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EFFECTS OF SPATIAL STRUCTURE AND DIFFUSION ON THE PERFORMANCES OF THE CHEMOSTAT

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Abstract. Given hydric capacity and nutrient flow of a chemostat-like system, we analyse the influence of a spatial structure on the output concentrations at steady-state. Three configurations are compared: perfectly-mixed, serial and parallel with diffusion rate. We show the existence of a threshold on the input concentration of nutrient for which the benefits of the serial and parallel configurations over the perfectly-mixed one are reversed. In addition, we show that the dependency of the output concentrations on the diffusion rate can be non-monotonic, and give precise conditions for the diffusion effect to be advantageous. The study encompasses dead-zone models.

1. **Introduction.** The chemostat is a popular apparatus, invented simultaneously by Monod [21] and Novick & Szilard [24], for the so-called *continuous culture* of micro-organisms. It has the advantage to study bacteria growth at steady state, in contrast to batch cultivation. In the classical experiments, the medium is assumed to be perfectly mixed, that justifies mathematical models described by systems of ordinary differential equations [30]. The chemostat model is also used in ecology for studying populations of micro-organisms, such as lake plankton or wetlands ecosystems. In natural ecosytems, or in industrial applications that use large bioreactors, the assumption of perfectly mixed medium is questionable. This is why spatial considerations have been introduced in the classical model of the chemostat, such as the gradostat model [17] that is a series of interconnected chemostats (of identicalvolumes). Segregated habitats are also considered in lakes, where the bottom can be modeled as a *dead zone* and nutrient mixing between the two zones is achieved by diffusion rate [22]. The consideration of dead zones is also often used in chemical or bioprocesses modelling [16, 15, 7, 27, 26, 34, 28]. In a similar way, stagnant zones are well-known to occur in porous media such as soils, at various extents depending on soil structure. The effect of such dead zones on reactive and conservative mass transport, and thus in turn on the biogeochemical cycles of elements, can also be significant [33, 32].

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Series of chemostats, instead of single chemostat, have shown to potentially improve the performances of bioprocesses, reducing the total residence time [14, 18, 11, 12, 13] or allowing species persistence [31, 25]. These properties have of course economical impacts for the biotechnological industry, and there is a significant literature on the design of series of reactors and comparison with plug-flow reactors (that can be seen as the *limiting case* of an arbitrary large number of tanks of arbitrary small volumes) [35, 1, 23, 2, 3, 4, 5]. Sometimes a radial diffusion is also considered in plug-flow reactors [8], but surprisingly,configurations of tanks in parallel have been much less investigated, apart simple considerations in chemical reaction engineering [16, 6]. One can argue that knowing input rates and volumes of tanks in parallel, their dynamical characteristics can be studied separately, and there is no need of devoting a specific study for these configurations. This is no longer the case if one considers a passive communication between the tanks, through a membrane for instance. In saturated soils or wetlands, a spatial structure could be simply represented by separated domains with diffusive communication. This consideration is similar to patches models or *islands models*, commonly used in ecology [19, 10], or lattice differential equations [29]. For instance, a recent investigation studies the influence of such structures on a consumer/resource model [9]. Consumer/resource models in ecology are similar to chemostat models, apart the source terms that are modeled as constant intakes of nutrient, instead of dilution rates that one rather met in liquid media.

In this paper, we propose to bring new insight on parallel configurations of chemostats with communication, in a spirit different than the one usually taken in bioprocesses design. One usually chooses a target for the output concentration of substrate, and looks for minimizing the total volume, or equivalently the residence time, among all the configurations that provide the same desired output at steady state. Here, we fix both the total hydric volume and the input flow and study the input-output map at steady-state, investigating the role of the spatial structure on the performances of the system. The performance is here measured by the level of substrate that is degraded by the system, and collected at the output. We draw precise comparisons between the three configurations: perfectly mixed, serial and parallel (with diffusion rate) with the same total hydric volume and flow rate. This set of configurations is far from be exhaustive, being limited to two compartments only, but it is a first attempt to grasp this input-output map of a structured chemostat, and study how a spatial structure can modify this map, and what are the key parameters. We believe that this study is of interest for the modelling of ecosystems such as saturated soils for which it is not easy to know the spatial structure, and where one has only access to *input-output* observations of the substrate degradation.

The paper is organized as follows. In Section 2, we present the three configurations under investigation and give the equations of the models. The main part of the paper is devoted to the analysis of the steady states, given in Section 3. The proofs of the global stability of the equilibriums are postponed to the Appendix, for lightening the presentation. Finally, discussion and numerical simulations are given in Section 4.

2. **The models.** The flow rate is labeled Q and V is the total capacity of the system. The three simple patterns we analyze are depicted on Figure 1:

- one single compartment of volume V

- two compartments of volume V_1, V_2 such that $V = V_1 + V_2$ connected in cascade
- two compartments of volume V_1, V_2 such that $V = V_1 + V_2$ in parallel with a diffusive connection.

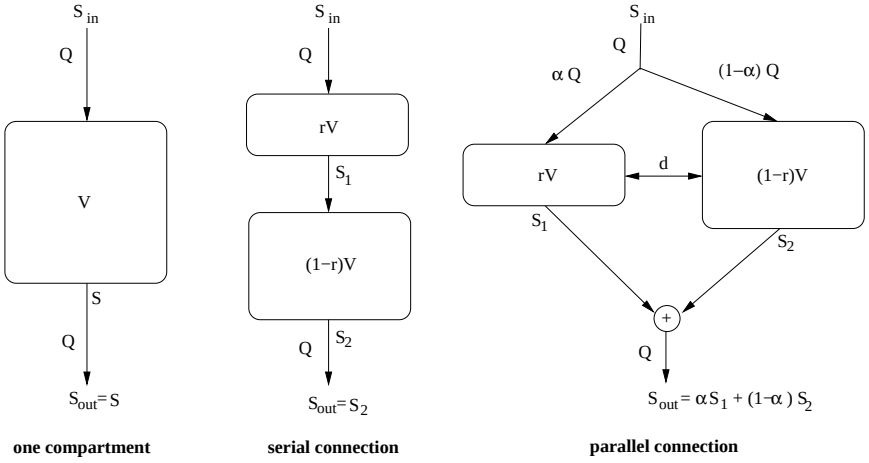

FIGURE 1. The set of configurations under investigation.

We recall the dynamical equations of resource (nutrient) and biomass concentrations, respectively denoted by S_i and X_i in a compartment i of volume V_i fed from a compartment i_- with a flow rate Q_i and connected by diffusion rate d to a compartment i_d (see Figure 2).

$$\begin{aligned} \dot{S}_i &= -\frac{\mu(s_i)}{y} X_i + \frac{Q_i}{V_i}(S_{i_-} - S_i) + \frac{d}{V_i}(S_{i_d} - S_i) \\ \dot{X}_i &= \mu(s_i) X_i + \frac{Q_i}{V_i}(X_{i_-} - X_i) + \frac{d}{V_i}(X_{i_d} - X_i) \end{aligned}$$

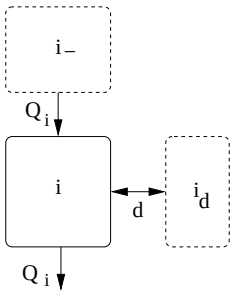

FIGURE 2. Possible interconnections of a compartment.

