The buffered chemostat with non-monotonic response functions ⋆

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Abstract: We show how a particular spatial structure with a buffer globally stabilizes the chemostat dynamics with non-monotonic response function, while this is not possible with single, serial or parallel chemostats of the same total volume and input flow. We give a characterization of the set of such configurations that satisfy this property, as well as the configuration that ensures the best nutrient conversion. Furthermore, we characterize the minimal buffer volume to be added to a single chemostat for obtaining the global stability. These results are illustrated with the Haldane kinetic function.

Keywords: chemostat, interconnection, bi-stability, global asymptotic stability, optimization.

1. INTRODUCTION

The mathematical model of the chemostat has been extensively studied in the literature (see e.g. [21]). However, in many applications, the assumption of perfectly mixed chemostats has to be relaxed. In the eighties, the gradostat has been proposed to represent spatial gradient [10], and has led to several mathematical studies [23, 18, 20, 4]. An interest for series of bioreactors appeared in biochemical industry, with tanks of possibly different volumes to be optimized [11, 8, 7]. Relatively few studies have considered non-serial interconnections of chemostats [19]. In natural reservoirs such as in undergrounds or ground-waters, a spatial structure with interconnections between several volumes is often considered, each of them being approximated as perfectly mixed. Those interconnections can be parallel, series or built up in more complex networks. To our knowledge, the influence of the topology of a network of chemostats on the overall dynamics has been sparsely investigated in the literature. However, the simple consideration of two different habitats can lead to non-intuitive behaviors [22, 12, 16, 9] and influence significantly the overall performances [13, 5].
It happens also that microbial growth can be inhibited by large concentrations of nutrient [1] and lead to instability in the chemostat [2, 21]. Several control strategies of the input flow have been proposed in the literature to globally stabilize such systems [3, 6, 15, 17] but the ability of a spatial structure to passively stabilize such dynamics has not been yet studied. This is the matter of the present work. Because of lack of place and technicalities, the proofs are not given but are all available in a research report [14].

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2. THE BUFFERED CONNECTION

We consider the chemostat model with a single tank of volume V and input flow Q, where S and X denote the substrate and biomass concentration, respectively:

$$\begin{aligned} \dot{S} &= -\mu(S)X + \frac{Q}{V}(S_{in} - S) \ , \\ \dot{X} &= \mu(S)X - \frac{Q}{V}X \ , \end{aligned} \tag{1}$$

Without loss of generality, we shall keep $Q/V = 1$. We assume that the growth function $\mu(\cdot)$ present an inhibition:

Assumption A1. The function $\mu(\cdot)$ is $C^\infty([0, +\infty))$ and such that $\mu(0) = 0$, $\mu(S) > 0$ for any $S > 0$. Moreover there exists a number $\hat{S} > 0$ such that μ is increasing on $(0, \hat{S})$ and decreasing on $(\hat{S}, +\infty)$.

Classically, we consider the set $\Lambda = \{S > 0 \mid \mu(S) > 1\} = (\lambda_-, \lambda_+)$. We assume to be in the bi-stable case, that is: there exists two stable equilibria: the (undesired) wash-out and a (desired) positive one:

Assumption A2. $\lambda_- < \lambda_+ < S_{in}$.

We consider spatial configurations with the same total volume V and input flow Q. Under Assumption A2, one can check that having a volume V split in several smaller volumes V_i interconnected in series or in parallel leads necessarily to a global dynamics with bi-stability or the wash-out as the only equilibrium in at least one of the tanks. In the present work, we study a particular spatial configuration of two tanks, one of them serving as a buffer (see Figure 1) The dynamical equations of this system are

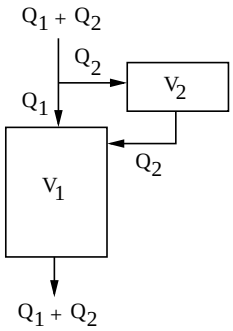

Fig. 1. The buffered chemostat.

