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A MATHEMATICAL STUDY OF A SYNTROPHIC RELATIONSHIP OF A MODEL OF ANAEROBIC DIGESTION PROCESS

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Abstract. A mathematical model involving the syntrophic relationship of two major populations of bacteria (acetogens and methanogens), each responsible for a stage of the methane fermentation process is proposed. A detailed qualitative analysis is carried out. The local and global stability analyses of the equilibria are performed. We demonstrate, under general assumptions of monotonicity, relevant from an applied point of view, the global asymptotic stability of a positive equilibrium point which corresponds to the coexistence of acetogenic and methanogenic bacteria.

1. Introduction.

"Methane fermentation" or "anaerobic digestion" is a process that converts organic matter into a gaseous mixture, mainly composed of methane and carbon dioxide (CH_4 and CO_2) through the concerted action of a close-knit community of bacteria (cf. Figure 1) by catabolizing anaerobically degradable organic matter to the end-products. It is often used for the treatment of concentrated wastewaters or to stabilize the excess sludge produced in waste-water treatment plants into more stable products. There is also considerable interest in plant-biomass-fed digesters, since the produced methane can be valorized as a source of energy. It is usually considered that three major metabolic groups of bacteria are involved in such a three-steps process:

- *Hydrolysis and acidogenesis*. Fermentative bacteria hydrolyze materials such as lipids, proteins, and polysaccharides, ferment most products with excretion of acetate and other saturated fatty acids, CO_2 and H_2 as major end-products.
- *Acetogenesis and dehydrogenation*. This second step is achieved by a consortium of mainly unknown species, the H_2-producing acetogenic bacteria,

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which produce acetate and H_2 from end-products of the first step (that is from Volatile Fatty Acids).

- *Methanogenesis*. The methanogenic bacteria catabolize the end-products, mainly acetate, CO_2 and H_2 produced jointly by the other two groups, to the terminal products [11].

The mathematical modeling of the anaerobic digestion process has been an active research area during the last three decades. Anaerobic digesters often exhibit significant stability problems, that may be avoided only through appropriate control strategies. Such strategies require, in general, the development of appropriate mathematical models, which adequately portray the key biological processes that take place in the reactor. Graef et al. [6] proposed a single anaerobic bacteria model involving only the acetoclastic methanogens. Hill et al. [7] developed a dynamic mathematical model for simulating the anaerobic digestion process. The entire process, from the introduction of insoluble organic material to the final production of carbon dioxide, ammonia, and methane, was considered during the design process. Carbonate equilibrium relationships are used to calculate pH while mass balances are maintained on volatile matter, volatile acids, soluble organics, two groups of bacteria, cations, nitrogen, and carbon dioxide. Inhibition of the bacteria by ammonia and un-ionized acids was also determined. Mosey [12] considered the hydrogen partial pressure as the key regulatory parameter of the anaerobic digestion of glucose. This influences the redox potential in the liquid phase. The model considers four bacterial groups to participate in the conversion of glucose to CO_2 and CH_4: the acid-forming bacteria, which are fast-growing and ferment glucose to produce a mixture of acetate, propionate and butyrate, the acetogenic bacteria convert the propionate and butyrate to acetate, the acetoclastic methane bacteria convert acetate to CO_2 and CH_4, and the hydrogen-utilizing methane bacteria reduce CO_2 to CH_4. Bernard *et al.* proposed a two step model for control purposes including the inhibition of the acidogenic consortium by VFA [2]. While these models were basically developed for control purposes, the IWA[1] task group on the modeling of anaerobic digestion recently proposed the Anaerobic Digestion Model No.1 (ADM1) which is however far too complex to be used for control design [1].

One specific characteristic of the anaerobic process is that it includes, within the second and third steps, a number of bacteria populations exhibiting obligatory mutualistic relationships. Such a syntrophic[2] relationship is necessary for the biological reactions to be thermodynamically possible. Indeed, an excess of hydrogen in the medium inhibits the growth of acetogenic bacteria. Their association with H_2 consuming bacteria is thus necessary for the second step of the reaction to be fulfilled. Such a syntrophic relationship has been pointed out in a number of experimental works. One of the first results was obtained by Bryant *et al.* who performed the following experiments. Two bacterial species were isolated from cultures of *Methanobacillus omelianskii* grown on media containing ethanol as oxidizable substrate [3]. One of these, the S organism, is a gram negative, motile, anaerobic rod which ferments ethanol with production of H_2 and acetate but is inhibited by inclusion of 0.5 arm of H_2 in the gas phase of the medium. The other organism is a gram

[1] International Water Association.

[2] which exhibits obligatory mutualistic (symbiotic) relationship but where at least one of the species can grow without the other at the opposite of a purely symbiotic relationship where both species must always grow together. It is actually one of the most important differences of the present paper with [4].

variable, nonmotile, anaerobic rod which utilizes H_2 but not ethanol for growth and methane formation. The results indicate that *M. omelianslcii* maintained in ethanol media is actually a symbiotic association of the two species (called syntrophic in microbial ecology to specify that at least one of the species can grow alone as it is the case for the H_2 consuming microorganism). Experimental results of these studies show that *M. omelianskii* as usually cultured in ethanol-carbonate medium consists of a symbiotic association of two species of bacteria, neither of which will grow well as pure cultures in ethanol-carbonate media even with complex sources of growth factors such as rumen fluid, trypticase and yeast extract added. One of these species, the S organism, oxidizes ethanol with production of H_2 and acetate. Its failure to grow well in ethanol media is at least partially explained by the fact that it is inhibited by the H_2 produced during growth. The other species, the methanogenic microorganisms, utilize H_2 but not ethanol as the source of electrons for growth and methane formation.

In this paper we restrict our attention to the reactionary part of the anaerobic digestion involving only two major bacteria populations (acetogens x_1 and methanogens x_2) and study their syntrophic relationship. The volatile fatty acids products (s) are degraded by acetogens, forming hydrogen (p), acetate and carbon dioxide. This same intermediate product is required by anaerobic methanogens in order to carry out anaerobic respiration. In the absence of H_2-producing bacteria (x_1), methanogens cannot grow.

Quite similar models have already been proposed in the literature as the one by Kreikenbohm et al. (cf. [9]). However, the model considered in the present paper is more general than the latter in the senss that the kinetics are not explicitely described. Rather, a number of qualitative assumptions are proposed and thus the performed analysis is more general. In addition, only the influence of the dilution rate on the number of equilibria is looked at while, in the present paper, we describe the qualitative behavior of the trajectories.

