, x_0 - \mu_1(s_1, s_2)\, x_1 = 0 \qquad (5)$$

$$-Ds_2 + \mu_1(s_1, s_2)\, x_1 - \omega\mu_0(s_0, s_2)\, x_0 - \mu_2(s_2)\, x_2 = 0 \qquad (6)$$

- $x_0 = 0 \Longrightarrow x_1 = 0$ and $x_2 = 0$, $x_1 = 0 \Longrightarrow x_0 = 0$ and $x_2 = 0$
- If $x_0 = 0$, then (4) $\Longrightarrow s_0 = s_0^{\text{in}}$ and (5) $\Longrightarrow Ds_1 + \mu_1(s_1, s_2)x_1 = 0$, Thus $s_1 = 0$ and $\mu_1(s_1, s_2)x_1 = 0$. Therefore (2) $\Longrightarrow x_1 = 0$ and (6) $\Longrightarrow Ds_2 + \mu_2(s_2)x_2 = 0$ Thus $s_2 = 0$ and $\mu_2(s_2)x_2 = 0$. Therefore, (3) $\Longrightarrow x_2 = 0$.
- If $x_1 = 0$, then (6) $\Longrightarrow Ds_2 + \omega\mu_0(s_0, s_2)x_0 + \mu_2(s_2)x_2 = 0$. Thus $s_2 = 0$, $\mu_0(s_0, s_2)x_0 = 0$ and $\mu_2(s_2)x_2 = 0$. Therefore, (1) $\Longrightarrow x_0 = 0$.

Steady-state SS1

- **Proposition 1**. The only steady-state, for which $x_0 = 0$ or $x_1 = 0$, is the steady-state

$$\mathrm{SS1} = (x_0 = 0, x_1 = 0, x_2 = 0, s_0 = s_0^{\mathrm{in}}, s_1 = 0, s_2 = 0)$$

where all species are washed out. This steady-state always exists. It is always stable.

Besides the steady-state SS1, the system can have at most two other steady-states.

- SS2 : $x_0 > 0$, $x_1 > 0$ and $x_2 = 0$, where species x_2 is washed out while species x_0 and and x_1 exist.
- SS3 : $x_0 > 0$, $x_1 > 0$, and $x_2 > 0$, where all populations are maintained.

SS2 : $x_0 > 0$, $x_1 > 0$ and $x_2 = 0$

$$[\mu_0(s_0, s_2) - D - a_0]\, x_0 = 0 \tag{7}$$

$$[\mu_1(s_1, s_2) - D - a_1]\, x_1 = 0 \tag{8}$$

$$[\mu_2(s_2) - D - a_2]\, x_2 = 0 \tag{9}$$

$$D\left(s_0^{\mathrm{in}} - s_0\right) - \mu_0(s_0, s_2)\, x_0 = 0 \tag{10}$$

$$-Ds_1 + \mu_0(s_0, s_2)\, x_0 - \mu_1(s_1, s_2)\, x_1 = 0 \tag{11}$$

$$-Ds_2 + \mu_1(s_1, s_2)\, x_1 - \omega\mu_0(s_0, s_2)\, x_0 - \mu_2(s_2)\, x_2 = 0 \tag{12}$$

- If $x_0 > 0$ and $x_1 > 0$, then, (7) and (8) imply $\mu_0(s_0, s_2) = D + a_0$ and $\mu_1(s_1, s_2) = D + a_1$. Hence, $s_0 = M_0(D + a_0, s_2)$ and $s_1 = M_1(D + a_1, s_2)$.
- (10) and (11) imply $x_0 = \frac{D}{D+a_0}(s_0^{\mathrm{in}} - s_0)$ and $x_1 = \frac{D}{D+a_1}(s_0^{\mathrm{in}} - s_0 - s_1)$
- Therefore

$$(12) \Longrightarrow -s_2 + (s_0^{\mathrm{in}} - s_0 - s_1) - \omega(s_0^{\mathrm{in}} - s_0) = 0$$

