



Qualitative analysis of a chemostat model with inhibitory exponential substrate uptake [☆]

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Abstract

In this paper, we consider a simple chemostat model involving a single species feeding on redundant substrate with a constant yield term. Many experiments indicate that very high substrate concentrations actually inhibit growth. Instead of assuming the prevalent Monod kinetics for growth rate of cells, we use a non-monotonic functional response function to describe the inhibitory effect. A detailed qualitative analysis about the local and global stability of its equilibria (including all critical cases) is carried out. Numerical simulations are performed to show that the dynamical properties depend intimately upon the parameters.

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1. Introduction

The chemostat is an important laboratory apparatus used to culture microorganisms (see, for example, [1–6,9–12] and the references therein). Species grow in continuously stirred homogenous fermenters which are fed continuously by a nutrient and the cells are drawn off continuously. It is of both ecological and mathematical interest since its applicability in many areas, for example, waste water treatment and the operation of industrial fermenters. The continuous culture model with Monod kinetics for nutrient uptake has received a great deal of attention since it was first introduced and a complete mathematical theory of this model has been developed. In addition, the model has been modified frequently in order to account for various phenomena that are relevant in the actual experiments. A detailed exposition of the mathematical theory of the chemostat that includes nine modifications to the original model is given in [11]. When such modifications are made, it is always a central question of interest to find criteria under which the new model predicts that the microorganisms will be able to persist at a steady state in the culture vessel for an indefinitely long period of time. An accompanying question is to determine the steady-state microorganism and nutrient concentrations as functions of the model parameters.

So far, for the nutrient uptake rate, large numbers of models are established on the basis of Monod kinetics function (Michaelis-Menten or Holling type II), which takes the form of $\mu(S) = \mu_m S / (k_m + S)$ and satisfies the following conditions:

$$\mu(0) = 0, \quad \mu'(S) > 0, \quad \lim_{S \rightarrow +\infty} \mu(S) = \mu_m < \infty.$$

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Here $\mu_m > 0$ is called the maximal specific growth rate; k_m is the half-saturation constant, such that $\mu(k_m) = \mu_m/2$. Clearly, $\mu(S)$ is an increasing function of S over the entire interval $0 \leq S < \infty$. However, in some cases, very high substrate concentrations actually inhibit the growth of cells. Moreover, with the substrate concentrations increase unlimitedly, some kind of microorganism will die eventually. To describe this phenomenon accurately, we consider $\mu(S)$ from a different point of view. Assume that, there exists a constant $0 < S^* < \infty$ such that $\mu(S)$ is increasing over the interval $0 \leq S < S^*$, $\mu(S) \approx \mu_m$ for all S less than but sufficiently close to S^* , and is decreasing on the interval $S^* < S < \infty$. More precisely, we use the so-called Tissett functional response of the form of $\mu(S) = \mu_m S e^{-S/k_i} / (k_m + S)$ (see, for example, [3]).

This paper is organized as follows. The model is described in Section 2. In Section 3, we study the existence of equilibria and their local stability in details. The global dynamics are considered in Section 4. Some discussions are given in Section 5.

2. Statement of the model

Owing to the fact that nutrient is supplied continuously at a constant rate, we can take for granted that substrate concentration and microorganism concentration are all continuous functions of time. Let $S(t)$ and $X(t)$ denote, respectively, the concentration of substrate and microorganism at time t . Our model is described by the following ordinary differential equations (see [3–5,11,12]):

$$\begin{cases} \dot{S}(t) = D(S^0 - S) - \frac{1}{\delta} \mu(S)X, \\ \dot{X}(t) = (\mu(S) - D)X, \end{cases} \tag{2.1}$$

where S^0 denotes the input concentration of nutrient, D is referred to as the dilution rate, δ is yield term, $\mu(S) = \mu_m S e^{-S/k_i} / (k_m + S)$ describes the specific growth rate of cells. It is biologically natural to assume that all of the parameters are non-negative and the initial conditions of (2.1) are given as

$$S(0) = S_0 \geq 0, \quad X(0) = X_0 \geq 0. \tag{2.2}$$

It is convenient to introduce dimensionless variables. In particular, we define

$$X = \delta S^0 x, \quad S = S^0 y, \quad t = \tau/D, \quad m = \mu_m/D, \quad b = S^0/k_i, \quad a = k_m/S^0,$$

and still denote τ with t , then system (2.1) becomes

$$\begin{cases} \dot{x}(t) = \frac{mxye^{-by}}{a+y} - x, \\ \dot{y}(t) = 1 - y - \frac{mxye^{-by}}{a+y}, \end{cases} \tag{2.3}$$

and the initial conditions of (2.3) are

$$x(0) = x_0, \quad y(0) = y_0. \tag{2.4}$$

where $0 \leq x_0 = X_0/(\delta S^0) < +\infty$, $0 \leq y_0 = S_0/S^0 \leq 1$.

From the biological meanings, we consider (2.3) on the following set Ω :

$$\Omega = \{(x, y) | x \geq 0, 0 \leq y \leq 1\}.$$

It is easily to be shown that Ω is positive invariant with respect to (2.3). In fact, note that on the part of $\partial\Omega$ where $y = 0$, the vector field is pointing strictly inside Ω since $y' \equiv 1 > 0$. The set $L_1 = \{(x, y) | x = 0, 0 \leq y \leq 1\}$ consists of the trajectories of (2.3). Let $L_2 = \{(x, y) | y = 1, x \geq 0\}$. It has that $y' = \frac{mxye^{-by}}{a+y} < 0$, which implies that any trajectory of (2.3) started from Ω will still stay in Ω for all $t \geq 0$. This proves the positive invariance of Ω .

If one adds the two equations of (2.3), then one obtains a single equation

$$(x(t) + y(t))' = 1 - (x(t) + y(t)) \tag{2.5}$$

with $x(0) + y(0) \geq 0$. Obviously

$$x(t) + y(t) = 1 + (x(0) + y(0) - 1) \exp(-t)$$

for all $t \geq 0$, this gives the dissipativeness of (2.3) and that

$$\lim_{t \rightarrow +\infty} (x(t) + y(t)) = 1.$$

It also has that the set $L_3 = \{(x, y) | x + y = 1, x \geq 0, y \geq 0\}$ is positive invariant with respect to (2.3).

3. Existence and local stability of equilibria

For the existence of the equilibria of (2.3), we have the following results.

