Journal of Applied Analysis and Computation
Volume 9, Number 3, June 2019, 981–1006
Website:http://jaac.ijournal.cn
DOI:10.11948/2156-907X.20180195

A MICROBIAL CONTINUOUS CULTURE SYSTEM WITH DIFFUSION AND DIVERSIFIED GROWTH*

Jingli Ren[1,†] and Ying Xu[1]

Abstract A reaction-diffusion model is presented to describe the microbial continuous culture with diversified growth. The existence of nonnegative solutions and attractors for the system is obtained, the stability of steady states and the steady state bifurcation are studied under three growth conditions. In the case of no growth inhibition or only product inhibition, the system admits one positive constant steady state which is stable; in the case of growth inhibition only by substrate, the system can have two positive constant steady states, explicit conditions of the stability and the steady state bifurcation are also determined. In addition, numerical simulations are given to exhibit the theoretical results.

Keywords Continuous culture, diffusion, diversified growth, stability, steady state bifurcation.

MSC(2010) 35Q92, 35K57, 35B32.

1. Introduction

Microbial continuous culture is widely used in many fields of industry, such as biological phosphorus removal in waste-water treatment [1], production of bioethanol from lignocellulosic materials [4], and bioconversion of industrial by-product glycerol to 1,3-propanediol [5].

In recent decades, studies on microbial continuous culture fascinate biochemical and mathematical researchers. Up to now, many fruits, including experiment results, numerical simulations and theoretical analyses, were achieved, see [1–8, 10–12, 14–16, 19–24, 26] and references therein. For example, in [22], Xiu et al. numerically analyzed the dynamics behavior of a continuous culture subject to metabolic overflow and growth inhibition by substrate and/or product, and showed three positive constant equilibriums are possible in a certain range of operating conditions. Afterwards, Gao et al. [12] discussed the parameters identification problem in microbial continuous cultures, and Ye et al. [24] studied the existence and stability of equilibriums for the proposed system in [12]. Very recently, Ren and Yuan [19] investigated the complex dynamics of a period forced microbial continuous culture model with bifurcation theory, and obtained various solutions by numerical simulations.

†the corresponding author. Email address: renjl@zzu.edu.cn(J. Ren)
1School of Mathematics and Statistics, Zhengzhou University, 450001 Zhengzhou, China
*The authors were supported by National Natural Science Foundation of China (11771407).

Note that above works [2,6,8,10–12,14–16,19,21–24,26] all considered the corresponding ordinary differential system in the absence of diffusion. As a matter of fact, diffusion is ubiquitous in the liquid medium, including the simple diffusion which is a movement of molecules from a region of higher concentration to one of lower concentration, the facilitated diffusion known as a process of passive and transmembrane transport [7], and so on. As a preliminary study, we explore the effect of simple diffusion on the substrate consumption and product formation. In this paper, we give two assumptions

A1. the biochemical reaction takes place in a tubular culture vessel, which is thin and long enough. Then the vessel is approximate to be one dimensional, and its capacity is quantified by the length;
A2. feed streams are not from the two ends of the vessel, but flow into it in the vertical direction. Thus there is no flow along x-axis and nothing crosses the boundary.

Under above assumptions, the microorganism continuous culture process can be seen as the following diffusion-reaction system

$$\begin{cases} u_t = d_1 u_{xx} + u(r - D), & x \in (0, L), t > 0, \\ v_t = d_2 v_{xx} + D(a_0 - v) - u(n_s + \frac{r}{Y_s}), & x \in (0, L), t > 0, \\ w_t = d_3 w_{xx} + u(n_p + Y_p r) - Dw, & x \in (0, L), t > 0, \\ u_x(x,t) = v_x(x,t) = w_x(x,t) = 0, & x = 0, L, t > 0, \\ u(x,0) = u_0(x), v(x,0) = v_0(x), w(x,0) = w_0(x), & x \in (0, L). \end{cases} \tag{1.1}$$

Here $u(x,t)$, $v(x,t)$, $w(x,t)$ are the concentrations of biomass, substrate and product at location x and time t; the initial functions $u_0(x), v_0(x), w_0(x) \in \Phi$ with

$$\Phi = \{\phi(x) : \phi(x) \in \mathcal{C}^{2+\alpha}((0,L)), \phi(x) \geq, \not\equiv 0, \quad 0 < \alpha < 1\}.$$

For $i = 1, 2, 3$, d_i denotes the diffusion rate of biomass, substrate and product, respectively; a_0 means substrate concentration in medium; D is the dilution rate; n_s, n_p account for the maintenance requirement of substrate consumption and product formation; Y_s, Y_p are biomass and product yield coefficients. And d_i, a_0, D, n_s, n_p, Y_s and Y_p are given constants.

