Ordinary Differential Equations

A Lyapunov function for the chemostat with variable yields

Une fonction de Lyapunov pour le chemostat avec des rendements variables

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A R T I C L E   I N F O

A B S T R A C T

In this Note, we give a global asymptotic stability result for the competition mathematical model between several species in a chemostat, by using a new Lyapunov function. The model includes both monotone and non-monotone response functions, distinct removal rates for the species and variable yields, depending on the concentration of substrate. We obtain, as corollaries of our result, three global stability theorems which were considered in the literature.

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R É S U M É

Dans cette Note on propose une nouvelle fonction de Lyapunov pour l'étude de la stabilité asymptotique globale dans un modèle mathématique de compétition entre esspèces dans le chemostat. Le modèle inclut des fonctions de croissance monotones ou non monotones, des taux de mortalité différents pour chaque espèce et des taux de rendement variables, fonctions de la concentration en substrat. On obtient, comme corollaires de notre résultat, trois théorèmes de stabilité globale qui ont été considérés dans la litérature.

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Dans cet article on étudie la dynamique globale du modèle mathématique où n espèces de micro-organismes sont en compétition dans le chemostat pour un unique substrat limitant, voir (1). Dans ce modèle $S(t)$ représente la concentration du substrat ; $x_i(t)$ représente la concentration de l'espèce i de micro-organismes ; $f_i(S)$ est la quantité de substrat consommé par la population i ; $p_i(S)$ est le taux de croissance de la population i. Ainsi la fonction $y_i(S)$ définie par $y_i(S) = \frac{p_i(S)}{f_i(S)}$ est le taux de rendement de la population i ; S^0 et D sont la concentration du substrat en entrée et le taux de dilution du chemostat, respectivement ; D_i représente le taux de prélèvement de la population i.

Ce modèle a été considéré dans [4], dans le cas de Monod [7] où les taux de croissance sont de la forme de Michaelis–Menten $p_i(S) = \frac{a_i S}{b_i + S}$, les taux de rendement sont constants $y_i(S) = Y_i$, et $D_i = D$ pour $i = 1, \dots, n$. Ces auteurs ont montré que l'espèce qui a le plus petit $\lambda_i = p_i^{-1}(D)$ survit à la compétition. Donc le principe d'exclusion compétitive (CEP) a lieu : une seule espèce survit, celle qui fait la meilleure utilisation de la ressource. Hsu [3] a utilisé une fonction de Lyapunov pour obtenir une preuve élégante et simple du résultat de [4] dans le cas où les D_i sont différents.

Le CEP a été prouvé sous des hypothèses variées [2,6,12,13], mais la question importante de savoir si le CEP est vrai lorsque les p_i sont croissantes et sans restriction sur les D_i reste sans réponse depuis trente ans [5]. L'article [12] représente l'un des progrès majeurs dans l'extension du résultat de [3] à des fonctions de croissance générales. Pour des informations plus complètes sur les contributions des divers auteurs on peut consulter [5,6,10] ainsi que le livre de Smith et Waltman [11]. Le cas où les taux de rendement dépendent du substrat a été considéré par [1,8,10]. Pour les motivations biologiques des taux de rendement dépendant du substrat le lecteur peut consulter [1,8] et leur références.

Dans cet article on généralise le résultat principal de [12] en permettant aux taux de rendement d'être variables et on généralise un résultat de [1] en considérant plusieurs espèces dans le modèle au lieu d'une seule. Par ailleurs on étend [10] en imposant des conditions moins restrictives au système. On utilise pour cela la fonction de Lyapunov (2). Cette fonction de Lyapunov se réduit à la fonction de Lyapunov de [1] lorsque $n = 1$ et à la fonction de Lyapunov de [12] lorsque $y_i(S) = Y_i$.