Theorem 1. (2.3) always has a washout equilibria $E_0 = (0, 1)$. For the existence of the positive equilibrium, there are four cases:

- (1) If $0 < m \leq 1$ or $m > 1, b \leq 2, me^{-b}(1-b) \geq 1, me^{-b} \leq a+1$, or $m > 1, me^{-b}(1-b) < 1, me^{-b} < a+1, b\bar{y}^2 + ab\bar{y} - a < 0$, then there does not exist any positive equilibrium, where \bar{y} denoted the root of $f'(y) = me^{-by}(1-by) - 1 = 0$.
- (2) If $m > 1, me^{-b} > a+1$ or $m > 1, me^{-b}(1-b) < 1, me^{-b} = a+1$, then there exists a single positive equilibrium, denoted by $E_1^+ = (1 - y_1^*, y_1^*)$.
- (3) If $m > 1, me^{-b} < a+1, me^{-b}(1-b) < 1, b\bar{y}^2 + ab\bar{y} - a = 0$, then there also exists a single equilibrium, denoted by $E_3^+ = (1 - y_3^*, y_3^*)$.
- (4) If $m > 1, me^{-b} < a+1, me^{-b}(1-b) < 1, b\bar{y}^2 + ab\bar{y} - a > 0$, then there exist two equilibria, denoted, respectively, by $E_{21}^+ = (1 - y_{21}^*, y_{21}^*)$ and $E_{22}^+ = (1 - y_{22}^*, y_{22}^*)$.

Proof. From the right part of Eq. (2.3), we can get the washout solution $(0, 1)$ easily, which we denotes as $E_0 = (0, 1)$. As far as other equilibria are concerned, the analysis of the equation $mye^{-by}/(a+y) = 1$ is needed. We define

$$f(y) = mye^{-by} - a - y,$$

then, accordingly we have

$$f'(y) = me^{-by}(1-by) - 1, \quad f''(y) = mbe^{-by}(by-2).$$

Firstly, we study the function $f''(y)$. $f''(y) = 0$ has a simple root $y = \frac{2}{b}$ and $f''(y) < 0$ for $0 \leq y < \frac{2}{b}$, which informs that $f'(y)$ decreases monotonously over this interval; $f''(y) > 0$ for $y > \frac{2}{b}$, which informs that $f'(y)$ increases monotonously over this interval. Notice that $f(0) = -a < 0, f(1) = me^{-b} - a - 1, f'(0) = m - 1, f'(1) = me^{-b}(1-b) - 1, f'(\frac{2}{b}) = -me^{-2} - 1 < 0$, we proceed our discussions into five steps:

- (1) (see Fig. 1) When $\frac{2}{b} < 1$, i.e. $b > 2$, at the same time, $m < 1$, then $f'(y)$ decreases from $m - 1 (< 0)$ to $f'(\frac{2}{b}) < 0$, then rises from $f'(\frac{2}{b}) < 0$ to $f'(1)$, where $f'(1) < 0$ can be judged easily. On the whole, $f'(y) < 0, \forall y \in [0, 1]$, accordingly, $f(y)$ will decreases from $-a$ to $f(1)$, and it is impossible for $f(y)$ to intersect axis y . So, in this case, there will be no root at all for $f(y) \forall y \in [0, 1]$.
- (2) (see Fig. 2) When $\frac{2}{b} < 1$, i.e. $b > 2$, at the same time, $m > 1$, then $f'(y)$ decreases from $m - 1 (> 0)$ to $f'(\frac{2}{b}) < 0$, after that, rises from $f'(\frac{2}{b}) < 0$ to $f'(1)$, where $f'(1) < 0$ can be judged easily. Because $f'(0) > 0, f'(\frac{2}{b}) < 0$, and in the interval of $y \in [0, \frac{2}{b}]$, $f'(y)$ monotonously decreases, there must exist a point, at which $f'(y) = 0$. We denote this point by \bar{y} , and notice that $f'(y) > 0, \forall y \in [0, \bar{y}]$, which implies that $f(y)$ increases monotonously over this interval, and $f'(y) < 0 \forall y \in [\bar{y}, 1]$, which implies that $f(y)$ decreases monotonously over this interval. So far, we can only detect that $f(\bar{y}) > f(1)$ but the sign of $f(1)$ is still uncertain, which needs to be discussed in three steps:
 - (a) If $me^{-b} > a+1$, i.e. $f(1) > 0$, then incontrovertibly $f(\bar{y}) > 0$. Because $f(0) < 0, f(\bar{y}) > 0$, and in the interval of $y \in [0, \frac{2}{b}]$, $f(y)$ increases monotonously, there must exist a point in the interval $y_1^* \in [0, \bar{y}]$, such that $f(y_1^*) = 0$. Furthermore, we can perceive that $f'(y_1^*) > 0$ from the tendency of $f'(y)$.
 - (b) If $me^{-b} > a+1$, i.e. $f(1) = 0$, then using the same argument as in (a), we can get that there is a root y_1^* on the interval $[0, 1)$.
 - (c) If $me^{-b} < a+1$, i.e. $f(1) < 0$, then the sign of $f(\bar{y})$ becomes changeable, so we should break it down into three steps. As has been noted that \bar{y} is the solutions of $f'(\bar{y}) = 0$, so it must satisfy that $me^{-b\bar{y}}(1-b\bar{y}) = 1$, i.e. $me^{-b\bar{y}} = 1/(1-b\bar{y})$. Substitute it into $f(y)$, we have $f(\bar{y}) = m\bar{y}e^{-b\bar{y}} - a - \bar{y} = (b\bar{y}^2 + ab\bar{y} - a)/(1-b\bar{y})$, here $1-b\bar{y}$ must be positive, or else $f'(\bar{y})$ will permanently negative, which contradicts with $f'(\bar{y}) = 0$. But the sign of $b\bar{y}^2 + ab\bar{y} - a$ is insecure either, so the discussion in three steps is necessary.

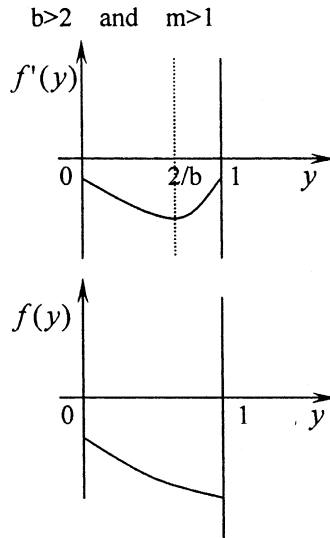


Fig. 1.

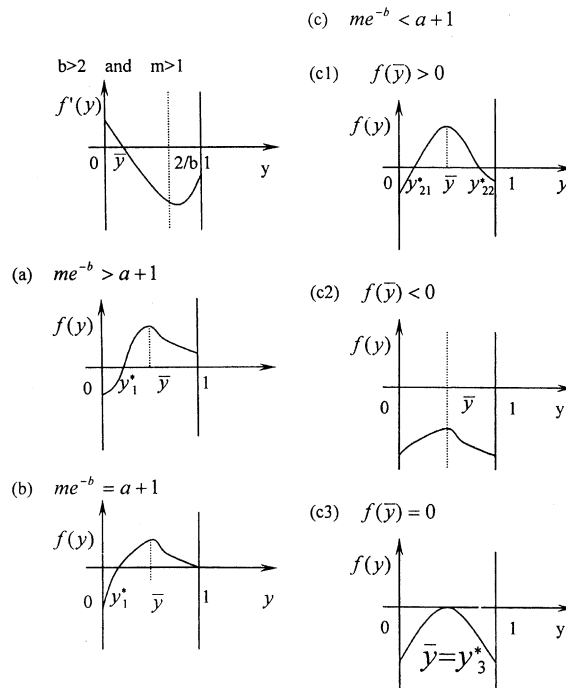


Fig. 2.