In Section 2, we propose a system of four differential equations as a model for this association. The positive equilibria are determined in Section 3. Next, in Section 4, their local and global stability properties are established. The global asymptotic stability results are demonstrated through Dulac's criterion (see for instance [8, Chapter 6]) that rules out the possibility of the existence of periodic solutions for the reduced planar system and the Poincaré-Bendixon Theorem (see for instance [8, Chapter 6]). In particular, we show that for every positive initial conditions, and under general and natural assumptions on the substrate input concentration and on the growth functions, the solutions converge to a positive equilibrium point which corresponds to the coexistence of acetogenic and methanogenic bacteria. Simulations are presented in Section 5. Finally, concluding remarks in Section 6 end the paper.

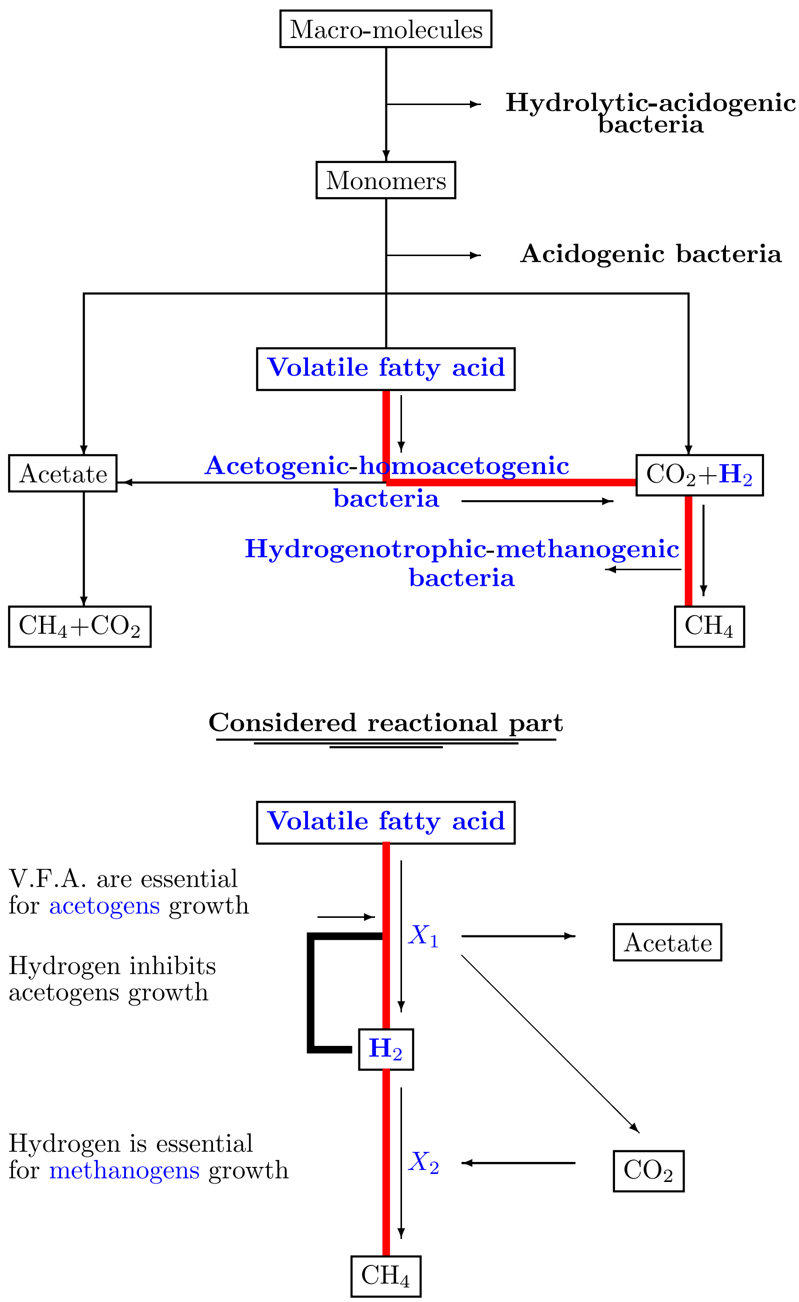

FIGURE 1. Anaerobic fermentation process

1.1. **Notations and definitions.** • We let $\mathbb{R}_+ = [0, +\infty)$, $\mathbb{R}_+^* = (0, +\infty)$, $\mathcal{C} = (0, +\infty)^4$ and $\overline{\mathcal{C}} = \mathbb{R}_+^4$.
• We will say that a point is positive (resp. nonnegative) if all its components are positive (resp. nonnegative).
• We will say that a system

$$\dot{\chi} = \mathcal{F}(\chi), \tag{1}$$

with $\chi \in \mathbb{R}^n$ which admits a positively invariant set $\mathcal{P} \subset \mathbb{R}^n$ and an equilibrium point $E \in \mathcal{P}$ admits E as a globally asymptotically stable equilibrium point of (1) on $\mathcal{P}$ if all the solutions of (1) with initial condition $\chi(0) \in \mathcal{P}$ are defined for all $t \geq 0$ and converge to E. When $\mathcal{P} = \mathbb{R}_+^n$ or $\mathcal{P} = (0, +\infty)^n$, then we will simply say that (1) admits E as a globally asymptotically stable equilibrium point whenever no confusion can arise from the context.
• The argument of the functions will be omitted or simplified whenever no confusion can arise from the context.

2. **Mathematical model.** Let S, X_1, X_2 and P denote, respectively, the concentrations of volatile fatty acid, acetogenic bacteria, hydrogenotrophic-methanogenic bacteria, and hydrogen present in the reactor at time t. We neglect all species-specific death rates and take into account the dilution rate only. Hence our model is described by the following ordinary differential equations:

$$\left\{ \begin{array}{rcl} \dot{S} & = & D(S_{in} - S) - k_3\mu_1(S,P)X_1 \ , \\ \dot{X}_1 & = & \mu_1(S,P)X_1 - DX_1 \ , \\ \dot{X}_2 & = & \mu_2(P)X_2 - DX_2 \ , \\ \dot{P} & = & k_1\mu_1(S,P)X_1 - k_2\mu_2(P)X_2 - DP \ , \end{array} \right. \tag{2}$$

where S_{in} denotes the input concentration of volatile fatty acid and D is the dilution rate. The parameters S_{in}, D, k_1, k_2, k_3 are positive and constant and the functional responses of the species $\mu_1 : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $\mu_2 : \mathbb{R}_+ \to \mathbb{R}_+$ are of class C^1. We introduce some assumptions.
A1. $\mu_1(S_{in} - 2P, P) > D$, for all $P \geq 0$ such that $\mu_2(P) \leq D$.
A2. $\mu_1(0, P) = 0$, for all $P \in \mathbb{R}_+$.
A3. $\dfrac{\partial \mu_1}{\partial S}(S, P) > 0$, for all $(S, P) \in \mathbb{R}_+^2$.
A4. $\dfrac{\partial \mu_1}{\partial P}(S, P) < 0$, for all $(S, P) \in \mathbb{R}_+^2$.
A5. $\mu_2(0) = 0$, $\mu_2(S_{in}) > D$, $\mu_2'(P) > 0$, for all $P \in \mathbb{R}_+$.

