Polytopic Lyapunov functions for the stability analysis of persistence of competing species

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***Abstract*— We show that intra-specific competition can explain coexistence of several species in a chemostat where they compete for a single substrate. It is indeed known that, without such a competition, only one of the species will survive. The proof technique, which is based on the construction of a polytopic Lyapunov function, is then used to extend this result to a more general class of systems.**

I. INTRODUCTION

In this paper, we will analyze the stability of the non-trivial equilibrium that arises in some mixed culture in competition for a single substrate. It is well known that, when the growth rate of the different species is Monod-like (strictly increasing from zero and upper-bounded), the generic equilibrium state for a given dilution rate consists in the survival of only one of the species (competitive exclusion [12]), that is the species that requires the smallest substrate concentration to have a growth-rate equivalent to the dilution rate: it is the survival of the most efficient species at this rate. This observation has been validated through laboratory experiments [6], but it can also be seen that coexistence of the species is observed in real life. This coexistence has been explained in different cases by a time-varying nutrient feed [13], [7], [5], [2], multi-resource models [9], [8], turbidity operating conditions [4] or a crowding effect [3]. It has been first shown in [10] that the coexistence of the different species can simply be explained by an intra-specific dependency of the growth function, which represents an intra-specific competition; the approach that was used for the proof made use of a multi-phase plane analysis. it leads to a possible generalization of the result to systems modeling competition in a culture, where the competing aspect is not directly linked to the sum of the concentrations of the competing species, but to a more general monotonic function.

We will here present a Lyapunov strategy for the proof of stability of the competition model. It will be based on the construction of a non-smooth Lyapunov function that explicitly takes into account the fact that the competition is linked to the sum of the concentrations of the competing species. It will then be generalized to more general kinds of competition.

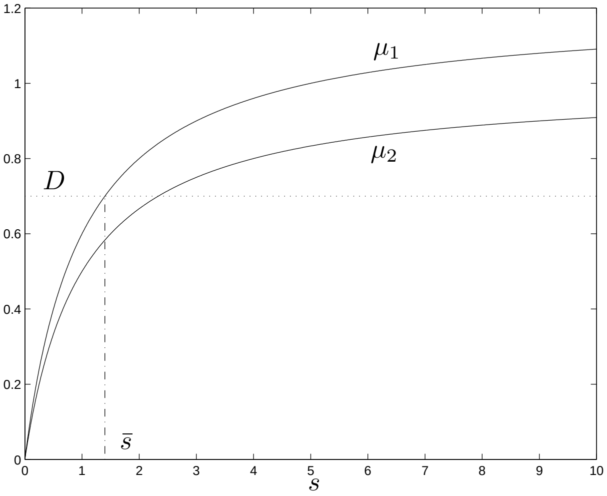

Fig. 1. Graphic representation of the $\mu_i(s) = D$ equations, with the value $\bar{s}$ of the substrate at the stable equilibrium

II. SINGLE-NUTRIENT COMPETITION IN THE CHEMOSTAT

The classical model of a mixed culture in competition for a single substrate in a chemostat is given by the following equations:

$$\left\{ \begin{array}{lcl} \dot{s} & = & -\sum_{j=1}^{n} \frac{\mu_j(s)}{k_j} x_j + D(s_{in} - s) \\ \dot{x}_i & = & x_i(\mu_i(s) - D) \end{array} \right. \qquad (1)$$

where $s \in I\!\!R_+$ represents the substrate, s_{in} the substrate concentration in the input, $x_i \in I\!\!R_+$ a competing species ($i \in \{1, \cdots, n\}$), $\mu_i(s)$ the growth-rate of the species x_i on the substrate s and $D \in I\!\!R_+$ the constant dilution rate.

As stated in the introduction, when the growth-rates are different, such that $\mu_i(0) = 0$, non-decreasing and upper-bounded, the generic globally asymptotically stable equilibrium of this system only presents one persisting species (the others being washed-out). We indeed see, from the analysis of the $\dot{x}_i = 0$ equation that, if two species (i_1 and i_2) are to be present at the same time at the equilibrium, the equations

$$\begin{array}{lcl} \mu_{i_1}(\bar{s}) & = & D \\ \mu_{i_2}(\bar{s}) & = & D \end{array}$$

should both be satisfied. As we can see on Figure 1, this is generically not the case for two arbitrary Monod functions and an arbitrary dilution rate. A local stability analysis shows that only one equilibrium where a singles species survives is stable: the one having the population that requires the smallest substrate value for having $\mu_i(s) = D$.