- (c₁) If $b\bar{y}^2 + ab\bar{y} - a > 0$, then on the interval $[0, \bar{y}]$, $f(y)$ increases monotonously, and $f(0) < 0, f(\bar{y}) > 0$, there must exist a point in the interval $y_{21}^* \in [0, \bar{y}]$, such that $f(y_{21}^*) = 0$. Furthermore, we can perceive that $f'(y_{21}^*) > 0$ from the tendency of $f'(y)$; Conversely, on the interval $[\bar{y}, 1], f(y)$ decreases monotonously, and $f(\bar{y}) > 0, f(1) < 0$ there must also exist a point in the interval $y_{22}^* \in [\bar{y}, 1]$, such that $f(y_{22}^*) = 0$. Also, we can perceive that $f'(y_{22}^*) < 0$ from the tendency of $f'(y)$.
- (c₂) If $b\bar{y}^2 + ab\bar{y} - a < 0$, then on the interval $[0, 1]$, all values of $f(y)$ are negative because $f(\bar{y})$ is the maximum value of $f(y)$ when y belongs to $[0, 1]$, and it is impossible for $f(y)$ to intersect axis y . So, in this case, there will be no root at all for $f(y) \forall y \in [0, 1]$.

(c₃) If $b\bar{y}^2 + ab\bar{y} - a = 0$, then on the interval $[0, 1]$, \bar{y} is the only zero of $f(y)$. We denote this point as y_3^* .

Furthermore, we can perceive that $f'(y_3^*) = 0$ from the tendency of $f'(y)$.

In terms of $\frac{2}{b} \geq 1$, i.e. $b \leq 2$, $f'(y)$ will always decrease over the interval $y \in [0, 1]$;

(3) (see Fig. 3) When $b \leq 2$, at the same time, $m < 1$, then $f'(y)$ decreases from $m - 1 (< 0)$. On the whole, $f'(y) < 0, \forall y \in [0, 1]$, accordingly, $f(y)$ will decrease from $-a$ to $f(1)$, and it is impossible for $f(y)$ to intersect axis y . So, in this case, there will be no root at all for $f(y) \forall y \in [0, 1]$.

On the other hand, if $b \leq 2$, at the same time, $m > 1$, then $f'(y)$ decreases from $m - 1 (> 0)$ to $f'(1)$, but the sign of $f'(1)$ is doubtful, so a further discussion in (4) and (5) is needed.

(4) (see Fig. 4) When $b \leq 2$, at the same time, $m > 1$, and $f'(1) = me^{-b}(1 - b) - 1 \geq 0$, then although $f'(y)$ decreases, it will not traverse y axis, which inform that $f(y)$ increases monotonously on the interval $[0, 1]$. But the sign of $f(1)$ needs the following discussions:

(a) If $me^{-b} > a + 1$, i.e. $f(1) > 0$, then, obviously there must exist a point $y_1^* \in [0, 1]$ such that $f(y_1^*) = 0$. Furthermore, we can perceive that $f'(y_1^*) > 0$ from the tendency of $f'(y)$.

(b) If $me^{-b} = a + 1$, i.e. $f(1) = 0$, then $y = 1$ is the only solution of $f(y) = 0 \forall y \in [0, 1]$. Actually, it coincides with the washout point, so we ignore it.

(c) If $me^{-b} < a + 1$, i.e. $f(1) < 0$, then obviously, it is impossible for $f(y)$ to intersect axis y . So, in this case, there will be no root at all for $f(y) = 0$.

(5) (see Fig. 5) When $b \leq 2$, at the same time, $m > 1$, and $f'(1) = me^{-b}(1 - b) - 1 < 0$, then it follows from $f'(0) > 0$ and $f'(1) < 0$ that $f'(y)$ monotonously decreases on the interval $[0, 1]$. There must exist a point, in which $f'(y) = 0$. We denote this point by \bar{y} . Notice that $f'(y) > 0 \forall y \in [0, \bar{y}]$, which implies that $f(y)$ increases monotonously over this interval, and $f'(y) < 0, \forall y \in [\bar{y}, 1]$, which implies that $f(y)$ decreases monotonously over this interval. So far, we can only detect that $f(\bar{y}) > f(1)$, but the sign of $f(1)$ is still uncertain. Using the same argument as (2), we have:

(a) If $me^{-b} > a + 1$, there must exist a point in the interval $[0, \bar{y}]$, in which $f(y) = 0$. We denote this point as y_1^* with $f'(y_1^*) > 0$.

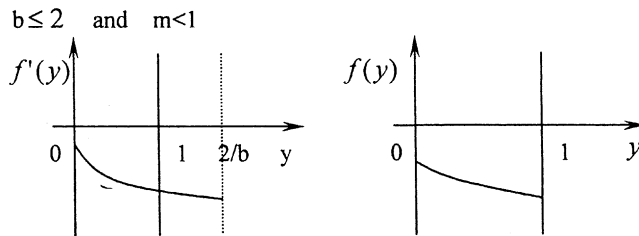


Fig. 3.

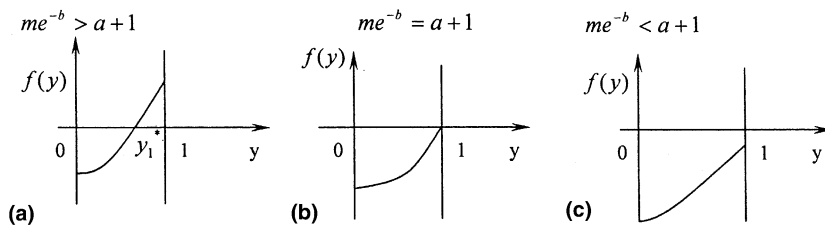
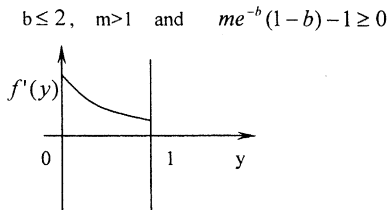


Fig. 4.