Dans la Section 2, on suppose que les fonction $p_i, f_i : \mathbf{R}_+ \to \mathbf{R}_+$ sont continues, qu'elles s'annulent en 0 et que $p_i(S) > 0$ et $f_i(S) > 0$ pour $S > 0$. On considère le cas où les fonctions de croissance ne sont pas monotones. Plus précisément on suppose comme dans [2] qu'il existe λ_i et μ_i tels que $\lambda_i \leqslant \mu_i \leqslant +\infty$ et vérifiant $p_i(S) < D_i$ si $S \notin [\lambda_i, \mu_i]$, et $p_i(S) > D_i$ si $S \in]\lambda_i, \mu_i[$. Par conséquent il y a au plus 2 valeurs de S, $S = \lambda_i$ et $S = \mu_i$, telles que $p_i(S) = D_i$. On en déduit que le système (1), dont les solutions sont positivement bornées et qui laisse invariant le cône positif (voir Theorem 4.1 de [1]) peut admettre plusieurs points d'équilibre : l'équilibre de lessivage $E_0 = (S^0, 0, \ldots, 0)$ et les points d'équilibre E_i^* and E_i^{**} dont toutes les composantes sont nulles à l'exception de la première qui vaut λ_i ou μ_i et de celle d'indice $i + 1$ qui vaut $x_i^* = F_i(\lambda_i)$ ou $x_i^{**} = F_i(\mu_i)$, où $F_i(S) = D\frac{S^0 - S}{f_i(S)}$.

On considère le cas $\lambda_1 < \lambda_2 \leqslant \cdots \leqslant \lambda_n$ et $\lambda_1 < S^0 < \mu_1$ (voir hypothèse (i) du Théorème 2.1). Dans ce cas l'équilibre $E_1^* = (\lambda_1, x_1^*, 0, \ldots, 0)$ est localement exponentiellement stable si et seulement si $F_1'(\lambda_1) < 0$. On s'intéresse alors à la stabilité asymptotique globale de E_1^*. On suppose de plus qu'il existe des constantes $\alpha_i > 0$ telles que pour tout $i \geqslant 2$ pour lequel $\lambda_i < S^0$ les conditions (3) sont satisfaites. Enfin on suppose que la fonction $F(S) = \frac{f_1(S)}{S^0 - S}$ est plus petite que $F(\lambda_1)$ si $S \in]0, \lambda_1[$, et qu'elle est plus grande que $F(\lambda_1)$ si $S \in]\lambda_1, S^0[$. Sous ce hypothèses (illustrées dans la Fig. 1), le Théorème 2.1 affirme que l'équilibre E_1^* est globalement asymptotiquement stable, pour (1), dans le cône positif. Dans la section 3 on montre comment ce théorème généralise des résultats de [1,10,12].

1. Introduction

In this Note we study the global dynamics of the following model of the chemostat in which n populations of microorganisms compete for a single growth-limiting substrate:

$$S'(t) = D[S^0 - S(t)] - \sum_{i=1}^{n} f_i(S(t))x_i(t), \qquad x_i'(t) = [p_i(S(t)) - D_i]x_i(t), \quad i = 1, \ldots, n, \tag{1}$$

where $S(0) \geqslant 0$ and $x_i(0) > 0$, $i = 1, \ldots, n$, and S^0, D and D_i are positive constants. In these equations, $S(t)$ denotes the concentration of the substrate at time t; $x_i(t)$ denotes the concentration of the ith population of microorganisms at time t; $f_i(S)$ represents the uptake rate of substrate of the ith population; $p_i(S)$ represents the per-capita growth rate of the ith population and so the function $y_i(S)$ defined by $y_i(S) = \frac{p_i(S)}{f_i(S)}$ is the growth yield; S^0 and D denote, respectively, the concentration of substrate in the feed bottle and the flow rate of the chemostat; each D_i represents the removal rate of the ith population.