Assumption *A1* means that, in spite of being inhibiting by the product, the first species still grows for concentrations that are limiting for the second species. It is a necessary and sufficient condition for the existence of the positive equilibrium point which corresponds to the coexistence of the two species. Hypothesis *A2* results from the fact that no growth can take place for acetogens without volatile fatty acid. Hypothesis *A3* means that the growth of acetogens increases with volatile fatty acid. Hypothesis *A4* reflects that acetogens is inhibited by the hydrogen H_2 that it produces. The equality $\mu_2(0) = 0$ in Hypothesis *A5* means that the presence of hydrogen is necessary for the growth of methanogens and, in Hypothesis *A5*, the fact that μ_2' is positive means that the growth of methanogens increases with hydrogen produced by acetogens. As underlined in the introduction, note that there is a kind of mutualism between the two species which is necessary for methanogens and optional for acetogens (called "syntrophy" in the present paper).

We do not claim that the system (2) endowed with the hypotheses *A1*-*A5* is a realistic model for complete anaerobic fermentation stage. We simply study part of the methane fermentation: we are interested in the specific role of hydrogen for a class of microorganisms. The model (2) is a first step and its greatest advantage is that it is completely tractable from the mathematical point of view.

We transform (2) by means of the following changes of variables and notations: $x_1 = k_1X_1; x_2 = k_2X_2,\ p = P,\ s = \dfrac{2k_1}{k_3}S,\ s_{in} = \dfrac{2k_1}{k_3}S_{in},\ f(s,p) = \mu_1(S,P)$ and $g(p) = \mu_2(P)$. The equations thus obtained are

$$\left\{\begin{array}{rcl} \dot{s} & = & D(s_{in} - s) - 2f(s,p)x_1 \ , \\ \dot{x}_1 & = & f(s,p)x_1 - Dx_1 \ , \\ \dot{x}_2 & = & g(p)x_2 - Dx_2 \ , \\ \dot{p} & = & f(s,p)x_1 - g(p)x_2 - Dp \ , \end{array}\right. \tag{3}$$

where $s_{in} > 0$, $D > 0$ and $f : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $g : \mathbb{R}_+ \to \mathbb{R}_+$ are functions of class C^1. Assumptions *A1* to *A5* become:
H1. $f(s_{in} - 2p, p) > D$ for all $p \geq 0$ such that $g(p) \leq D$.
H2. $f(0,p) = 0$, for all $p \in \mathbb{R}_+$.
H3. $\dfrac{\partial f}{\partial s}(s,p) > 0$, for all $(s,p) \in \mathbb{R}_+^2$.
H4. $\dfrac{\partial f}{\partial p}(s,p) < 0$, for all $(s,p) \in \mathbb{R}_+^2$.
H5. $g(0) = 0$, $g(s_{in}) > D$, $g'(p) > 0$, for all $p \in \mathbb{R}_+$.

3. Preliminary results.

3.1. Technical results.

To establish our main results, we need some technical Lemmas.

Lemma 1. *If a function $g : \mathbb{R}_+ \to \mathbb{R}_+$ satisfies Assumption H5, then there exists a unique value $p_* \in (0, s_{in})$ such that*

$$g(p_*) = D \ . \tag{4}$$

Proof. The result is a consequence of the fact that $g(0) = 0$, $g(s_{in}) > D$ and g is continuous and increasing. □

Remark 1. We deduce from Lemma 1 that if the system (3) is such that the function g satisfies Assumption *H5* and the function f satisfies Assumptions *H2* to *H4*, then this system satisfies Assumption *H1* if and only if $f(s_{in} - 2p_*, p_*) > D$.

Lemma 2. *Assumptions H1 to H5 ensure that there exists a unique value $\bar{p} \in \left(0, \frac{1}{2}s_{in}\right)$ such that*

$$f\left(s_{in} - 2\bar{p}, \bar{p}\right) = D \ . \tag{5}$$

Proof. Assumption *H2* ensures that $f(0,p) = 0$ for all $p \geq 0$. Assumptions *H1* and *H5* imply that $f(s_{in}, 0) > D$ and Assumptions *H3* and *H4* imply that the function $p \to f(s_{in} - 2p, p)$ is continuous and decreasing. The result is deduced. □

Lemma 3. *Consider a solution (s, x_1, x_2, p) of (3). Let*

$$z = s + x_1 + x_2 + p \ , \quad \zeta = s + 2x_1 \ . \tag{6}$$

Then,

$$\dot{z} = -D(z - s_{in}) \ , \tag{7}$$
$$\dot{\zeta} = -D(\zeta - s_{in}) \ , \tag{8}$$

and

$$\begin{cases} \dot{x}_2 = g(p)x_2 - Dx_2 \ , \\ \dot{p} = f(2(z - x_2 - p) - \zeta, p)\,[x_2 + p + \zeta - z] - g(p)x_2 - Dp \ . \end{cases} \tag{9}$$

Proof. The lemma can be proved through routine calculations. □

3.2. **Invariant and attractive sets.** One can prove that the system (3) is dissipative. More precisely, we establish below the following result:

Proposition 1. *(i) Any solution of (3) with initial condition in $\overline{\mathcal{C}}$ is bounded and defined for all $t \geq 0$. The sets $\overline{\mathcal{C}}$ and $\mathcal{C}$ are positively invariant sets of (3).*
(ii) The set $\mho = \Big\{(s, x_1, x_2, p) \in \overline{\mathcal{C}} : \ s + x_1 + x_2 + p = s_{in}, \ s + 2x_1 = s_{in}\Big\}$ is a positively invariant attractor of all solutions of system (3) in $\overline{\mathcal{C}}$.

Proof. To begin with note that since g of class C^1 and $g(0) = 0$ there exists a continuous function $\hat{g}(p)$ such that, for all $p \geq 0$, $g(p) = \hat{g}(p)p$.

Consider now a solution of (3) with an initial condition $(s(0), x_1(0), x_2(0), p(0)) \in \overline{\mathcal{C}}$. Let $T > 0$ be such that the solution is defined over $[0, T]$.