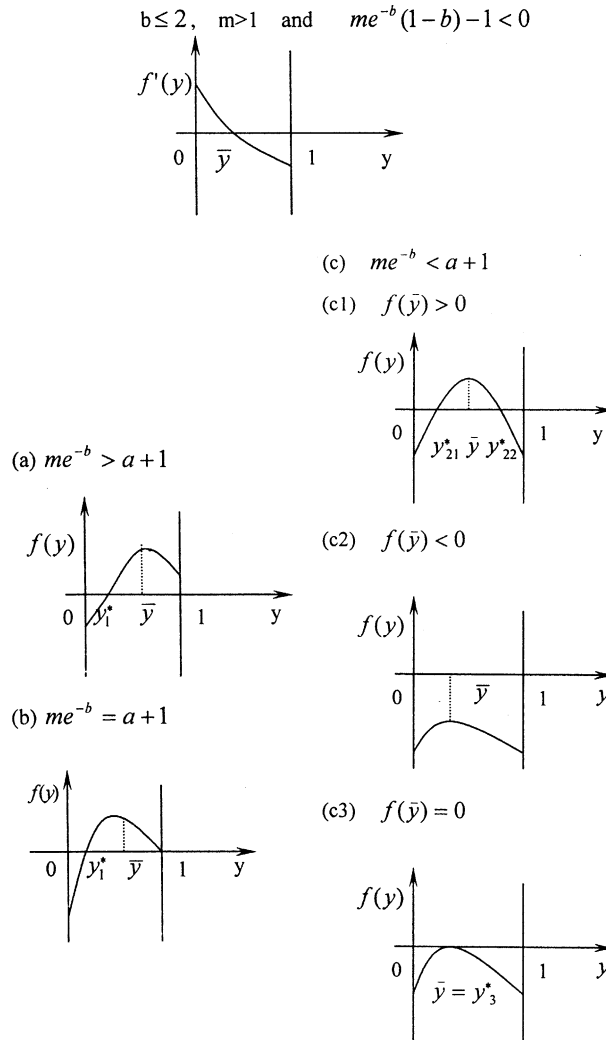


Fig. 5.

- (b) If $me^{-b} = a + 1$, there still be one root on the interval $[0, 1]$, we also denote it as y_1^* .
- (c) If $me^{-b} < a + 1$, the sign of $b\bar{y}^2 + ab\bar{y} - a$ is uncertain too, the discussions of three steps is necessary.
 - (c₁) If $b\bar{y}^2 + ab\bar{y} - a > 0$, then on the interval $[0, \bar{y}]$, there must exist a point in the interval $y_{21}^* \in [0, \bar{y}]$, in which $f(y_{21}^*) = 0$, with $f'(y_{21}^*) > 0$; Conversely, on the interval $[\bar{y}, 1]$, there must also exist a point in the interval $y_{22}^* \in [\bar{y}, 1]$, in which $f(y_{22}^*) = 0$, with $f'(y_{22}^*) < 0$.
 - (c₂) If $b\bar{y}^2 + ab\bar{y} - a < 0$, there will be no root at all for $f(y) \forall y \in [0, 1]$.
 - (c₃) If $b\bar{y}^2 + ab\bar{y} - a = 0$, then on the interval $[0, 1]$, \bar{y} is the only zero of $f(y)$. We denote this point as y_3^* , with $f'(y_3^*) = 0$.

Substitute all values of y into the right part of Eq. (2.3), we easily derive $x = 1 - y$, accordingly, we obtain all equilibrium points.

This completes the proof of Theorem 1. \square

Theorem 2

- (i) If $a + 1 < me^{-b}$, E_0 is a saddle point; If $a + 1 > me^{-b}$, E_0 is locally asymptotically stable; If $a + 1 = me^{-b}$, the stability of E_0 belongs to the degenerate case, which needs further discussion.
- (ii) E_1^+ and E_{21}^+ are locally asymptotically stable, when they exist; E_{22}^+ is unstable, when it exists; and the stability of E_3^+ (if exists), belongs to the degenerate case, which needs further discussion.

Proof. To study the local stability of E_0 , we first consider the coefficient matrix J_0 of the linearizing system (2.3) about E_0 , where

$$J_0 = \begin{pmatrix} \frac{me^{-b}-(a+1)}{a+1} & 0 \\ \frac{-me^{-b}}{a+1} & -1 \end{pmatrix}$$

the two eigenvalues are $\lambda_1 = -1$, and $\lambda_2 = (me^{-b} - (a + 1))/(a + 1)$. Obviously, the two eigenvalues are all real numbers, and if $a + 1 < me^{-b}$, J_0 has one positive real eigenvalue root and one negative real eigenvalue root, which infers that E_0 is a saddle point; If $a + 1 > me^{-b}$, J_0 has two negative real eigenvalue roots, which infers that E_0 is locally asymptotically stable; If $a + 1 = me^{-b}$, J_0 has one zero eigenvalue, which infers that E_0 is degenerate.

On the other hand, the local stability of positive equilibrium involves the coefficient matrix J_1 of the linearizing system (2.3) about E_i^+ ($i = 1, 21, 22, 3$). We denotes (x^*, y^*) as the assemblage of all positive equilibria. Note that $x^* = 1 - y^*$.

$$J_1 = \begin{pmatrix} 0 & \frac{-x^*(by^{*2}+aby^*-a)}{y^*(a+y^*)} \\ -1 & \frac{-x^*(by^{*2}+aby^*-a)}{y^*(a+y^*)-1} \end{pmatrix}$$

The two eigenvalues are $\lambda_1 = -1$ and $\lambda_2 = x^*(by^{*2} + aby^* - a)/(y^*(a + y^*))$. Obviously, the two eigenvalues are all real numbers. As noted that y^* is the solution of $f(y) = 0$, so it must satisfy that $my^*e^{-by^*} - a - y^* = 0$, i.e. $me^{-by^*} = (a + y^*)/y^*$, substitute it into $f'(y)$, we have $f'(y^*) = me^{-by^*}(1 - by^*) - 1 = (by^{*2} + aby^* - a)/(-y^*)$. In the proof of Theorem 1, we have shown that $f'(y_1^*) > 0$, which implies that $by_1^{*2} + aby_1^* - a < 0$. Similarly, $f'(y_{21}^*) > 0$ implies that $by_{21}^{*2} + aby_{21}^* - a < 0$; $f'(y_{22}^*) < 0$ implies that $by_{22}^{*2} + aby_{22}^* - a > 0$; and $f'(y_3^*) = 0$ implies that $by_3^{*2} + aby_3^* - a = 0$. Thus, the local asymptotical behavior of E_i^+ depends on the sign of $by^{*2} + aby^* - a$. We have the following conclusions:

E_{11}^+ and E_{21}^+ are locally asymptotically stable, as long as they exist; E_{22}^+ is unstable, as long as it exists; E_3^+ is degenerate if it exists. This completes the proof of Theorem 2. □

The two degenerate cases referred in Theorem 2 are considered in the following two theorems.

Theorem 3. For the degenerate case of E_0 , i.e. when $me^{-b} = a + 1$, the phase portrait of (2.3) in the vicinity of E_0 is given in Fig. 6, here E_0 is a saddle-node.