In (1.1), the specific growth rate r is a function of v and/or w. There are several growth functions reported in [2,8,16,22,26] for different types of continuous culture. In this paper, we aim at the following three popular growth functions to compare the effects of growth limiting and/or different inhibiting factors on the continuous fermentation process.

$$\text{Case I.} \quad r = r_m \frac{v}{v + K},$$

where r_m is the maximum specific growth rate, K is the Monod saturation constant. Case I is the well-known Monod growth function, which implies that substrate is the growth limiting factor, and the growth of microorganisms is not inhibited by substrate or product. It is known that the Monod relationship provides a reasonable fit for continuous culture systems such as those used in biological processes for waste treatment [2].

$$\text{Case II.} \quad r = r_m \frac{v}{v + K}(1 - \frac{v}{c}),$$

where c is the critical concentration of the substrate above which microorganisms cease to grow, $c \geq a_0$. As suggested in [2, 10, 23], inhibition of microbial growth is observed at high concentration of substrate, and the second term in Case II describes substrate inhibition.

$$\text{Case III.} \quad r = r_m \frac{v}{v+K}(1 - \frac{w}{d}),$$

where d is the critical concentration of product above which microorganisms stop growing. It means that high product concentration may inhibit the growth of microorganisms, see [3, 5, 15, 16, 26], and the second term in Case III represents product inhibition.

This paper is devoted to the reaction-diffusion model under above three cases. The properties of the nonnegative solution to (1.1) are analyzed in Section 2, and the attractor is obtained in Section 3. The stability of positive constant steady states, nonexistence of Hopf bifurcation and existence of steady state bifurcation are studied in Section 4. Some numerical results are given in Section 5 and the paper is concluded by some discussion.

2. Preliminaries

In the following text, denote

$$s = -K + \sqrt{K^2 + cK}, \tag{2.1}$$

$$\Theta = (0,0,0), \quad \mathrm{M} = (\frac{Da_0}{n_s}, a_0, d), \quad \mathrm{S} = (\frac{Da_0}{n_s}, a_0, (n_p + r_m Y_p)\frac{a_0}{n_s}), \tag{2.2}$$

$$\underline{\mathrm{M}} = (0, s, 0), \quad \tilde{\mathrm{M}} = (D\frac{a_0 - s}{n_s + \frac{r_m}{Y_s}}, a_0, \frac{a_0 - s}{n_s + \frac{r_m}{Y_s}}(n_p + Y_p r_m)), \tag{2.3}$$

$$\mathrm{U}_0(x) = (u_0(x), v_0(x), w_0(x)), \quad \mathrm{U}(x,t) = (u(x,t), v(x,t), w(x,t)), \tag{2.4}$$

and define

$$\langle \underline{\mathrm{U}}, \bar{\mathrm{U}} \rangle \equiv \{u, v, w \in \mathcal{C}^2([0,L]) : \underline{u} \leq u \leq \bar{u}, \underline{v} \leq v \leq \bar{v}, \underline{w} \leq w \leq \bar{w}\}, \tag{2.5}$$

where $\underline{\mathrm{U}} = (\underline{u}, \underline{v}, \underline{w})$, $\bar{\mathrm{U}} = (\bar{u}, \bar{v}, \bar{w})$. Particularly,

$$\langle \Theta, \bar{\mathrm{U}} \rangle \equiv \{u, v, w \in \mathcal{C}^2([0,L]) : 0 \leq u \leq \bar{u}, 0 \leq v \leq \bar{v}, 0 \leq w \leq \bar{w}\}. \tag{2.6}$$

Lemma 2.1. *Suppose*

$$r_m \leq D \quad or \quad \begin{cases} r_m > D, \\ a_0 \leq \frac{DK}{r_m - D}, \end{cases} \tag{2.7}$$

then for any $\mathrm{U}_0(x) \in \langle \Theta, \mathrm{M} \rangle$, *problem (1.1) has a unique solution* $\mathrm{U}(x,t)$ *in* $\langle \Theta, \mathrm{M} \rangle$ *if*

(i) Case I;

(ii) Case III with $d > (n_p + r_m Y_p)\frac{a_0}{n_s}$.

Proof. Case I. $r = r_m \frac{v}{v+K}$, then (1.1) can be rewritten as

$$\begin{cases} u_t = d_1 u_{xx} + r_m \frac{uv}{v+k} - Du, & x \in (0,L), t > 0, \\ v_t = d_2 v_{xx} + D(a_0 - v) - n_s u - \frac{r_m}{Y_s}\frac{uv}{v+K}, & x \in (0,L), t > 0, \\ w_t = d_3 w_{xx} + n_p u + r_m Y_p \frac{uv}{v+k} - Dw, & x \in (0,L), t > 0, \\ u_x(x,t) = v_x(x,t) = w_x(x,t) = 0, & x = 0, L; t > 0, \\ u(x,0) = u_0(x), v(x,0) = v_0(x), w(x,0) = w_0, \, x \in (0,L). \end{cases} \tag{2.8}$$

Firstly, we show $f = (f_1, f_2, f_3)$ is mixed quasimonotone in $\langle \Theta, \mathrm{M} \rangle$, where f_1, f_2 and f_3 are expressed as

$$\begin{cases} f_1 = r_m \frac{uv}{v+k} - Du, & x \in (0,L), \\ f_2 = D(a_0 - v) - n_s u - \frac{r_m}{Y_s}\frac{uv}{v+K}, & x \in (0,L), \\ f_3 = n_p u + r_m Y_p \frac{uv}{v+k} - Dw, & x \in (0,L). \end{cases} \tag{2.9}$$