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We have seen that this wash-out was not always observed in real-life, and that several explanations have been given for such a phenomenon: time-varying nutrient feed, multi-resource models, turbidity operating conditions or a crowding effect. In this paper, we show that intra-specific competition is sufficient for creating such an equilibrium that presents more than one subsisting species. In order to express this intra-specific competition, we simply replace the $\mu_i(\cdots)$ functions with functions h_i of s and x_i:

$$\left\{ \begin{array}{lll} \dot{s} & = & -\sum_{j=1}^{n} \frac{h_j(s,x_j)}{k_j} x_j + D(s_{in} - s) \\ \dot{x}_i & = & x_i(h_i(s,x_i) - D) \end{array} \right. \quad (2)$$

where h_i satisfies

Assumption *1:* The Lipschitz functions $h_i : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+$ satisfy

(i) $h_i(0,.) = 0$

(ii) $\frac{\partial h_i}{\partial s}(.,.) > 0$ (for all $s, x \geq 0$) and $\frac{\partial h_i}{\partial x_i}(.,.) < 0$ (for all $s > 0$, $x \geq 0$).

(iii) The inequality $h_i(s_{in}, 0) > D$ holds and, for all fixed $s > 0$, we have

$$lim_{x_i \rightarrow +\infty} h_i(s, x_i) = 0$$

(iv) For the maximal value $\tilde{s}$ of s such that there exists some k such that $h_k(\tilde{s}, 0) = D$, the $\dot{x}_i = 0$ equations yield non-trivial solutions $\tilde{x}_i > 0$ (except for $\tilde{x}_k = 0$) such that

$$\sum_{j=1}^{n} \frac{\tilde{x}_j}{k_j} < s_{in} - \tilde{s}$$

Point (i) ensures that no growth can take place without substrate; point (ii) shows that the growth of the x_i species is improved by the increase of substrate concentration and is inhibited by its own concentration (intra-specific competition); $h_i(s_{in}, 0) > D$ is necessary because, if it is not satisfied for one of the species, this species is necessarily washed out; with the addition of the technical hypotheses (iii) and (iv), the existence of an equilibrium where all species are present is guaranteed.

This last point is shown as follows; first make the following change of coordinates:

$$(s, x_1, \cdots, x_n) \rightarrow (z, x_1, \cdots, x_n) = (s + \sum_{j=1}^{n} \frac{x_j}{k_j}, x_1, \cdots, x_n)$$

so that the system (2) becomes

$$\left\{ \begin{array}{lll} \dot{z} & = & D(s_{in} - z) \\ \dot{x}_i & = & x_i \left(h_i \left(z - \sum_{j=1}^{n} \frac{x_j}{k_j}, x_i \right) - D \right) \end{array} \right. \quad (3)$$

We directly see that $\bar{z} = s_{in}$, so that, at a positive equilibrium, $\bar{x}_i$ must satisfy

$$h_i \left(s_{in} - \sum_{j=1}^{n} \frac{\bar{x}_j}{k_j}, \bar{x}_i \right) = D$$

Let us now replace $\sum_{j=1}^{n} \frac{\bar{x}_j}{k_j}$ with a constant u. The equilibrium value of x_i is then a function of u that we will denote $\tilde{x}_i(u)$ and that satisfies

$$h_i \left(s_{in} - u, \tilde{x}_i(u) \right) = D \text{ for } u < s_{in}$$

For $u = 0$, point (ii) and (iii) of Assumption 1 ensures that, for each i, there exists a single value $\tilde{x}_i(0) > 0$ such that $h_i \left(s_{in}, \tilde{x}_i(0) \right) = D$; the sum of all these $\frac{\tilde{x}_i(0)}{k_j}$ is then larger than $u = 0$. Differentiating $h_i \left(s_{in} - u, \tilde{x}_i(u) \right) - D = 0$ with respect to u yields

$$-\frac{\partial h_i}{\partial s} + \frac{\partial h_i}{\partial x_i} \frac{d\tilde{x}_i}{du} = 0$$

so that point (ii) implies that

$$\frac{d\tilde{x}_i}{du} < 0$$

For increasing values of u, the value of the sum $\sum_{j=1}^{n} \frac{\tilde{x}_j(u)}{k_j}$ then decreases until $u = s_{in} - \tilde{s}$. At this moment, point (iv) shows that the sum is smaller than $u = s_{in} - \tilde{s}$. There exists therefore a single value $\bar{u}$ of u (that belongs to the open interval $(0, s_{in} - \tilde{s})$) such that we have

$$\bar{u} = \sum_{j=1}^{n} \frac{\tilde{x}_j(\bar{u})}{k_j}$$

There is therefore a single equilibrium to system (3) inside the positive orthant, and it is defined by:

$$(\bar{z}, \bar{x}_1, \cdots, \bar{x}_n) = (s_{in}, \tilde{x}_1(\bar{u}), \cdots, \tilde{x}_n(\bar{u}))$$

We can then state the main theorem of this section:

Theorem 1: The single positive equilibrium of system (2) is asymptotically stable with a basin of attraction containing the positive orthant.