Proof. Firstly, we translate the washout critical point to the origin. Define $u = x$, $v = y - 1$, still denote u, v with x, y , and (2.3) can be written as the following system:

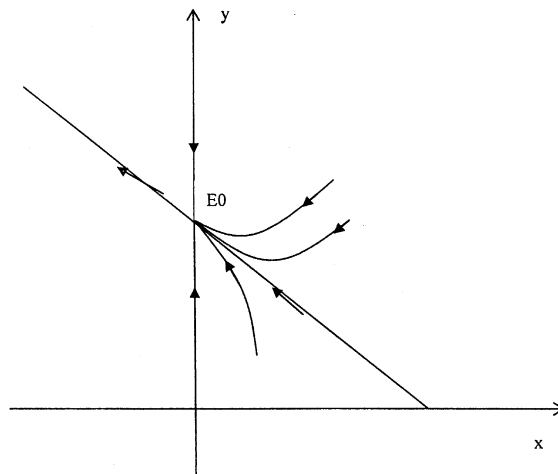


Fig. 6. The phase portrait of (2.3) in the vicinity of E_0 when $me^{-b} = a + 1$, i.e., E_0 is degenerate.

$$\begin{cases} \dot{x}(t) = \frac{mx(y+1)e^{-b(y+1)}}{a+y+1} - x, \\ \dot{y}(t) = -y - \frac{mx(y+1)e^{-b(y+1)}}{a+y+1}. \end{cases} \tag{3.1}$$

Using polar coordinates, define $x = r \cos(\theta)$, $y = r \sin(\theta)$, we have

$$\begin{aligned} \dot{r}(t) = & \frac{-r(a - mre^{-b(r \sin(\theta)+1)}) \sin(\theta) \cos^2(\theta) + r \sin(\theta) + 1}{a + r \sin(\theta) + 1} + \frac{mre^{-b(r \sin(\theta)+1)} \cos(\theta) - mre^{-b(r \sin(\theta)+1)} \cos^3(\theta)}{a + r \sin(\theta) + 1} \\ & - \frac{me^{-b(r \sin(\theta)+1)} \cos^2(\theta) + me^{-b(r \sin(\theta)+1)} \sin(\theta) \cos(\theta)}{a + r \sin(\theta) + 1}, \end{aligned} \tag{3.2}$$

$$\dot{\theta}(t) = \frac{-me^{-b(r \sin(\theta)+1)}(r \sin(\theta) + 1)(\cos(\theta) \sin(\theta) + 1 - \sin^2(\theta))}{a + r \sin(\theta) + 1}. \tag{3.3}$$

We denote $U(\theta)$ as the coefficient of the minimum power about r in Eq. (3.3), and $R(\theta)$ as the coefficient of the minimum power about r in Eq. (3.2). Then, we obtain

$$\begin{aligned} U(\theta) &= \frac{-me^{-b}(\sin(\theta) \cos(\theta) + \cos^2(\theta))}{a + 1}, \\ R(\theta) &= \frac{-a + me^{-b} \cos^2(\theta) - 1 - me^{-b} \cos(\theta) \sin(\theta)}{a + 1}, \end{aligned}$$

then, accordingly

$$U'(\theta) = -\sqrt{2} \cos\left(2\theta + \frac{\pi}{4}\right).$$

When $\theta = \frac{\pi}{2}$ and $\frac{3\pi}{2}$, they satisfy $U(\theta) = 0$, $R(\theta) < 0$, $U'(\theta) > 0$ (see [13]). We know that the trajectories of system (3.1) approach $(0, 0)$ along $\theta = \frac{\pi}{2}$ and $\frac{3\pi}{2}$ as $t \rightarrow \infty$, that is, the trajectories of (2.3) along y axis approach E_0 .

For other trajectories, make the transformation of coordinates

$$\begin{cases} x = -\bar{x}, \\ y = \bar{x} + \bar{y}, \end{cases} \tag{3.4}$$

and time transformation $t = -\tau$. (3.1) becomes

$$\begin{cases} \dot{\bar{x}}(t) = \frac{\bar{x}((-me^{-b(\bar{x}+\bar{y}+1)}+1)\bar{x}-me^{-b(\bar{x}+\bar{y}+1)}\bar{y}-me^{-b(\bar{x}+\bar{y}+1)}a+\bar{y}+1)}{a+\bar{x}+\bar{y}+1}, \\ \dot{\bar{y}}(t) = \bar{y}. \end{cases} \tag{3.5}$$

As referred in [7], we get

$$\varphi(\bar{x}, \bar{y}) = \frac{-m\bar{x}^2e^{-b(1+\bar{y}+\bar{x})}}{a + \bar{x} + \bar{y} + 1} - \frac{m\bar{x}\bar{y}e^{-b(1+\bar{y}+\bar{x})}}{a + \bar{x} + \bar{y} + 1} - \frac{m\bar{x}e^{-b(1+\bar{y}+\bar{x})}}{a + \bar{x} + \bar{y} + 1} + \frac{\bar{x}a + \bar{x}^2 + \bar{x}\bar{y} + \bar{x}}{a + \bar{x} + \bar{y} + 1},$$

and $\psi(\bar{x}, \bar{y}) = 0$ can be easily discerned from the second equation of (3.5), so $\bar{y} = 0$ is incontrovertible. Substitute $\bar{y} = 0$ into $\varphi(\bar{x}, \bar{y})$, and make a Taylor expansion for $\varphi(\bar{x}, 0)$ in $(0,0)$, then the coefficient of the square term about \bar{x} is

$$g_2 = \frac{-m}{(a + 1)e^b} < 0.$$

At the same time, noticing the time transformation $t = -\tau$, the coordinate transformation $\bar{x} = -x$, $\bar{y} = x + y$, and $u = x$, $v = y - 1$, in the x - y plane, we give the phase portrait showed in Fig. 6 from which we find that E_0^+ is a saddle-node (see [7,13]). This completes the proof. \square

Theorem 4. For the degenerate case of E_3^+ , i.e. when the case (3) of Theorem 1 holds, the phase portrait of (2.3) in the vicinity of E_3^+ is given in Fig. 7, here E_3^+ is a saddle-node.

Proof. Firstly, we translate E_3^+ to the origin. Define $u = x - x_3^*$, $v = y - y_3^*$. Still denote x, y for u, v , then (2.3) can be transformed to

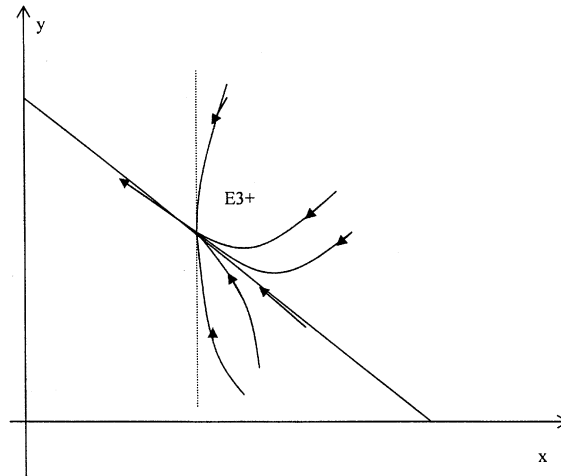


Fig. 7. The phase portrait of (2.3) in the vicinity of E_3^+ when the case (3) of Theorem 1 holds, i.e., E_3^+ is degenerate.

$$\begin{cases} \dot{x}(t) = \frac{m(x+1-y_3^*)(y+y_3^*)e^{-b(y+y_3^*)}}{a+y+y_3^*} - x - 1 + y_3^*, \\ \dot{y}(t) = 1 - y - y_3^* - \frac{m(x+1-y_3^*)(y+y_3^*)e^{-b(y+y_3^*)}}{a+y+y_3^*}. \end{cases} \quad (3.6)$$