For any $(u, v, w) \in \langle \Theta, \mathrm{M} \rangle$, it is easy to see

$$\begin{cases} \frac{\partial f_1}{v} = r_m \frac{uK}{(v+K)^2} \geq 0, & \frac{\partial f_1}{w} = 0; \\ \frac{\partial f_2}{u} = -n_s - \frac{r_m}{Y_s}\frac{v}{v+K} < 0, & \frac{\partial f_2}{w} = 0; \\ \frac{\partial f_3}{u} = n_p + r_m Y_p \frac{v}{v+K} > 0, & \frac{\partial f_3}{v} = r_m Y_p \frac{uK}{(v+K)^2} \geq 0, \end{cases}$$

which implies $f = (f_1, f_2, f_3)$ is quasimonotone in $\langle \Theta, \mathrm{M} \rangle$.

Secondly, we show $\mathrm{M} = (\frac{Da_0}{n_s}, a_0, d)$ and $\Theta = (0, 0, 0)$ are coupled upper and lower solutions of (1.1).

According to Definition 8.1.2 in [17], if $(\bar{u}, \bar{v}, \bar{w})$ and $(\underline{u}, \underline{v}, \underline{w})$ satisfy

$$\begin{cases} \bar{u}_t - d_1 \bar{u}_{xx} \geq f_1(\bar{u}, \bar{v}), \\ \bar{v}_t - d_2 \bar{v}_{xx} \geq f_2(\bar{v}, \underline{u}), \\ \bar{w}_t - d_3 \bar{w}_{xx} \geq f_3(\bar{w}, \bar{u}, \bar{v}), \end{cases} \tag{2.10}$$

and

$$\begin{cases} \underline{u}_t - d_1 \underline{u}_{xx} \leq f_1(\underline{u}, \underline{v}), \\ \underline{v}_t - d_2 \underline{v}_{xx} \leq f_2(\underline{v}, \bar{u}), \\ \underline{w}_t - d_3 \underline{w}_{xx} \leq f_3(\underline{w}, \underline{u}, \underline{v}), \end{cases} \tag{2.11}$$

then $(\bar{u}, \bar{v}, \bar{w})$ and $(\underline{u}, \underline{v}, \underline{w})$ are coupled upper and lower solutions of (1.1).

$(\underline{u}, \underline{v}, \underline{w}) = (0, 0, 0)$ and $\bar{u} = \frac{Da_0}{n_s}$ directly yield

$$\begin{cases} f_1(\underline{u}, \underline{v}) = 0, \\ f_2(\underline{v}, \bar{u}) = Da_0 - n_s \bar{u} = 0, \\ f_3(\underline{w}, \underline{u}, \underline{w}) = 0, \end{cases}$$

which satisfies (2.11).

In addition, $f_1(\bar{u},\bar{v}) = r_m\frac{\bar{u}\bar{v}}{(\bar{v}+K)} - D\bar{u}$.

It is clear that $f_1(\bar{u},\bar{v}) < 0$ for $r_m \leq D$. For $r_m > D$, $a_0 \leq \frac{DK}{r_m - D}$ implies $\frac{r_m a_0}{(a_0+K)} \leq D$, which deduces

$$f_1(\bar{u},\bar{v}) = r_m\frac{\bar{u}\bar{v}}{(\bar{v}+K)} - D\bar{u} = \bar{u}[\frac{r_m a_0}{(a_0+K)} - D] \leq 0. \tag{2.12}$$

By $\bar{v} = a_0$, it is easy to get

$$f_2(\bar{v},\underline{u}) = D(a_0 - \bar{v}) = 0. \tag{2.13}$$

It follows from $\bar{u} = \frac{Da_0}{n_s}$ and $d \geq (n_p + r_m Y_p)\frac{a_0}{n_s}$ that

$$f_3(\bar{w},\bar{u},\bar{v}) = n_p\bar{u} + r_m Y_p\frac{\bar{u}\bar{v}}{(\bar{v}+K)} - D\bar{w} \leq n_p\bar{u} + r_m Y_p\bar{u} - D\bar{w} \leq 0. \tag{2.14}$$

(2.12), (2.13) and (2.14) indicate that (2.10) holds. Hence Θ and M are coupled lower and upper solutions to (1.1).