Proof: In order to prove the stability of this equilibrium, we will first study the system on the attractive manifold defined by $z = s_{in}$. Indeed, we directly see from (3) that z exponentially converges towards s_{in}. We will study the stability of the interconnected system afterwards. The system that we need to analyze therefore has the form

$$\dot{x}_i = x_i \left(h_i \left(s_{in} - \sum_{j=1}^{n} \frac{x_j}{k_j}, x_i \right) - D \right) \quad (4)$$

which is defined in the set

$$\mathcal{D} = \{x \in \mathbb{R}^n | x_i \geq 0 \text{ for } i \in \{1, \cdots, n\}, \sum_{j=1}^{n} \frac{x_j}{k_j} \leq s_{in}\}$$

We will also define $\mathcal{D}_+ = \{x \in \mathbb{R}^n | x_i > 0, \sum_{j=1}^{n} \frac{x_j}{k_j} \leq s_{in}\}$.

We will then introduce the following functions; for any $x \in \mathbb{R}^n$, define

$$S(x) = \sum_{j=1}^{n} \frac{x_j - \bar{x}_j}{k_j}$$

and the $\max$ functions

$$S_j^+(x_j) = \max(\frac{x_j - \bar{x}_j}{k_j}, 0) \text{ for } j \in \{1, \cdots, n\}$$

$$S_j^-(x_j) = \max(\frac{\bar{x}_j - x_j}{k_j}, 0) \text{ for } j \in \{1, \cdots, n\}$$

which allow for the definitions of

$$S^+(x) = \sum_{j=1}^{n} S_j^+(x_j) \geq 0$$

$$S^-(x) = \sum_{j=1}^{n} S_j^-(x_j) \geq 0$$

then $S(x) = S^+(x) - S^-(x)$ and the function (when considered in $I\!\!R^n$)

$$V(x) = \max(S^+(x), S^-(x)) \tag{5}$$

is positive definite, radially unbounded, has its unique minimum in $V(\bar{x}) = 0$, and is a $\mathcal{C}^0$ polytopic function (because it is the maximum of continuous functions). We will use $V(x)$ as our Lyapunov function inside $\mathcal{D}$ and instead of checking $\dot{V} < 0$, as is usually done, and which is impossible here because V is non-differentiable, we will verify, for each solution $x(.)$, that the composite map $t \to V(x(t))$ is decreasing everywhere except at $x = \bar{x}$, so that the equilibrium is attractive [1].

The stability analysis is then separated into two cases, the one where $S^+(x) \geq S^-(x)$ and the opposite; in this first part, we suppose that $x_j > 0$ for all $j \in \{1, \cdots, n\}$

$\underline{S^+(x) \geq S^-(x)}$: In this region, our choice of V makes us consider the time evolution of $S^+(x)$. It is easily seen that, when some $x_j > \bar{x}_j$, we have $\dot{x}_j < 0$ because

$$\begin{array}{rcl} \dot{x}_j & = & x_j \left(h_j(s_{in} - \sum_{l=1}^{n} \frac{x_l}{k_l}, x_j) - D \right) \\ & = & x_j \left(h_j(s_{in} - \sum_{l=1}^{n} \frac{\bar{x}_l}{k_l} - S(x), x_j) - D \right) \end{array}$$

Noticing that

$$-S(x) = -S^+(x) + S^-(x) \leq 0$$

and the fact that

$$h_j \left(s_{in} - \sum_{l=1}^{n} \frac{\bar{x}_l}{k_l}, \bar{x}_j \right) - D = 0$$

we can use Assumption (ii) to see that for all $x_j > \bar{x}_j$

$$h_j \left(s_{in} - \sum_{l=1}^{n} \frac{\bar{x}_l}{k_l} - S(x), x_j \right) - D < 0 \tag{6}$$

so that $\dot{x}_j < 0$. This implies that $\dot{S}_j^+(x_j) < 0$. In the case where $x_j = \bar{x}_j$, we see, by continuity, that $\dot{x}_j \leq 0$.