$$\begin{aligned}
\dot{S}_1 &= -\mu(S_1)X_1 + \frac{Q_1 S_{in} + Q_2 S_2 - Q S_1}{V_1} \ , \\
\dot{X}_1 &= \mu(S_1)X_1 + \frac{Q_2 X_2 - Q X_1}{V_1} \ , \\
\dot{S}_2 &= -\mu(S_2)X_2 + \frac{Q_2 S_{in} - Q_2 S_2}{V_2} \ , \\
\dot{X}_2 &= \mu(S_2)X_2 - \frac{Q_2 X_2}{V_2} \ .
\end{aligned} \tag{2}$$

with $V = V_1 + V_2$ and $Q = Q_1 + Q_2$. We describe the set of all such configurations by two parameters $r \in (0,1)$ and $\alpha > 0$, defined as follows:

$$r = \frac{V_1}{V}, \quad \alpha = \frac{Q_2}{(1-r)Q} \ .$$

Notice that $r = 0$ corresponds to a "by-pass" of the volume V, a limiting case already considered in [7].

3. STUDY OF EQUILIBRIA

One can easily see that the equilibria $(S_1^\star, X_1^\star, S_2^\star, X_2^\star)$ of (2) are solutions of the system of equations:

$$\begin{aligned}
1 + \frac{1-r}{r}\left(1 - \alpha\frac{S_{in} - S_2^\star}{S_{in} - S_1^\star}\right) = \mu(S_1^\star) \text{ or } S_1^\star = S_{in} \ , \\
X_1^\star = S_{in} - S_1^\star \ , \\
\mu(S_2^\star) = \alpha \text{ or } S_2^\star = S_{in} \ , \\
X_2^\star = S_{in} - S_2^\star \ .
\end{aligned}$$

Due to the cascade structure of the model (2), the study of the dynamics of the second reactor can be done independently of the first one. Under Assumptions A1 and A2, one can straightforwardly check that

- there exists an unique positive equilibrium $(S_2^\star, X_2^\star)$ in the second tank exactly when α belongs to the set $(0, \mu(S_{in})]$. Let us then denote $S_2^\star(\alpha)$ the unique solution of $\mu(S_2) = \alpha$ in $(0, S_{in})$.
- for any fixed $\alpha \in (0), \mu(S_{in})]$, a positive equilibrium $(S_1^\star, X_1^\star)$ has to fulfill

$$\phi_{\alpha,r}(S_1^\star) = \mu(S_1^\star)$$

where the function $\phi_{\alpha,r}(\cdot)$ is defined as follows:

$$\phi_{\alpha,r}(s) = 1 + \frac{1-r}{r}\left(1 - \alpha\frac{S_{in} - S_2^\star(\alpha)}{S_{in} - s}\right)$$

that is to claim that $S_1^\star$ is the abscissa of an intersection of the graph of $\mu(\cdot)$ with the hyperbola $H_{\alpha,r}$, graph of the function $\phi_{\alpha,r}(\cdot)$. We define then the family of sets

$$\mathcal{R}(\alpha) = \{r \in (0,1) \mid \exists! s \in (0, S_{in}) \text{ s.t. } \phi_{\alpha,r}(s) = \mu(s)\}$$

parametrized by $\alpha \in (0, \mu(S_{in})]$, so that the set $\mathcal{C}$ of pairs (α, r) such that dynamics (2) admits an unique positive equilibrium is given by

$$\mathcal{C} = \{(\alpha, r) \,|\, \alpha \in (0, \mu(S_{in})],\ r \in \mathcal{R}(\alpha)\} \ . \tag{3}$$

For convenience, we shall consider the set of s at which the hyperbola $H_{\alpha,r}$ is tangent to the graph of the function $\mu(\cdot)$ and is locally on one side:

$$\mathcal{S}_{\alpha,r} = \{s \in (\lambda_-, S_{in}) \text{ s.t. } 0 \text{ is a local ext. of } \phi_{\alpha,r} - \mu \text{ at } s\}$$

and define the number

$$\underline{S}(\alpha) = \alpha S_2^\star(\alpha) + (1-\alpha) S_{in} \ . \tag{4}$$