Then, make the following transformation of coordinates:

$$\begin{cases} x = -\bar{x}, \\ y = \bar{x} + \bar{y}, \end{cases} \quad (3.7)$$

and time transformation $t = -\tau$. As in Theorem 3, the square coefficient about \bar{x} is

$$g_2 = \frac{mae^{-by_3^*}(y_3^{*2} + (a-2)y_3^* - a)}{2y_3^*(a+y_3^*)^3}.$$

To determine the sign of g_2 , define

$$f_1(y) = 2y^2 + (a-2)y - a.$$

Obviously, over the interval $[0, 1)$, the quadratic function $f_1(y) < 0$, and because $0 < y_3^* < 1$, we have $f_1(y_3^*) < 0$, that is $g_2 < 0$. At the same time, owing to the time transformation $t = -\tau$, the coordinate transformation $\bar{x} = -x$, $\bar{y} = x + y$, and $u = x - x_3^*$, $v = y - y_3^*$, in the x - y plane, we can draw the phase portrait Fig. 7 from which we find that E_3^* is a saddle-node. This completes the proof. \square

4. Global behavior of equilibria

Theorem 5

- (i) If the case (1) of Theorem 1 holds, then E_0 is globally asymptotically stable with respect to Ω for $me^{-b} < a + 1$, and globally attractive with respect to Ω for $me^{-b} = a + 1$.
- (ii) If $m > 1$, $me^{-b} > a + 1$ (one of the conditions in the case (2) of Theorem 1) holds, then E_1^+ is globally asymptotically stable with respect to $\Omega_1 = \{(x, y) | (x, y) \in \Omega, x > 0\}$.
- (iii) If the case (3) of Theorem 1 holds, then E_0 attracts all solutions with initial condition (x_0, y_0) satisfying $(x_0, y_0) \in \Omega_2 = \{(x, y) | 0 \leq x \leq x_3^*, 0 \leq y \leq 1\} \setminus \{E_3^+\}$.

(iv) If the case (4) of Theorem 1 holds, then E_0 attracts all solutions with initial condition (x_0, y_0) satisfying $(x_0, y_0) \in \Omega_3 = \{(x, y) \mid 0 < x \leq x_{22}^*, y_{22}^* < y \leq 1\}$; E_{21}^+ attracts all solutions with initial condition (x_0, y_0) satisfying $(x_0, y_0) \in \Omega_4 = \{(x, y) \mid 0 < y \leq y_{22}^*, 1 - y \leq x < +\infty\} \setminus \{E_{22}^+\}$.

Proof. (i) We only need to show that E_0 is globally attractive. We shall use the Liapunov–LaSalle invariant principle to prove attractivity. Consider the non-negative function $V = x$ on the compact set Ω . It is clear that $V = x$ is continuous on Ω and the derivative along the solutions of (2.3) satisfies

$$\dot{V} = \dot{x} = \frac{x[y(me^{-by} - 1) - a]}{a + y} = \frac{xf(y)}{a + y} \leq 0.$$

This implies that $V = x$ is a Liapunov function of (2.3) on Ω . Define the subset G of Ω as

$$G = \{(x, y) \mid (x, y) \in \Omega, \dot{V} = 0\},$$

and let M be the largest invariant set of (2.3) in Ω .

If $me^{-b} < a + 1$, it has that $f(y) < 0$ for any $0 \leq y \leq 1$ and hence,

$$G = \{(x, y) \mid (x, y) \in \Omega, \dot{V} = 0\} = \{(x, y) \mid (x, y) \in \Omega, x = 0\}.$$

By the invariance of M and (2.3), we can easily show that

$$G = \{(0, 1) \in \Omega\} = \{E_0\}.$$

If $me^{-b} = a + 1$, it has that $f(y) < 0$ for any $0 \leq y < 1$ and that $f(y) = 0$ for $y = 1$. Hence,

$$G = \{(x, y) \mid (x, y) \in \Omega, \dot{V} = 0\} = \{(x, y) \mid (x, y) \in \Omega, x = 0 \text{ or } y = 1\}.$$

Also from the invariance of M and (2.3), we can show that

$$G = \{(0, 1) \in \Omega\} = \{E_0\}.$$

Therefore, it follows from well-known Liapunov–LaSalle invariant principle (see, for example, [7]) that E_0 is globally attractive.

(ii) When $m > 1$ and $me^{-b} > a + 1$ (one of the conditions of the case (2) of Theorem 1 holds), we have known that the equilibrium E_0 is a saddle point and that the equilibrium E_1^+ is locally asymptotically stable. For any $(x_0, y_0) \in \Omega_1$, it has that the solution $(x(t), y(t))$ of (2.3) with (2.4) belongs to Ω_1 for all $t \geq 0$ and that $(x(t), y(t))$ is bounded. Thus, it follows from well-known Poincare–Bendixson theorem (see, for example, [7,8,13]) that one of the following cases holds: (a) the ω limit set, denoted by Q , of $(x(t), y(t))$ is an equilibrium; (b) Q is a periodic orbit; (c) Q is a singular closed orbit. On the other hand, note that E_0 is a saddle point and that E_1^+ is locally asymptotically stable, and that $\lim_{t \rightarrow +\infty} (x(t) + y(t)) = 1$, we see that Q must be the equilibrium E_1^+ . This shows that E_1^+ is globally asymptotically stable with respect to $\Omega_1 = \{(x, y) \mid (x, y) \in \Omega, x > 0\}$.

As Theorem 1 has shown that E_1^+ is locally asymptotically stable if the case (2) of Theorem 1 holds. Now we derive that when $m > 1$ and $me^{-b} > a + 1$, E_1^+ is globally asymptotically stable. On the other hand, as for another condition of Theorem 1: $m > 1$, $me^{-b}(1 - b) < 1$ and $me^{-b} = a + 1$, E_0 will also attract some trajectories of (2.3). Hence, E_1 cannot be globally attractive. We give a numerical simulation in Fig. 12.

(iii) In the case of (3) in Theorem 1, we know that $f(y) < 0$ for $0 \leq y < y_3^*$ and $y_3^* < y \leq 1$. If $(x_0, y_0) \in \Omega_2$ and $x_0 = 0$, it easily has that $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (0, 1)$. If $(x_0, y_0) \in \Omega_2$ and $x_0 > 0$, it has that

$$\dot{x} = \frac{x}{a + y} f(y) \leq 0 \tag{4.1}$$

for $(x(t), y(t)) \in \Omega_2$, from which we can easily have that $(x(t), y(t)) \in \Omega_2$ for all $t \geq 0$. Hence, $\lim_{t \rightarrow +\infty} x(t) = x^*$ and $\lim_{t \rightarrow +\infty} y(t) = 1 - x^*$ for some x^* . Clearly, it must have $(x^*, 1 - x^*) = (0, 1)$. This shows that E_0 attracts all solutions with $(x_0, y_0) \in \Omega_2$.