Therefore, as long as $S^+(x) \geq S^-(x)$, the composite map $t \to S_j^+(x_j(t))$ is non-increasing. Moreover, as long as $x \neq \bar{x}$, there is always at least one k such that $x_k > \bar{x}_k$ (otherwise, $S^+(x) = 0$, which implies that $S^-(x) = 0$, and the considered x is the equilibrium). The composite map $t \to S_k^+(x_k(t))$ is therefore decreasing so that the composite map

$$t \to S^+(x(t))$$

is decreasing (it is the sum of non-increasing maps, including at least a decreasing one).

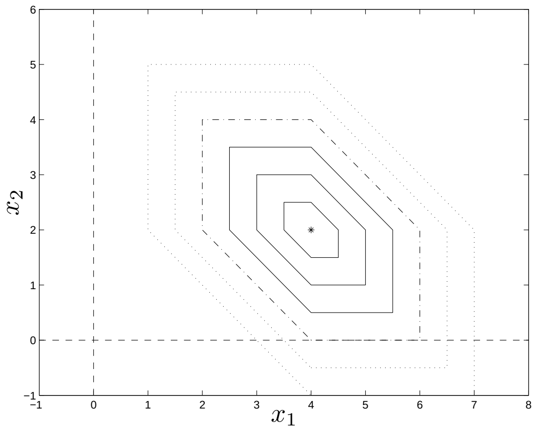

Fig. 2. Level sets of the polytopic Lyapunov functions for a 2D system having its equilibrium in $(x_1, x_2) = (4, 2)$.

$\underline{S^+(x) \leq S^-(x)}$: Through a similar reasoning, we can show that, in this region, the composite map

$$t \to S^-(x(t))$$

is decreasing with the use of

$$h_j \left(s_{in} - \sum_{l=1}^{n} \frac{\bar{x}_l}{k_l} - S(x), x_j \right) - D > 0 \tag{7}$$

Note, however, that troubles could arise when some of the x_js are equal to zero, so that $\dot{x}_j = 0$.

If we now consider the composite map

$$t \to V(x(t)) = \max(S^+(x(t)), S^-(x(t)))$$

we see that it is always decreasing when $x \neq \bar{x}$ and $S^+(x) \neq S^-(x)$ because, in this case, it is equivalent to only one of the functions S^+ or S^- at a time. If $x \neq \bar{x}$ and $S^+(x(t)) = S^-(x(t))$, both composite functions decrease, so that $t \to V(x(t)) = \max(S^+(x(t)), S^-(x(t)))$ also decreases.

It is to be noted that the analysis is not completed here yet. Indeed, we can wonder if convergence can take place towards one of the axes or faces of $\mathcal{D}$ (extinction of one or several of the species)? We have indeed only shown that V is strictly decreasing inside $\mathcal{D}_+$, and not on the border of the orthant. The face $\sum_{j=1}^{n} \frac{x_j}{k_j} = s_{in}$ is not a problem because $h_j(.,.) = 0$ on that face, so that $\sum_{j=1}^{n} \frac{\dot{x}_j}{k_j} = -D \sum_{j=1}^{n} \frac{x_j}{k_j}$, and it is therefore repulsive towards the interior of $\mathcal{D}$.

Looking at Figure 2, we see that the solid level sets are within the positive orthant and that the dash-dotted level set touches the boundary of the orthant. Any solution initiated within this dash-dotted level set then converges to the equilibrium. On the other hand, the dotted level sets cross the border of the orthant, so that a solution having its initial condition within them could very well go to the boundary (e.g. towards one of the equilibria that can be found there).

Let us first note that $S^-(x)$ can be rewritten as a $\max$ function. Indeed, it is easily seen that

$$S^-(x) = \sum_{j=1}^{n} S_j^-(x_j) = \max_{\mathcal{C}_p} \sum_{j \in \mathcal{C}_p \subset \{1, \cdots, n\}} \frac{\bar{x}_j - x_j}{k_j}$$

where the maximum is taken from the 2^n combinations $\mathcal{C}_p$ of arbitrary numbers of indices taken in $\{1, \cdots, n\}$. We will denote $\sum_{j \in \mathcal{C}_p \subset \{1,\cdots,n\}} \frac{\bar{x}_j - x_j}{k_j}$ a partial sum. We will now order the partial sums according to $\sum_{j \in \mathcal{C}_p} \frac{\bar{x}_j}{k_j}$, that is their value in 0 (which is, incidently, also their maximal value within $\mathbb{R}_+^n$); we will write