For sake of simplicity of the analytical analysis, we assume that the growth function $\mu(\cdot)$ is a linear function of the resource concentration:

$$\mu(S) = mS$$

In Section 4, we shall consider Monod growth function and show that the qualitative results of our study are not changed. The yield coefficient y of the bio-conversion

is kept equal to one (this is always possible by choosing the unit measuring the biomass). It is convenient to write dimensionless concentrations: for each concentration C_i in the compartment i (C_i can denote S_i or X_i), we define

$$c_i = m\frac{V}{Q}C_i \ ,$$

and

$$r_i = \frac{V_i}{V} \ .$$

We shall also consider that the time t is measured in units such that $Q = V$. Finally, we assume that the input concentration S_{in} is large enough to avoid the (trivial) wash-out equilibrium to be the only steady-state in each compartment.

Remark 1. The particular case of the parallel configuration with $\alpha = 0$ corresponds to a configuration of a perfectly mixed tank of volume $(1 - r)V$ connected to a so-called *dead-zone* of volume rV (see Figure 3.

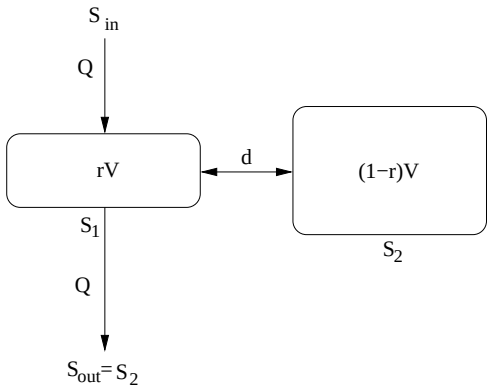

FIGURE 3. The dead-zone configuration is a special case of the parallel configuration with $\alpha = 0$.

This is a way to approximate a non well-mixed tank or *segregated* bioreactors of total volume V, estimating the fraction of the volume occupied by the highly agitated area.

3. Steady-state analysis of the three configurations.

3.1. Configuration with one compartment.

The dynamical equations of the configuration with a single compartment are

$$\left\{ \begin{array}{rcl} \dot{s} & = & -sx + s_{in} - s \\ \dot{x} & = & sx - x \end{array} \right.$$

The non-trivial equilibrium is $(1, s_{in} - 1)$ under the condition $s_{in} > 1$. Then, one has

$$s^{\star}_{out} = 1 \ .$$

Remark 2. This is a well known property from the theory of the chemostat that the output concentration at steady state is independent of the input concentration, provided this latter to be large enough (i.e. $s_{in} \geq 1$).

3.2. **Serial connection of two compartments.** The dynamical equations of the model with two compartments in series (see Figure 1), assuming r to be different to 0 and 1, are

$$\left\{\begin{array}{rcl} \dot{s}_1 &=& -s_1x_1 + \dfrac{1}{r}(s_{in} - s_1) \\ \dot{x}_1 &=& s_1x_1 - \dfrac{1}{r}x_1 \\ \dot{s}_2 &=& -s_2x_2 + \dfrac{1}{1-r}(s_1 - s_2) \\ \dot{x}_2 &=& s_2x_2 + \dfrac{1}{1-r}(x_1 - x_2) \end{array}\right. \tag{1}$$

with $r = V_1/V$.

Proposition 1. *When $s_{in} > 1/r$, there exists an unique equilibrium $(s_1^\star, x_1^\star, s_2^\star, x_2^\star)$ of (1) on the positive orthant. One has necessarily $s_1^\star = 1/r$ and $s_2^\star < \min(1/r, 1/(1-r))$. Furthermore, one has*

$$s_{out}^\star < 1 \Longleftrightarrow s_{in} > 1 + 1/r \ .$$

Proof. One can readily check that there exists a non-trivial equilibrium $(1/r, s_{in} - 1/r)$ for the first compartment exactly when $s_{in} > 1/r$. Furthermore, this equilibrium is unique. Then, any equilibrium for the overall system (1) has to be $(s_2^\star, s_{in} - s_2^\star)$ for the second compartment, with $s_2^\star$ solution of the equation

$$s_2(s_{in} - s_2) = \frac{1}{1-r}(1/r - s_2) \tag{2}$$

with $s_2^\star < 1/r$. One can easily verify that there exists a unique $s_2^\star$ solution of (2) on $(0, 1/r)$. Graphically, $s_2^\star$ is the abscissa of the intersection of the graphs (see Figure 4) of the polynomial function

$$\phi(s_2) = s_2(s_{in} - s_2)$$

and the affine function

$$l(s_2) = \frac{1}{1-r}(1/r - s_2) \ .$$

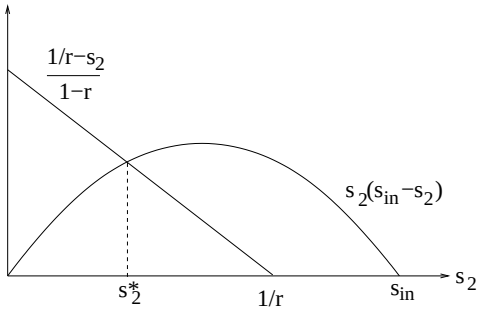

FIGURE 4. Graphical determination of $s_2^\star$.

Remark that $s_{in} > 1/r$ implies the inequality $\phi(1/(1-r)) > l(1/(1-r))$, from which one deduces $s_2^\star < 1/(1-r)$. Finally one can compare $s_{out} = s_2^\star$ with the value obtained in the configuration of one compartment:

$$s_{out}^\star < 1 \Longleftrightarrow \phi(1) > l(1) \Longleftrightarrow s_{in} > 1 + 1/r \ .$$

□

The global stability of the non-trivial equilibrium is proved in the Appendix (Proposition 4).

3.3. **Parallel interconnection of two compartments.** The dynamical equations of the model with two compartments in parallel and diffusion (see Figure 1), assuming r to be different to 0 and 1, are the following

$$\left\{\begin{array}{rcl} \dot{s}_1 &=& -s_1 x_1 + \dfrac{\alpha}{r}(s_{in} - s_1) + \dfrac{d}{r}(s_2 - s_1) \\ \dot{x}_1 &=& s_1 x_1 - \dfrac{\alpha}{r} x_1 + \dfrac{d}{r}(x_2 - x_1) \\ \dot{s}_2 &=& -s_2 x_2 + \dfrac{1-\alpha}{1-r}(s_{in} - s_2) + \dfrac{d}{1-r}(s_1 - s_2) \\ \dot{x}_2 &=& s_2 x_2 - \dfrac{1-\alpha}{1-r} x_2 + \dfrac{d}{1-r}(x_1 - x_2) \end{array}\right. \tag{3}$$

where the output concentration s_{out} is given by

$$s_{out} = \alpha s_1 + (1-\alpha) s_2 \ .$$

The wash-out in both tanks corresponds to the trivial equilibrium $(s_{in}, 0, s_{in}, 0)$, that leads to the trivial steady-state $s_{out}^\star = s_{in}$. For convenience, we posit

$$\alpha_1 = \frac{\alpha}{r} \ , \ \alpha_2 = \frac{1-\alpha}{1-r} \ ,$$

and assume, without any loss of generality that one has $\alpha_2 \geq \alpha_1$ (if it is not the case one can just exchange indexes 1 and 2).