(iv) In the case of (4) in Theorem 1, we know that $f(y) < 0$ for $0 < y \leq y_{21}^*$ and $y_{22}^* \leq y < 1$ and $f(y) > 0$, for $y_{21}^* < y < y_{22}^*$. For convenience, we let

$$\begin{aligned}
 C_1 &= \{(x, y) \mid 1 - y < x \leq x_{22}^*, y_{22}^* < y \leq 1\}, \\
 C_2 &= \{(x, y) \mid 0 < x \leq 1 - y, y_{22}^* < y \leq 1\}, \\
 C_3 &= \{(x, y) \mid 1 - y \leq x < \infty, y_{21}^* < y < y_{22}^*\}, \\
 C_4 &= \{(x, y) \mid 1 - y \leq x < \infty, 0 < y \leq y_{21}^*\}, \\
 C_5 &= \{(x, y) \mid x_{22}^* < x < \infty, y_{22}^* < y \leq 1\}, \\
 C_6 &= \{(x, y) \mid 0 < x < 1 - y, 0 < y \leq y_{22}^*\}.
 \end{aligned}$$

Then we have the following discussions in five steps:

- (1) If $(x_0, y_0) \in C_1$, we have $y_{22}^* < y_0 \leq 1$. Hence, from (4.1) we see that $x(t)$ strictly decreases as t increases and $(x(t), y(t)) \in C_1$. Note that the orbit cannot cross the line $x + y = 1$. By a similar argument as in (iii), we can show that $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (0, 1)$.
- (2) If $(x_0, y_0) \in C_2$ and $x_0 + y_0 = 1$, from (2.5) we see that $(x(t), y(t)) \in C_2$ and $(x(t), y(t)) = 1$ for all $t \geq 0$. Hence, $\dot{x}(t) < 0$ and

$$\dot{y}(t) = 1 - y - x - \frac{x}{a + y} f(y) > 0 \tag{4.2}$$

for $t \geq 0$. From the monotonicity of $x(t)$ and $y(t)$, we can also easily see that

$$\lim_{t \rightarrow +\infty} (x(t), y(t)) = (0, 1).$$

If $(x_0, y_0) \in C_2$ and $x_0 + y_0 < 1$, we see that $x(t) + y(t) < 1$ for all $t \geq 0$. Furthermore, it has from $y_{22}^* < y_0 \leq 1$ that $x(t)$ strictly decreases and $y(t)$ strictly increases as t increases and $(x(t), y(t)) \in C_2$. From the monotonicity of $x(t)$ and $y(t)$, we can also easily see that $(x(t), y(t)) \in C_2$ for all $t \geq 0$ and that $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (0, 1)$.

- (3) If $(x_0, y_0) \in C_3$ and $x_0 + y_0 = 1$, it also has that $(x(t), y(t)) \in C_3$ and $x(t) + y(t) = 1$ for all $t \geq 0$. Hence, $\dot{x}(t) > 0$ and

$$\dot{y}(t) = 1 - y - x - \frac{x}{a + y} f(y) < 0$$

for $t \geq 0$. Also from the monotonicity of $x(t)$ and $y(t)$, we have that $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (1 - y_{21}^*, y_{21}^*)$.

If $(x_0, y_0) \in C_3$ and $x_0 + y_0 > 1$, it has that $x(t) + y(t) > 1$ for all $t \geq 0$. It follows from $y_{21}^* < y_0 < y_{22}^*$ that $x(t)$ strictly increases and $y(t)$ strictly decreases as t increases and $(x(t), y(t)) \in C_3$. Thus, the orbit $(x(t), y(t))$ either stays in C_3 for all $t \geq 0$ or enters into C_4 . Clearly, if the orbit $(x(t), y(t))$ stays in C_3 for all $t \geq 0$, it must have $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (1 - y_{21}^*, y_{21}^*)$.

- (4) If $(x_0, y_0) \in C_4$ and $x_0 + y_0 = 1$, it also has that $(x(t), y(t)) \in C_4$ and $x(t) + y(t) = 1$ for all $t \geq 0$. Hence, $\dot{x}(t) < 0$ and $\dot{y}(t) > 0$ for all $t \geq 0$. We also have that $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (1 - y_{21}^*, y_{21}^*)$.

If $(x_0, y_0) \in C_4$ and $x_0 - y_0 > 1$, it has from $0 < y_0 \leq y_{22}^*$ that $x(t)$ strictly decreases and $y(t)$ strictly increases as t increases and $(x(t), y(t)) \in C_4$. Hence, it must also have that $\lim_{t \rightarrow +\infty} (x(t), y(t)) = (1 - y_{21}^*, y_{21}^*)$.

- (5) If $(x_0, y_0) \in C_5$ or $(x_0, y_0) \in C_6$, there exists orbit $(x(t), y(t))$ such that it tends E_0 or E_{21}^+ .

Now let $\Omega_2 = C_1 \cup C_2$ and $\Omega_3 = C_3 \cup C_4$, we see that the conclusion (iv) of Theorem 5 holds. This completes the proof of Theorem 5. \square

5. Discussion

In this paper, we have explored a model involving a single species feeding on a redundant substrate with the Tisiet functional response as the specific growth rate of cells, which accounts for some natural phenomena more reasonably. Our results show the dynamical properties depend intimately upon the value of its experimental parameters. For some values, the continuous fermentation can succeed. We also give some numerical simulations for some fixed parameter (see Fig. 8–14). Fig. 8–10 belong to the case (1) of Theorem 1, in the case E_0 is globally asymptotically stable. Fig. 11 belongs to the first case of the case (2) of Theorem 1, in this case E_1^+ is globally asymptotically stable.

Fig. 12 is approximate to the second of the case (2) of Theorem 1, in this case E_1^+ attracts majority of trajectories and theoretically E_0 also attracts some Fig. 13 belongs to the case (3) of Theorem 1, in this case E_3^+ and E_0 are attractors of some trajectories. Fig. 14 belongs to the case (4) of Theorem 1, in this case E_{21}^+ and E_0 are attractors of some trajectories.

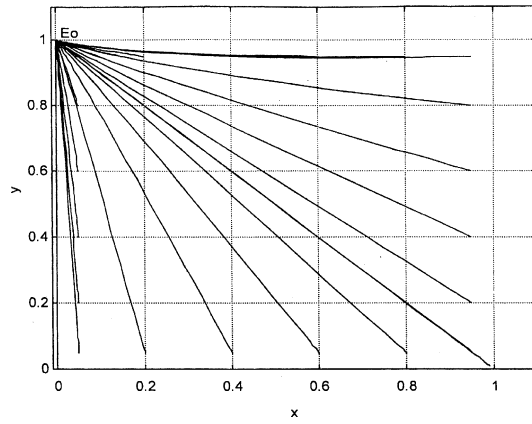


Fig. 8. $a = 0.9, b = 0.2, m = 0.2, me^{-b} \approx 0.1637 < a + 1 = 1.9, me^{-b}(1 - b) = 0.131, \bar{y}$ does not exist. The only equilibrium of (2.3) is E_0 .