$$W_l^-(x) = \sum_{j \in \mathcal{C}_p} \frac{\bar{x}_j - x_j}{k_j}$$

with $W_0^-(x) = 0$ and $W_{2^n-1}^-(x) = -S(x)$ (corresponding to the empty and full combinations of indices) and, if we consider $W_{l_1}^-(x)$ and $W_{l_2}^-(x)$, we will have

$$l_1 < l_2 \text{ if } W_{l_1}^-(0) < W_{l_2}^-(0)$$

No ordering is specified when two partial sums have the same value in 0. For convenience, we will define $W_l^+(x) = -W_l^-(x)$ and some $W_{2^n}^-(0) = +\infty$. We can rewrite

$$S^-(x) = \max_{l \in \{0,\cdots,2^n-1\}} W_l^-(x)$$

$$S^+(x) = \max_{l \in \{0,\cdots,2^n-1\}} W_l^+(x)$$

so that

$$V(x) = \max_{l \in \{0,\cdots,2^n-1\}} \left| W_l^-(x) \right|$$

Going back to Figure 2, it is clear that the level corresponding to the dash-dotted line is $W_1^-(0) = \min_j \frac{\bar{x}_j}{k_j}$; indeed, as long as $V(x) < W_1^-(0)$, we can easily see that no x_j can be equal to 0: if such a case would occur, there would be a term $\frac{\bar{x}_j - 0}{k_j} \geq W_1^-(0)$ in $S_j^-(x_j)$ so that $S^-(x)$ (and $V(x)$) would be larger than $W_1^-(0)$, which is a contradiction. On the other hand, the border is touched by this level set $V(x) = W_1^-(0)$; indeed, if we consider, for the corresponding j, the element $x = (\bar{x}_1, \cdots, \bar{x}_{j-1}, 0, \bar{x}_{j+1}, \cdots, \bar{x}_n)$, which belongs to the border of the orthant, we see that $S^-(x) = S_j^-(x) = W_1^-(0)$ and that $S^+(x) = S_j^+(x) = -W_1^-(0)$, so that $V(x) = S^-(x) = W_1^-(0)$. As we have seen, within $\{x \in \mathbb{R}_+^n | V(x) \leq W_1^-(0)\}$, the classical Lyapunov approach applies (with the exception of the part that touches the border).

We will now prove by induction that the set $\{x \in \mathbb{R}_+^n | V(x) \leq W_1^-(0)\}$ is reached in finite time.

Let us suppose that there exists $1 \leq l \leq 2^{n-1}$ such that $W_l^-(0) < V(x(t_0)) < W_{l+1}^-(0)$, where $x(t_0)$ is the value of $x(t)$ at time t_0. We will show that the level set $V(x) = W_l^-(0)$ is reached in finite time. In order to do that, we define the sets

$$\begin{array}{rcl} \Omega & = & \{x \in \mathcal{D} | W_l^-(0) \leq V(x) \leq V(x(t_0))\} \\ \Omega_m^+ & = & \Omega \cap \{x \in \mathcal{D} | V(x) = W_m^+(x)\} \\ \Omega_m^- & = & \Omega \cap \{x \in \mathcal{D} | V(x) = W_m^-(x)\} \end{array}$$

Each set Ω_m^+ and Ω_m^- can be rewritten as

$$\Omega_m^\pm = \Omega \cap \{x \in \mathcal{D} | W_m^\pm(x) \geq \max_{l \in \{0,\cdots,2^n-1\} \setminus m} W_l^\pm(x)\}$$

and is therefore compact (the $^\pm$ notation is a short notation to say that this is valid for $^+$ and $^-$).

Remembering that $S(x) \geq 0$ inside Ω_m^+, the use of (6) induces that $\frac{d}{dt}(W_m^+(x)) < 0$ inside the compact set Ω_m^+, so that there exists a positive constant σ_m^+ such that, inside Ω_m^+

$$\frac{d}{dt}(W_m^+(x)) \leq -\sigma_m^+$$

If we now consider a certain Ω_m^- set with $m \leq l$, we see that it is empty or only contains points that have $x_j = 0$ for the js belonging to the $\mathcal{C}_p$ combination that helped define $W_m^-(x)$. Indeed, the maximal value of some $W_m^-(x)$ within $\mathcal{D}$ is $W_m^-(0)$, so that, if $m \leq l$, the maximal value of $W_m^-(x)$ that can be reached is smaller or equal to $W_l^-(0)$. We will not consider those degenerate Ω_m^- sets because they only come into play after the level $W_l^-(0)$ is reached.