The global analysis of this model was considered by Hsu, Hubbell and Waltman [4], in the Monod case [7] when the response functions are of Michaelis–Menten form $p_i(S) = \frac{a_i S}{b_i + S}$, and the yields are constant $y_i(S) = Y_i$, and $D_i = D$ for $i = 1, \ldots, n$. The authors showed that only the species with the lowest break-even concentration $\lambda_i = p_i^{-1}(D)$ survives. Thus the competitive exclusion principle (CEP) holds: only one species survives, namely the species which makes optimal use of the resources. Hsu [3] applied a Lyapunov–LaSalle argument to give a simple and elegant proof of the result in [4] for the case of different removal rates D_i.

CEP has been proved under a variety of hypothesis [2,6,12,13], but an important open question remains: *is the CEP true assuming only that the p_i are monotone with no restriction on the D_i?* This major open problem remains unresolved after more than thirty years [5]. Despite the fact that the hypothesis of [12] are not satisfied by all growth functions, the work of Wolkowicz and Lu [12] represents a major step in the extension of the result of Hsu [3] to general growth functions. For a survey on the contribution of each paper the reader may consult the introductions of the papers [5,6,10]. For general background on model (1), in the constant yield case $y_i(S) = Y_i$, the reader is referred to the monograph of Smith and Waltman [11]. The variable yield case was considered, for $n = 1$ and $n = 2$ by Pilyugin and Waltman [8], with a particular interest to linear and quadratic yields. The model (1) was considered by Arino, Pilyugin and Wolkowicz [1] and by Sari and Mazenc [10]. For biological motivations concerning the dependence of the yields on the substrate, the reader is referred to [1,8] and the references therein. Our result concern mainly the case of variable yields, for which it is known [1,8] that exotic dynamical behaviours, including limit cycles ad chaos, are possible. Thus in the case of variable yields, it is of great importance to have criteria ensuring the global convergence to an equilibrium with at most one surviving species.

In this Note we generalize [12] by allowing variable yields and we generalize [1] by allowing multi species. We further extend [10] by providing less restrictive assumptions on the system. We use the Lyapunov function

$$V = \frac{S^0 - \lambda_1}{f_1(\lambda_1)} \int_{\lambda_1}^{S} \frac{p_1(\sigma) - D_1}{S^0 - \sigma}\, d\sigma + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi}\, d\xi + \sum_{i=2}^{n} \alpha_i x_i, \tag{2}$$

where λ_1, x_1^* and α_i are real numbers to be determined. This Lyapunov function reduces to the Lyapunov function considered in [1] in the case when $n = 1$. It reduces to the Lyapunov function considered in [12] in the case when the yields are constant. The paper is organized as follows. In Section 2 we give our main result (Theorem 2.1). In Section 3 we show how Theorem 2.1 extends results in [1,10,12].

2. Global asymptotic stability

We assume that $p_i, f_i : \mathbf{R}_+ \to \mathbf{R}_+$ are continuous functions such that $p_i(0) = f_i(0) = 0$ and for all $S > 0$, $p_i(S) > 0$ and $f_i(S) > 0$. Following Butler and Wolkowicz [2], we make the following assumptions on the form of the response functions p_i: there exist positive extended real numbers λ_i and μ_i with $\lambda_i \leqslant \mu_i \leqslant +\infty$ such that $p_i(S) < D_i$ if $S \notin [\lambda_i, \mu_i]$, and $p_i(S) > D_i$ if $S \in]\lambda_i, \mu_i[$. Hence there exist at most two values of S, $S = \lambda_i$ and $S = \mu_i$, called the break-even concentrations, satisfying the equation $p_i(S) = D_i$. We adopt the convention $\mu_i = \infty$ if this equation has only one solution and $\lambda_i = \infty$ if it has no solution.