Let also define the subsets:

$$R^-(\alpha) = \{r \mid \exists s \in \mathcal{S}_{\alpha,r} \text{ s.t. } (s - \underline{S}(\alpha))(\lambda_+ - \underline{S}(\alpha)) < 0\} \ ,$$

$$R^+(\alpha) = \{r \mid \exists s \in \mathcal{S}_{\alpha,r} \text{ s.t. } (s - \lambda_+)(\lambda_+ - \underline{S}(\alpha)) \geq 0\} \ .$$

We state now our main result about the multiplicity of equilibria of dynamics (2):

Proposition 1. Assume that A1 and A2 are fulfilled. For any $\alpha \in (0, \mu(S_{in})]$ and $r \in (0,1)$ the dynamics (2) admits a positive equilibrium with $S_1^\star$ such that

$$(\underline{S}(\alpha) - S_1^\star)(\lambda_+ - \underline{S}(\alpha)) \geq 0 \ . \tag{5}$$

The set $R^+(\alpha)$ is non empty, and the set $R^-(\alpha)$ is not reduced to a singleton when it is not empty. One has

$$\mathcal{R}(\alpha) = \begin{cases} (0, \min R^+(\alpha)) \text{ when } R^-(\alpha) = \emptyset \ , \\ (0, \min R^+(\alpha)) \cap (0,1) \setminus [\min R^-(\alpha), \max R^-(\alpha)] \\ \qquad \text{when } R^-(\alpha) \neq \emptyset \ . \end{cases}$$

Furthermore, one has the following properties

- For any $r \in (\min R^+(\alpha), 1)$, there exists at least two equilibria such that $(\underline{S}(\alpha) - S_1^\star)(\lambda_+ - \underline{S}(\alpha)) \geq 0$, and at least four for r in a subset of $(\min R^+(\alpha), 1)$ when $R^+(\alpha)$ is not reduced to a singleton.

- When $R^-(\alpha)$ is non empty, for any r in the interval $(\min R^-(\alpha), \max R^-(\alpha))$, there exists at least three equilibria such that $(\underline{S}(\alpha) - S_1^\star)(\lambda_+ - \underline{S}(\alpha)) < 0$.

Proof. See [14] for the complete proof. One can first check that the equality $\phi_{\alpha,r}(\underline{S}(\alpha)) = 1$ is fulfilled whatever is r. Therefore, we distinguish two cases depending on the relative position of $\underline{S}(\alpha)$ w.r.t. λ^+. The proof consists in giving conditions for the hyperbola $H_{\alpha,r}$ to intersect in only one point the graph of the function $\mu(\cdot)$. The limiting cases correspond to tangent intersections, with abscissa less or greater than λ^+ (see Figures 2 and 3 as illustrations).

For each $\alpha \in (0, \mu(S_{in})]$, we define the number

$$\bar{r}(\alpha) = \sup \mathcal{R}(\alpha) \ .$$

Remark 2. According to Proposition 1, for any α and r such that $r \in \mathcal{R}(\alpha)$, one can define uniquely a number $S_1^\star(\alpha, r) \in (0, S_{in})$ such that

$$\phi_{\alpha,r}(S_1^\star(\alpha, r)) = \mu(S_1^\star(\alpha, r)) \ .$$

The map $(\alpha, r) \mapsto S_1^\star(\alpha, r)$ is clearly continuous and one can then consider the limiting map:

$$\bar{S}_1^\star(\alpha) = \lim_{r < \bar{r}(\alpha), r \to \bar{r}(\alpha)} S_1^\star(\alpha, r) \ .$$

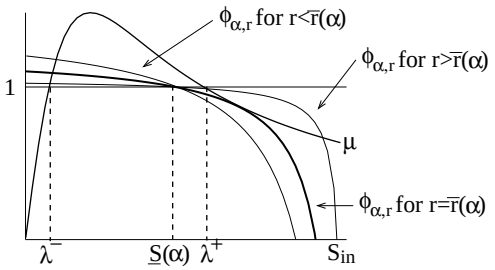

Fig. 2. Family of functions $\phi_{\alpha,r}(\cdot)$ when $\underline{S}(\alpha) < \lambda_+$.