In the case where $m > l$, we have $W_m^-(0) > V(x(t_0))$, so that all x_js that participate in the definition of $W_m^-(.)$ cannot be equal to zero together in $x \in \Omega_m^-$. Using (7) and $S(x) \leq 0$, it is therefore straightforward to see that $\frac{d}{dt} W_m^-(x) < 0$ inside the compact set Ω_m^-. There exists therefore a positive constant σ_m^- such that, inside Ω_m^-

$$\frac{d}{dt}(W_m^-(x)) \leq -\sigma_m^-$$

If x belongs to a single $\Omega_m^\pm$, $\dot{V} = \frac{d}{dt}(W_m^\pm(x))$, so that it is upper-bounded with $-\sigma_m^\pm$. On the other hand, if $x(t)$ belongs to several $\Omega_{m_i}^\pm$, $\dot{V}$ might not be defined; two cases occur at such an $x(t)$:

- there exists a m_i such that $x(.)$ belongs to $\Omega_{m_i}^\pm$ during the small time interval $[t - \epsilon, t + \epsilon]$; $\dot{V}(x(t))$ is then well-defined as $\dot{W}_{m_i}^\pm(x(t)$ and upper-bounded with $-\sigma_{m_i}^\pm$;
- there exists a m_i such that $x(.)$ belongs to $\Omega_{m_i}^\pm$ during the time interval $[t - \epsilon, t]$ and a m_j such that $x(.)$ belongs to $\Omega_{m_j}^\pm$ during the time interval $[t, t + \epsilon]$; during the time interval $[t - \epsilon, t]$. The left time-derivative of V is then defined as $\dot{W}_{m_i}^\pm(x(t))$ and its right derivative as $\dot{W}_{m_j}^\pm(x(t))$. Both are upper-bounded with $\max(-\sigma_{m_i}^\pm, -\sigma_{m_j}^\pm)$

It is then easily understood that, inside Ω, the rate of decrease of $V(x(t))$ is upper-bounded with the maximum of the $-\sigma_m^+$ and $-\sigma_m^-$ of the considered Ω_m^+ and Ω_m^- sets.

$$\max_{m \in \{l+1,\cdots,2^n-1\}} \left(\max(-\sigma_m^-, -\sigma_m^+)\right)$$

so that the level $V(x) = W_l^-(0)$ is reached in finite time (at $x(t_1)$). Moreover, this level is not reached on the boundary of the positive orthant because this boundary is invariant and can therefore not be reached in finite time. We can then conclude that $t \to V(x(t))$ is also decreasing for some time after time t_1 because, as long as all $x_j > 0$, and whether we have to consider S^- or S^+, $t \to V(x(t))$ is decreasing. There exists therefore a small time ϵ such that $V(x(t_1 + \epsilon)) < V(x(t_1)) = W_l^-(0)$.

The induction approach can therefore keep going until we see that $x(t)$ belongs to the interior of the set $\{x \in \mathcal{D} | V(x) \leq W_1^-(0)\}$, where the equilibrium is attractive.

The analysis of the interconnected system is concluded by noting that a solution of the interconnected system (3) either goes to the equilibrium, goes to the boundary of the positive orthant or goes unbounded. This last option is clearly not possible because we can easily see that $z(t)$ is upper-bounded with $\max(s_{in}, z(0))$ and $\sum_{j=1}^{n} \frac{x_j}{k_j}$ is upper-bounded with $z(t)$ because of the way z was defined through a change of coordinates. We will show that no solution can go to the boundary of the positive orthant.

In order to do that, it suffices to use a theorem that was given by Thieme [14] and Markus [11], in a version that can be found in [12] about triangular systems

$$\begin{array}{rcll} \dot{y} & = & Ay & y \in \mathbb{R}^m \\ \dot{x} & = & f(x,z) & x \in \mathbb{R}_+^n \end{array}$$

where A is Hurwitz and $\dot{x} = f(x,0)$ has isolated equilibria. In our case, $m = 1$, $y = z - s_{in}$ and $\dot{x} = f(x,0)$ represents the $\dot{x}_i$ equations with $z = s_{in}$; it has a single equilibrium $\bar{x}$, which is asymptotically stable and attractive inside $\mathcal{D}_+$, and the other equilibria $\bar{x}^j$, which lie on faces of the orthant, have their stable manifold nested in their own face, and of dimension p^j. The result states that the stable manifold of the equilibrium $(0, \bar{x}^j)$ for the (y,x) system is then of dimension $m+p^j$, from which we can conclude that this stable manifold cannot go outside $\mathbb{R}^m \times$the considered face. The equilibrium $(z,x) = (s_{in}, \bar{x})$ is then asymptotically stable with $\mathbb{R}_+ \times \mathcal{D}_+$ as region of attraction.

