MILED EL HAJJI, NEJMEDDINE CHORFI, MOHAMED JLELI

Communicated by Vicențiu D. Rădulescu

Abstract. In this article, we present a mathematical six-dimensional dynamical system involving a three-tiered microbial food web without maintenance. We give a qualitative analysis of the model, and an analysis of the local stability of equilibrium points. Under general assumptions of monotonicity, we prove the uniqueness and the local stability of the positive equilibrium point corresponding to the persistence of the three bacteria. Possibilities of periodic orbits are not excluded and asymptotic coexistence is satisfied.

1. Introduction

The anaerobic digestion model No. 1 (ADM1) is a sophisticated mathematical model developed by the international water association (IWA) modelling the anaerobic digestion processes created for full-scale industrial plants design, systems operational analysis and control [1]. This generic model permits to produce a platform for dynamic simulations of a variety of anaerobic processes. A way to facilitate the study of such a sophisticated model is by considering reduced models to better understand the biological phenomena of sub-processes while reducing the number of variables and parameters of the system in order to simplify the mathematical analysis.

It has been proved previously that simplifying or reducing the complexity of the model ADM1 can preserve biological significance while reducing the computational effort needed to find mathematical solutions to the equations of this model [9]. Note that when using gross simplification of a biological system, analytical techniques are unable to provide general solutions for the system and then numerical simulations must suffice.

In this work, we shall revisit the model proposed by Wade et al. [8] and analyzed by Sari and Wade [5] in considering two main changes relevant from an applied point of view. The contents of this paper is arranged as following. First, we present, in Section 2, a description of the model to be investigated, which is a reduction of the one given by [8]. Then existence, uniqueness and local stability of the 3D reduced system is analyzed in Section 3. Global stability of the reduced system is also
discussed. In section 4, asymptotic behavior of the 6D-system is then deduced. Finally, in section 5, numerical simulations are given when using Monod’s growth functions which are currently used in biotechnology.

2. **Mathematical model and results**

The model developed here has six components, three substrate and three biomass variables based on Anaerobic Digestion Model No. 1 (ADM1) (Batstone et al. [1]). The chlorophenol degrader ($X_1$) uses both chlorophenol ($S_1$) and hydrogen ($S_3$) for growth, producing phenol ($S_2$) as a product. Phenol ($S_2$) is consumed by the phenol degrader ($X_2$), which is inhibited by the hydrogen. The methanogen ($X_3$) growth on the hydrogen. In the actual paper, we revisit the model proposed by Wade et al. [8] and analyzed by Sari and Wade [5] in considering two main changes relevant from an applied point of view. First, we neglect all species specific mortality (maintenance) rates and take into account the dilution rate only. The second modification of the model is that we neglect the part of hydrogen produced by the phenol degrader. Chlorophenol, phenol and hydrogen are introduced into the reactor with a constant dilution rate $D$ and an input concentration $S_i^{in}$, $i = 1, 2, 3$, respectively.

Biomass and substrate concentrations are then modelled by the following six-dimensional dynamical system of ODEs:

\[
\begin{align*}
\dot{X}_1 &= (\mu_1(S_3, S_1) - D)X_1, \\
\dot{S}_1 &= D(S_1^{in} - S_1) - \mu_1(S_3, S_1)\frac{X_1}{Y_1}, \\
\dot{X}_2 &= (\mu_2(S_3, S_2) - D)X_2, \\
\dot{S}_2 &= D(S_2^{in} - S_2) + \mu_1(S_3, S_1)\frac{X_1}{Y_4} - \mu_2(S_3, S_2)\frac{X_2}{Y_2}, \\
\dot{X}_3 &= (\mu_3(S_3) - D)X_3, \\
\dot{S}_3 &= D(S_3^{in} - S_3) - \mu_1(S_3, S_1)\frac{X_1}{Y_5} - \mu_3(S_3)\frac{X_3}{Y_3},
\end{align*}
\]

with initial conditions $(S_1(0), S_2(0), S_3(0), X_1(0), X_2(0), X_3(0)) \in \mathbb{R}_+^6$, where $Y_i$, $i = 1, 2, 3, 4$ are the yield coefficients.

**Figure 1.** Three-tiered microbial food web
Assume that the functional response of each species $\mu_1, \mu_2 : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $\mu_3 : \mathbb{R}_+ \to \mathbb{R}_+$ satisfies

(A1) $\mu_1, \mu_2 : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $\mu_3 : \mathbb{R}_+ \to \mathbb{R}_+$ are of class $C^1$,
(A2) $\mu_1(0, S_1) = \mu_2(S_3, 0) = \mu_2(S_3, 0) = \mu_3(0) = 0$, for all $S_3, S_1 \in \mathbb{R}_+$,
(A3) $\frac{\partial \mu_3}{\partial S_3}(S_3, S_1) > 0$, $\frac{\partial \mu_3}{\partial S_3}(S_3, S_1) > 0$, for all $S_3, S_1 \in \mathbb{R}_+$,
(A4) $\frac{\partial \mu_3}{\partial S_3}(S_3, S_2) > 0$, $\frac{\partial \mu_3}{\partial S_3}(S_3, S_2) < 0$, for all $S_2, S_3 \in \mathbb{R}_+$,
(A5) $\mu_3(S_3) > 0$, for all $S_3 \in \mathbb{R}_+$.

Assumption (A2) means that species $X_1$ cannot grow without substrates $S_1$ and $S_3$ and that the intermediate product $S_2$ is obligate for the growth of species $X_2$ and that the substrate $S_3$ is obligate for the growth of species $X_3$. Hypothesis (A3) expresses that the growth of species $X_1$ increases with the substrate $S_1$ and the substrate $S_3$. Hypothesis (A4) expresses that the species $X_2$ growth increases with intermediate product $S_2$ produced by species $X_1$ whereas $X_2$ is inhibited by the substrate $S_3$. Hypothesis (A5) expresses that the growth of species $X_3$ increases with the substrate $S_3$.

This proposed mathematical six-dimensional dynamical system describe a three-tiered microbial food web without maintenance. Previous works on two-tier ecological systems gave complete stability analysis, locally and globally (El Hajji et al. [3]; Sari et al. [4], Weissemann et al. [9]).