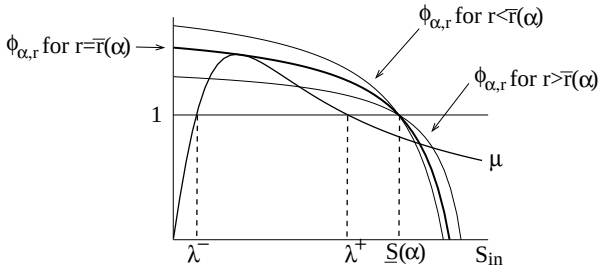

Fig. 3. Family of functions $\phi_{\alpha,r}(\cdot)$ when $\underline{S}(\alpha) > \lambda_+$.

Furthermore, accordingly to Proposition 1, one has $\bar{S}_1^\star(\alpha) \leq \lambda_+$ (resp. $\bar{S}_1^\star(\alpha) \geq \lambda_+$) when $\underline{S}(\alpha) < \lambda_+$ (resp. $\underline{S}(\alpha) > \lambda_+$). Consider, if it exists, a value of α, denoted by $\underline{\alpha}$, that is such that $\underline{S}(\underline{\alpha}) = \lambda_+$. Although one has $\phi_{\underline{\alpha},r}(\lambda_+) = \mu(\lambda_+)$ for any r, there is no reason to have

$$\lim_{\alpha<\underline{\alpha},\alpha\to\underline{\alpha}} \bar{S}_1^\star(\alpha) = \lambda_+ \quad \text{or} \quad \lim_{\alpha>\underline{\alpha},\alpha\to\underline{\alpha}} \bar{S}_1^\star(\alpha) = \lambda_+ \ .$$

Consequently, the map $\alpha \mapsto \bar{r}(\alpha)$ might be discontinuous at such point $\underline{\alpha}$.

Proposition 3. For any configuration $(\alpha, r) \in \mathcal{C}$, any trajectory of the dynamics (2) with $X_2(0) > 0$ converges exponentially to the steady state $E^\star(\alpha, r)$ in forward time.

Proof. see [14].

4. PERFORMANCE OF THE BUFFERED CHEMOSTAT

We first aim at characterizing among all the configurations in the set $\mathcal{C}$ the ones that provide the best conversion of the nutrient at steady state, that is the smallest value of $S_1^\star(\alpha, r)$. For convenience, we consider the function

$$\psi(s) = \mu(s)(S_{in} - s) \tag{6}$$

and define the number

$$\psi^\star = \max_{s\in[0,\bar{s}]} \psi(s) \tag{7}$$

where $\bar{s}$ is defined by

$$\bar{s} = \lim_{\alpha\to\mu(S_{in})} S_2^\star(\alpha) \ .$$

Note that the number $\bar{s}$ is such that $\mu(\bar{s}) = \mu(S_{in})$ with $\bar{s} < S_{in}$. Assumptions A1 and A2 provide the uniqueness of $s^\star$ realizing the maximum in (7), and one can then define the number

$$\alpha^\star = \mu(s^\star) \ . \tag{8}$$

Proposition 4. Assume that Hypotheses A1 and A2 are fulfilled. The best stable configuration consists in choosing $\alpha = \alpha^\star$ (or α arbitrarily close to $\mu(S_{in})$ if $\alpha^\star = \mu(S_{in})$) and

- having a by-pass of the volume V with a flow rate equal to $(1-\alpha)Q$, when $\psi^\star < S_{in} - \lambda_+$. The output concentration at steady state is then equal (or arbitrarily close) to $S_{in} - \psi^\star$.

- choosing any value of $r \in \mathcal{R}(\alpha)$, when $\psi^\star = S_{in} - \lambda_+$. The output concentration at steady state is then equal (or arbitrarily close) to λ_+.

- taking r smaller and arbitrarily close to $\bar{r}(\alpha)$, when $\psi^\star > S_{in} - \lambda_+$. The output at steady state is then arbitrary close to the infimum of $S_1^\star$ on $\mathcal{S}$ (that is necessarily less than λ_+).

Proof. see [14].