Since $\dot{s}(t) = Ds_{in} > 0$ if $s(t) = 0$, we deduce that $s(t) > 0$ for all $t \in (0, T]$. Now, observe that for all $t \in [0, T]$ the equalities

$$x_1(t) = x_1(0)\exp(\int_0^t (f(s(\ell), p(\ell)) - D)d\ell), x_2(t) = x_2(0)\exp(\int_0^t (g(p(\ell)) - D)d\ell) \tag{10}$$

hold. Therefore the sign of $x_1(t)$ and $x_2(t)$ cannot change. Next, let us assume that $p(0) > 0$ and let us proceed by contradiction and prove that, for all $t \in [0, T]$, $p(t) > 0$. Assume that there exists $t_c \in (0, T]$ such that the solution is defined over $[0, t]$ and $p(m) > 0$ for all $m \in [0, t_c)$ and $p(t_c) = 0$. We deduce that, for all $m \in [0, T]$, the inequality

$$p(m) \geq p(0)\exp(\int_0^m [-\hat{g}(p(\ell))x_2(\ell) - D]d\ell) \tag{11}$$

holds. It follows that $p(t_c) > 0$. This yields a contradiction. Therefore $p(t) > 0$ for all $t \in [0, T]$.

Next, assume that $p(0) = 0$ and $x_1(0) = 0$. Then the uniqueness of the solutions implies that $p(t) = 0$ for all $t \in [0, T]$. Next, assume that $p(0) = 0$ and $x_1(0) > 0$. Then $\dot{p}(0) = f(s(0), 0)x_1(0)$. If $s(0) > 0$, $\dot{p}(0) > 0$ and therefore there exists $t_1 \in (0, T]$ such that $p(t) > 0$ for all $t \in (0, t_1)$. If $s(0) = 0$, then $\dot{p}(0) = 0$ and, according to Assumption H3, $\ddot{p}(0) = \dfrac{\partial f}{\partial s}(0, 0)x_1(0) > 0$. Therefore there exists $t_2 \in (0, T]$ such that $p(t) > 0$ for all $t \in (0, t_2)$. Therefore when $p(0) = 0$ and $x_1(0) > 0$, arguing as we did when $p(0) > 0$, one can prove that $p(t) \geq 0$ for all $t \in [0, T]$.

It follows that, for all $T > 0$ such that the solution is defined over $[0, T]$, we have $s(t) \geq 0$, $x_1(t) \geq 0$, $x_2(t) \geq 0$, $p(t) \geq 0$ for all $t \in [0, T]$. Therefore $\overline{\mathcal{C}}$ is a positively invariant set of (3). Similarly, one can prove that $\mathcal{C}$ is a positively invariant set of (3).

From (6), (7) and the fact that $s(t)$, $x_1(t)$, $x_2(t)$, $p(t)$ are nonnegative we deduce that $s(t)$, $x_1(t)$, $x_2(t)$, $p(t)$ are bounded. Therefore the finite escape time phenomenon does not occur. It follows that the solutions are defined for all $t \geq 0$. Hence, the first item of Proposition 1 holds.

Let us establish the second item of Proposition 1.

The equations (7) and (8) imply that $\mho$ is positively invariant and that, if $(s(t), x_1(t), x_2(t), p(t))$ is a solution of $\overline{\mathcal{C}}$ then it satisfies, for all $t \geq 0$,

$$s(t)+x_1(t)+x_2(t)+p(t) = s_{in}+K_1e^{-Dt} \quad \text{where} \quad K_1 = s(0)+x_1(0)+x_2(0)+p(0)-s_{in}$$

and

$$s(t) + 2x_1(t) = s_{in} + K_2e^{-Dt} \quad \text{where} \quad K_2 = s(0) + 2\,x_1(0) - s_{in} \ .$$

This allows us to conclude. □

3.3. **Nonnegative equilibrium points of (3).** The next result is devoted to the equilibrium points of the system (3) in $\overline{\mathcal{C}}$.

Theorem 1. *Assume that the system (3) satisfies Assumptions H1 to H5. Then the system (3) admits three and only three equilibrium points in $\overline{\mathcal{C}}$. There exists $s_* \in \mathbb{R}$ such that*

$$0 < s_* < s_{in} \ , \ f(s_*, p_*) = D \ , \ x_{1*} = \frac{s_{in} - s_*}{2} > 0 \ , \ x_{2*} = \frac{s_{in} - s_*}{2} - p_* > 0 \quad (12)$$

with p_* given by Lemma 1 and the equilibrium points of (3) are

$$E^0 = (s_{in}, 0, 0, 0), \quad E^1 = (s_{in} - 2\bar{p}, \bar{p}, 0, \bar{p}) \quad \text{and} \quad E^* = (s_*, x_{1*}, x_{2*}, p_*) \quad (13)$$

with $\bar{p}$ defined in (5) and moreover, the constants $\bar{p}$, p_* satisfy

$$0 < p_* < \bar{p} < \frac{s_{in}}{2} \ . \quad (14)$$

Assume that the system (3) satisfies Assumptions H2 to H5 but not Assumption H1. Then the system (3) admits two and only two equilibrium points in $\overline{\mathcal{C}}$. These equilibrium points are $E^0 = (s_{in}, 0, 0, 0)$, $E^1 = (s_{in} - 2\bar{p}, \bar{p}, 0, \bar{p})$. Moreover $\bar{p}$, p_* satisfy the inequalities

$$0 < \bar{p} \leq p_* < s_{in} \ . \quad (15)$$

Proof. We assume that (3) satisfied Assumptions *H2* to *H5*.

$E_e = (s_e, x_{1e}, x_{2e}, p_e)$ is a nonnegative equilibrium point of (3) if and only if its components are nonnegative and such that

$$\begin{aligned} D(s_{in} - s_e) - 2f(s_e, p_e)x_{1e} &= 0 \ , \\ f(s_e, p_e)x_{1e} - Dx_{1e} &= 0 \ , \\ g(p_e)x_{2e} - Dx_{2e} &= 0 \ , \\ f(s_e, p_e)x_{1e} - g(p_e)x_{2e} - Dp_e &= 0 \ . \end{aligned} \quad (16)$$

These equalities are equivalent to

$$\begin{aligned} f(s_e, p_e)x_{1e} &= Dx_{1e} \ , \\ g(p_e)x_{2e} &= Dx_{2e} \ , \\ s_e &= s_{in} - 2x_{1e} \ , \\ x_{1e} &= x_{2e} + p_e \ . \end{aligned} \quad (17)$$

If $x_{1e} = 0$, then the last equation implies that $x_{2e} = p_e = 0$. We deduce easily that $E_e = E^0$. If $x_1 \neq 0$ and $x_2 = 0$, then

$$\begin{array}{rcl} f(s_{in} - 2p_e, p_e) & = & D\ , \\ s_e & = & s_{in} - 2x_{1e}\ , \\ x_{1e} & = & p_e\ . \end{array} \tag{18}$$

We deduce from Assumptions *H3* and *H4* that $p_e = \bar{p}$. We deduce easily that $E_e = E^1$.