Remark 3. One has necessarily $\alpha_2 \geq 1$ and $\alpha_1 \leq 1$.

When $d = 0$ (no diffusion), the equilibrium of the system can be determined independently in the two compartments as simple chemostats. In this case, there is an unique globally stable equilibrium $(s_1^*, s_{in} - s_1^\star, s_2^*, s_{in} - s_2^\star)$ in the non-negative orthant, where $s_i^* = \min(\alpha_i, s_{in})$ $(i = 1, 2)$.

When $d > 0$, we define the functions

$$\begin{aligned} \phi_2(s_1) &= s_1 + \frac{r}{d}(s_{in} - s_1)(s_1 - \alpha_1) \ , \\ \phi_1(s_2) &= s_2 + \frac{1-r}{d}(s_{in} - s_2)(s_2 - \alpha_2) \ , \end{aligned}$$

and

$$g(s_1) = \phi_1(\phi_2(s_1)) - s_1 \ .$$

Proposition 2. *When $s_{in} > 1$ and $d > 0$, there exists a unique equilibrium $(s_1^\star, x_1^\star, s_2^\star, x_2^\star)$ of (3) in the positive orthant, where $(s_1^\star, s_2^\star)$ is the unique solution of the system*

$$s_2^\star = \phi_2(s_1^\star) \text{ and } s_1^\star = \phi_1(s_2^\star) \ , \tag{4}$$

on the domain $(0, s_{in}) \times (0, s_{in})$, *with* $x_i^\star = s_{in} - s_i^\star$ $(i = 1, 2)$. *Furthermore,* $s_1^\star = s_2^\star = 1$ *when* $\alpha_2 = \alpha_1$ *and*

$$\alpha_1 < s_1^\star < s_2^\star < \min(\alpha_2, s_{in}) \tag{5}$$

when $\alpha_2 > \alpha_1$.

Proof. At equilibrium, one has

$$\begin{aligned} r(\dot{s}_1 + \dot{x}_1) + (1-r)(\dot{s}_2 + \dot{x}_2) &= 0, \\ r(\dot{s}_1 + \dot{x}_1) &= 0, \end{aligned}$$

which amounts to write, from equations (3)

$$\begin{aligned} \alpha(s_{in} - s_1^\star - x_1^\star) + (1-\alpha)(s_{in} - s_2^\star - x_2^\star) &= 0, \\ \alpha(s_{in} - s_1^\star - x_1^\star) + d(s_2^\star + x_2^\star - s_1^\star - x_1^\star) &= 0, \end{aligned}$$

or equivalently

$$\underbrace{\begin{bmatrix} \alpha & 1-\alpha \\ \alpha + d & -d \end{bmatrix}}_{M} \begin{pmatrix} s_{in} - s_1^\star - x_1^\star \\ s_{in} - s_{12}^\star - x_2^\star \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

One has $det(M) = \alpha^2 - \alpha - d \leq -d < 0$ and deduces the property

$$s_1^\star + x_1^\star = s_2^\star + x_2^\star = s_{in} \ .$$

Consequently, an equilibrium in the positive orthant has to fulfill $s_i^\star \in [0, s_{in}]$ for $i = 1, 2$. Replacing $x_i^\star$ by $s_{in} - s_i^\star$ in equations (3) at equilibrium, one obtains the equations

$$\begin{aligned} d(s_2^\star - s_1^\star) &= r(s_{in} - s_1^\star)(s_1^\star - \alpha_1) \\ d(s_1^\star - s_2^\star) &= (1-r)(s_{in} - s_2^\star)(s_2^\star - \alpha_2) \end{aligned} \tag{6}$$

which amounts to write that $(s_1^\star, s_2^\star)$ is solution of the system (4) (see Figure 5) or equivalently $s_1^\star$ is a zero of the function $g(\cdot)$.

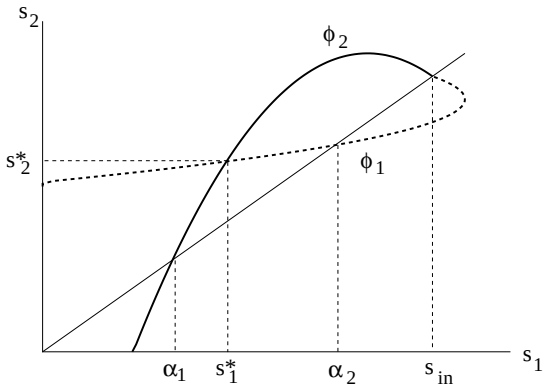

FIGURE 5. Graphical determination of steady states (when $\alpha_1 < \alpha_2 < s_{in}$).

When $\alpha_2 = \alpha_1 = 1$, one can check that $s_1^\star = s_2^\star = 1 < s_{in}$ is solution of (4). When $\alpha_2 > \alpha_1$, one has necessarily $\alpha_1 < 1$ and the condition $s_{in} > 1$ implies $g(\alpha_1) < 0$. We distinguish now two cases:

Case $\alpha_2 < s_{in}$. If $\phi_2(\alpha_2) \leq s_{in}$, notice that one has $\phi_2(\alpha_2) > \alpha_2$ and then $g(\alpha_2) > 0$. If $\phi_2(\alpha_2) > s_{in}$, notice that $\phi_2(\alpha_1) = \alpha_1 < s_{in}$ and by the Mean Value Theorem, there exists $\tilde{s}_2 \in (\alpha_1, \alpha_2)$ such that $\phi_2(\tilde{s}_2) = s_{in}$ which implies $g(\tilde{s}_2) = s_{in} - \tilde{s}_2 > 0$. In both cases, one deduces by the Mean Value Theorem the existence of $s_1^\star \in (\alpha_1, \alpha_2)$ such that $g(s_1^\star) = 0$.
Case $\alpha_2 \geq s_{in}$. One has $g(s_{in}) = 0$ with

$$g'(s_{in}) = \frac{r(1-r)}{d^2}(\alpha_1 - s_{in})(\alpha_2 - s_{in}) + \frac{1 - s_{in}}{d} < 0 \ .$$

Rolle and Mean Value Theorems allow to conclude the existence of $s_1^\star \in (\alpha_1, s_{in})$ such that $g(s_1^\star) = 0$.