Under Assumptions A1 and A2, we study now the benefit of adding to a single chemostat of volume V a buffer of volume V_2 under a constant total input flow $Q = Q_1 + Q_2$, and characterize the minimal value of V_2/V to obtain a global stability of the positive equilibrium.

Similarly, we describe the set of configurations by two non-negative parameters:

$$\alpha = \frac{Q_2}{V_2} \ , \quad \beta = \frac{V_2}{V} \ ,$$

but here one has $V_1 = V$ whatever is the volume V_2. For any number $\alpha \in (0, \mu(S_{in})]$, there exists an unique $S_2^\star(\alpha) \in (0, \bar{s})$ such that $\mu(S_2^\star(\alpha)) = \alpha$, and consequently there exists an unique positive equilibrium in the second tank. The parameter α being fixed, one can straightforwardly check on equations (2) that a positive equilibrium in the first tank fulfills

$$\varphi(S_1^\star) = \alpha\beta(S_{in} - S_2^\star(\alpha)) \tag{9}$$

where the function φ is defined as

$$\varphi(s) = (S_{in} - s)(1 - \mu(s)) \ .$$

Consequently, we are looking for the smallest value of β such that there exists an unique positive solution of (9) on the interval $(0, S_{in})$ (see Figure 4).

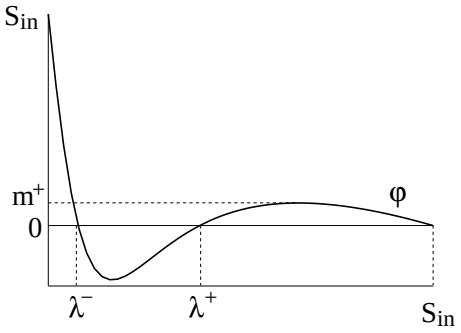

Fig. 4. Graph of the function φ

Proposition 5. Under Assumptions A1 and A2, there exists a buffered configuration with an additional tank of

volume V_2 that possesses a unique globally exponentially stable positive equilibrium from any initial condition with $S_2(0) > 0$, exactly when V_2 fulfills the condition

$$\beta = \frac{V_2}{V} > \frac{\max\limits_{s\in(\lambda_+,S_{in})} \varphi(s)}{\psi^\star} \ , \tag{10}$$

where $\psi^\star$ is defined in (7), with any $\alpha \in (0, \mu(S_{in})]$ such that

$$\max_{s\in(\lambda_+,S_{in})} \varphi(s) < \alpha\beta(S_{in} - S_2^\star(\alpha)) < S_{in} \ .$$

Proof. see [14].

Remark 6. Section 3 has shown the benefit of the buffered chemostat in terms of global stability of the system, but with a price to pay in performances when one imposes to have the same residence time (i.e. the nutrient concentration at steady state is larger than λ_-). When adding a buffer, this is no longer true (i.e. the steady state necessarily exhibits a better performance than λ_-): there always exists a solution $S_1^\star \in (0, \lambda_-)$ of (9), that is unique under conditions of Proposition 5, because $\varphi(0) = S_{in}$, $\varphi(\lambda_-) = 0$ and $\alpha\beta(S_{in} - S_2^\star) \in (0, S_{in})$.

5. ILLUSTRATION AND DISCUSSION

We illustrate the results of the former sections on an non-monotonic uptake function given by the Haldane expression

$$\mu(S) = \frac{\bar\mu S}{K + S + S^2/K_I} \ .$$

One can easily check that for this function the set Λ defined is non empty exactly when the condition

$$\bar\mu > 1 + 2\sqrt{\frac{K}{K_I}}$$

is fulfilled.

Lemma 7. Assume that $\mu(\cdot)$ is an Haldane function and that Assumptions A1 and A2 are fulfilled. For any $\alpha \in (0, \mu(S_{in})]$, the following properties are satisfied.

- the set $R^+(\alpha)$ is a singleton,
- for any $r \in (0, 1)$, the set $\mathcal{S}_{r,\alpha}$ defined is either empty or a singleton,
- if the set $R^-(\alpha)$ is non empty, then one has $\max R^-(\alpha) < R^+(\alpha)$.