To complete the study, only one case remains to be investigated: $x_1 \neq 0$ and $x_2 \neq 0$. In this case,

$$\begin{array}{rcl} f(s_e, p_e) & = & D\ , \\ g(p_e) & = & D\ , \\ s_e & = & s_{in} - 2x_{1e}\ , \\ x_{1e} & = & x_{2e} + p_e\ . \end{array} \tag{19}$$

From Assumption *H5* and Lemma 1, we deduce that $p_e = p_*$ and therefore

$$\begin{array}{rcl} f(s_{in} - 2(x_{2e} + p_*), p_*) & = & D\ , \\ s_e & = & s_{in} - 2x_{1e}\ , \\ x_{1e} & = & x_{2e} + p_*\ . \end{array} \tag{20}$$

If Assumption *H1* is satisfied, necessarily $f(s_{in} - 2p_*, p_*) > D$. It follows from the continuity of f and Assumptions *H2* and *H3* that there exists $x_{2e} > 0$ such that $f(s_{in} - 2(x_{2e} + p_*), p_*) = D$ and $s_e = s_{in} - 2x_{1e} = s_{in} - 2(x_{2e} + p_*) > 0$. Therefore E_e is a positive equilibrium point and $E_e = E^*$.

If Assumption *H1* is not satisfied, necessarily $f(s_{in} - 2p_*, p_*) \leq D$. It follows from Assumption H3 that there exists no value $x_{2e} > 0$ such that $f(s_{in} - 2(x_{2e} + p_*), p_*) = D$. Therefore (3) has not positive equilibrium points. Finally, observe that $f(s_{in} - 2p_*, p_*) \leq f(s_{in} - 2\bar{p}, \bar{p})$. It follows from Assumptions *H3* and *H4* that $\bar{p} \leq p_*$. We deduce that (15) is satisfied. □

4. **Stability analysis.** In this section, we study the asymptotic behavior of the solutions of the system (3). One might think that, due to the attractivity of the set $\mho$, one can straightforwardly deduce from the stability properties of the system (3) restricted to the invariant set $\mho$ what are the stability properties of the system (3). But this is false in general as highlighted by examples: see [16, 17]. However fortunately, in the case we consider, it turns out that this is true: we will manage to deduce what is the behavior of the positive solutions of (3) from the asymptotic behavior of the solutions of the system

$$\left\{ \begin{array}{rcl} \dot{x}_2 & = & \lambda_1(x_2, p)\ , \\ \dot{p} & = & \lambda_2(x_2, p)\ , \end{array} \right. \tag{21}$$

with

$$\begin{pmatrix} \lambda_1(x_2, p) \\ \\ \lambda_2(x_2, p) \end{pmatrix} = \begin{pmatrix} (g(p) - D)\, x_2 \\ \\ f(s_{in} - 2\,p - 2\,x_2, p)(p + x_2) - g(p)x_2 - Dp \end{pmatrix} \tag{22}$$

and with

$$\mathcal{S} = \left\{ (x_2, p) \in (\mathbb{R}_+^*)^2 \ : \ 0 < x_2 + p < \frac{s_{in}}{2} \right\} \tag{23}$$

as state space. We shall prove in Section 4.2.1 that $\mathcal{S}$ is a positively invariant set of (21). Observe that the system (21) is obtained by considering the system (9) with $z = \zeta = s_{in}$.

To begin with, we determine what are the local stability properties of the equilibria of (3). These results are interesting for their own sake and will be instrumental when establishing the global results.

4.1. **Analysis of the local stability properties of the equilibria of (3).** In this section, we prove the following result.

Theorem 2. *Assume that the system (3) satisfies Assumptions H2 to H5. Then E^0 is locally unstable. If in addition the system (3) satisfies Assumption H1, then E^1 is locally unstable and E^* is a locally exponentially stable. If the system (3) does not satisfy Assumption H1 and $f(s_{in} - p_*, p_*) < D$, then E^1 is locally exponentially stable.*

Proof. From Lemma 3 and Theorem 1, we deduce that the planar system (21) admits $F^0 = (0, 0)$, $F^1 = (0, \bar{p})$ and, when Assumption *H1* holds, $F^* = (x_2^*, p_*)$ as equilibrium points and that E^0, E^1, E^* are locally exponentially stable (resp. unstable) equilibrium points of (3) if and only if F^0, F^1, F^* are locally exponentially stable (resp. unstable) equilibrium points of (21). Therefore the result of Theorem 2 holds if the following lemma holds:

Lemma 4. *Assume that the system (3) satisfies Assumptions H2 to H5. Then F^0 is a locally unstable equilibrium point of the associated system (21). If in addition the system (3) satisfies Assumption H1, then F^1 is a locally unstable equilibrium point of (21) and F^* is a locally exponentially stable equilibrium point of (21). If the system (3) does not satisfy Assumption H1 and $f(s_{in} - p_*, p_*) < D$, then F^1 is a locally exponentially stable equilibrium point of (3).*

To prove Lemma 4, we determine first what is the Jacobian matrix of the function $\Lambda(x_2, p) = (\lambda_1(x_2, p)\ \lambda_2(x_2, p))^\top$ at a point (x_2, p) in the closure in $\mathcal{S}$, denoted by $\overline{\mathcal{S}}$. Simple calculations give the Jacobian matrix $J((x_2, p)) = (J_{ij}(x_2, p)) \in \mathbb{R}^{2\times 2}$ with

$$\begin{array}{rcl}
J_{11}(x_2,p) &=& g(p) - D\ , \\
J_{12}(x_2,p) &=& g'(p)x_2\ , \\
J_{21}(x_2,p) &=& -2\dfrac{\partial f}{\partial s}(s_{in} - 2p - 2x_2, p)(x_2 + p) + f(s_{in} - 2p - 2x_2, p) - g(p)\ , \\
J_{22}(x_2,p) &=& \left(-2\dfrac{\partial f}{\partial s}(s_{in} - 2p - 2x_2, p) + \dfrac{\partial f}{\partial p}(s_{in} - 2p - 2x_2, p)\right)(x_2 + p) \\
&& +f(s_{in} - 2p - 2x_2, p) - g'(p)x_2 - D\ .
\end{array} \tag{24}$$

Now, we consider successively the matrices $J(F^0)$, $J(F^1)$, $J(F^*)$.