To scale the system (2.1) consider the following change of variables and parameters:

\[
\begin{align*}
s_1 &= S_1, & s_2 &= \frac{Y_4}{Y_1} s_2, & s_3 &= \frac{Y_5}{Y_1} S_3, & x_1 &= \frac{X_1}{Y_1}, & x_2 &= \frac{Y_4}{Y_1 Y_2} x_2, \\
x_3 &= \frac{Y_5}{Y_1 Y_3} X_3, & s_1^i &= S_1^i, & s_2^i &= \frac{Y_4}{Y_1} s_2^i, & s_3^i &= \frac{Y_5}{Y_1} S_3^i.
\end{align*}
\]

The dimensionless equations thus obtained are:

\[
\begin{align*}
\dot{x}_1 &= (f_1(s_3, s_1) - D)x_1, \\
\dot{s}_1 &= D(s_1^i - s_1) - f_1(s_3, s_1)x_1, \\
\dot{x}_2 &= (f_2(s_3, s_2) - D)x_2, \\
\dot{s}_2 &= D(s_2^i - s_2) + f_1(s_3, s_1)x_1 - f_2(s_3, s_2)x_2, \\
\dot{x}_3 &= (f_3(s_3) - D)x_3, \\
\dot{s}_3 &= D(s_3^i - s_3) - f_1(s_3, s_1)x_1 - f_3(s_3)x_3.
\end{align*}
\]

Here, functions $f_1, f_2 : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $f_3 : \mathbb{R}_+ \to \mathbb{R}_+$ are given by

\[
\begin{align*}
f_1(s_3, s_1) &= \mu_1(\frac{Y_1}{Y_5} s_3, s_1), & f_2(s_3, s_2) &= \mu_1(\frac{Y_1}{Y_5} s_3, \frac{Y_1}{Y_4} s_2), & f_3(s_3) &= \mu_3(\frac{Y_1}{Y_5} s_3).
\end{align*}
\]

Then the Assumptions (A1)–(A5) satisfied by the functions $\mu_1, \mu_2$ and $\mu_3$ are translated to the following assumptions on the functions $f_1, f_2$ and $f_3$:

(A6) $f_1, f_2 : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $f_3 : \mathbb{R}_+ \to \mathbb{R}_+$ are of class $C^1$,
(A7) $f_1(0, s_1) = f_1(s_3, 0) = f_2(s_3, 0) = f_3(0) = 0$, for all $s_1, s_3 \in \mathbb{R}_+$,
(A8) $\frac{\partial f_1}{\partial s_3}(s_3, s_1) > 0$, $\frac{\partial f_1}{\partial s_3}(s_3, s_1) > 0$, for all $s_1, s_3 \in \mathbb{R}_+$,
(A9) $\frac{\partial f_2}{\partial s_3}(s_3, s_2) > 0$, $\frac{\partial f_2}{\partial s_3}(s_3, s_2) < 0$, for all $s_2, s_3 \in \mathbb{R}_+$,
(A10) $f_3'(s_3) > 0$, for all $s_3 \in \mathbb{R}_+$. 

The closed non-negative cone $\mathbb{R}_+^6$, in $\mathbb{R}^6$, is positively invariant by the system (2.2). More precisely we have the following result.

**Proposition 2.1.** (1) For all initial condition in $\mathbb{R}_+^6$, the solution of system (2.2) is bounded and has positive components and thus is defined for all $t > 0$.
(2) System (2.2) admits a positive invariant attractor set of all solution given by
$$
\Omega = \{(s_1, s_2, s_3, x_1, x_2, x_3) \in \mathbb{R}_+^6 / s_1 + x_1 = s_1^{in}, x_1 + s_3 + x_3 = s_3^{in}, s_2 + x_2 + s_3 + x_3 = s_2^{in} + s_3^{in}\}.
$$

**Proof.** (1) The positivity of the solution is proved by the fact that: If $s_i = 0$ then $\dot{s}_i = Ds_i^{in} > 0$ for $i = 1, 3$, and if $x_i = 0$ then $\dot{x}_i = 0$ for $i = 1, 2, 3$. Now, if $s_2 = 0$ then $\dot{s}_2 = Ds_2^{in} + f_1(s_3, s_1)x_1 > 0$. Next we have to prove the boundedness of solutions of (2.2). By adding the two first equations of system (2.2), one obtains, for $s_1 = s_1 + x_1 - s_1^{in}$, a single equation: $\dot{z}_1 = -Dz_1$ then
$$
\dot{s}_1(t) + x_1(t) = s_1^{in} + (s_1(0) + x_1(0) - s_1^{in})e^{-Dt}
$$
Similarly, by adding the first and the two last equations of system (2.2), one obtains, for $z_2 = x_1 + s_3 + x_3 - s_3^{in}$, a single equation: $\dot{z}_2 = -Dz_2$ then
$$
x_1(t) + s_3(t) + x_3(t) = s_3^{in} + (x_1(0) + s_3(0) + x_3(0) - s_3^{in})e^{-Dt}
$$
Finally, by adding the last four equations of system (2.2), one obtains, for $z_3 = s_2 + x_2 + s_3 + x_3 - s_2^{in} - s_3^{in}$, a single equation: $\dot{z}_3 = -Dz_3$ then
$$
\dot{s}_2(t) + x_2(t) + s_3(t) + x_3(t) = s_2^{in} + s_3^{in} + (s_2(0) + x_2(0) + s_3(0) + x_3(0) - s_2^{in} - s_3^{in})e^{-Dt}
$$
Since all terms of the two sums are positive, then the solution is bounded.
(2) The second point is simply a direct consequence of equalities (2.3) -(2.5).

3. Restriction to $\mathbb{R}_+^3$

Trajectories of the 6D-system (2.2) converge exponentially inside the set $\Omega$ and our aim is to study the asymptotic behavior of these trajectories. The idea is to restrict the study of the asymptotic behavior of the system (2.2) onto the attractive set $\Omega$. Using Theme’s results [7], the asymptotic behavior of the solutions of the reduced system will be informative for the complete system (2.2) (cf. EL Hajji et al. [2] and Sari et al. [3]). Note that in our case, periodic orbits are not excluded.