Proof. In the case of the Haldane function, the equality $\phi_{\alpha,r}(s) = \mu(s)$ can be rewritten as

$$\begin{aligned}(S_{in} - s - \alpha(1-r)(S_{in} - S_2^\star(\alpha))(K + S + S^2/K_I) \\ = r\bar\mu s(S_{in} - s) \ .\end{aligned}$$

So $S_1^\star$ is the root of a polynomial P of degree three, and there exists at most three solutions of $\phi_{\alpha,r}(s) = \mu(s)$. We then deduce from Proposition 1 that $R^+(\alpha)$ is a singleton.

Requiring to have $\phi_{\alpha,r}(s) = \mu(s)$ and $\phi'_{\alpha,r}(s) = \mu'(s)$ simultaneously implies that s is solution of $P = 0$ and $P'(s) = 0$ i.e. that s is a double root of P. P being of degree three, there is a most one such solution. So the set $\mathcal{S}_{r,\alpha}$ possesses at most one element, and this implies $R^-(\alpha) \cap R^+(\alpha) = \emptyset$.

When $R^-(\alpha)$ is non empty, we know from Proposition 1 that for $r \in (\min R^-(\alpha), \max R^-(\alpha))$, $\phi_{\alpha,r}(s) = \mu(s)$ has at least three solutions on an interval I, and for $r \in (\min R^+(\alpha), 1)$ at least two on another interval J, where I and J are disjoint. Consequently, one should have $\max R^-(\alpha) < \min R^+(\alpha)$, otherwise there would exists at least 5 solutions of $\phi_{\alpha,r}(s) = \mu(s)$ on $(0, S_{in})$. *q.e.d.*

Lemma 7 implies that for any $\alpha \in (0, \mu(S_{in})]$, the number $\bar r(\alpha)$ is the single element of $R^+(\alpha)$. It can then be determined numerically as the unique minimizer of the function

$$F_\alpha(r, s) = (\mu(s) - \phi_{\alpha,r}(s))^2 + \left(\mu'(s) - \phi'_{\alpha,r}(s)\right)^2$$

on $(0, 1) \times \{s \in (\lambda^-, S_{in}) \text{ s.t. } (s - \lambda^+)(\lambda^+ - \underline{S}(\alpha)) \geq 0\}$. One can also easily check that for the Haldane growth, the function ψ defined in (6) is increasing up to $\psi^\star$ and decreasing. Its maximum on the interval $(0, S_{in})$ is achieved for the value

$$\bar s^\star = \frac{\sqrt{K^2 + KS_{in}(1 + S_{in}/K_I)} - K}{1 + S_{in}/K_I} \ .$$

Consequently, one has

$$s^\star = \min(\bar s^\star, \bar s) \ ,$$

that allows to determine the optimal value $\alpha^\star = \mu(s^\star)$.

The parameters given in Table 1 have been chosen for the numerical simulations. On Figure 5, the domain $\mathcal{C}$ defined

$\bar\mu$	K	K_I	λ_-	λ_+
12	1	0.8	$\simeq 0.103$	$\simeq 0.777$

Table 1.

in (3) is drawn for different values of S_{in}. According

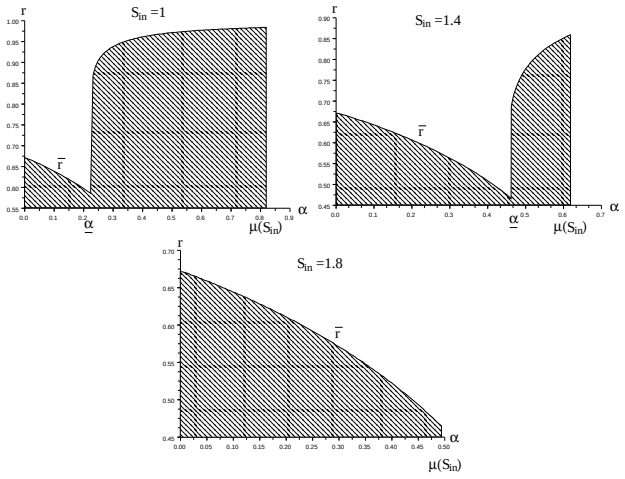

Fig. 5. Domains $\mathcal{C}$ of stable configurations.