Since

$$J(F^0) = \begin{bmatrix} -D & 0 \\ J_{21}(F^0) & f(s_{in}, 0) - D \end{bmatrix},$$

the eigenvalues of $J(F^0)$ are $-D$ and $f(s_{in}, 0) - D$. Assumptions *H1* and *H5* imply that $f(s_{in}, 0) - D > 0$. It follows that if Assumption *H2* is satisfied then one of the eigenvalues of $J(F^0)$ is a positive real number. Consequently, F^0 is an exponentially unstable equilibrium point of (21).

Since

$$J(F^1) = \begin{bmatrix} g(\bar{p}) - D & 0 \\ J_{21}(F^1) & \left(-2\frac{\partial f}{\partial s}(s_{in} - 2\bar{p}, \bar{p}) + \frac{\partial f}{\partial p}(s_{in} - 2\bar{p}, \bar{p})\right)\bar{p} \end{bmatrix},$$

one of the eigenvalues of $J(F^1)$ is $g(\bar{p}) - D$. If Assumption *H1* is satisfied, the inequalities (14), the equality $D = g(p_*)$ and Assumption *H5*, which ensures that g is increasing, imply that

$$g(\bar{p}) - D > 0 \ . \tag{25}$$

Consequently, F^1 is an exponentially unstable equilibrium point of (21).

If Assumption *H1* is satisfied, one can check readily that

$$\det(J(F^*)) = 2\frac{\partial f}{\partial s}(s_*, p_*)(x_{2*} + p_*)g'(p_*)x_{2*} \tag{26}$$

and

$$\mathrm{tr}(J(F^*)) = \left(-2\frac{\partial f}{\partial s}(s_*, p_*) + \frac{\partial f}{\partial p}(s_*, p_*)\right)(x_{2*} + p_*) - g'(p_*)x_{2*} \ . \tag{27}$$

Assumptions *H3*, *H4* and *H5* imply that $\det(J(F^*)) > 0$ and $\mathrm{tr}J(F^*) < 0$. Therefore the matrix $J(F^*)$ admits two eigenvalues with a negative real part. Thus the linear approximation of (21) at F^* is exponentially stable.

Finally, assume that the system (3) is such that $f(s_{in} - p_*, p_*) < D$ and Assumptions *H2* to *H5* are satisfied. Then $g(\bar{p}) - D = g(\bar{p}) - g(p_*) < 0$ because $\bar{p} < p_*$. We deduce that the eigenvalues of $J(F^1)$ are negative. Consequently, F^1 is an exponentially stable equilibrium point of (21). □

4.2. **Global analysis of the system (3).** In this section, we investigate what are the global stability properties of (3). Our analysis splits up into two parts. In a first part, we analyze the stability properties of the reduced order system (21). In the second part, we take advantage of the result obtained in the first to establish the global stability properties of the system (3) on $\mathcal{C}$.

4.2.1. *Global analysis of the system (21).* In this section, we investigate what are the global stability properties of (21). First, we need to prove that the set $\mathcal{S}$ defined in (23) and $\overline{\mathcal{S}}$ are positively invariant sets of (21) and that (21) admits neither periodic orbits nor polycycles inside $\overline{\mathcal{S}}$.

Lemma 5. *Assume that the system (3) satisfies Assumptions H2 to H5 and consider the associated system (21). The sets $\mathcal{S}$ and $\overline{\mathcal{S}}$ are positively invariant set of (21). The system (21) admits no periodic solution inside $\overline{\mathcal{S}}$.*

Proof. One can prove that $\mathcal{S}$ and $\overline{\mathcal{S}}$ are positively invariant sets of (21) using the fact that

$$\dot{x}_2 + \dot{p} \quad = [f(s_{in} - 2p - 2x_2, p) - D][p + x_2] \ .$$

Next, we consider a trajectory of (21) belonging to $\mathcal{S}$. Transforming the system (21) through the change of coordinates

$$\xi = \ln(x_2) \ , \ \beta = \ln(p + x_2) = \ln\left(p + e^{\xi}\right) \ ,$$

the following system

$$\begin{cases} \dot{\xi} &= h_1(\xi, \beta) \ , \\ \dot{\beta} &= h_2(\xi, \beta) \ , \end{cases} \tag{28}$$

with

$$\left(\begin{array}{c} h_1(\xi,\beta) \\ h_2(\xi,\beta) \end{array} \right) = \left(\begin{array}{c} g\left(e^{\beta}-e^{\xi}\right)-D \\ f\left(s_{in}-2e^{\beta},\ e^{\beta}-e^{\xi}\right)-D \end{array} \right) \tag{29}$$

is obtained. From Assumptions *H3* and *H4*, we deduce that the function

$$\begin{aligned} \Gamma(\xi,\beta) \quad &:= \frac{\partial h_1}{\partial \xi}(\xi,\beta)+\frac{\partial h_2}{\partial \beta}(\xi,\beta) \\ &= -e^{\xi}g'\left(e^{\beta}-e^{\xi}\right)-2e^{\beta}\frac{\partial f}{\partial s}\left(s_{in}-2e^{\beta},e^{\beta}-e^{\xi}\right) \\ &+e^{\beta}\frac{\partial f}{\partial p}\left(s_{in}-2e^{\beta},e^{\beta}-e^{\xi}\right) \end{aligned} \tag{30}$$

is such that

$$\Gamma(\xi,\beta) \quad < \quad 0\ , \text{ when } \quad e^{\beta}-e^{\xi}>0 \text{ and } \quad s_{in}-2e^{\beta}>0\ .$$

This allows us to apply Dulac's criterion (see [8, Chapter 6]) to (28) for trajectories belonging to the simply connected region

$$\mathcal{D}=\left\{(\beta,\xi)\in\mathbb{R}^2 : \ln\left(\frac{s_{in}}{2}\right)>\beta>\xi\right\}\ .$$

Since $\Gamma(\beta,\xi)$ does not change sign in $\mathcal{D}$, this criterion ensures that the system (28) has no periodic trajectory in $\mathcal{D}$. Then we deduce that the system (21) has no periodic orbit in $\mathcal{S}$. Besides it cannot have polycycles because there is only one equilibrium point in $\mathcal{S}$. Next, let us proceed by contradiction to prove that the system (21) has no periodic orbit in $\overline{\mathcal{S}}$. Assume that there exists in $\overline{\mathcal{S}}$ a periodic solution of (21) that we denote $(x_2(t),p(t))$. We deduce easily from the fact that $\mathcal{S}$ is positively invariant that necessarily either $x_2(t)=0$ for all $t\geq 0$ or $p(t)=0$ for all $t\geq 0$. If $x_2(t)=0$ for all $t\geq 0$, then necessarily, for all $t\geq 0$, $\dot{p}(t)=[f(s_{in}-2p(t),p(t))-D]p(t)$. Thanks to Assumptions *H3* and *H4*, we deduce that necessarily $p(t)$ converges either to 0 or $\bar{p}$ when the time goes to the infinity. If $p(t)=0$ for all $t\geq 0$, then necessarily, for all $t\geq 0$, $\dot{x}_2(t)=-Dx_2(t)$ and $x_2(t)$ converges to zero when the time goes to the infinity. This concludes the proof. □

We are ready to establish a crucial result for planar system (21).