If $\omega \geq 1$ this equation has no solution. If $\omega < 1$ this equation is equivalent to

$$s_0^{\mathrm{in}} = s_0 + \frac{s_1 + s_2}{1 - \omega}.$$

Steady-state SS2

Proposition 2. If $\omega \geq 1$ then SS2 does not exist. If $\omega < 1$ then SS2 exists if, and only if, $s_0^{\mathrm{in}} \geq F_1(D)$. If $s_0^{\mathrm{in}} \geq F_1(D)$ then each solution s_2 of equation $\psi(s_2) = s_0^{\mathrm{in}}$ gives a steady-state $\mathrm{SS2} = (x_0, x_1, x_2 = 0, s_0, s_1, s_2)$ where

$$s_0 = M_0(D + a_0, s_2), \quad s_1 = M_1(D + a_1, s_2)$$

$$x_0 = \frac{D}{D + a_0}(s_0^{\mathrm{in}} - s_0), \quad x_1 = \frac{D}{D + a_1}(s_0^{\mathrm{in}} - s_0 - s_1)$$

$$s_0 = M_0(D + a_0, s_2) \Longleftrightarrow D + a_0 = \mu_0(s_0, s_2)$$

$$s_1 = M_1(D + a_1, s_2) \Longleftrightarrow D + a_1 = \mu_1(s_1, s_2)$$

$$\psi(s_2) = M_0(D + a_0, s_2) + \frac{M_1(D + a_1, s_2) + s_2}{1 - \omega},$$

$$F_1(D) = \inf_{s_2} \psi(s_2)$$

The function $\psi(s_2)$ and $F_1(D)$

- The function $\psi(s_2) = M_0(D + a_0, s_2) + \frac{M_1(D+a_1,s_2)+s_2}{1-\omega}$ is defined for $s_2^1 < s < s_2^1$ where s_2^1 and s_2^2 are given by

$$\mu_0(+\infty, s_2^0) = D + a_0, \quad \mu_1(+\infty, s_2^1) = D + a_1$$

- $\psi(s_2) > 0$ for $s_2^0 < s_2 < s_2^1$ and

$$\lim_{s_2 \to s_2^0} \psi(s_2) = \lim_{s_2 \to s_2^1} \psi(s_2) = +\infty$$

- We define $F_1(D) = \inf_{s_2 \in (s_2^0, s_2^1)} \psi(s_2)$
- If $s_0^{\text{in}} > F_1(D)$ then equation $\psi(s_2) = s_0^{\text{in}}$ has exactly two solutions denoted by $s_2^\flat$ and $s_2^\sharp$. To these solutions, $s_2^\flat$ and $s_2^\sharp$, correspond two steady-states of SS2, which are denoted by $\mathrm{SS2}^\flat$ and $\mathrm{SS2}^\sharp$.

SS3 : $x_0 > 0$, $x_1 > 0$ and $x_2 > 0$

$$\left[\mu_0\left(s_0, s_2\right) - D - a_0\right] x_0 = 0 \tag{13}$$
$$\left[\mu_1\left(s_1, s_2\right) - D - a_1\right] x_1 = 0 \tag{14}$$
$$\left[\mu_2\left(s_2\right) - D - a_2\right] x_2 = 0 \tag{15}$$
$$D\left(s_0^{\text{in}} - s_0\right) - \mu_0\left(s_0, s_2\right) x_0 = 0 \tag{16}$$
$$-Ds_1 + \mu_0\left(s_0, s_2\right) x_0 - \mu_1\left(s_1, s_2\right) x_1 = 0 \tag{17}$$
$$-Ds_2 + \mu_1\left(s_1, s_2\right) x_1 - \omega\mu_0\left(s_0, s_2\right) x_0 - \mu_2\left(s_2\right) x_2 = 0 \tag{18}$$

- If $x_0 > 0$, $x_1 > 0$ and $x_2 > 0$, then, (13), (14) and (15) imply $\mu_0(s_0, s_2) = D + a_0$, $\mu_1(s_1, s_2) = D + a_1$ and $\mu_2(s_2) = D + a_2$. Hence, $s_2 = M_2(D + a_2)$, $s_0 = M_0(D + a_0, s_2)$ and $s_1 = M_1(D + a_1, s_2)$.
- (16), (17) and (18) imply $x_0 = \frac{D}{D+a_0}(s_0^{\text{in}} - s_0)$, $x_1 = \frac{D}{D+a_1}(s_0^{\text{in}} - s_0 - s_1)$ and $x_2 = \frac{D}{D+a_2}\left((1-\omega)(s_0^{\text{in}} - s_0) - s_1 - s_2\right)$
- $x_i > 0$ iff $s_0^{\text{in}} > \psi\left(s_2\right)$