to Remark 2, one can see that the map $\alpha \mapsto \bar r(\alpha)$ is discontinuous at $\alpha = \underline{\alpha}$, where $\underline{\alpha}$ is such that $\underline{s}(\underline{\alpha}) = \lambda_+$ (when it exists). On Figure 6 one can see that the two limiting hyperbolas $H_{\alpha,\bar r(\alpha)}$ about $\underline{\alpha}$ are different for such a case. Our study has revealed the role of the

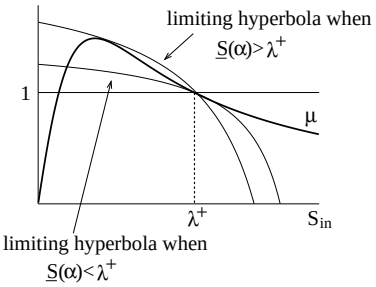

Fig. 6. The limiting hyperbolas $H_{\alpha,\bar{r}(\alpha)}$ about $\alpha = \underline{\alpha}$.

input concentration S_{in} on the shape of the domain $\mathcal{C}$. So we have computed numerically the best configurations $(\alpha^\star, r^\star)$ given by Proposition 4 as functions of S_{in}, as well as the corresponding output concentration $S_1^\star$ (see Figure 7). The map $S_{in} \mapsto \alpha^\star$ given by (7) and (8) being

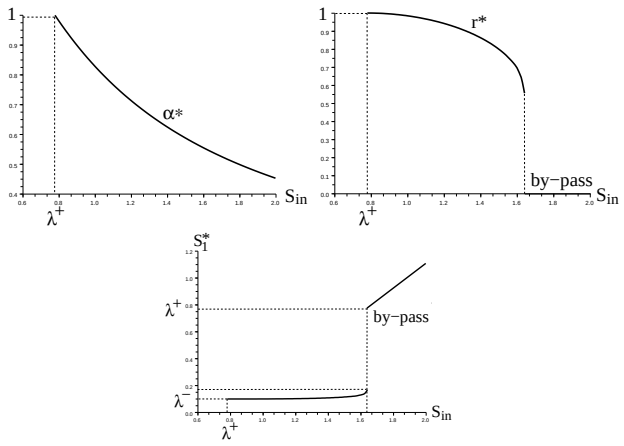

Fig. 7. $\alpha^\star$, $r^\star$ and $S_1^\star$ as functions of S_{in}.

continuous, the discontinuity of the map $\alpha \mapsto \bar{r}(\alpha)$ leads to a discontinuity of the map $S_{in} \mapsto S_1^\star$. Consequently, there exists a threshold of S_{in} such that

- below the threshold, the optimal buffered chemostat provides global stability, with performance close to the single chemostat i.e. $S_1^\star$ is close to λ_-;
- above the threshold, the optimal stable configuration consists in a by-pass of the single chemostat without any buffer. The performance is significantly modified as $S_1^\star$ is larger than λ_+.

According to Propositions 1 and 4, this threshold corresponds to a value of S_{in} such that $\underline{S}^\star(\alpha^\star) = \lambda_+$, where $\underline{S}$ is defined in (4). For values of S_{in} smaller than this threshold, the output concentration at steady state $S_1^\star$ of the best configuration is thus bounded by the one computed for the limiting case when S_{in} get arbitrary close to the threshold The values of S_{in} and $S_1^\star$ obtained at the threshold are given in Table 2. One can see on this example that the

S_{in}	$\alpha^\star$	$r^\star$	$S_1^\star$
$\simeq 1.641$	$\simeq 0.543$	$\simeq 0.561$	$\simeq 0.167$

Table 2.

buffered chemostat allows a global stability for any value of S_{in} in the interval $[0.777, 1.641]$ with an output at steady state less than 0.167, to be compared with the value 0.103 of the locally stable equilibrium of the single chemostat (see also Figure 7).