Theorem 3. *Assume that the system (3) satisfies Assumptions H1 to H5 and consider the associated system (21). Then the point F^* is a globally asymptotically stable equilibrium of (21) on $\mathcal{S}$.*

Proof. Consider a solution $(x_2(t),p(t))$ of (21) belonging to $\mathcal{S}$. The system (21) has no unbounded trajectory in $\mathcal{S}$ because $\overline{\mathcal{S}}$ is a positively invariant compact set. Therefore $(x_2(t),p(t))$ is a bounded. Consequently, it admits a compact ω-limit set, that we denote ω, which is included in $\overline{\mathcal{S}}$. According to the Poincaré-Bendixon Theorem [8], ω either contains an equilibrium point or (21) admits a periodic solution in $\overline{\mathcal{S}}$. Since Lemma 5 ensures there exist no periodic solutions of (21) in $\overline{\mathcal{S}}$, necessarily ω contains an equilibrium point of (21). If $F^*\in\omega$, then $F^*=\omega$ because F^* is locally exponentially stable (see Lemma 4). Next, let us prove that $F^*\in\omega$ by proceeding by contradiction. Assume that $F^*\notin\omega$. Then, necessarily, either $F^0\in\omega$ or $F^1\in\omega$.

Let us prove that $F^0\notin\omega$. We have, for all $t\geq 0$

$$\dot{x}_2+\dot{p}=f(s_{in}-2p-2x_2,p)(p+x_2)-Dp-Dx_2\ .$$

From Assumption H4, we deduce that, for all $t\geq 0$

$$\dot{x}_2+\dot{p}\geq\left[f(s_{in}-2p-2x_2,p+x_2)-D\right]\left[p+x_2\right]\ .$$

Then from Assumption *H1* and Assumption *H5*, we deduce that $f(s_{in}, 0) > D$ and therefore there exist $T > 0$ and $\delta > 0$ such that, for all $t \geq T$, $p(t) + x_2(t) \geq \delta$. It follows that $F^0 \notin \omega$.

Assume that $F^1 = \omega$. Using (25), one can prove that it follows that there exist two real numbers $T > 0$ and $\delta > 0$ such that, for all $t \geq T$, $\dot{x}_2(t) \geq \delta x_2(t)$. It follows that $(p(t) + x_2(t))$ is unbounded. This yields a contradiction with the fact that $\mathcal{S}$ is a positively invariant compact set.

We deduce that ω is a polycycle with F_1 as unique equilibrium point. Such a polyclycle cannot exist because any polycycle contains necessarily more than only one equilibrium point. We deduce that neither $F^0 \in \omega$ nor $F^1 \in \omega$ and therefore we have obtained a contradiction. Therefore $F^* \in \omega$.

This allows us to conclude that all the solutions of the system (21) in $\mathcal{S}$ converge asymptotically to F^*. □

Next, we establish the following result.

Theorem 4. *Assume that the system (3) satisfies Assumptions H2 to H5 and that $f(s_{in} - p_*, p_*) < D$. Consider the associated system (21). The point F^1 is a globally asymptotically stable equilibrium of (21) on $\mathcal{S}$.*

Proof. Consider a solution $(x_2(t), p(t))$ of (21) belonging to $\mathcal{S}$. The system (21) has no unbounded trajectory in $\mathcal{S}$ because $\overline{\mathcal{S}}$ is a positively invariant compact set. Therefore $(x_2(t), p(t))$ is a bounded. Consequently, it admits a compact ω-limit set, that we denote ω. According to the Poincaré-Bendixon Theorem [8], ω either contains an equilibrium point or (21) admits a periodic solution in $\overline{\mathcal{S}}$. Since Lemma 5 ensures there exist no periodic solutions of (21) in $\overline{\mathcal{S}}$, necessarily ω contains an equilibrium point of (21). Arguing as in the proof of Theorem 3, one can prove that $F^0 \notin \omega$. Therefore, necessarily, $F^1 \in \omega$. Since F^1 is locally exponentially stable, it follows that $F^1 = \omega$. □

4.2.2. *Global analysis of (3).* In this section, we state and prove the main results of the paper.

Theorem 5. *Assume that the system (3) satisfies Assumptions H1 to H5. Then the equilibrium point E^* is globally asymptotically stable.*

Proof. The new coordinates

$$z_1 = s + x_1 + x_2 + p - s_{in}\ , \quad z_2 = s + 2x_1 - s_{in}$$

lead us to consider the system

$$\left\{ \begin{array}{rcl} \dot{Z} & = & AZ \\ \dot{x}_2 & = & g(p)x_2 - Dx_2 \\ \dot{p} & = & f(2z_1 + s_{in} - 2x_2 - 2p - z_2, p)\,[x_2 + p + z_2 - z_1] \\ & & -g(p)x_2 - Dp \end{array} \right. \tag{31}$$

with $Z = (z_1, z_2)^\top$, $A = -D.Id_2$, where Id_2 denotes the identity matrix of $\mathbb{R}^{2\times 2}$. To analyze the stability properties of this system, we use the convergence theorem given in [15, Appendix F]. We let the Z-subsystem of (31) play the role of the z-subsystem of (F.1) in [15] and the (x_2, p)-subsystem of (31) play the role of the y-subsystem of (F.1) in [15]. The set which corresponds to D in [15, Appendix F] is the positively invariant set

$$D_1 = \left\{ (x_2, p, z_1, z_2) \in \mathbb{R}^4 \;\middle|\; x_2 \geq 0, p \geq 0,\ z_2 \geq z_1 - x_2 - p \geq \frac{1}{2}(z_2 - s_{in}) \right\}\ .$$

Thus, the set which corresponds to Ω in [15, Appendix F] is $\Omega_1 = \overline{\mathcal{S}}$, i.e.

$$\Omega_1 = \left\{ (x_2, p) \in \mathbb{R}_+^2 \;\middle|\; x_2 + p \leq \frac{1}{2} s_{in} \right\} .$$