In any case, we obtain the existence of $(s_1^\star, s_2^\star)$ solution of (4) with $s_1^\star$ belonging to the interval $(\alpha_1, \min(\alpha_2, s_{in}))$, that implies $s_2^\star = \phi_2(s_1^\star) > s_1^\star$. But then $s_1^\star = \phi_1(s_2^\star) < s_2^\star$ implies $s_2^\star < \min(\alpha_2, s_{in})$. Thus, the inequalities (5) are fulfilled.

Finally, notice that functions $\phi_1(\cdot)$, $\phi_2(\cdot)$ are both strictly concave, and steady states $(s_1^\star, s_2^\star)$ are intersections of $\mathcal{G}_1$, the graph of the function $\phi_1(\cdot)$, and $\mathcal{G}_2$ the symmetric of the graph of $\phi_2(\cdot)$ with respect to the first diagonal. Consequently, if $(s_1^\star, s_2^\star)$ is a steady state different from (s_{in}, s_{in}), $\mathcal{G}_1$ and $\mathcal{G}_2$ are respectively above and below the line segment $(s_1^\star, s_2^\star) - (s_{in}, s_{in})$. We conclude that there exists at most one non-trivial equilibrium. □

Corollary 1. *When $s_{in} > 1$ and $d > 0$, the value $s_1^\star$ of the non trivial equilibrium is the unique zero of the function $g(\cdot)$ on $(\alpha_1, \min(\alpha_2, s_{in}))$. Furthermore, one has $g'(s_1^\star) > 0$.*

Proof. When $\alpha_1 = \alpha_2$, one has $s_1^\star = s_2^\star = 1$ and one can easily check

$$g'(s_1^\star) = \left(1 + \frac{r}{d}(s_{in} - 1)\right)\left(1 + \frac{1-r}{d}(s_{in} - 1)\right) - 1 > 0 \ .$$

When $\alpha_2 > \alpha_1$, one has $g(\alpha_1) < 0$ and we recall from the proof of Proposition 1 that $s_1^\star$ is the unique zero of $g(\cdot)$ on $(\alpha_1, \min(\alpha_2, s_{in}))$. We conclude that g is non decreasing at $s_1^\star$. Notice that ϕ_1 and ϕ_2 are concave functions and that

$$\phi_1'(\phi_2(s_1^\star))) = 1 + \frac{1-r}{d}(s_{in} + \alpha_2 - 2s_2^\star) > 0$$

implies

$$g''(s_1^\star) = \phi_1''(\phi_2(s_1^\star)).\left[\phi_2'(s_1^\star)\right]^2 + \phi_1'(\phi_2(s_1^\star)).\phi_2''(s_1^\star) < 0$$

We deduce that $g'(s_1^\star)$ cannot be equal to zero, and consequently one has $g'(s_1^\star) > 0$. □

The global stability of the non-trivial equilibrium is proved in the Appendix (Proposition 5).

Proposition 2 defines properly the map $d \mapsto s_{out}^\star = \alpha s_1^\star + (1-\alpha)s_2^\star$ for the unique non-trivial steady-state, that we aim at studying as a function of d. Accordingly to Proposition 2, $s_{out}^\star$ is equal to one for any value of the parameter d in the non-generic case $\alpha_2 = \alpha_1$. We shall focus on the case $\alpha_2 \neq \alpha_1$ (and without loss of generality we shall consider $\alpha_2 > \alpha_1$). We start by the two extreme situations: no diffusion and infinite diffusion.

Lemma 3.1. *For the non trivial equilibrium, one has*

$$s^\star_{out}(0) \geq 1 \Longleftrightarrow s_{in} \geq s^0_{in} = \frac{r-\alpha^2}{r(1-\alpha)}$$

with $s^0_{in} \in (1,2)$.

Proof. Under the assumptions $s_{in} > 1$ and $\alpha_2 \geq \alpha_1$, we distinguish two cases when $d = 0$.
If $s_{in} \geq \alpha_2$, one has $s^\star_1 = \alpha_1$ and $s^\star_2 = \alpha_2$. Then, one can write

$$s^\star_{out} = \frac{\alpha^2}{r} + \frac{(1-\alpha)^2}{1-r} = 1 + \frac{(\alpha-r)^2}{r(1-r)} \geq 1 \ .$$

If $s_{in} < \alpha_2$, on has $s^\star_1 = \alpha_1$, $s^\star_2 = s_{in}$ and

$$s^\star_{out} \geq 1 \Longleftrightarrow s_{in} \geq \frac{1-\alpha\alpha_1}{1-\alpha} = s^0_{in} \ .$$

(recall that assuming $\alpha_2 \geq \alpha_1$ imposes to have $\alpha < 1$, and s^0_{in} is well defined). Notice that the number s^0_{in} is necessarily larger than one because $\alpha_1 \leq 1$, and one has also

$$\alpha_2 - s^0_{in} = \frac{(r-\alpha)^2}{r(1-r)(1-\alpha)} \geq 0.$$

Consequently one concludes that $s^\star_{out} \geq 1$ exactly when $s_{in} \geq s^0_{in}$. Finally, remark that one has

$$s^0_{in} = \frac{r-\alpha^2}{r(1-\alpha)} = 1 - \frac{(\alpha-r)^2}{r(r-\alpha)} + \frac{r-\alpha}{1-\alpha} < 2 \ .$$

□

Lemma 3.2. *For* $s_{in} > 1$, *the non trivial equilibrium fulfill*

$$\lim_{d\to+\infty} s^\star_1(d) = \lim_{d\to+\infty} s^\star_2(d) = \lim_{d\to+\infty} s^\star_{out}(d) = 1 \ .$$

Proof. For any $d > 0$, Proposition 2 guarantees the existence of a unique non trivial equilibrium $(s^\star_1, s^\star_2) \in (0, s_{in}) \times (0, s_{in})$ that is solution of (6). When d is arbitrary large, one obtains from (6)

$$\lim_{d\to+\infty} s^\star_1(d) - s^\star_2(d) = 0 \ .$$

From equations (6), one deduces also the following equality valid for any d

$$r(s_{in} - s^\star_1)(s^\star_1 - \alpha_1) + (1-r)(s_{in} - s^\star_2)(s^\star_2 - \alpha_2) = 0 \ ,$$

that can rewritten, taking into account the equality $r\alpha_1 + (1-r)\alpha_2 = 1$:

$$(s_{in} - s^\star_1)(s^\star_1 - 1) = (1-r)(s^\star_1 - s^\star_2)(s_{in} + \alpha_2 - s^\star_1 - s^\star_2) \ .$$

Consequently, one has

$$\lim_{d\to+\infty} s^\star_1(d) = \lim_{d\to+\infty} s^\star_2(d) = 1 \text{ or } \lim_{d\to+\infty} s^\star_1(d) = \lim_{d\to+\infty} s^\star_2(d) = s_{in} \ .$$

If $\alpha_2 < s_{in}$, the property $s^\star_1 < \alpha_2$ valid for any $d > 0$ implies that $s^\star_1$ cannot converges to s_{in}.
If $\alpha_2 \geq s_{in}$ and $\lim s^\star_1 = \lim s^\star_2 = s_{in}$, there exists d such that $rs^\star_1 + (1-r)s^\star_2 > (s_{in}+1)/2$. Then, one has

$$g'(s^\star_1) = \frac{r(1-r)}{d^2}(s_{in}+\alpha_1-2s^\star_1)(s_{in}+\alpha_2-2s^\star_2) + \frac{s_{in}+1-2(rs^\star_1+(1-r)s_{2^\star})}{d} < 0$$

that contradicts Corollary 1. Finally, one has $\lim s_1^\star = \lim s_2^\star = 1$ and consequently $\lim s_{out}^\star = 1$. □

We present now our main result concerning properties of the map $d \mapsto s_{out}^\star(d)$ defined at the non-trivial steady-state.