In industrial applications, the attraction of the wash-out equilibrium is undesired because it presents a risk that may ruin the culture in case of disturbance, temporarily pump breakdown or presence of toxic material that could drive the state in the attracting basin of the wash-out equilibrium. It imposes also to ensure that initial condition belongs to the attracting basin of the desired equilibrium. A common technique to overcome theses difficulties and allow an initial stage with a small concentration of biomass, is to control the input flow rate Q with a stabilizing feedback [3, 17] (it consists in finding a feedback law that reduces the flow rate when the state belongs to the attracting basin of the wash-out equilibrium). But this solution requires an upstream storage and an actuator. The design of a buffered chemostat is thus an alternative that does not require any upstream storage nor feedback control. In real world applications, it may happen that the growth function $\mu(\cdot)$ is not perfectly known or uncertain. Then choosing a buffered configuration not too close from the boundary of the domain $\mathcal{C}$ provides a robustness margin for the global stability.

When the characteristics of the input flow cannot be changed, a simple solution consists in increasing the volume of the vessel, so that the dilution rate is small enough to ensure a unique globally asymptotically stable equilibrium of the dynamics (1). The relative increment $\Delta V/V$ has then to satisfy the condition

$$S_{in} \notin \left\{ S > 0 \mid \mu(S) > \frac{1}{1 + \frac{\Delta V}{V}} \right\} \tag{11}$$

that is equivalent to have

$$\frac{\Delta V}{V} > \frac{1}{\mu(S_{in})} - 1 \ . \tag{12}$$

Note that under Assumptions A1 and A2, this last number is positive. This solution increases significantly the residence time in the tank and induces additional financial costs. Instead of choosing a larger volume V, we show that adding a buffer can be an interested alternative to improve the stability of a given bioprocess. For the parameters given in Table 1, we have compared numerically

- the smallest relative increment of the volume of the single chemostat to be globally stable, given in (12),
- the smallest relative size of the buffer to be added for the buffered chemostat to be globally stable, given by Proposition 5 (that imposes to choose $\alpha = \alpha^\star$),

as functions of the input concentration S_{in} (for values larger than λ_+ for which the bi-stability occurs with a dilution rate equal to one, cf Proposition 1). One can clearly see on Figure 8 the advantage of the buffered chemostat that requires less volume augmentation. The output concentrations are also drawn for both configurations with the minimal volume augmentation. According to Remark 6, these concentrations are always smaller than λ_-. This example demonstrates the flexibility of the buffered chemostat in the choice of possible configurations, with two parameters than can be tuned, while the single

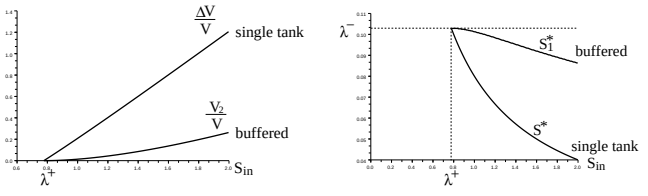

Fig. 8. Comparison of minimal increase of volume, and output nutrient concentration.

chemostat is penalized with only one parameter, requiring larger increments of volume and providing (too) low output concentrations.

Finally note that due to the robustness property that is obtained for the stability in the first tank when using a buffered chemostat, the presence of biomass at initial time is necessarily only in the buffer tank (see Proposition 3). This property possesses some advantages for the practitioners in industrial frameworks for the seeding phase.

6. CONCLUSION

The present work considers non-monotonic response functions with a particular interconnection of two chemostats of different volumes, one being a buffer tank. To our knowledge, this spatial structure, that is neither serial nor parallel, has not yet been considered in the literature. The idea is to decouple the residence time of microorganisms in two vessels such that the wash-out equilibrium is repulsive in both tanks. We prove that this is possible with such a configuration, while any serial, parallel or single tank structures with the same total volume exhibits bi-stability. This result brings new insights in microbial ecology for the understanding of the role of spatial patterns in the stability of bio-conversion processes in natural environments, where natural buffers can occur, such as in soil ecosystems. It has also potential impact on the design of robust industrial bio-processes.

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