The projection on the three-dimensional space $(x_1, x_2, x_3)$ of the restriction of system (2.2) on $\Omega$ is given by the following reduced system.
$$
\begin{align*}
\dot{x}_1 &= \left(f_1(s_3^{in} - x_3, s_2^{in} - x_1) - D\right)x_1, \\
\dot{x}_2 &= \left(f_2(s_3^{in} - x_3, s_2^{in} + x_1 - x_2) - D\right)x_2, \\
\dot{x}_3 &= \left(f_3(s_2^{in} - x_1 - x_3) - D\right)x_3.
\end{align*}
$$

Thus, for (3.1) the state-vector $(x_1, x_2, x_3)$ belongs to the following subset of $\mathbb{R}_+^3$:
$$
S = \{(x_1, x_2, x_3) \in \mathbb{R}_+^3 : 0 \leq x_1 \leq s_1^{in}, 0 \leq x_2 \leq x_1 + s_2^{in}, 0 \leq x_1 + x_3 \leq s_3^{in}\}.
$$

3.1. Local analysis.
3.1.1. Equilibrium points. The system can have the following eight types of equilibrium points.

- Trivial equilibria \( F^0 = (0, 0, 0) \).
- Boundary equilibria \( F^1 = (\bar{x}_1, 0, 0) \), where \( x_1 = \bar{x}_1 \) is solution, if it exists, of equation
  \[
  f_1(x_3^{in} - x_1, s_1^{in} - x_1) = D. \tag{3.2}
  \]
- Boundary equilibria \( F^2 = (0, \bar{x}_2, 0) \), where \( x_2 = \bar{x}_2 \) is a solution, if it exists, of equation
  \[
  f_2(s_3^{in}, s_2^{in} - x_2) = D. \tag{3.3}
  \]
- Boundary equilibria \( F^3 = (0, 0, s_3^{in} - s^*) \), where \( s^* = f_3^{-1}(D) \).
- Boundary equilibria \( F^{13} = (x_1^*, 0, s_1^{in} - s^* - x_1^*) \), where \( x_1 = x_1^* \) is solution, if it exists, of equation
  \[
  f_1(s_1^*, s_1^{in} - x_1) = D. \tag{3.4}
  \]
- Boundary equilibria \( F^{23} = (0, \bar{x}_2, s_3^{in} - s^*) \), where \( x_2 = \bar{x}_2 \) is solution, if it exists, of equation
  \[
  f_2(s^*, s_2^{in} - x_2) = D. \tag{3.5}
  \]
- Boundary equilibria \( F^{12} = (\bar{x}_1, \bar{x}_2, 0) \), where \( x_2 = \bar{x}_2 \) is solution, if it exists, of equation
  \[
  f_2(s_3^{in} - \bar{x}_1, s_2^{in} + \bar{x}_1 - x_2) = D. \tag{3.6}
  \]
- Positive equilibria \( F^* = (x_1^*, x_2^*, s_3^{in} - s^* - x_1^*) \), where \( x_2 = x_2^* \) is solution, if it exists, of equation
  \[
  f_2(s^*, s_2^{in} + x_1^* - x_2) = D. \tag{3.7}
  \]

**Existence and uniqueness.** For a given \( D \), let \( s^* = f_3^{-1}(D) \), \( x_1^* \) the unique solution, if it exists, of \( f_1(s^*, s_1^{in} - x_1) = D \) and \( \bar{x}_1 \) the unique solution, if it exists, of \( f_1(s_3^{in} - x_1, s_1^{in} - x_1) = D \). We use the following notation

\[
\begin{align*}
D_1 &= f_1(s_3^{in}, s_1^{in}), & D_2 &= f_2(s_3^{in}, s_2^{in}), & D_3 &= f_3(s_3^{in}), \\
D_4 &= f_1(s^*, s_1^{in}), & D_5 &= f_2(s^*, s_2^{in}), & D_6 &= f_2(s^*, s_2^{in} + x_1^*), \\
D_7 &= f_2(s_3^{in} - \bar{x}_1, s_2^{in} + \bar{x}_1), & D_8 &= f_3(s_3^{in} - \bar{x}_1).
\end{align*}
\]

**Remark 3.1.** By assumptions (A6)–(A10), one can easily verify that

\[
D_2 < D_5 < D_6, \quad D_3 < D_7, \quad D_4 < D_1, \quad D_8 < D_3.
\]

Existence and uniqueness conditions of the equilibrium points \( F^0, F^1, F^2, F^3, F^{12}, F^{13}, F^{23} \) and \( F^* \) are given in the following theorem.

**Theorem 3.2.**

- \( F^0 = (0, 0, 0) \) exists always and is unique,
- \( F^1 \) exists and is unique if and only if \( D < D_1 \),
- \( F^2 \) exists and is unique if and only if \( D < D_2 \),
- \( F^3 \) exists and is unique if and only if \( D < D_3 \),
- \( F^{13} \) exists and is unique if and only if \( D < \min(D_3, D_4) \),
- \( F^{23} \) exists and is unique if and only if \( D < \min(D_3, D_5) \),
- \( F^{12} \) exists and is unique if and only if \( D < \min(D_1, D_7) \),
- \( F^* \) exists and is unique if and only if \( D < \min(D_3, D_4, D_6) \).

**Proof.**

- \( F^0 = (0, 0, 0) \) exists always.
• The mapping \( x_1 \mapsto f_1(s_3^{in} - x_1, s_1^{in} - x_1) \) is decreasing. Hence, there exists a unique \( \bar{x}_1 \) such that \( f_1(s_3^{in} - \bar{x}_1, s_1^{in} - \bar{x}_1) = D \) if and only if \( D < D_1 = f_1(s_3^{in}, s_1^{in}) \). Then, \( F^1 \) exists and is unique if and only if \( D < D_1 \).