The non-negative cone is invariant under the flow of (1), and all solutions are defined and remain bounded for all $t \geqslant 0$, see Theorem 4.1 [1]. System (1) can have many equilibria: the washout equilibrium $E_0 = (S^0, 0, \ldots, 0)$, which is locally exponentially stable if and only if for all $i = 1, \ldots, n$, $S^0 \notin [\lambda_i, \mu_i]$ and the equilibria E_i^* and E_i^{**} where all components of E_i^* and E_i^{**} vanish except for the first and the $(i+1)$th, which are $S = \lambda_i$, $x_i = x_i^* := F_i(\lambda_i)$, for E_i^*, and $S = \mu_i$, $x_i = x_i^{**} := F_i(\mu_i)$, for E_i^{**}, respectively, where $F_i(S) = D\frac{S^0 - S}{f_i(S)}$.

The equilibrium E_i^* lies in the non-negative cone if and only if $\lambda_i \leqslant S^0$. If $\lambda_i < \lambda_j$ for all $i \neq j$ and $F_i'(\lambda_i) < 0$ then it is locally exponentially stable. It coalesces with E_0 when $\lambda_i = S^0$. The equilibrium E_i^{**} lies in the non-negative cone if and only if $\mu_i \leqslant S^0$ and is locally exponentially unstable if it exists. Its coalesces with E_0 when $\mu_i = S^0$. Besides these equilibria, the system (1) can have a continuous set of non-isolated equilibria in the non-generic cases where two or more of the break-even concentrations are equal. In what follows we assume, that $\lambda_1 < \lambda_2 \leqslant \cdots \leqslant \lambda_n$, and $\lambda_1 < S^0 < \mu_1$. Hence E_0 is locally exponentially unstable and the equilibrium $E_1^* = (\lambda_1, x_1^*, 0, \ldots, 0)$, where $x_1^* = F_1(\lambda_1) = D\frac{S^0 - \lambda_1}{f_1(\lambda_1)}$, lies in the non-negative cone. It is locally exponentially stable if and only if $F_1'(\lambda_1) < 0$. Our aim is to give sufficient conditions for which E_1^* is globally asymptotically stable (GAS).

Theorem 2.1. *Assume that*

(i) $\lambda_1 < \lambda_2 \leqslant \cdots \leqslant \lambda_n$, and $\lambda_1 < S^0 < \mu_1$.
(ii) *Let $\rho_i = \min(\lambda_i, S^0)$. There exist constants $\alpha_i > 0$ for each $i \geqslant 2$ satisfying $\lambda_i < S^0$ such that*

$$\max_{0 < S < \lambda_1} g_i(S) \leqslant \alpha_i \leqslant \min_{\lambda_i < S < \rho_i} g_i(S), \quad \text{where } g_i(S) = \frac{f_i(S)}{f_1(\lambda_1)} \frac{p_1(S) - D_1}{p_i(S) - D_i} \frac{S^0 - \lambda_1}{S^0 - S}. \tag{3}$$

(iii) *The function $F(S) = \frac{f_1(S)}{S^0 - S}$ satisfies $F(S) < F(\lambda_1)$ if $S \in]0, \lambda_1[$, and $F(S) > F(\lambda_1)$ if $S \in]\lambda_1, S^0[$.*

Then the equilibrium E_1^* is GAS for (1) *with respect to the interior of the positive cone.*

Proof. Consider the function $V = V(S, x_1, \ldots, x_n)$ defined by (2) where $\alpha_i > 0$ are the positive constants satisfying (3) if $\lambda_i < S^0$ and $\alpha_i > 0$ are arbitrary if $\lambda_i > S^0$. The function V is continuously differentiable for $0 < S < S^0$ and $x_i > 0$ and positive except at the point E_1^*, where it is equal to 0. The derivative of V along the trajectories of (1) is given by

$$V' = x_1\left[p_1(S) - D_1\right]\left[1 - \frac{F(S)}{F(\lambda_1)}\right] + \sum_{i=2}^{n} x_i\left[p_i(S) - D_i\right]\left[\alpha_i - g_i(S)\right].$$