Thirdly, we show that, for $i = 1,2,3$, f_i satisfies Lipschitz condition

$$|f_i(\mathrm{U}_1) - f_i(\mathrm{U}_2)| \leq K_i|\mathrm{U}_1 - \mathrm{U}_2|, \quad \mathrm{U}_1,\mathrm{U}_2 \in \langle\Theta,\mathrm{M}\rangle, \tag{2.15}$$

where $\mathrm{U}_1 = (u_1,v_1,w_1)$, $\mathrm{U}_2 = (u_2,v_2,w_2)$, $|\mathrm{U}_1-\mathrm{U}_2| = |u_1-u_2|+|v_1-v_2|+|w_1-w_2|$, $K_i \equiv K_i(t,x)$ is a bounded function in $(0,T]\times(0,L)$ for each $T>0$.

$$\begin{aligned}
&|f_1(\mathrm{U}_1) - f_1(\mathrm{U}_2)|\\
=&|\ r_m\frac{u_1v_1}{v_1+K} - r_m\frac{u_2v_2}{v_2+K} + Du_2 - Du_1\ |\\
\leq& r_m\ |\ \frac{u_1v_1}{v_1+K} - \frac{u_2v_2}{v_2+K}| + D|u_2 - u_1\ |,
\end{aligned}$$

and

$$\begin{aligned}
&|\ \frac{u_1v_1}{v_1+K} - \frac{u_2v_2}{v_2+K}\ |\\
=&\frac{1}{(v_1+K)(v_2+K)}\ |\ u_1v_1v_2 + Ku_1v_1 - u_2v_2v_1 - Ku_2v_2\ |\\
\leq&\frac{1}{K^2}\ |\ v_1v_2(u_1-u_2) + Ku_1v_1 - Ku_2v_1 + Ku_2v_1 - Ku_2v_2\ |\\
=&\frac{1}{K^2}\ |\ v_1v_2(u_1-u_2) + Kv_1(u_1-u_2) + Ku_2(v_1-v_2)\ |\\
\leq&(\frac{\bar{v}}{K})^2\ |\ u_1-u_2\ | + \frac{\bar{v}}{K}\ |\ u_1-u_2\ | + \frac{\bar{u}}{K}\ |\ v_1-v_2\ |\\
=&[(\frac{\bar{v}}{K})^2 + \frac{\bar{v}}{K}]\ |\ u_1-u_2\ | + \frac{\bar{u}}{K}\ |\ v_1-v_2\ |.
\end{aligned}$$

Then

$$\begin{aligned}
|f_1(\mathrm{U}_1) - f_1(\mathrm{U}_2)| &\leq [r_m(\frac{\bar{v}}{K})^2 + r_m\frac{\bar{v}}{K} + D]\ |\ u_1-u_2\ | + r_m\frac{\bar{u}}{K}\ |\ v_1-v_2\ |\\
&= [r_m(\frac{a_0}{K})^2 + r_m\frac{a_0}{K} + D]\ |\ u_1-u_2\ | + r_m\frac{Da_0}{Kn_s}\ |\ v_1-v_2\ |\\
&\leq K_1\ |\ \mathrm{U}_1 - \mathrm{U}_2\ |,
\end{aligned} \tag{2.16}$$

where $K_1 = \max\{[r_m(\frac{a_0}{K})^2 + \frac{r_m a_0}{K} + D], \frac{r_m D a_0}{K n_s}\}$.

Similarly, we get (2.15) holds for $i = 2, 3$.

$$|f_i(\mathrm{U}_1) - f_i(\mathrm{U}_2)| \le K_i |\mathrm{U}_1 - \mathrm{U}_2|, \quad i = 2, 3. \tag{2.17}$$

Therefore, f_i satisfies Lipschitz condition (2.15), $i = 1, 2, 3$. Thanks to Theorem 8.1 of Chapter 8 in [17], we obtain part (i) of Lemma 2.1.

Case III. The results can be proved by the similar method, so we omit the details. □

For convenience, some hypotheses are listed as follows

(H1) $r_m \le D, a_0 \le \min\{c, s\}$,

(H2) $r_m > D, a_0 \le \min\{c, \dfrac{DK}{r_m - D}, s\}$,

(H3) $r_m \le D, \quad s \le a_0$,

(H4) $r_m > D, \quad \Delta_1 \le 0, \quad s \le a_0$,

(H5) $\begin{cases} r_m > D, \quad \Delta_1 > 0, \\ 0 < s \le \min\{a_0, \frac{c(1-\frac{D}{r_m}-\sqrt{\Delta_1})}{2}\} \quad \text{or} \quad \frac{c(1-\frac{D}{r_m}+\sqrt{\Delta_1})}{2} \le s \le a_0, \end{cases}$

where $\Delta_1 = (1 - \frac{D}{r_m})^2 - \frac{4DK}{c r_m}$.

Lemma 2.2. *For Case II, the following statements are valid.*

(i) Suppose either (H1) *or* (H2) *holds, then for any* $\mathrm{U}_0(x) \in \langle \Theta, \mathrm{S} \rangle$*, problem (1.1) admits a unique solution* $\mathrm{U}(x, t) \in \langle \Theta, \mathrm{S} \rangle$.

(ii) Suppose one of (H3)−(H5) *holds, then for any* $\mathrm{U}_0(x) \in \langle \underline{\mathrm{M}}, \tilde{\mathrm{M}} \rangle$*, problem (1.1) admits a unique solution* $\mathrm{U}(x, t) \in \langle \underline{\mathrm{M}}, \tilde{\mathrm{M}} \rangle$.