• The mapping \( x_2 \mapsto f_2(s_3^{in}, s_2^{in} - x_2) \) is decreasing. Hence, there exists a unique \( \bar{x}_2 \) such that \( f_2(s_3^{in}, s_2^{in} - \bar{x}_2) = D \) if and only if \( D < D_2 = f_2(s_3^{in}, s_2^{in}) \). Then, \( F^2 \) exists and is unique if and only if \( D < D_2 \).

• The mapping \( s_3 \mapsto f_3(s_3) \) is increasing. Hence, there exists a unique \( s^* \) such that \( f_3(s^*) = D \) if and only if \( D < D_3 = f_3(s_3^{in}) \). Then, \( F^3 \) exists and is unique if and only if \( D < D_3 \).

\( s^* \) exists if and only if \( D < D_3 \). The mapping \( x_1 \mapsto f_1(s^*, s_1^{in} - x_1) \) is decreasing. Hence, there exists a unique \( x_1^* \) such that \( f_1(s^*, s_1^{in} - x_1^*) = D \) if and only if \( D < D_4 = f_1(s^*, s_1^{in}) \). Then, \( F^{13} \) exists and is unique if and only if \( D < \min(D_3, D_4) \).

Similarly, the mapping \( x_2 \mapsto f_2(s^*, s_2^{in} - x_2) \) is decreasing. Hence, there exists a unique \( x_2^* \) such that \( f_2(s^*, s_2^{in} - x_2^*) = D \) if and only if \( D < D_5 = f_2(s^*, s_2^{in}) \). Then, \( F^{23} \) exists and is unique if and only if \( D < \min(D_3, D_5) \).

\( x_1 \) exists and is unique if and only if \( D < D_1 \). For \( D < D_1 \), the mapping \( x_2 \mapsto f_2(s_3^{in} - x_1, s_2^{in} + \bar{x}_1 - x_2) \) is decreasing. Hence, there exists a unique \( \bar{x}_2 \) such that \( f_2(s_3^{in} - x_1, s_2^{in} + \bar{x}_1 - \bar{x}_2) = D \) if and only if \( D < D_7 = f_2(s_3^{in} - x_1, s_2^{in} + \bar{x}_1) \). One deduce that \( F^{12} \) exists and is unique if and only if \( D < \min(D_1, D_7) \).

\( s^* = f_3^{-1}(D) \) exists and is unique if and only if \( D < D_3 \). \( x_1^* \) exists and is unique if and only if \( D < D_4 \). For \( D < \min(D_3, D_4) \), the mapping \( x_2 \mapsto f_2(s^*, s_2^{in} + x_1^* - x_2) \) is decreasing. Hence, there exists a unique \( x_2^* \) such that \( f_2(s^*, s_2^{in} + x_1^* - x_2^*) = D \) if and only if \( D < D_6 \). One deduce that \( F^* \) exists and is unique if and only if \( D < \min(D_3, D_4, D_6) \).

\( \square \)

Local stability. The Jacobian matrix of (3.1), at point \((x_1, x_2, x_3)\), is

\[
J = \begin{bmatrix}
    f_1 - D - \frac{\partial f_1}{\partial s_3} x_1 - \frac{\partial f_1}{\partial s_1} x_1 & 0 & -\frac{\partial f_1}{\partial x_1} \\
    \frac{\partial f_2}{\partial s_3} x_2 + \frac{\partial f_2}{\partial s_2} x_2 & f_2 - D - \frac{\partial f_2}{\partial s_2} x_2 & -\frac{\partial f_2}{\partial x_2} \\
    -\frac{\partial f_3}{\partial x_3} & 0 & f_3 - D - \frac{\partial f_3}{\partial x_3}
\end{bmatrix}
\]

where the function \( f_1 \) is evaluated at \((s_3^{in} - x_1 - x_3, s_1^{in} - x_1)\), \( f_2 \) is evaluated at \((s_3^{in} - x_1 - x_3, s_2^{in} + x_1 - x_2)\) and \( f_3 \) is evaluated at \( s_3^{in} - x_1 - x_3 \). In the following lemma, the nature of the equilibrium point \( F^0 \) is given.

Lemma 3.3. If \( D > \max(D_1, D_2, D_3) \) then \( F^0 \) is a stable node.
If \( \min(D_1, D_2, D_3) < D < \max(D_1, D_2, D_3) \) then \( F^0 \) is a saddle point.
If \( D < \min(D_1, D_2, D_3) \) then \( F^0 \) is an unstable node.

Proof. The Jacobian matrix at \( F^0 \) is

\[
J^0 = \begin{bmatrix}
    D_1 - D & 0 & 0 \\
    0 & D_2 - D & 0 \\
    0 & 0 & D_3 - D
\end{bmatrix}
\]

The eigenvalues are \( D_1 - D, D_2 - D \) and \( D_3 - D \). Thus, if \( D > \max(D_1, D_2, D_3) \) then \( F^0 \) is a stable node. If \( \min(D_1, D_2, D_3) < D < \max(D_1, D_2, D_3) \) then \( F^0 \) is a saddle point. If \( D < \min(D_1, D_2, D_3) \) then \( F^0 \) is an unstable node. \( \square \)
In the following lemmas, the nature of the boundary equilibrium points $F^1$, $F^2$, $F^3$, $F^{12}$, $F^{13}$ and $F^{23}$ is given.

**Lemma 3.4.** $F^1$ is a stable node if $D > \max(D_7, D_8)$. $F^1$ is a saddle point if $D < \max(D_7, D_8)$.

*Proof.* The Jacobian matrix at $F^1$ is

$$J^1 = \begin{bmatrix} \frac{\partial f_1}{\partial s_3} \bar{x}_1 - \frac{\partial f_1}{\partial s_1} \bar{x}_1 & 0 & 0 \\ 0 & D_7 - D & 0 \\ 0 & 0 & D_8 - D \end{bmatrix}$$

where $f_1$ is evaluated at $(s_3^{in} - \bar{x}_1, s_1^{in} - \bar{x}_1)$. The eigenvalues are given by

$$\frac{\partial f_1}{\partial s_3} \bar{x}_1 - \frac{\partial f_1}{\partial s_1} \bar{x}_1 < 0, \quad D_7 - D, \quad D_8 - D.$$ 