Steady-state SS3

Proposition 3. If $\omega \geq 1$ then SS3 does not exist. If $\omega < 1$ then SS3 exists if, and only if, $s_0^{\text{in}} > F_2(D)$. If $s_0^{\text{in}} > F_2(D)$ then the steady-state $\mathrm{SS3} = (x_0, x_1, x_2, s_0, s_1, s_2)$ is given by

$$s_0 = M_0(D + a_0, M_2(D + a_2))$$
$$s_1 = M_1(D + a_1, M_2(D + a_2))$$
$$s_2 = M_2(D + a_2)$$

and

$$x_0 = \frac{D}{D + a_0}(s_0^{\text{in}} - s_0), \quad x_1 = \frac{D}{D + a_1}(s_0^{\text{in}} - s_0 - s_1)$$
$$x_2 = \frac{D}{D + a_2}\left((1 - \omega)(s_0^{\text{in}} - s_0) - s_1 - s_2\right)$$

$$s_2 = M_2(D + a_2) \Longleftrightarrow D + a_2 = \mu_2(s_2)$$

$$F_2(D) = \psi\left(M_2(D + a_2)\right)$$

Notations

$$s_0 = M_0(D + a_0, s_2) \iff D + a_0 = \mu_0(s_0, s_2)$$

$$s_1 = M_1(D + a_0, s_2) \iff D + a_1 = \mu_1(s_1, s_2)$$

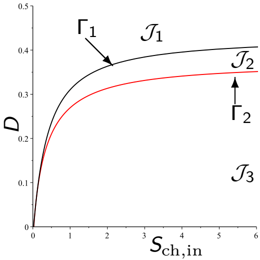
$$s_2 = M_2(D + a_2) \iff D + a_2 = \mu_2(s_2)$$

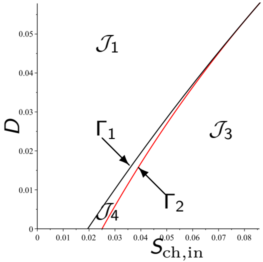
$$\psi(s_2) = M_0(D + a_0, s_2) + \frac{M_1(D + a_1, s_2) + s_2}{1 - \omega},$$

$$F_1(D) = \inf_{s_2} \psi(s_2)$$

$$F_2(D) = \psi\left(M_2(D + a_2)\right)$$

Since $F_1(D) \leq F_2(D)$, the condition $s_0^{\mathrm{in}} > F_2(D)$ for the existence of SS3 implies that the condition $s_0^{\mathrm{in}} > F_2(D)$ for the existence of $\mathrm{SS2}^{\flat}$ and $\mathrm{SS2}^{\sharp}$ is satisfied.





Region	Steady states
$\mathcal{J}_1$	SS1
$\mathcal{J}_2 \cup \mathcal{J}_4$	SS1, $\mathrm{SS2}^\flat$, $\mathrm{SS2}^\sharp$
$\mathcal{J}_3$	SS1, $\mathrm{SS2}^\flat$, $\mathrm{SS2}^\sharp$, SS3

Model without maintenance

The change of variables

$$z_0 = s_0 + x_0, \quad z_1 = s_1 + x_1 - x_0, \quad z_2 = s_2 + x_2 + \omega x_0 - x_1$$

Therefore, the model with $a_0 = a_1 = a_2 = 0$, become

$$\begin{aligned}
\frac{\mathrm{d}x_0}{\mathrm{d}t} &= -Dx_0 + \mu_0\left(z_0 - x_0, z_2 - \omega x_0 + x_1 - x_2\right)x_0 \\
\frac{\mathrm{d}x_1}{\mathrm{d}t} &= -Dx_1 + \mu_1\left(z_1 + x_0 - x_1, z_2 - \omega x_0 + x_1 - x_2\right)x_1 \\
\frac{\mathrm{d}x_2}{\mathrm{d}t} &= -Dx_2 + \mu_2\left(z_2 - \omega x_0 + x_1 - x_2\right)x_2 \\
\frac{\mathrm{d}z_0}{\mathrm{d}t} &= D\left(s_0^{\mathrm{in}} - z_0\right) \\
\frac{\mathrm{d}z_1}{\mathrm{d}t} &= -Dz_1 \\
\frac{\mathrm{d}z_2}{\mathrm{d}t} &= -Dz_2
\end{aligned}$$

Stability without maintenance

Proposition 4.