Proposition 3. *Assume $\alpha_2 > \alpha_1$.*

- *When $s_{in} \geq 2$, the map $d \mapsto s_{out}^\star(d)$ (for the non trivial equilibrium) is decreasing and $s_{out}^\star(d) > 1$ for any $d \geq 0$.*
- *When $s_{in} < 2$, the map $d \mapsto s_{out}^\star(d)$ (for the non trivial equilibrium) admits a minimum in $d^\star < +\infty$, that is strictly less than one. Furthermore, one has*

$$s_{in} > \underline{s}_{in} = \frac{2\alpha_1\alpha_2}{\alpha_1+\alpha_2} \quad \Longrightarrow \quad d^\star > 0$$

with $\underline{s}_{in} < \min(2, \alpha_2)$.

Proof. Let differentiate with respect to d the equations (6) at steady state:

$$\begin{aligned}
(s_2^\star - s_1^\star) + d\,(\partial_d s_2^\star - \partial_d s_1^\star) &= \underbrace{r(s_{in} - 2s_1^\star + \alpha_1)}_{A}\,\partial_d s_1^\star \\
(s_1^\star - s_2^\star) + d\,(\partial_d s_1^\star - \partial_d s_2^\star) &= \underbrace{(1-r)(s_{in} - 2s_2^\star + \alpha_2)}_{B}\,\partial_d s_2^\star
\end{aligned}$$

that can rewritten as follows

$$\underbrace{\begin{bmatrix} A+d & -d \\ d & -B-d \end{bmatrix}}_{\Gamma} \begin{pmatrix} \partial_d s_1^\star \\ \partial_d s_2^\star \end{pmatrix} = (s_2^\star - s_1^\star) \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$

Remark that one has

$$\begin{aligned}
A + d &= d\phi_2'(s_1^\star) \\
B + d &= d\phi_1'(s_2^\star) \\
det(\Gamma) &= d^2(1 - \phi_1'(s_2^\star)\phi_2'(s_1^\star)) = -d^2 g'(s_1^\star)
\end{aligned}$$

From Corollary 1, one has $det(\Gamma) < 0$ and one deduces that the derivatives $\partial_d s_1^\star$, $\partial_d s_2^\star$ are defined as follows

$$\begin{aligned}
\partial_d s_1^\star &= (s_2^\star - s_1^\star)\frac{-B}{det(\Gamma)} \\
\partial_d s_2^\star &= (s_2^\star - s_1^\star)\frac{A}{det(\Gamma)}
\end{aligned} \tag{7}$$

Notice from inequalities (5) that we obtain $B > 0$ and deduce $\partial_d s_1^\star > 0$ for any d. With Lemma 3.2 we conclude that $s_1^\star(d) < 1$ for any d.
From equations (7), we can write

$$\partial_d s_{out}^\star = (s_2^\star - s_1^\star)\frac{\alpha B - (1-\alpha)A}{-det(\Gamma)} = \underbrace{[\alpha_1(s_{in} - 2s_2^\star) - \alpha_2(s_{in} - 2s_1^\star)]}_{\sigma}\frac{(s_2^\star - s_1^\star)r(1-r)}{-det(\Gamma)}$$

When $s_{in} \geq 2$, one has $A > 0$ and then $\partial_d s_2^\star < 0$. With Lemma 3.2 we conclude that $s_2^\star(d) > 1$ for any d. Then, one obtain the inequality

$$\sigma < (s_{in} - 2)(\alpha_1 - \alpha_2) \leq 0$$

which proves with Lemma 3.2 that $s^\star_{out}$ is a decreasing function of d that converges to one.

When $s_{in} < 2$, we write

$$\sigma = (s_{in} - 2)(\alpha_1 - \alpha_2) + 2(\alpha_1(1 - s^\star_2) - \alpha_2(1 - s^\star_1))$$

As $s^\star_1$ and $s^\star_2$ tend to one when d takes arbitrary large values, we conclude that there exists $\bar{d} < +\infty$ such that $\sigma > 0$ for any $d > \bar{d}$ and consequently $s^\star_{out}$ is smaller than one and increasing for $d > \bar{d}$. We conclude that the map $d \mapsto s^\star_{out}(d)$ admits a minimum, say at $d^\star < +\infty$, that is strictly less than one.

When $d = 0$, one has $s^\star_1 = \alpha_1$ and $s^\star_2 = \alpha_2$ if $s_{in} \geq \alpha_2$. Then, one obtains $\sigma = s_{in}(\alpha_1 - \alpha_2) < 0$. So the map $d \mapsto \partial_d s^\star_{out}(d)$ is decreasing at $d = 0$ and consequently $d^\star > 0$.

When $d = 0$ with $s_{in} < \alpha_2$, one has $s^\star_2 = s_{in}$ and then $\sigma = 2\alpha_1\alpha_2 - s_{in}(\alpha_1 + \alpha_2)$, for which we conclude

$$\sigma < 0 \Longleftrightarrow s_{in} > \frac{2\alpha_1\alpha_2}{\alpha_1 + \alpha_2} = \underline{s}_{in} \ .$$

Remark that this case is feasible because of the inequality $2\alpha_1\alpha_2 < \min(2, \alpha_2)(\alpha_1 + \alpha_2)$. We conclude that for s_{in} larger than this last value, $d^\star$ is necessarily strictly positive. □

4. **Numerical computation and discussion.** Propositions 1 and 3 reveal the existence of a threshold on the value of the input concentration s_{in} (equal to 2 for our choice of the parameters units) that reverses the performances of the serial and parallel configurations in terms of $s^\star_{out}$, compared to the single tank case (for which $s^\star_{out} = 1$):

- for $s_{in} > 2$, there exist serial configurations such that $s^\star_{out} < 1$ for r large enough (i.e. the first tank has to be large enough), but any parallel configuration produces $s^\star_{out} > 1$,
- for $s_{in} < 2$, there exists parallel configurations such that $s^\star_{out} < 1$, while any serial configuration has $s^\star_{out} > 1$. There exists another threshold $s^0_{in} \in (1, 2)$ such that configurations with $s^\star_{out} < 1$ require to have d large enough when $s_{in} > s^0_{in}$ (see Lemma 3.1).