Thus $F^1$ is a stable node if $D > \max(D_7, D_8)$. $F^1$ is a saddle point if $D < \max(D_7, D_8)$. $\square$

**Lemma 3.5.** $F^2$ is a stable node if $D > \max(D_1, D_3)$. It is a saddle point if $D < \max(D_1, D_3)$.

*Proof.* The Jacobian matrix at $F^2$ is

$$J^2 = \begin{bmatrix} \frac{D_1 - D}{\partial s} \bar{x}_2 & \frac{\partial f_2}{\partial s_2} \bar{x}_2 & 0 \\ 0 & \frac{\partial f_2}{\partial s_2} \bar{x}_2 & 0 \\ 0 & 0 & D_3 - D \end{bmatrix}$$

where the function $f_2$ is evaluated at $(s_3^{in}, s_2^{in} - \bar{x}_2)$. The eigenvalues are

$$\frac{\partial f_2}{\partial s_2} \bar{x}_2 < 0, \quad D_1 - D, \quad D_3 - D.$$ 

Thus $F^2$ is a stable node if $D > \max(D_1, D_3)$. It is a saddle point if $D < \max(D_1, D_3)$. $\square$

**Lemma 3.6.** $F^3$ is a stable node if $D > \max(D_4, D_5)$. $F^3$ is a saddle point if $D < \max(D_4, D_5)$.

*Proof.* The Jacobian matrix at $F^3$ is

$$J^3 = \begin{bmatrix} D_4 - D & 0 & 0 \\ 0 & D_5 - D & 0 \\ -f'_3(s^*)(s_3^{in} - s^*) & 0 & -f'_3(s^*)(s_3^{in} - s^*) \end{bmatrix}$$

The eigenvalues are

$$-f'_3(s^*)(s_3^{in} - s^*) < 0, \quad D_4 - D, \quad D_5 - D.$$ 

Thus $F^3$ is a stable node if $D > \max(D_4, D_5)$. $F^3$ is a saddle point if $D < \max(D_4, D_5)$. $\square$

**Lemma 3.7.** $F^{12}$ is a stable node if $D > D_8$. $F^{12}$ is a saddle point if $D < D_8$.

*Proof.* The Jacobian matrix at $F^{12}$ is

$$J^{12} = \begin{bmatrix} \frac{\partial f_1}{\partial s_3} \bar{x}_1 - \frac{\partial f_1}{\partial s_1} \bar{x}_1 & 0 & 0 \\ \left(-\frac{\partial f_2}{\partial s_3} + \frac{\partial f_2}{\partial s_2}\right) \bar{x}_2 & -\frac{\partial f_2}{\partial s_2} \bar{x}_2 & -\frac{\partial f_2}{\partial s_1} \bar{x}_2 \\ 0 & 0 & D_8 - D \end{bmatrix}.$$
where the function $f_1$ is evaluated at $(s_3^{in} - \tilde{x}_1, s_1^{in} - \tilde{x}_1)$, $f_2$ is evaluated at $(s_3^{in} - \tilde{x}_1, s_2^{in} + \tilde{x}_1 - \tilde{x}_2)$. Then eigenvalues are $\lambda_1 = D_8 - D$, $\lambda_2 = -\frac{\partial f_2}{\partial s_2} \tilde{x}_2 < 0$ and $\lambda_3 = -(\frac{\partial f_1}{\partial s_3} \tilde{x}_1 + \frac{\partial f_1}{\partial s_1} \tilde{x}_1) < 0$. Thus $F^{12}$ is a stable node if $D > D_8$. $F^{12}$ is a saddle point if $D < D_8$. 

**Lemma 3.8.** $F^{13}$ is a stable node if $D > D_6$. $F^{13}$ is a saddle point if $D < D_6$.

**Proof.** The Jacobian matrix at $F^{13}$ is

$$
J^{13} = \begin{bmatrix}
-\frac{\partial f_1}{\partial s_3} x_1 - \frac{\partial f_1}{\partial s_1} x_1^* & 0 & \frac{\partial f_1}{\partial s_3} x_1^*
\frac{\partial f_2}{\partial s_2} x_2 & 0 & -\frac{\partial f_2}{\partial s_3} \tilde{x}_2
-(s_3^{in} - s^* - x_1^*) f_3'(s^*) & 0 & -(s_3^{in} - s^* - x_1^*) f_3'(s^*)
\end{bmatrix}
$$

where the function $f_1$ is evaluated at $(s^*, s_1^{in} - x_1^*)$ and $f_2$ is evaluated at $(s^*, s_2^{in} + x_1^*)$.

The characteristic polynomial is

$$(D_6 - D - \lambda) \left[ \lambda^2 + \lambda \left( \frac{\partial f_1}{\partial s_3} x_1 + \frac{\partial f_1}{\partial s_1} x_1^* \right) + \left( \frac{\partial f_2}{\partial s_2} x_2 + \frac{\partial f_2}{\partial s_3} \tilde{x}_2 \right) \right]$$

Eigenvalues are then $\lambda_1 = D_6 - D$ and two other negative eigenvalues (by Routh’s Stability Criterion). Thus $F^{13}$ is a stable node if $D > D_6$. $F^{13}$ is a saddle point if $D < D_6$.

**Lemma 3.9.** $F^{23}$ is a stable node if $D > D_4$ and it is a saddle point if $D < D_4$.

**Proof.** The Jacobian matrix at $F^{23}$ is

$$
J^{23} = \begin{bmatrix}
D_4 - D & 0 & 0
-(s_3^{in} - s^*) f_3'(s^*) & 0 & -(s_3^{in} - s^*) f_3'(s^*)
\end{bmatrix}
$$

where the function $f_2$ is evaluated at $(s^*, s_2^{in} - \tilde{x}_2)$.

The eigenvalues are

$D_4 - D, -\frac{\partial f_2}{\partial s_2} \tilde{x}_2 < 0, -(s_3^{in} - s^*) f_3'(s^*) < 0$.

Thus $F^{23}$ is a stable node if $D > D_4$ and it is a saddle point if $D < D_4$.

Let us discuss now the local stability of the positive equilibria $F^* = (x_1^*, x_2^*, x_3^*)$ where $x_1^* > 0, x_2^* > 0$ and $x_3^* > 0$.