We now check that the assumptions of [15, Theorem F.1] are satisfied. To begin with, observe that f and g are continuously differentiable. Next, we prove that (31) is dissipative. Since the Z-subsystem of (31) is exponentially stable, every solution of (31) with initial condition in D_1 eventually enters and remains in the compact set

$$\left\{ (x_2, p, z_1, z_2) \in \mathbb{R}_+^2 \times \mathbb{R}^2 \;\middle|\; |z_2| + |z_1| \leq 1 \;,\; z_2 \geq z_1 - x_2 - p \geq \frac{1}{2}(z_2 - s_{in}) \right\}$$

i.e. (31) is dissipative. Assumption H1 is satisfied because the eigenvalues of A are equal to $-D < 0$. From Section 4.1, we deduce easily that Assumptions H2 and H3 are satisfied. One can prove easily that Assumption H4 is satisfied if the equilibrium point $\overline{p} \in (0, \frac{1}{2} s_{in})$ (see Lemma 2) of the system $\dot{p} = [f(s_{in} - 2p, p) - D]p$ admits a basin of attaction larger than $[0, \frac{1}{2} s_{in}]$. This property is satisfied because $p \rightarrow f(s_{in} - 2p, p)$ is continuous and decreasing between 0 and $\frac{1}{2} s_{in}$. Finally, from Theorem 3, we deduce that Assumption H5 is satisfied.

We conclude that [15, Theorem F.1] applies. It follows that every trajectory with initial condition in D_1 converges to one of the equilibrium points $(0,0,0,0)$, $(0,0,0,\overline{p})$, $(0,0,x_{2*},p_*)$. Consider now a solution belonging to the interior of D_1 and let us show by contradiction that this solution converges to the equilibrium point $(0,0,x_{2*},p_*)$. Assume that this solution converges to $(0,0,0,0)$. It follows that (3) admits a solution $(s(t), x_1(t), x_2(t), p(t))$, with positive initial conditions, which converges to E^0. Therefore $x_1(t) = x_1(0) \exp\left(\int_0^t (f(s(m), p(m)) - D) dm \right)$ converges to 0. Since $x_1(0) > 0$, it follows that $\int_0^t (f(s(m), p(m)) - D) dm$ converges to $-\infty$. This is in contradiction with the fact that $\lim_{t\to\infty} [f(s(t), p(t)) - D] = f(s_{in}, 0) - D > 0$. Next, assume that this solution, that we denote $(z_1(t), z_2(t), x_2(t), p(t))$, converges to $(0,0,0,\overline{p})$. Then $x_2(t) = x_2(0) \exp\left(\int_0^t [g(p(m)) - D] dm \right)$ converges to 0. Since $x_2(0) > 0$, it follows that $\int_0^t [g(p(m)) - D] dm$ converges to $-\infty$. This leads to a contradiction with the fact that Assumption H1 of the model implies that $\lim_{t\to\infty} [g(p(t)) - D] = g(\overline{p}) - D > g(p_*) - D = 0$. This allows us to conclude.

$\square$

Remark 2. *Theorem 5 can be proved through an alternative approach (cf. [4]). It turns out that (21) contains only locally exponentially stable and unstable equilibria, and neither periodic orbits nor cyclic chains. Thus Thiemes's results [16] can be applied to deduce the asymptotic behaviors of the solutions of the complete system (3) from the asymptotic behaviors of the solutions of the reduced system (21).*

We conclude the section with a result for the case where $f(s_{in} - p_*, p_*) < D$. We do not study the particular case where $f(s_{in} - p_*, p_*) = D$ because this is not a generic case and has no specific interest.

Theorem 6. *Assume that the system (3) satisfies Assumptions H2 to H5 and that* $f(s_{in} - p_*, p_*) < D$. *Then the equilibrium point* E^1 *is a globally asymptotically and a locally exponentially stable equilibrium point of the system (3) on* $\mathcal{C}$.

Proof. The proof of Theorem 6, which is similar and simpler than the proof of Theorem 5, is omitted. □

5. **Numerical simulations.** We performed numerical simulations for the particular model:

$$\left\{\begin{array}{rcl} \dot{s} &=& (8-s) - 2\,\dfrac{8s}{2+s}\,\dfrac{4}{2+p}\,x_1 \ , \\ \dot{x}_1 &=& \Big(\dfrac{8s}{2+s}\,\dfrac{4}{2+p} - 1\Big)x_1 \ , \\ \dot{x}_2 &=& \Big(\dfrac{2p}{0.2+p} - 1\Big)x_2 \ , \\ \dot{p} &=& \dfrac{8s}{2+s}\dfrac{4}{2+p}x_1 - \dfrac{2p}{0.2+p}x_2 - p \ . \end{array}\right. \tag{32}$$

The parameters values are chosen such that the system (32) satisfies Assumptions *H2* to *H5*. Let us check that Assumption *H1* is satisfied too. With our general notations, we have $s_* = \dfrac{22}{149}$, $x_{1*} = \dfrac{585}{149}$, $x_{2*} = \dfrac{2779}{745}$, $p_* = 0.2$, $s_{in} = 8$, $D = 1$, $f(s_{in} - 2p_*, p_*) = \dfrac{380}{33} > 1 = D$.

As expected, the trajectories filling the whole positive cone converge to the positive point $(x_{1*}, x_{2*}) = \left(\dfrac{585}{149}, \dfrac{2779}{745}\right)$.

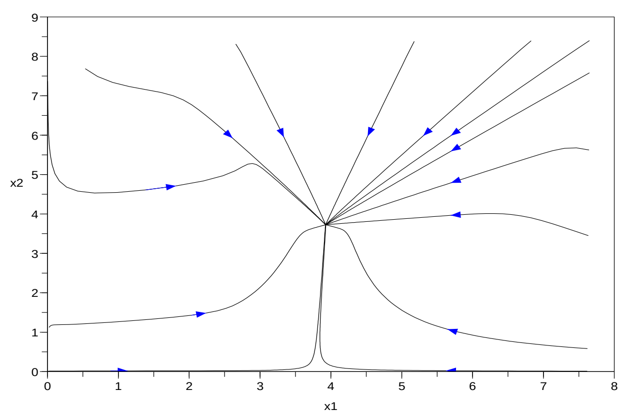

FIGURE 2. $x_1 - x_2$ behavior

6. **Conclusion.** We have proposed a mathematical model involving a part of the population consortium responsible for the second and the third stages of the anaerobic fermentation process. The analysis of the model is mainly based on an application of the Poincaré-Bendixon Theorem and Dulac's criterion that rules out the possibility of periodic solutions for a reduced planar system whose stability properties are linked with the stability properties of the overall system. It results from this

analysis that, under general and natural assumptions of monotonicity on the functional responses, the stable asymptotic coexistence of acetogenic and methanogenic bacteria occurs.

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