Proof. For any $(u, v, w) \in \langle \Theta, \mathrm{S} \rangle$, some direct calculations yield

$$\begin{cases} \frac{\partial f_1}{v} = u \frac{r_m}{(v+K)^2}(-v^2 - 2vK + cK) \ge 0, \ \frac{\partial f_1}{w} = 0, \\ \frac{\partial f_2}{u} = -n_s - \frac{r_m}{Y_s}\frac{v}{v+K}(1 - \frac{v}{c}) < 0, \qquad \frac{\partial f_2}{w} = 0, \\ \frac{\partial f_3}{u} = n_p + r_m Y_p \frac{v}{v+K}(1 - \frac{v}{c}) > 0, \qquad \frac{\partial f_3}{v} = Y_p \frac{r_m}{(v+K)^2}(-v^2 - 2vK + cK) \ge 0. \end{cases}$$

For any $(u, v, w) \in \langle \mathrm{m}, \tilde{\mathrm{M}} \rangle$, it is easy to get

$$\begin{cases} \frac{\partial f_1}{v} < 0, \ \frac{\partial f_1}{w} = 0, \\ \frac{\partial f_2}{u} < 0, \ \frac{\partial f_2}{w} = 0, \\ \frac{\partial f_3}{u} > 0, \ \frac{\partial f_3}{v} < 0. \end{cases}$$

Then $f = (f_1, f_2, f_3)$ is quasimonotone in $\langle \Theta, \mathrm{M} \rangle$ or $\langle \underline{\mathrm{M}}, \tilde{\mathrm{M}} \rangle$.

One must check S and Θ satisfy (2.10) and (2.11) to show they are coupled upper and lower solutions of (1.1).

Part (i) can be proved by the similar process to Lemma 2.1.

Part (ii). Using some straightforward computations, one can get $\bar{\mathrm{U}} = \tilde{\mathrm{M}}$ and $\underline{\mathrm{U}} = \underline{\mathrm{M}}$ satisfy

$$\begin{cases} \bar{u}_t - d_1 \bar{u}_{xx} \ge f_1(\bar{u}, \underline{v}), \\ \bar{v}_t - d_2 \bar{v}_{xx} \ge f_2(\bar{v}, \underline{u}), \\ \bar{w}_t - d_3 \bar{w}_{xx} \ge f_3(\bar{w}, \bar{u}, \underline{v}), \end{cases} \tag{2.18}$$

and

$$\begin{cases} \underline{u}_t - d_1\underline{u}_{xx} \le f_1(\underline{u}, \bar{v}), \\ \underline{v}_t - d_2\underline{v}_{xx} \le f_2(\underline{v}, \bar{u}), \\ \underline{w}_t - d_3\underline{w}_{xx} \le f_3(\underline{w}, \underline{u}, \bar{v}), \end{cases} \tag{2.19}$$

if one of (H3)–(H5) holds. This means $\tilde{\mathrm{M}}$ and $\underline{\mathrm{M}}$ are coupled upper and lower solutions of (1.1). Then part (ii) can be obtained by similar process to the proof of Lemma 2.1. □

Next we give the estimates of $u(x,t), v(x,t)$ and $w(x,t)$.

Proposition 2.1. *For $0 < \varepsilon \ll 1$, there exists $T \gg 1$ such that, when $0 < x < L$ and $t > T$, the solution $(u(x,t), v(x,t), w(x,t))$ of system (1.1) with Case I–III satisfies*

$$v(x,t) \le a_0 + \varepsilon,$$

$$\begin{cases} u(x,t) < \varepsilon, \\ w(x,t) < \varepsilon, \end{cases} \quad \text{for } D > br_m, \qquad \begin{cases} u(x,t) < \bar{u}(0), \\ w(x,t) < \frac{G}{D} + \varepsilon, \end{cases} \quad \text{for } D = br_m,$$

where $b = \frac{a_0+\varepsilon}{a_0+\varepsilon+K}$, $\bar{u}(0) = \sup\limits_{0<x<L} u_0(x)$, $G = (n_p + r_m Y_p b)\bar{u}(0)$.

Proof. Case I. The second function of (2.8) yields $v_t \le d_2 v_{xx} + D(a_0 - v)$.

Let

$$\begin{cases} \bar{v}_t = d_2\bar{v}_{xx} + D(a_0 - \bar{v}), \\ \bar{v}(0) = \sup\limits_{0<x<L} v_0(x), \end{cases} \tag{2.20}$$

hence $\bar{v} = a_0 - (a_0 - \bar{v}(0))e^{-Dt}$ is one solution to (2.20), and $\lim\limits_{t\to\infty} v = a_0$.

By comparison principles, for $0 < \varepsilon \ll 1$, there exists $T_1 \gg 1$ such that

$$v(x,t) \le a_0 + \varepsilon, \tag{2.21}$$

for $0 < x < L$ and $t > T_1$.