■

In this section, we have shown how intra-specific competition could prevent inter-specific competition from resulting in extinction of all but one of the species competing for the same nutrient. This idea is in fact quite intuitive: if one of the species starts growing and eliminating the others, the intra-specific competition will limit its growth rate, so that the other species stand a chance of survival.

The polytopic Lyapunov function that has been used is also quite intuitive: while working on the manifold $z = s_{in}$, the growth-rate is not limited by the actual $s(t)$, but rather by the crowding of the bioreactor: the crowding of the bioreactor is equivalent to the possibility of accessing the substrate for each species. If the reactor is very crowded, the species that are above their target equilibrium have a limited growth-rate because of this crowding that limit their access and by the intra-specific competition, so that their concentrations are guaranteed to decrease; if the bioreactor is lightly populated, the species that are under their target equilibrium have an important growth-rate because they have an easy access to the substrate and because they have little competition with their own peers. The polytopic Lyapunov function simply expresses this observation in mathematical terms.

III. GENERALIZATION TO SYSTEMS PRESENTING ADDITIVE CONNECTIONS

The proof technique can be generalized to the interconnection of stable scalar systems through a connection that takes the form of a sum of increasing functions of the states. This could again be interpreted as a competition between the elements of the system; however, we will not impose conditions on the signs of the partial derivatives of the considered functions, but rather on the signs of the functions in some points of the state-space. We will now work in $\mathbb{R}^n$ (and not in the positive orthant):

Theorem 2: Let the system of n equations with input

$$\dot{x}_i = f_i(x_i, u)$$

with $x_i, u \in \mathbb{R}$ and $f_i(.,.)$ Lipschitz continuous in its arguments be such that

$$\begin{array}{ll} (A) & f_i(x_i,u) < 0 \text{ if } x_i > 0 \text{ and } u \leq 0 \\ (B) & f_i(x_i,u) > 0 \text{ if } x_i < 0 \text{ and } u \geq 0 \end{array}$$

Then the autonomous system of n equations

$$\dot{x}_i = f_i(x_i, -\sum_{j=1}^{n} x_j) \tag{8}$$

has a unique equilibrium in $(0, \cdots, 0)$, and it is globally asymptotically stable (GAS).

Proof: It is first clear that $f_i(0,0) = 0$ for all i. Indeed, we have $f_i(x_i, 0) > 0$ for $x_i < 0$ and $f_i(x_i, 0) < 0$ for $x_i > 0$, so that $f_i(0,0) = 0$ by continuity. System (8) then has an equilibrium in $(0, \cdots, 0)$.

We can show that system (8) cannot have an equilibrium with $\sum_{j=1}^{n} x_j > 0$ (resp < 0) by noting that there must then exist k such that $x_k > 0$, so that $\dot{x}_k = f(x_k, -\sum_{j=1}^{n} x_j) < 0$ (because of assumption (B)). The same reasoning can be held for a potential equilibrium x such that $\sum_{j=1}^{n} x_j = 0$ and some $x_k > 0$. The origin is therefore the unique equilibrium.

In order to show stability, we will build a polytopic Lyapunov function similar to the one of the competition case. For any $x \in \mathbb{R}^n$, define

$$S(x) = \sum_{j=1}^{n} x_j$$

and the $\max$ functions

$$S_j^+(x_j) = \max(x_j, 0) \text{ for } j \in \{1, \cdots, n\}$$

$$S_j^-(x_j) = \max(-x_j, 0) \text{ for } j \in \{1, \cdots, n\}$$

which allow for the definitions of

$$S^+(x) = \sum_{j=1}^{n} S_j^+(x_j) \geq 0$$

$$S^-(x) = \sum_{j=1}^{n} S_j^-(x_j) \geq 0$$

then $S(x) = S^+(x) - S^-(x)$ and the function

$$V(x) = \max(S^+(x), S^-(x)) \tag{9}$$

is positive definite, radially unbounded, has its unique minimum in $V(0) = 0$, and is a $\mathcal{C}^0$ polytopic function. We then have two cases for the analysis of the evolution of $V(x(t))$:

$\underline{S^+(x) \geq S^-(x)}$: In this region, our choice of V makes us consider the time evolution of $S^+(x)$. It is easily seen that, when some $x_j > 0$, we have $\dot{x}_j < 0$ because

$$\dot{x}_j \;=\; f_j(x_j, -\textstyle\sum_{l=1}^{n} x_l) = f_j(x_j, -S(x))$$

where

$$-S(x) = -S^+(x) + S^-(x) \le 0$$

This implies that $\dot{S}_j^+(x_j) < 0$. In the case where $x_j = \bar{x}_j$, we can also show that $\dot{x}_j \le 0$.

Therefore, as long as $S^+(x) \ge S^-(x)$, the composite map $t \to S_j^+(x_j(t))$ is non-increasing. Moreover, as long as $x \ne 0$, there is always at least one k such that $x_k > 0$ (otherwise, $S^+(x) = 0$, which implies that $S^-(x) = 0$, and the considered x is the equilibrium). The composite map $t \to S_k^+(x_k(t))$ is therefore decreasing so that the composite map

$$t \to S^+(x(t))$$

is decreasing.

$\underline{S^+(x) \le S^-(x)}$: Through a similar reasoning, we can show that, in this region, the composite map

$$t \to S^-(x(t))$$

is decreasing.

If we now consider the composite map

$$t \to V(x(t)) = \max(S^+(x(t)), S^-(x(t)))$$

we see that it is always decreasing when $x \ne 0$ and $S^+(x) \ne S^-(x)$ because, in this case, it is equivalent to only one of the functions S^+ or S^- at a time. If $x \ne \bar{x}$ and $S^+(x(t)) = S^-(x(t))$, both composite functions decrease, so that $t \to V(x(t)) = \max(S^+(x(t)), S^-(x(t)))$ also decreases, which implies that the origin is GAS. ■

Remark *1:* Note that this can be extended to the same family of systems where the family of feedbacks takes the form

$$u = -\sum_{j=1}^{n} g_j(x_j)$$

where $g_j'(x_j) > 0$, $g_j(0) = 0$, and g_j is bijective ($I\!R \to I\!R$). It then suffices to apply the change of coordinates $y_j = g_j(x_j)$ to be back in the previous case.

The shape of this Lyapunov function is the same as in the previous case as can be seen on Figure 3, except that it is now centered at the origin. We have also added simulations of the system

$$\left\{ \begin{array}{rcl} \dot{x}_1 & = & -x_1(1.01 - \sin(10x_1)) + u(1.01 - \sin(7u)) \\ \dot{x}_2 & = & -x_2(1.01 - \sin(10x_2)) + 2u(1.01 - \sin(7u)) \end{array} \right. \tag{10}$$

with $u = -x_1 - x_2$ which satisfies the hypotheses of the theorem. We see that this system does not satisfy monotonicity hypotheses as the model of competition of Section II did, but it satisfies the sign hypothesis that was used in Theorem 2. This justifies that, along the solutions of this system, the Lyapunov function decreases.

IV. CONCLUSION

In this paper, we have shown, through a non-smooth Lyapunov approach, that persistence of all the species in a chemostat where all species are in competition for the same nutrient, can be explained through intra-specific competition. We have then used this same Lyapunov function to show stability of the origin in a different system of interconnected scalar differential equations.

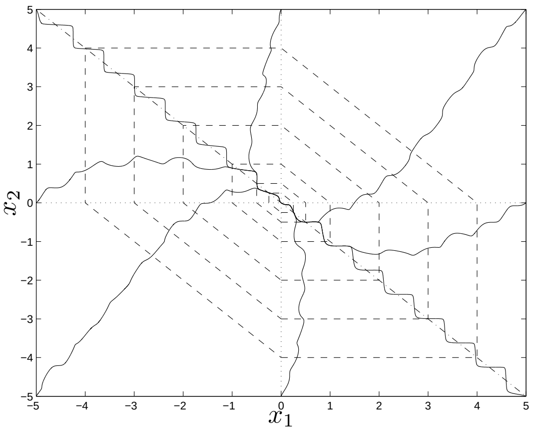

Fig. 3. Level sets of the polytopic Lyapunov functions for the 2D system (8): dashed lines; simulations of system (10): solid lines; $x_1 + x_2 = 0$: dash-dotted line.

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