- SS2 is stable if, and only if, $\mu_2(s_2) < D$ and $\frac{d\psi}{ds_2} > 0$.
- If $F_3(D) \geq 0$ then SS3 is stable as long as it exists.
- If $F_3(D) < 0$ then SS3 is stable if, and only if, $F_4\left(D, s_0^{\text{in}}\right) > 0$.

$$F_3(D) = \frac{d\psi}{ds_2}\left(M_2(D)\right)$$

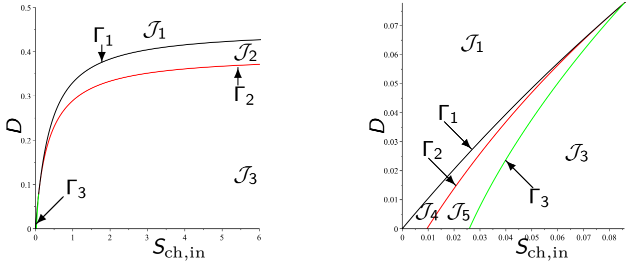
$$F_4\left(D, s_0^{\text{in}}\right) = \left(EIx_0x_2 + \left[E(G+H) - (1-\omega)FG\right]x_0x_1\right)f_2 \\ + \left(Ix_2 + (G+H)x_1 + \omega Fx_0\right)GIx_1x_2$$

where $f_2 = Ix_2 + (G+H)x_1 + (E+\omega F)x_0$ and

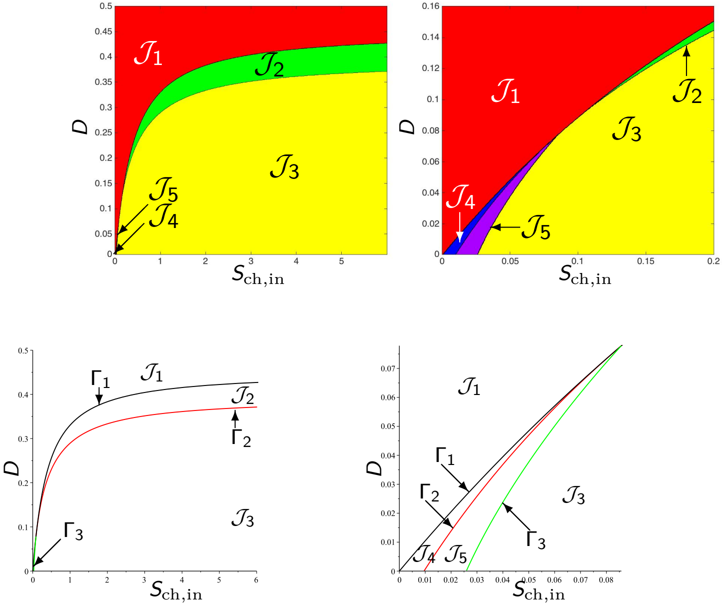
$$E=\frac{\partial\mu_0}{\partial s_0}, \quad F=\frac{\partial\mu_0}{\partial s_2}, \quad G=\frac{\partial\mu_1}{\partial s_1}, \quad H=-\frac{\partial\mu_1}{\partial s_2}, \quad I=\frac{d\mu_2}{ds_2}$$

evaluated at the steady-state SS3, that is to say, for

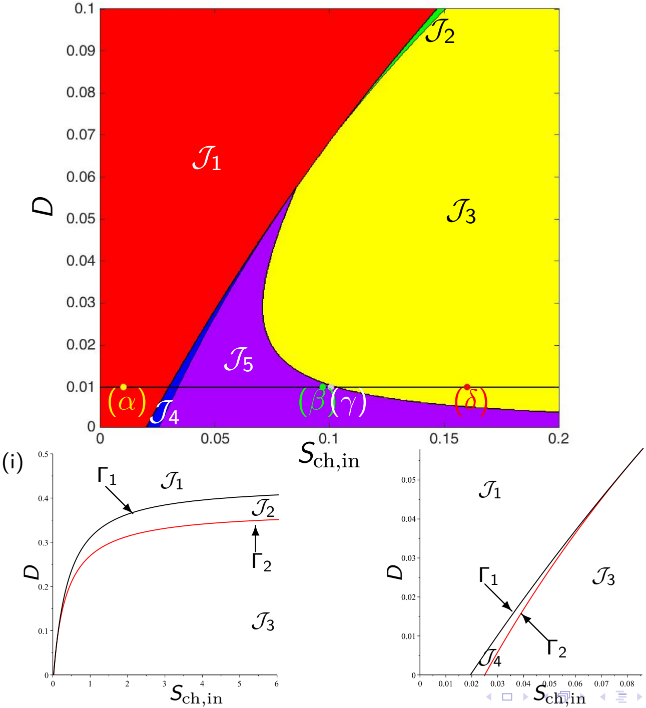
$$s_2 = M_2(D), \quad s_0 = M_0(D, s_2), \quad s_1 = M_1(D, s_2)$$