It follows from (2.21) and the first function of (2.8)

$$u_t \le d_1 u_{xx} + r_m \frac{u(a_0+\varepsilon)}{a_0+\varepsilon+K} - Du.$$

Let

$$b = \frac{a_0+\varepsilon}{a_0+\varepsilon+K} < 1,$$

and

$$\begin{cases} \bar{u}_t = d_1\bar{u}_{xx} + r_m \frac{\bar{u}(a_0+\varepsilon)}{a_0+\varepsilon+K} - D\bar{u}, \\ \bar{u}(0) = \sup\limits_{0<x<L} u_0(x). \end{cases} \tag{2.22}$$

One can see that $\bar{u} = \bar{u}(0)e^{(br_m - D)t}$ is one solution to (2.22), then

$$\lim_{t\to\infty} \bar{u} = \begin{cases} 0, & D > br_m, \\ \bar{u}(0), & D = br_m, \\ \infty, & D < br_m. \end{cases}$$

In fact, for any $t > 0$, $\bar{u} = \bar{u}(0)$ if $D = br_m$.

As a result, for $0 < \varepsilon \ll 1$, there exists $T_2 \gg 1$ such that

$$\begin{cases} u(x,t) < \varepsilon, & D > br_m, \\ u(x,t) \leq \bar{u}(0), & D = br_m, \end{cases} \tag{2.23}$$

with $0 < x < L$ and $t > T_2$.

For $D > br_m$, it is clear that $w_t \leq d_3 w_{xx} + \varepsilon(n_p + r_m Y_p b) - Dw$ from $u(x,t) < \varepsilon$ and the third equation of (2.8).

Denote $G_1 = n_p + r_m Y_p b$, and

$$\begin{cases} \bar{w}_t = d_1 \bar{w}_{xx} + \varepsilon(n_p + r_m Y_p b) - D\bar{w} = d_1 \bar{w}_{xx} + \varepsilon G_1 - D\bar{w}, \\ \bar{w}(0) = \sup\limits_{0<x<L} w_0(x), \end{cases} \tag{2.24}$$

then $\bar{w} = \frac{G_1}{D}\varepsilon - (\frac{G_1}{D}\varepsilon - \bar{w}(0))e^{-Dt}$ is one solution to (2.22). For simplicity, we rewrite $\bar{w} = \varepsilon_1 - (\varepsilon_1 - \bar{w}(0))e^{-Dt}$. Thus $\lim\limits_{t\to\infty} \bar{w} = 0$, which means there exists $T_3 \gg 1$ such that

$$w(x,t) < \varepsilon, \quad \text{if} \quad D > br_m, \tag{2.25}$$

for $0 < x < L$ and $t > T_3$.

For $D = br_m$, from $u(x,t) < \bar{u}(0)$, $v(x,t) \leq a_0 + \varepsilon$ and the third equation of (2.8), there holds

$$w_t \leq d_3 w_{xx} + n_p \bar{u}(0) + r_m Y_p b \bar{u}(0) - Dw = d_3 w_{xx} + \bar{u}(0)(n_p + r_m Y_p b) - Dw.$$

Let

$$G = (n_p + r_m Y_p b)\bar{u}(0),$$

and

$$\begin{cases} \breve{w}_t = d_1 \breve{w}_{xx} + \bar{u}(0)(n_p + r_m Y_p b) - D\breve{w}, \\ \breve{w}(0) = \sup\limits_{0<x<L} w_0(x). \end{cases} \tag{2.26}$$

It is obvious that $\breve{w} = \frac{G}{D} - (\frac{G}{D} - \breve{w}(0))e^{-Dt}$ is one solution to (2.22), which implies $\lim\limits_{t\to\infty} \breve{w} = \frac{G}{D}$. Then for $0 < \varepsilon \ll 1$, there exists $T_4 \gg 1$ such that

$$w(x,t) < \frac{G}{D} + \varepsilon, \quad \text{if} \quad D = br_m, \tag{2.27}$$

with $0 < x < L$ and $t > T_3$.

Let $T = \max\{T_1, T_2, T_3, T_4\}$, according to (2.21), (2.23), (2.25), (2.27), then we get Proposition 2.1 for Case I.

For Case II and Case III, the desired statements can be checked by the similar process. □

Proposition 2.2. *For $0 < \varepsilon \ll 1$, there exists $T \gg 1$ such that, when $0 < x < L$ and $t > T$, the solution $(u(x,t), v(x,t), w(x,t))$ of system (1.1) with Case I– III satisfies*

$$\begin{cases} v(x,t) > a_0 - \varepsilon, & \textit{for } D > br_m, \\ v(x,t) > a_0 - \frac{\breve{K}}{D} - \varepsilon, & \textit{for } D = br_m, \end{cases}$$

where $\breve{K} = (n_s + \frac{r_m}{Y_s} b)\bar{u}(0)$.

Proof. We take Case I as an example to verify Proposition 2.2 since proofs for the other two cases are similar.

For $D > br_m$, it is easy to see

$$v_t > d_2 v_{xx} + Da_0 - (n_s + \frac{r_m}{Y_s} b)\varepsilon - Dv,$$

from $u(x,t) < \varepsilon$ and the second equation of (2.8).