Furthermore, the best performance of the parallel configuration is obtained

- for arbitrary large values of d when $s_{in} > 2$,
- for a finite positive $d^\star$ when $s_{in} \in (\underline{s}_{in}, 2)$ (where the expression of $\underline{s}_{in}$ is given in Proposition 3).

For the serial configuration, the graph of the function $s^\star_{out}$ is plotted as function of $r \in [1/s_{in}, 1]$ on Figure 6 for different values of the input concentration s_{in}.

For the parallel interconnection, we depict on Figure 7 the two kind of configurations that occur, depending on whether the number $\underline{s}_{in}$ is larger than one or not.

The values of the parameters are given on the table below

	α	r	$\underline{s}_{in}$	s^0_{in}
left figure	0.6	0.9	1.14	1.5
right figure	0.1	0.9	0.21	1.09

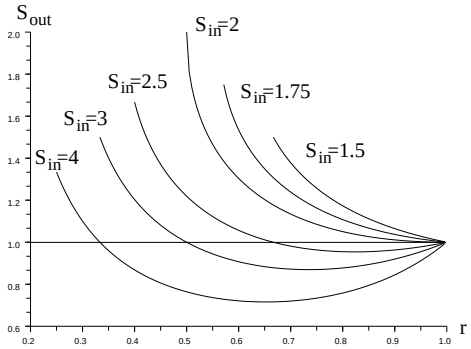

FIGURE 6. Comparison of $s^\star_{out}$ for the serial configuration.

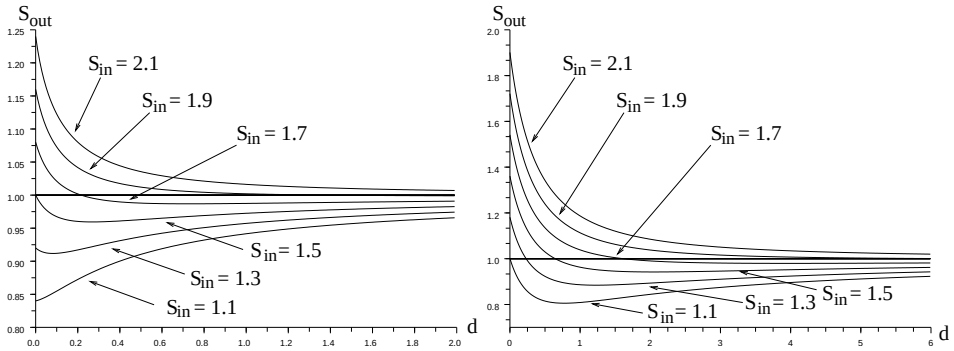

FIGURE 7. Comparison of $s^\star_{out}$ for the parallel configuration ($\underline{s}_{in} > 1$ on the left and $\underline{s}_{in} < 1$ on the right) .

The analytic analysis of Section 3 has been conducted under the assumption of the linearity of the function $\mu(\cdot)$. It is often in microbiology that the growth rate $\mu(\cdot)$ presents a concavity, as described by the usual Monod (or Michaelis-Menten) function. We have computed numerically the same curves $s^\star_{out}(\cdot)$ than Figures 6 and 7, considering the Monod function

$$\mu(S) = \frac{6S}{5+S}$$

instead of the linear function (see Figure 8).

This function has been chosen to fulfill $s^\star_{out} = 1$ for the single tank configuration, guaranteeing the same steady state than the linear growth for this configuration.

On Figures 9 and 10, we observe that the concavity of the growth function does not change qualitatively the theoretical results and the existence of threshold for s_{in} that favourites one of the configuration.

We notice on all the figures that the yield is better for the Monod function in the parallel configuration and worst for the serial one. This implies that the threshold on s_{in}, that was determined to be equal to 2 for the linear case is higher when the growth function is concave.

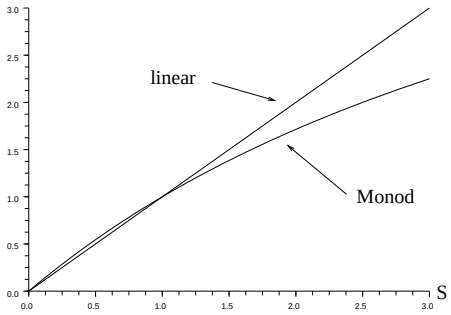

FIGURE 8. Linear and Monod growth functions.

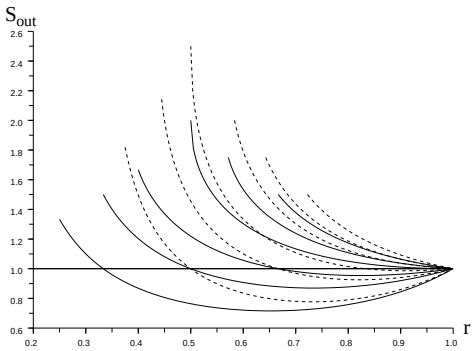

FIGURE 9. Comparison of $s^\star_{out}$ for Monod (dashed) and linear (plain) for the serial configuration.

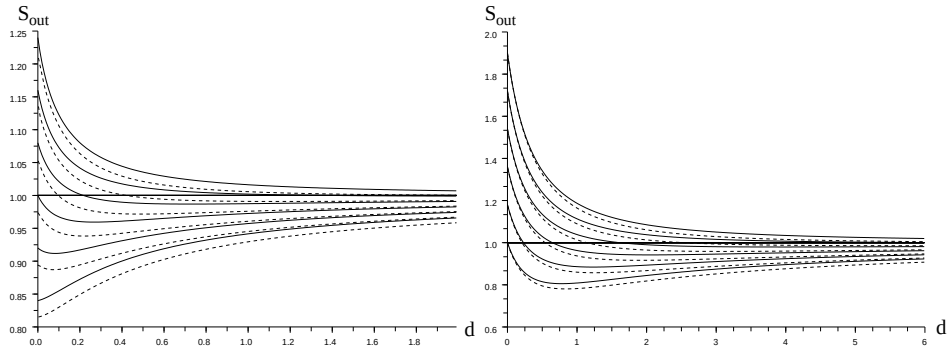

FIGURE 10. Comparison of $s^\star_{out}$ for the parallel configuration ($\underline{s}_{in} > 1$ on the left and $\underline{s}_{in} < 1$ on the right) .

Remark 4. The serial configuration for the limiting value $r = 1$ is equivalent to a single tank. This explains why all the curves on Figures 6 and 9 coincide for this value of the parameter r.

Remark 5. For the parallel configuration with $\alpha = 0.1$ and $r = 0.9$ one has $\alpha_2 = 9$. This implies that for the limiting value $d = 0$ the only equilibrium in the second tank is the wash-out when $s_{in} < 9$. This is not the case for the first tank but the

flow rate αQ being small, the output $s^\star_{out}$ remains closed to s_{in} in any case, as one can see on Figures 7 and 10 for small values of the parameter d.