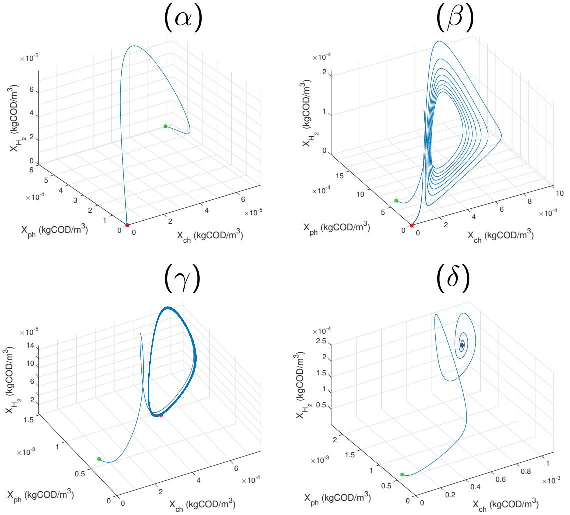
Region	SS1	$SS2^\flat$	$SS2^\sharp$	SS3
$\mathcal{J}_1$	S			
$\mathcal{J}_2$	S	U	S	
$\mathcal{J}_3$	S	U	U	S
$\mathcal{J}_4$	S	U	U	
$\mathcal{J}_5$	S	U	U	U



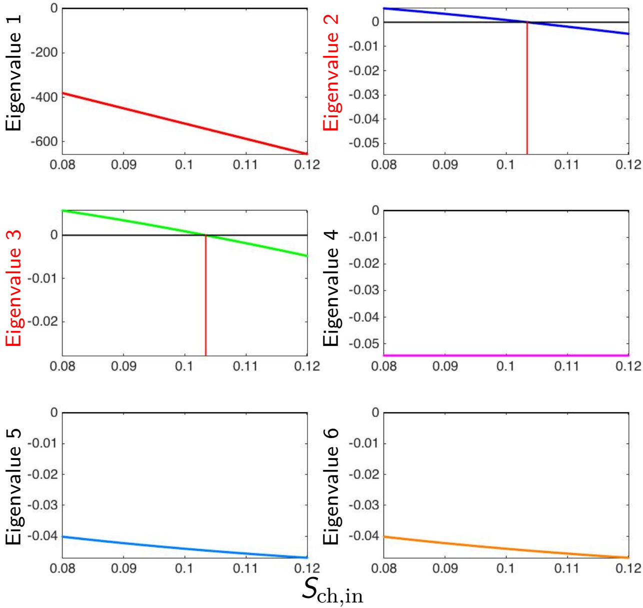
$\mathcal{J}_1$
$\mathcal{J}_2$
$\mathcal{J}_3$
$\mathcal{J}_4$
$\mathcal{J}_5$
D
$S_{\mathrm{ch,in}}$
Γ_1
Γ_2
Γ_3



$\mathcal{J}_1$
$\mathcal{J}_2$
$\mathcal{J}_3$
$\mathcal{J}_4$
$\mathcal{J}_5$
(α)
(β)
(γ)
(δ)
D
$S_{\mathrm{ch,in}}$
(i)
Γ_1
Γ_2



(α)
(β)
(γ)
(δ)
X_{H_2} (kgCOD/m^3)
X_{ph} (kgCOD/m^3)
X_{ch} (kgCOD/m^3)



Eigenvalue 1
Eigenvalue 2
Eigenvalue 3
Eigenvalue 4
Eigenvalue 5
Eigenvalue 6
0
-200
-400
-600
-0.01
-0.02
-0.03
-0.04
-0.05
0.08
0.09
0.1
0.11
0.12
$S_{\mathrm{ch,in}}$

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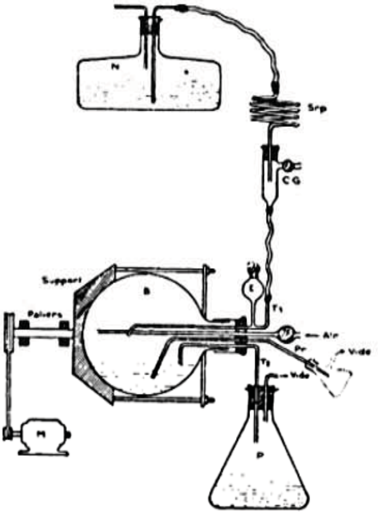

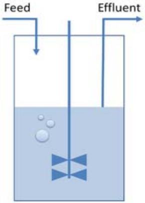

FIG. 4. — Montage d'un appareil à croissance continue. N, nourrice; Srp, serpentin capillaire; C.G., compte-gouttes; B, ballon rotatif; T_1, tubulure d'arrivée; E, tubulure d'ensemencement; Pr, tubulure de prélèvement (en pointillé, fiole de prélèvement); T_2, tubulure de niveau; P, produit; M, moteur.