Let $\acute{K} = n_s + \frac{r_m}{Y_s} b$, and

$$\begin{cases} \underline{v}_t = d_2 \underline{v}_{xx} + Da_0 - (n_s + \frac{r_m}{Y_s} b)\varepsilon - D\underline{v}, \\ \underline{v}(0) = \inf\limits_{0<x<L} v_0(x). \end{cases} \tag{2.28}$$

Then $\underline{v} = a_0 - \frac{\acute{K}}{D}\varepsilon - (a_0 - \frac{\acute{K}}{D}\varepsilon - \underline{v}(0))e^{-Dt}$ solves (2.28), which implies $\lim\limits_{t\to\infty} \underline{v} = a_0$.

In view to comparison principles, for $0 < \varepsilon \ll 1$, there exists $T_5 \gg 1$ such that

$$a_0 - \varepsilon \le v(x,t), \quad \text{if} \quad D > br_m, \tag{2.29}$$

for $0 < x < L$ and $t > T_5$.

For $D = br_m$, $u(x,t) < \bar{u}(0)$ and the second equation of (2.8) yield

$$v_t > d_2 v_{xx} + Da_0 - (n_s + \frac{r_m}{Y_s} b)\bar{u}(0) - Dv.$$

Denote $\breve{K} = (n_s + \frac{r_m}{Y_s} b)\bar{u}(0)$, and

$$\begin{cases} \underline{v}_t = d_2 \underline{v}_{xx} + Da_0 - (n_s + \frac{r_m}{Y_s} b)\bar{u}(0) - D\underline{v}, \\ \underline{v}(0) = \inf\limits_{0<x<L} v_0(x). \end{cases} \tag{2.30}$$

One can find that $\underline{v} = a_0 - \frac{\breve{K}}{D} - (a_0 - \frac{\breve{K}}{D} - \underline{v}(0)e^{-Dt}$ is one solution to (2.30). Hence $\lim\limits_{t\to\infty} \underline{v} = a_0 - \frac{\breve{K}}{D}$.

Thus there exists $T_6 \gg 1$ such that

$$a_0 - \frac{\breve{K}}{D} - \varepsilon \le v(x,t), \quad \text{if} \quad D = br_m, \tag{2.31}$$

for $0 < x < L$ and $t > T_6$.

Let $T = \max\{T_5, T_6\}$, then we get the results. □

From Proposition 2.1 and Proposition 2.2, the following theorem can be deduced directly.

Theorem 2.1. *For Case I- III, the solution $(u(x,t), v(x,t), w(x,t))$ of (1.1) satisfies*

(i) if $D > br_m$, then $(u(x,t), v(x,t), w(x,t)) \to (0, a_0, 0)$ uniformly on $[0,L]$ as $t \to \infty$.

(ii) if $D = br_m$, then for $0 < \varepsilon \ll 1$, there exists $T \gg 1$ such that $0 \le u(x,t) < \bar{u}(0)$, $a_0 - \frac{\breve{K}}{D} - \varepsilon < v(x,t) < a_0 + \varepsilon$, $0 \le w(x,t) < \frac{G}{D} + \varepsilon$.

3. Attractor

Theorem 3.1. *Suppose* (2.7) *holds, then for any* $\mathrm{U}_0(x) \in \langle \Theta, \mathrm{M} \rangle$, *the solution* $\mathrm{U}(x,t)$ *of (1.1) satisfies*

$$\underline{\mathrm{U}}^{(\infty)} \leq \lim_{t\to\infty} \inf \mathrm{U(t,x)} \leq \lim_{t\to\infty} \sup \mathrm{U(t,x)} \leq \bar{\mathrm{U}}^{(\infty)}, \tag{3.1}$$

if Case I, or Case III with $d > (n_p + r_m Y_p)\frac{a_0}{n_s}$. $\underline{\mathrm{U}}^{(\infty)} = (\underline{u}^{(\infty)}, \underline{v}^{(\infty)}, \underline{w}^{(\infty)})$ *and* $\bar{\mathrm{U}}^{(\infty)} = (\bar{u}^{(\infty)}, \bar{v}^{(\infty)}, \bar{w}^{(\infty)})$ *refer to* (3.3) *and satisfy (3.4), (3.5).*