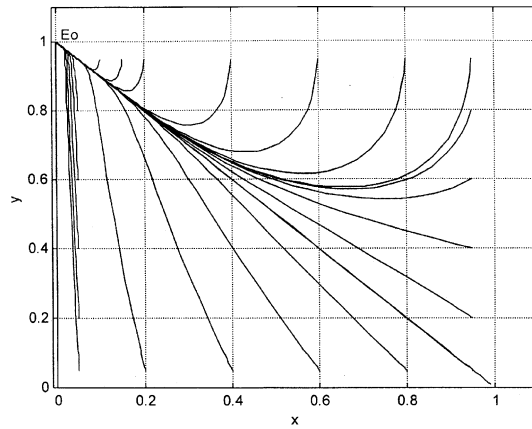


Fig. 9. $a = 9, b = 0.2, m = 12, me^{-b} \approx 9.82 < a + 1 = 10, me^{-b}(1 - b) = 7.8598, \bar{y}$ does not exist. The only equilibrium of (2.3) is E_0 .

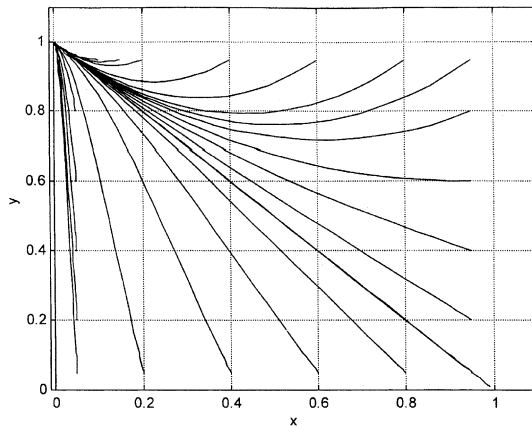


Fig. 10. $a = 0.9, b = 0.2, m = 1.2, me^{-b} \approx 0.9825 < a + 1 = 1.9, me^{-b}(1 - b) = 0.786, \bar{y} = 0.445, b\bar{y}^2 + ab\bar{y} - a = -0.7802$. The only equilibrium of (2.3) is E_0 .

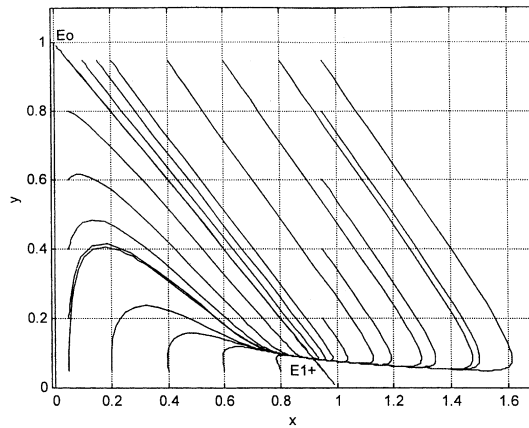


Fig. 11. $a = 0.9, b = 0.2, m = 12, me^{-b} \approx 9.82 < a + 1 = 1.9, me^{-b}(1 - b) = 7.85, \bar{y}$ does not exist. The equilibria of (2.3) are E_0 and $E_1^+ \approx (0.9167, 0.0833)$.

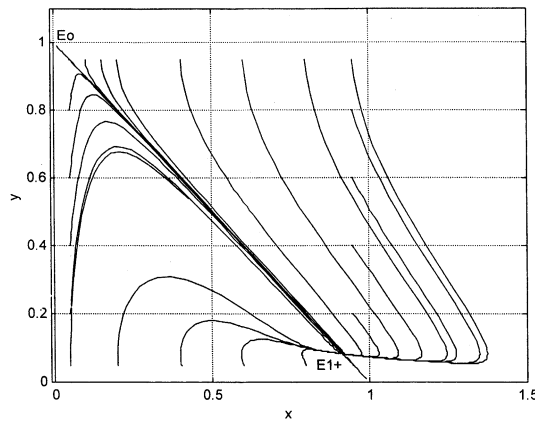


Fig. 12. $a = 0.9, b = 2, m = 14.0392, me^{-b} \approx 1.9 = a + 1 = 1.9, me^{-b}(1 - b) = -1.9, \bar{y} = 0.4179, b\bar{y}^2 + ab\bar{y} - a = 0.2013$. The equilibria of (2.3) are E_0 and $E_1^+ \approx (0.9175, 0.0825)$.

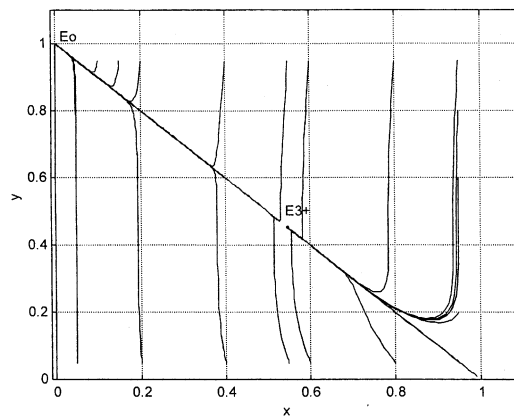


Fig. 13. $a = 0.0435, b = 0.2, m = 1.2, me^{-b} \approx 0.98 < a + 1 = 1.0435, me^{-b}(1 - b) = 0.786, \bar{y} = 0.445, b\bar{y}^2 + ab\bar{y} - a = 0$. The equilibria of (2.3) are E_0 and $E_3^+ \approx (0.565, 0.435)$.

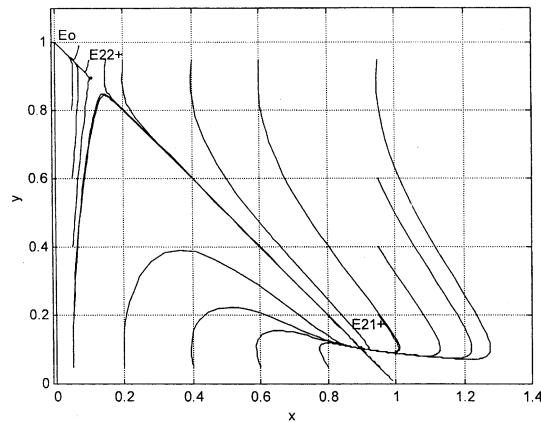


Fig. 14. $a = 0.9$, $b = 2$, $m = 12$, $me^{-b} \approx 1.62 < a + 1 = 1.9$, $me^{-b}(1 - b) = -1.62$, $\bar{y} = 0.4$, $b\bar{y}^2 + ab\bar{y} - a = 0.1609$. The equilibria of (2.3) are E_0 and $E_{21}^+ \approx (0.8943, 0.1057)$, $E_{22}^+ \approx (0.1026, 0.8974)$.

On the other hand, as far as the variant yield term and growth delays due to cells cycle are concerned (see, for example, [1,2,5,9,11] and the references therein), the model need further discussed in details.

Acknowledgement

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Appendix A

Let $f(y) = mye^{-by} - a - y$, $f(0) = -a$, $f(1) = me^{-b} - a - 1$, $f'(y) = me^{-by}(1 - by) - 1$, $f'(0) = m - 1$, $f'(1) = me^{-b}(1 - b) - 1$, $f''(y) = mbe^{-by}(by - 2)$ and \bar{y} be the solution of $f'(y) = 0$. After a detailed discussion, we have Figs. 1–5.

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