5. **Conclusion.** Given a flow rate and the total volume of a chemostat system, this study shows the existence of a threshold on the value of the input concentration s_{in} such that above and below this threshold, serial and the parallel configurations are respectively the best ones with respect to the criterion of minimizing the output concentration $s^\star_{out}$ at steady state. For the parallel scheme, the best performances are obtained for a precise value of the diffusion parameter that is proved to be positive when s_{in} is not too small. This study concerns also *dead-zone* configurations, as particular cases of the parallel configurations.

These results show that a single perfectly mixed chemostat (that does not lead toward the wash-out of the biomass) can be replaced by a configuration of two tanks with the same total volume (serial or parallel, depending on the value of the input concentration) that provides a better conversion rate of the substrate at steady state. In addition, we have proved in the Appendix that non-trivial steady states are unique and globally exponentially stable (under the assumption that the growth rate is linear).

Finally, this study reveals the role of the structure of the space on the performances of simple ecosystems or bioprocesses. The possibly non-monotonic influence of the diffusion parameter on the output steady state is not intuitive, and leave further investigations open for understanding or taking benefit of this property for natural ecosystems (such as saturated soils or wetlands) as well as for bioprocesses (such as waste-water treatments). This result can be also of interest for reverse engineering when deciding which among serial or parallel configurations is better fit for the modeling of chemostat-like ecosystems, providing that one has an estimation of the hydric capacity of the system.

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Appendix: Global exponential stability of the non-trivial equilibrium. First, one can easily check that the domain $D = \mathbb{R}^4_+$ is invariant by the dynamics (1) and (3). We consider the 2-dimensional vector z of variables $z_i = s_{in} - x_i - s_i$ $(i = 1, 2)$ whose dynamics are respectively for the serial and parallel configurations

$$\dot{z} = A_s z = \begin{bmatrix} -\frac{1}{r} & 0 \\ \frac{1}{1-r} & -\frac{1}{1-r} \end{bmatrix} z$$

$$\dot{z} = A_p z = \begin{bmatrix} -\alpha_1 - \frac{d}{r} & \frac{d}{r} \\ \frac{d}{1-r} & -\alpha_2 - \frac{d}{1-r} \end{bmatrix} z$$

Notice that matrices A_s and A_p are Hurwitz :

$$\mathrm{tr}(A_s) = -\frac{1}{r} - \frac{1}{1-r} < 0\ , \quad \det(A_s) = \frac{1}{r(1-r)} > 0$$

$$\mathrm{tr}(A_p) = -\alpha_1 - \alpha_2 - \frac{d}{r} - \frac{d}{1-r} < 0\ , \quad \det(A_p) = \alpha_1\alpha_2 + \frac{d}{r(1-r)} > 0$$

So z converges exponentially toward 0 for both systems, which implies that dynamics (1) and (3) are dissipative, in the sense that any solution of (1) or (3) in D

converge exponentially to the compact set $K = \{(s_1, x_1, s_2, x_2) \in D \text{ s.t. } x_1 + s_1 = s_{in} \text{ and } x_2 + s_2 = s_{in}\}$.

We recall a result from [20, Theorem 1.8] that shall be useful in the following.

Theorem 5.1. *Let Φ be an asymptotically autonomous semi-flow with limit semi-flow Θ, and let the orbit $\mathcal{O}_\Phi(\tau, \xi)$ have compact closure. Then the ω-limit set $\omega_\Phi(\tau, \xi)$ is non-empty, compact, connected, invariant and chain-recurrent by the semi-flow Θ and attracts $\Phi(t, \tau, \xi)$ when $t \to \infty$.*

We first give a result for the serial configuration.

Proposition 4. *Under the condition $s_{in} > 1/r$, any trajectory of (1) with initial condition in D such that $(s_1(0), x_1(0)) \neq (s_{in}, 0)$ converges exponentially to the unique non-trivial steady-state $(s_1^\star, x_1^\star, s_2^\star, x_2^\star)$ given by Proposition 1.*

Proof. Dynamics (1) has a cascade structure. It is straightforward to check that the solutions of the (s_1, x_1) sub-system converges asymptotically towards the non-trivial equilibrium $(1/r, s_{in} - 1/r)$ from any initial condition away from the wash-out equilibrium $(s_{in}, 0)$. From the convergence of z_2 toward 0, we deduce that the s_2 variable has to converge to the bounded interval $[0, s_{in}]$ and that its dynamics can be written as a scalar non autonomous differential equation:

$$\dot{s}_2 = -s_2(s_{in} - s_2 - z_2(t)) + \frac{1}{1-r}(s_1(t) - s_2) \tag{8}$$

This last dynamics has the property to be asymptotically autonomous with the limiting differential equation:

$$\dot{s}_2 = f(s_2) = -s_2(s_{in} - s_2) + \frac{1}{1-r}(1/r - s_2) \tag{9}$$

Statement of Proposition 1 implies that this last scalar dynamics has a unique equilibrium $s_2^\star$ that belongs to $[0, s_{in}]$. Furthermore, one has $f(0) > 0$ and $f(s_{in}) < 0$. Consequently any solution of (9) in $[0, s_{in}]$ converges asymptotically to $s_2^\star$. Then applying Theorem 5.1, we conclude that any bounded solution of (8) converges to $s_2^\star$. Finally any solutions of the (s_2, x_2) sub-system converges asymptotically to $(s_2^\star, s_{in} - s_2^\star)$.

The Jacobian matrix of dynamics (1) at the non-trivial equilibrium $(s_1^\star, x_1^\star, s_2^\star, x_2^\star)$ is of the following form in (z_1, z_2, s_1, s_2) coordinates

$$\begin{bmatrix} A_s & 0 \\ \star & J^\star \end{bmatrix} \quad \text{with} \quad J^\star = \begin{bmatrix} s_1^\star - s_{in} & 0 \\ \frac{1}{1-r} & 2s_2^\star - \frac{1}{1-r} - s_{in} \end{bmatrix}$$

Recall that A_s is Hurwitz. The eigenvalues of $J^\star$ are $-(s_{in} - s_1^\star)$, $-(s_{in} - s_2^\star) - (1/(1-r) - s_2^\star)$ that are both negative numbers, accordingly to Proposition 1. The exponential stability of the non-trivial equilibrium is thus proved. □

We give now a result for the parallel configuration.