First, note that, using hypothesis (i) and (iii), the first term of the above sum is always non-positive for $0 < S < S^0$ and equals 0 for $S \in]0, S^0[$ if and only if $S = \lambda_1$ or $x_1 = 0$. On the other hand, using (ii), the second term of the above sum is always non-positive for every $S \in]0, S^0[$ and equal to zero if and only if $x_i = 0$ for $i = 2, \ldots, n$. Hence $V' \leqslant 0$ and $V' = 0$ if and only if $x_i = 0$ for $i = 1, \ldots, n$ or $S = \lambda_1$ and $x_i = 0$ for $i = 2, \ldots, n$. By the Krasovskii–LaSalle extension theorem (see [11], Section 2.2) the ω-limit set of the trajectory is E_1^*. For the details of the proof see [9]. $\square$

The condition $\lambda_1 < \lambda_i$ for $i \neq 1$ in hypothesis (i) can be stated without loss of generality, by labelling the populations such that the index $i = 1$ corresponds to the lowest break-even concentration, but the condition $\lambda_1 < S^0 < \mu_1$ in hypothesis (i)
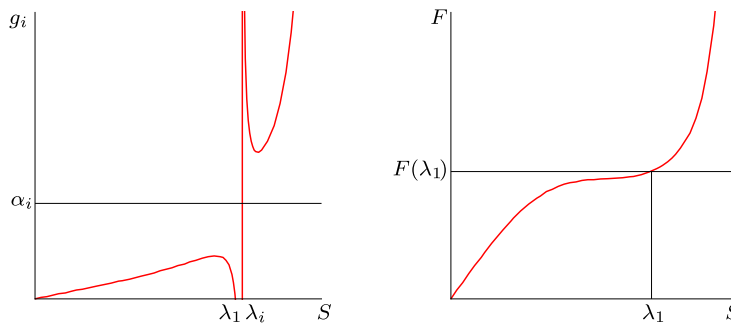
Fig. 1. Graphical depictions of the hypotheses in Theorem 2.1. On the left, hypothesis (ii). On the right, hypothesis (iii).

cannot be stated without loss of generality, see for instance [2], or the discussion in Section 2.5 of [11]. The hypotheses (ii) and (iii) are depicted in Fig. 1.

3. Applications

The system (1) was studied by Arino, Pilyugin and Wolkowicz [1]. However, these authors have considered the question of the global asymptotic stability of E_1^* only in the one species case $n = 1$ (see [1], Theorem 2.11). Using the Lyapunov function (notice that if $n = 1$, then $V = V_{APW}$)

$$V_{APW} = \frac{S^0 - \lambda_1}{f_1(\lambda_1)} \int_{\lambda_1}^{S} \frac{p_1(\sigma) - D_1}{S^0 - \sigma}\, d\sigma + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi}\, d\xi,$$

they proved the following result:

Corollary 3.1. *If $\lambda_1 < S^0 < \mu_1$ and $1 - \frac{f_1(S)(S^0 - \lambda_1)}{f_1(\lambda_1)(S^0 - S)}$ have exactly one sign change for $S \in (0, S^0)$ then E_1^* is GAS for (1), where $n = 1$, with respect to the interior of the positive quadrant.*

Proof. The result follows from Theorem 2.1 since the hypothesis on the change of sign is equivalent to hypothesis (iii) in Theorem 2.1. In the case when $n = 1$ the condition (3) is obviously satisfied. □

The constant yields case $y_i(S) = Y_i$ of (1) was considered by Wolkowicz and Lu (see [12], Theorem 2.3). Using the Lyapunov function (notice that if $y_i(S) = Y_i$, then $V = Y_1 V_{WL}$)

$$V_{WL} = \frac{S^0 - \lambda_1}{D_1} \int_{\lambda_1}^{S} \frac{p_1(\sigma) - D_1}{S^0 - \sigma}\, d\sigma + \frac{1}{Y_1}\int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi}\, d\xi + \sum_{i=2}^{n} \frac{\alpha_i^{WL}}{Y_i} x_i,$$

where α_i^{WL} are the positive constants satisfying (4), these authors proved the following result:

Corollary 3.2. *Assume that*

(i) $\lambda_1 < \lambda_2 \leqslant \cdots \leqslant \lambda_n$, and $\lambda_1 < S^0 < \mu_1$.
(ii) *Let $\rho_i = \min(\mu_i, S^0)$. There exist constants $\alpha_i^{WL} > 0$ for each $i \geqslant 2$ satisfying $\lambda_i < S^0$ such that*

$$\max_{0 < S < \lambda_1} g_i^{WL}(S) \leqslant \alpha_i^{WL} \leqslant \min_{\lambda_i < S < \rho_i} g_i^{WL}(S), \quad \text{where } g_i^{WL}(S) = \frac{p_i(S)}{D_1}\frac{p_1(S) - D_1}{p_i(S) - D_i}\frac{S^0 - \lambda_1}{S^0 - S}. \tag{4}$$

Then the equilibrium E_1^* is GAS stable for system (1), where $y_i(S) = Y_i$, with respect to the interior of the positive cone.

Proof. In the case when the yields are constant, we have $g_i(S) = \frac{Y_1}{Y_i} g_i^{WL}(S)$. Hence conditions (4) imply conditions (3) with $\alpha_i = \alpha_i^{WL} Y_1 / Y_i$. On the other hand $F(S) = \frac{p_1(S)}{(S^0 - S)Y_1}$. Thus, hypothesis (iii) in Theorem 2.1 follows from hypothesis $\lambda_1 < S^0 < \mu_1$. The result follows from Theorem 2.1. □

In [10], another Lyapunov function was proposed in the case when the yields are variable, leading to the following result:

Corollary 3.3. *Assume that*

(i) $\lambda_1 < \lambda_2 \leqslant \cdots \leqslant \lambda_n$, *and* $\lambda_1 < S^0 < \mu_1$.
(ii) *Let* $\rho_i = \min(\mu_i, S^0)$. *There exist constants* $\alpha_i^{SM} > 0$ *for each* $i \geqslant 2$ *such that*

$$\max_{0 < S < \lambda_1} g_i^{SM}(S) \leqslant \alpha_i^{SM} \leqslant \min_{\lambda_i < S < \rho_i} g_i^{SM}(S), \quad \text{where } g_i^{SM}(S) = \frac{f_i(S)}{f_1(S)} \frac{p_1(S) - D_1}{p_i(S) - D_i}. \tag{5}$$

(iii) *The function* $F(S) = \frac{f_1(S)}{S^0 - S}$ *satisfies* $F(S) < F(\lambda_1)$ *if* $S \in {]}0, \lambda_1[$, *and* $F(S) > F(\lambda_1)$ *if* $S \in {]}\lambda_1, S^0[$.

Then the equilibrium E_1^* *is GAS for* (1) *with respect to the interior of the positive cone.*

Proof. We have $g_i(S) = \frac{S^0 - \lambda_1}{f_1(\lambda_1)} F(S) g_i^{SM}(S)$. By hypotheses (ii) and (iii) we have hypothesis (iii) of Theorem 2.1, with appropriate constants α_i. The result follows from Theorem 2.1. □

Corollary 3.3 was obtained by Sari and Mazenc (see [10], Theorem 2.2). These authors used the following Lyapunov function:

$$V_{SM} = \int_{\lambda_1}^{S} \frac{p_1(\sigma) - D_1}{f_1(\sigma)} \, d\sigma + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} \, d\xi + \sum_{i=2}^{n} \alpha_i^{SM} x_i,$$

where α_i^{SM} are the positive constants satisfying (5). In the Monod case the Lyapunov function V_{SM} reduces to the Lyapunov function used by Hsu [3]. Notice that the Lyapunov function (2) we use is not proportional to the function V_{SM}.

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