**Lemma 3.10.** $F^*$, if it exists, is always a stable node.

**Proof.** The Jacobian matrix at $F^*$ is

$$
J^* = \begin{bmatrix}
-\frac{\partial f_1}{\partial s_3} x_1^* - \frac{\partial f_1}{\partial s_1} x_1^* & 0 & \frac{\partial f_1}{\partial s_3} x_1^*
(-\frac{\partial f_2}{\partial s_3} + \frac{\partial f_2}{\partial s_1}) x_2^* & 0 & \frac{\partial f_2}{\partial s_3} x_2^*
-f_3'(s^*) x_3^* & 0 & f_3'(s^*) x_3^*
\end{bmatrix}
$$

where the function $f_1$ is evaluated at $(s^*, s_1^{in} - x_1^*)$ and $f_2$ is evaluated at $(s^*, s_2^{in} + x_1^* - x_2^*)$.

The eigenvalues are

$-f_3'(s^*) x_3^* < 0, -\frac{\partial f_2}{\partial s_3} x_2^* < 0, -\frac{\partial f_1}{\partial s_3} x_1^* - \frac{\partial f_1}{\partial s_1} x_1^* < 0$.

Thus $F^*$, if it exists, is always a stable node.

**3.2. Summary.** Conditions of existence and uniqueness and the nature of equilibrium points are summarized in Table 1.
Table 1. Condition of existence and uniqueness and the nature of equilibrium points.

<table>
<thead>
<tr>
<th>Equil.</th>
<th>Existence/uniqueness</th>
<th>Stable node</th>
<th>Saddle point</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F^0$</td>
<td>always</td>
<td>$D &gt; \max(D_1, D_2, D_3)$</td>
<td>$\min(D_i) &lt; D &lt; \max(D_i)$, $i = 1, 2, 3$</td>
</tr>
<tr>
<td>$F^1$</td>
<td>$D &lt; D_1$</td>
<td>$D &gt; \max(D_2, D_3)$</td>
<td>$D &lt; \max(D_1, D_3)$</td>
</tr>
<tr>
<td>$F^2$</td>
<td>$D &lt; D_2$</td>
<td>$D &gt; \max(D_1, D_3)$</td>
<td>$D &lt; \max(D_1, D_3)$</td>
</tr>
<tr>
<td>$F^3$</td>
<td>$D &lt; D_3$</td>
<td>$D &gt; \max(D_2, D_3)$</td>
<td>$D &lt; \max(D_1, D_3)$</td>
</tr>
<tr>
<td>$F^{13}$</td>
<td>$D &lt; \min(D_3, D_4)$</td>
<td>$D &gt; D_6$</td>
<td>$D &lt; D_6$</td>
</tr>
<tr>
<td>$F^{23}$</td>
<td>$D &lt; \min(D_3, D_5)$</td>
<td>$D &gt; D_4$</td>
<td>$D &lt; D_4$</td>
</tr>
<tr>
<td>$F^{12}$</td>
<td>$D &lt; \min(D_2, D_7)$</td>
<td>$D &gt; D_8$</td>
<td>$D &lt; D_8$</td>
</tr>
<tr>
<td>$F^*$</td>
<td>$D &lt; \min(D_3, D_4, D_6)$</td>
<td>always</td>
<td>always</td>
</tr>
</tbody>
</table>

3.3. Global analysis. In the following, we consider only the case when

(A11) $D < \min(D_2, D_4, D_8)$

This hypothesis guarantees that $D < \min(D_1, D_2, D_3, D_4, D_5, D_6, D_7, D_8)$ which ensure the existence of $F^*$, the only stable node for the system (3.3). $F^1$, $F^2$, $F^3$, $F^{12}$, $F^{13}$ and $F^{23}$ are saddle points. $F^0$ is an unstable node.

Remark 3.11. Consider a solution of system (2.2) belonging to $\Omega$. Consider the transformation of the system (2.2) through the change of variables $\eta_i = \ln(x_i)$, $i = 1, 2, 3$. Then one gets the new system

\[
\begin{align*}
\dot{\eta}_1 &= h_1(\eta_1, \eta_2, \eta_3) := f_1(s_3^{in} - e^{i_n} - e^{i_3}, s_1^{in} - e^{i_1}) - D, \\
\dot{\eta}_2 &= h_2(\eta_1, \eta_2, \eta_3) := f_2(s_3^{in} - e^{i_n} - e^{i_3}, s_2^{in} + e^{i_1} - e^{i_2}) - D, \\
\dot{\eta}_3 &= h_3(\eta_1, \eta_2, \eta_3) := f_3(s_3^{in} - e^{i_n} - e^{i_3}) - D.
\end{align*}
\]

We have

\[
\frac{\partial h_1}{\partial \eta_1} + \frac{\partial h_2}{\partial \eta_2} + \frac{\partial h_3}{\partial \eta_3} = -\left(e^{i_1} + e^{i_2} + e^{i_3}\right) < 0.
\]

From Dulac criterion \( \bullet \), the system (3.8) has no invariant sets (including tori) with no-zero volume wholly inside $\Omega$. If there is a strange attractor it must be (typically) a fractal set with zero volume. Note that periodic orbits (of zeros volume) are not excluded.

- $\frac{\partial h_1}{\partial \eta_1} + \frac{\partial h_2}{\partial \eta_2} = -\left(e^{i_1} + e^{i_2} + e^{i_3}\right) < 0$. From Dulac criterion \( \bullet \), then the system (2.2) has no periodic trajectory in the plane $x_1x_2$ ($x_3 = 0$).
- $\frac{\partial h_1}{\partial \eta_1} + \frac{\partial h_3}{\partial \eta_3} = -\left(e^{i_1} + e^{i_3} + f_3^{'} e^{i_3}\right) < 0$. From Dulac criterion \( \bullet \), then the system (2.2) has no periodic trajectory in the plane $x_1x_3$ ($x_2 = 0$).
- $\frac{\partial h_2}{\partial \eta_2} + \frac{\partial h_3}{\partial \eta_3} = -\left(e^{i_2} + f_3^{'} e^{i_3}\right) < 0$. From Dulac criterion \( \bullet \), then the system (2.2) has no periodic trajectory in the plane $x_2x_3$ ($x_1 = 0$).