Proposition 5. *When $s_{in} > 1$ and $d > 0$, any trajectory of (3) with initial condition in D such that $x_1(0) > 0$ and $x_2(0) > 0$ converges exponentially to the unique non-trivial steady-state $(s_1^\star, x_1^\star, s_2^\star, x_2^\star)$ given by Proposition 2.*

Proof. Considering the time vector $z(\cdot)$, the (s_1, s_2) sub-system of dynamics (3) can be written as solution of a non-autonomous planar dynamics

$$\left\{ \begin{array}{rcl} \dot{s}_1 & = & s_1(z_1(t) + s_1 - s_{in}) + \alpha_1(s_{in} - s_1) + \frac{d}{r}(s_2 - s_1) \\ \dot{s}_1 & = & s_2(z_2(t) + s_2 - s_{in}) + \alpha_2(s_{in} - s_2) + \frac{d}{1-r}(s_1 - s_2) \end{array} \right. \tag{10}$$

We know that z converges to 0 and consequently the vector S of variables s_1, s_2 converges to the set $\mathcal{S} = [0, s_{in}] \times [0, s_{in}]$. We study now the limiting autonomous dynamics

$$\left\{ \begin{array}{rcl} \dot{s}_1 & = & (s_{in} - s_1)(\alpha_1 - s_1) + \frac{d}{r}(s_2 - s_1) \\ \dot{s}_2 & = & (s_{in} - s_2)(\alpha_2 - s_2) + \frac{d}{1-r}(s_1 - s_2) \end{array} \right. \tag{11}$$

on the domain $\mathcal{S}$. Let $\mathcal{B}$ be the boundary $\{s_1 = s_{in}\} \cup \{s_2 = s_{in}\}$. On the domain $\mathcal{S} \setminus \mathcal{B}$, we consider the vector σ of variables $\sigma_i = \log(s_{in} - s_i)$, whose dynamics can be written as follows

$$\dot{\sigma} = F(\sigma) = \left[\begin{array}{c} -\alpha_1 + s_{in} - e^{\sigma_1} - \frac{d}{r}\left(1 - e^{\sigma_2 - \sigma_1}\right) \\ -\alpha_2 + s_{in} - e^{\sigma_2} - \frac{d}{1-r}\left(1 - e^{\sigma_1 - \sigma_2}\right) \end{array} \right] \tag{12}$$

One can easily compute

$$\mathrm{div}(F) = -e^{\sigma_1} - e^{\sigma_2} - \frac{d}{r}e^{\sigma_2 - \sigma_1} - \frac{d}{1-r}e^{\sigma_1 - \sigma_2} < 0$$

From Poincaré-Bendixon theorem and Dulac criterion, we conclude that bounded trajectories of (12) cannot have limit cycle or closed path and necessarily converge to an equilibrium point. Consequently, any trajectory of (11) in $\mathcal{S}$ either converges to the rest point $S^\star = (s_1^\star, s_2^\star)$ or approaches the boundary $\mathcal{B}$. Notice that one has

$$s_i = s_{in},\ s_j < s_{in} \ \Rightarrow\ \dot{s}_i < 0 \qquad (i \neq j)$$

So the only possibility for approaching $\mathcal{B}$ is to converge to the other rest point $S^0 = (s_{in}, s_{in})$. This shows that the only non-empty, closed, connected, invariant and chain recurrent subsets of $\mathcal{S}$ are the singletons $\{S^\star\}$ and $\{S^0\}$.

Applying Theorem 5.1 we conclude that any trajectory of (10), issued from initial condition of dynamics (3) in $\mathcal{D}$, converges asymptotically to $S^\star$ or S^0. Consider now any initial condition with $x_1(0) > 0$ and $x_2(0) > 0$. We show that the solution $(s_1(\cdot), s_2(\cdot))$ of (3) cannot converge to S^0. If it is the case, there exists $T < +\infty$ such that one has

$$s_1(t) > \alpha_1 \quad \text{and} \quad r s_1(t) + (1-r)s_2(t) > 1 \quad \text{for any } t \geq T$$

under the assumption $s_{in} > 1$. Let us consider the function

$$V(x_1, x_2) = \min(r x_1 + (1-r)x_2, x_1)$$

(see Figure 11) and $v(t) = V(x_1(t), x_2(t))$ that is positive and tends to 0 when t tends to $+\infty$

If $x_1(t) < x_2(t)$, one has $v(t) = x_1(t)$ and

$$\dot{v} = \dot{x}_1 > (s_1(t) - \alpha_1)x_1 > 0 \text{ for } t \geq T$$

If $x_1(t) > x_2(t)$, one has $v(t) = r x_1(t) + (1-r)x_2(t)$ and

$$\begin{array}{rcl} \dot{v} & = & r\dot{x}_1 + (1-r)\dot{x}_2 = r(s_1 - \alpha_1)x_1 + (1-r)(s_2 - \alpha_2)x_2 \\ & > & (r s_1 + (1-r)s_2 - 1)x_2 > 0 \text{ for } t \geq T \end{array}$$

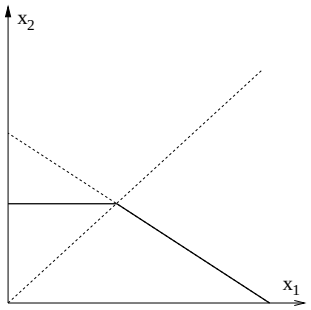

FIGURE 11. Iso-value of the V function.

We conclude that the function $t \mapsto v(t)$ is non-decreasing for $t \geq T$ and consequently cannot converge to zero, thus a contradiction.

The Jacobian matrix of dynamics (3) at the non-trivial equilibrium $(s_1^\star, x_1^\star, s_2^\star, x_2^\star)$ is of the following form in (z_1, z_2, s_1, s_2) coordinates

$$\begin{bmatrix} A_p & 0 \\ \star & J^\star \end{bmatrix} \quad \text{with} \quad J^\star = \begin{bmatrix} -\frac{d}{r}\phi_2'(s_1^\star) & \frac{d}{r} \\ \frac{d}{1-r} & -\frac{d}{1-r}\phi_1'(s_2^\star) \end{bmatrix}$$

Recall that A_p is Hurwitz. One has

$$\det(J^\star) = \frac{d^2}{r(1-r)}(\phi_1'(s_2^\star)\phi_2'(s_1^\star) - 1) \quad \text{and} \quad \operatorname{tr}(J^\star) = -\frac{d}{r}\phi_2'(s_1^\star) - \frac{d}{1-r}\phi_1'(s_2^\star)\ .$$

The function $\phi_1(\cdot)$ being concave, one has $\phi_1(s_{in}) \leq \phi_1(s_2^\star) + \phi_1'(s_2^\star)(s_{in} - s_2^\star)$. Along with the inequalities $s_{in} > s_2^\star$ and $\phi_1(s_{in}) = s_{in} > s_1^\star = \phi_1(s_2^\star)$, one deduces $\phi_1'(s_2^\star) > 0$. Recall from Corollary 1 that one has $g'(s_1^\star) = \phi_1'(s_2^\star)\phi_2'(s_1^\star) - 1 > 0$. Then the inequality $\phi_2'(s_1^\star) > 0$ is necessarily satisfied. Finally, we have shown $\det(J^\star) > 0$ and $\operatorname{tr}(J^\star) < 0$, that guarantee the exponential stability of the non-trivial equilibrium $(s_1^\star, x_1^\star, s_2^\star, x_2^\star)$. □

Remark 6. The wash-out equilibrium $(s_{in}, 0, s_{in}, 0)$ is not necessarily hyperbolic. This explains why we cannot use the Convergence Theorem for asymptotically autonomous dynamics given in Appendix F of [30].

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