Theorem 3.12. For every initial conditions $x_1(0) > 0$, $x_2(0) > 0$, $x_3(0) > 0$ in $\mathcal{S}$, three species coexist i.e.

\[
\lim_{t \to +\infty} x_1(t) > 0, \quad \lim_{t \to +\infty} x_2(t) > 0, \quad \lim_{t \to +\infty} x_3(t) > 0.
\]
Proof. Let \( x_1(0) > 0, x_2(0) > 0, x_3(0) > 0 \), and let \( \omega \) be the \( \omega \)-limit set of \((x_1(0), x_2(0), x_3(0))\) which is compact and invariant such that \( \omega \subset S \). Suppose that \( \omega \) contains a point \( M \) on the boundary of the positive cone \( \mathbb{R}^3_+ \) then:

- If \( F^0 \) is an unstable node then \( F^0 \) can’t be a part of the \( \omega \)-limit set of \((x_1(0), x_2(0), x_3(0))\), and thus \( M \) cannot be \( F^0 \).
- If \( M \in \{ \bar{x}_1, s_1^m \} \times \{ 0 \} \times \{ 0 \} \) (similarly \( M \in \{ 0 \} \times \{ \bar{x}_2, s_2^m \} \times \{ 0 \} \) or \( M \in \{ 0 \} \times \{ 0 \} \times \{ s_3^m - s^*, s_3^m \} \)). As \( \omega \) is invariant then \( \gamma(M) \subset \omega \) and this is impossible because \( \omega \) is bounded and \( \gamma(M) = ]\bar{x}_1, +\infty[ \times \{ 0 \} \) (similarly \( \gamma(M) = \{ 0 \} \times ]\bar{x}_1, +\infty[ \times \{ 0 \} \times s_3^m - s^*, +\infty[ \).
- If \( M \in ]0, \bar{x}_1[ \times \{ 0 \} \times \{ 0 \} \) (similarly \( M \in \{ 0 \} \times \{ 0 \} \times \{ \bar{x}_2, +\infty[ \times \{ 0 \} \) or \( M \in \{ 0 \} \times \{ \bar{x}_1, s_1^m + s^* \} \). As \( \omega \) is invariant then \( \gamma(M) \subset \omega \) and this is impossible because \( \gamma(M) = ]\bar{x}_1, +\infty[ \times \{ 0 \} \times s_3^m - s^*, +\infty[ \) (similarly \( \gamma(M) = \{ 0 \} \times ]\bar{x}_2, +\infty[ \times \bar{x}_1 \times +\infty[ \times \{ 0 \} \) or \( \gamma(M) = \{ 0 \} \times ]\bar{x}_1, +\infty[ \times s_3^m - s^*, s_3^m \} \). In particular, \( \omega \) contains \( F^0 \) and this is impossible.

- If \( M = F^1 \) (similarly \( M = F^2 \) or \( M = F^3 \)). \( \omega \) is not reduced to \( F^1 \) (similarly to \( F^2 \) or to \( F^3 \)). By Butler-McGehee theorem, \( \omega \) contains a point \( P \) of \( (0, +\infty) \times \{ 0 \} \times \{ 0 \} \) other that \( F^1 \) (similarly of \( \{ 0 \} \times \{ 0 \} \times \{ +\infty \} \) or \( \{ 0 \} \times \{ 0, +\infty \} \) other that \( F^3 \) and this is impossible.
- If \( M \in \{ \bar{x}_1, s_1^m \} \times \{ 0 \} \times \{ s_3^m - s^* \} \) (similarly \( M \in \{ 0 \} \times \{ \bar{x}_2, s_2^m \} \times \{ s_3^m - s^* \} \) or \( M \in \{ \bar{x}_1, s_1^m \} \times \{ \bar{x}_2, s_2^m \} \times \{ 0 \} \). As \( \omega \) is invariant then \( \gamma(M) \subset \omega \) and this is impossible because \( \gamma(M) = ]\bar{x}_1, +\infty[ \times ]\bar{x}_2, +\infty[ \times \{ 0 \} \times s_3^m - s^*, +\infty[ \) (similarly \( \gamma(M) = \{ 0 \} \times ]\bar{x}_1, +\infty[ \times s_3^m - s^*, +\infty[ \) or \( \gamma(M) = \{ 0 \} \times ]\bar{x}_2, +\infty[ \times s_3^m - s^*, +\infty[ \) or \( \gamma(M) = \{ 0 \} \times ]\bar{x}_1, +\infty[ \times s_3^m - s^*, +\infty[ \) or \( \gamma(M) = \{ 0 \} \times ]\bar{x}_2, +\infty[ \times s_3^m - s^*, +\infty[ \) or \( \gamma(M) = \{ 0 \} \times ]\bar{x}_1, +\infty[ \times s_3^m - s^*, +\infty[ \) (similarly \( \gamma(M) = \{ 0 \} \times ]\bar{x}_2, +\infty[ \times s_3^m - s^*, +\infty[ \) (similarly \( \gamma(M) = \{ 0 \} \times ]\bar{x}_1, +\infty[ \times s_3^m - s^*, +\infty[ \) or \( \gamma(M) = \{ 0 \} \times ]\bar{x}_2, +\infty[ \times s_3^m - s^*, +\infty[ \). In particular, \( \omega \) contains \( F^0 \) and this is impossible.

If \( M = F^{13} \) (similarly \( M = F^{23} \) or \( M = F^{12} \)). \( \omega \) is not reduced to \( F^{13} \) (similarly to \( F^{23} \) or to \( F^{12} \)). By Butler-McGehee theorem, \( \omega \) contains a point \( P \) of \( (0, +\infty) \times \{ 0 \} \times \{ 0, +\infty \} \) other that \( F^{13} \) (similarly of \( \{ 0 \} \times \{ 0, +\infty \} \times \{ 0, +\infty \} \) other that \( F^{23} \) or \( \{ 0, +\infty \} \times \{ 0 \} \times \{ 0, +\infty \} \) other that \( F^{12} \) and this is impossible.

No points on the boundary of the positive cone \( \mathbb{R}^3_+ \) can be inside the \( \omega \)-limit set. System (3.1) has possible “positive” periodic orbit inside \( S \). Using the Poincaré-Bendixon Theorem (3.1) the solution of system (3.1) converge asymptotically either to the unique stable node \( F^* \) or to a “positive” periodic orbit (if it exists) such that

\[
\lim_{t \to +\infty} x_1(t) > 0, \quad \lim_{t \to +\infty} x_2(t) > 0, \quad \lim_{t \to +\infty} x_3(t) > 0.
\]
Theorem 4.1. Consider the system \( (2.2) \) under Assumptions (A6)–(A11). For every initial conditions \( s_1(0) > 0, s_2(0) > 0, s_3(0) > 0, x_1(0) > 0, x_2(0) > 0, x_3(0) > 0 \) in \( \mathbb{R}_+^3 \), three species coexist i.e.

\[
\lim_{t \to +\infty} x_1(t) > 0, \quad \lim_{t \to +\infty} x_2(t) > 0, \quad \lim_{t \to +\infty} x_3(t) > 0.
\]

Proof. Let \((s_1(t), x_1(t), s_2(t), x_2(t), s_3(t), x_3(t))\) be a solution of \((2.2)\). From \((2.3), (2.4)\) and \((2.5)\) we deduce that

\[
s_1(t) = s_1^{in} - x_1(t) + K_1 e^{-Dt},
\]

\[
s_2(t) = s_2^{in} + x_1(t) - x_2(t) + K_3 e^{-Dt},
\]

\[
s_3(t) = s_3^{in} - x_1(t) - x_3(t) + K_2 e^{-Dt},
\]

where \(K_1 = s_1(0) + x_1(0) - s_1^{in}, K_2 = x_1(0) + x_3(0) - s_2^{in}\) and \(K_3 = -s_3^{in} - x_1(0) + x_2(0)\). Hence \((x_1(t), x_2(t), x_3(t))\) is a solution of the non-autonomous system of three differential equations:

\[
\dot{x}_1 = (f_1(s_1^{in} - x_1 - x_3 + K_2 e^{-Dt}, s_1^{in} - x_1 + K_1 e^{-Dt}) - D)x_1,
\]

\[
\dot{x}_2 = (f_2(s_2^{in} - x_1 - x_3 + K_2 e^{-Dt}, s_2^{in} + x_1 - x_2 + K_3 e^{-Dt}) - D)x_2,
\]

\[
\dot{x}_3 = (f_3(s_3^{in} - x_1 - x_3 + K_2 e^{-Dt}) - D)x_3.
\]

This system is an asymptotically autonomous differential system converging to the autonomous system \((3.1)\). Note that \(\Omega\) is an attractor of all trajectories in \(\mathbb{R}_+^3\) and that the phase portrait of the reduced (to \(\Omega\)) system \((3.1)\) contains only one locally stable node, one unstable node, and six saddle points and possible “positive” periodic trajectory. Thus applying Themes’s results [7] and concluding that the asymptotic behavior of solution of system \((4.2)\) is the same as the one of solution of the reduced system \((3.1)\). The result is then deduced.

\[\square\]

5. Numerical example

In this section we consider growth functions

\[
\begin{align*}
    f_1(s_3, s_1) &= \frac{m_1 s_1 s_3}{(K_1 + s_1)(L_1 + s_3)}, \\
    f_2(s_3, s_2) &= \frac{m_2 s_2}{(K_2 + s_2)(L_2 + s_3)},  \\
    f_3(s_3) &= \frac{m_3 s_3}{L_3 + s_3}.
\end{align*}
\]

These functions are currently used in biotechnology where the growth of a species is limited by one or more than one substrates. One can easily check that \((5.1)\) satisfy the given Assumptions (A6) to (A10).

**Table 2. Parameters for** \((5.1)\)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>(D)</th>
<th>(m_1)</th>
<th>(K_1)</th>
<th>(L_1)</th>
<th>(m_2)</th>
<th>(K_2)</th>
<th>(L_2)</th>
<th>(m_3)</th>
<th>(L_3)</th>
<th>(s_1^{in})</th>
<th>(s_2^{in})</th>
<th>(s_3^{in})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Value</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>12</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>(D_1)</td>
<td>(\frac{1}{36})</td>
<td>(\frac{1}{36})</td>
<td>(\frac{1}{36})</td>
<td>(\frac{1}{12})</td>
<td>15</td>
<td>(\frac{3}{4})</td>
<td>4.545</td>
<td>1.251</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Note that $D = 1 < \min(D_2, D_4, D_8)$. As it is shown in Figure 1 all trajectories inside the whole positive cone $\mathbb{R}_+^3$ converge to the positive equilibrium point $(x_1^*, x_2^*, x_3^*) = (3, 7.8, 1)$ corresponding to the persistence of the three bacteria.

Figure 2. The $x_1x_2x_3$ behavior.

**Conclusion.** A mathematical model involving a three-tiered microbial food web without maintenance was proposed. A detailed qualitative analysis is carried out. The local stability analysis of the equilibria are performed. It is concluded from this study that, under general and natural assumptions of monotonicity on the growth rates, the asymptotic persistence of the three bacteria is guaranteed.

**Acknowledgements.** The authors would like to extend their sincere appreciation to the Deanship of Scientific Research at King Saud University for its funding of this research through the Research Group Project No RGP-1436-034.

**References**


Miled El Hajji
General studies department, College of Telecom and Electronics, Technical and Vocational Training Corporation, Jeddah 2146, Saudi Arabia
E-mail address: miled.elhajji@enit.rnu.tn

Nejmeddine Chorfi (corresponding author)
Department of Mathematics, College of Sciences, King Saud University, Riyadh 11451, Saudi Arabia
E-mail address: nchorfi@ksu.edu.sa

Mohamed Jleli
Department of Mathematics, College of Sciences, King Saud University, Riyadh 11451, Saudi Arabia
E-mail address: jleli@ksu.edu.sa