Proof. For Case I, by using $(\bar{u}^0, \bar{v}^0, \bar{w}^0) = (\frac{Da_0}{n_s}, a_0, d)$ and $(\underline{u}^0, \underline{v}^0, \underline{w}^0) = (0,0,0)$ as a pair of coupled initial iterations in the iteration process

$$\begin{cases} -d_1 \bar{u}_{xx}^{(m)} + K_1 \bar{u}^{(m)} = K_1 \bar{u}^{(m-1)} + f_1(\bar{u}^{(m-1)}, \bar{v}^{(m-1)}), \\ -d_2 \bar{v}_{xx}^{(m)} + K_2 \bar{v}^{(m)} = K_2 \bar{v}^{(m-1)} + f_2(\bar{v}^{(m-1)}, \underline{u}^{(m-1)}), \\ -d_3 \bar{w}_{xx}^{(m)} + K_3 \bar{w}^{(m)} = K_3 \bar{w}^{(m-1)} + f_3(\bar{w}^{(m-1)}, \bar{u}^{(m-1)}, \bar{v}^{(m-1)}), \\ -d_1 \underline{u}_{xx}^{(m)} + K_1 \underline{u}^{(m)} = K_1 \underline{u}^{(m-1)} + f_1(\underline{u}^{(m-1)}, \underline{v}^{(m-1)}), \\ -d_2 \underline{v}_{xx}^{(m)} + K_2 \underline{v}^{(m)} = K_2 \underline{v}^{(m-1)} + f_2(\underline{v}^{(m-1)}, \bar{u}^{(m-1)}), \\ -d_3 \underline{w}_{xx}^{(m)} + K_3 \underline{w}^{(m)} = K_3 \underline{w}^{(m-1)} + f_3(\underline{w}^{(m-1)}, \underline{u}^{(m-1)}, \underline{v}^{(m-1)}), \\ \bar{u}_x^{((m))} = \bar{v}_x^{((m))} = \bar{w}_x^{((m))} = 0, \\ \underline{u}_x^{((m))} = \underline{v}_x^{((m))} = \underline{w}_x^{((m))} = 0, \end{cases} \tag{3.2}$$

where K_i is a Lipschitz constant of $f(\cdot, \mathrm{U})$ in $\langle \underline{\mathrm{U}}, \bar{\mathrm{U}} \rangle$.

It follows from [17, Lemma 8.10.1] that the corresponding sequences $\bar{\mathrm{U}}^{(m)} \equiv \{\bar{u}^{(m)}, \bar{v}^{(m)}, \bar{u}^{(w)}\}$ and $\underline{\mathrm{U}}^{(m)} \equiv \{\underline{u}^{(m)}, \underline{v}^{(m)}, \underline{u}^{(w)}\}$ possess the monotone property

$$\underline{\mathrm{U}} \leq \underline{\mathrm{U}}^{(m)} \leq \underline{\mathrm{U}}^{(m+1)} \leq \bar{\mathrm{U}}^{(m+1)} \leq \bar{\mathrm{U}}^{(m)} \leq \bar{\mathrm{U}},$$

and the limits

$$\lim_{m\to\infty} \underline{\mathrm{U}}^{(m)} = \underline{\mathrm{U}}^{(\infty)}, \quad \lim_{m\to\infty} \bar{\mathrm{U}}^{(m)} = \bar{\mathrm{U}}^{(\infty)}, \tag{3.3}$$

exist and satisfy

$$\begin{cases} d_1 u_{xx} + f_1(u, \underline{v}^{(\infty)}) = 0, & x \in (0,L), \\ d_2 v_{xx} + f_2(v, \bar{u}^{(\infty)}) = 0, & x \in (0,L), \\ d_3 w_{xx} + f_3(w, \underline{u}^{(\infty)}, \underline{v}^{(\infty)}) = 0, & x \in (0,L), \\ u_x = v_x = w_x = 0, & x = 0, L, \end{cases} \tag{3.4}$$

and

$$\begin{cases} d_1 u_{xx} + f_1(u, \bar{v}^{(\infty)}) = 0, & x \in (0,L), \\ d_2 v_{xx} + f_2(v, \underline{u}^{(\infty)}) = 0, & x \in (0,L), \\ d_3 w_{xx} + f_3(w, \bar{u}^{(\infty)}, \bar{v}^{(\infty)}) = 0, & x \in (0,L), \\ u_x = v_x = w_x = 0 & x = 0, L, \end{cases} \tag{3.5}$$

respectively.

Thanks to Theorem 2.1 in [18], for any $\mathrm{U}_0(x) \in \langle \Theta, \mathrm{M} \rangle$, the solution $\mathrm{U}(x,t)$ of (1.1) satisfies (3.1). That's to say, $\langle \underline{\mathrm{U}}^{(\infty)}, \bar{\mathrm{U}}^{(\infty)} \rangle$ is an attractor of (1.1) if $\mathrm{U}_0(x) \in \langle \Theta, \tilde{\mathrm{M}} \rangle$.

For Case III, just change (3.2), (3.4) and (3.5) as

$$\begin{cases} -d_1\bar{u}_{xx}^{(m)} + K_1\bar{u}^{(m)} = K_1\bar{u}^{(m-1)} + f_1(\bar{u}^{(m-1)}, \bar{v}^{(m-1)}, \underline{w}^{(m-1)}), \\ -d_2\bar{v}_{xx}^{(m)} + K_2\bar{v}^{(m)} = K_2\bar{v}^{(m-1)} + f_2(\bar{v}^{(m-1)}, \underline{u}^{(m-1)}, \bar{w}^{(m-1)}), \\ -d_3\bar{w}_{xx}^{(m)} + K_3\bar{w}^{(m)} = K_3\bar{w}^{(m-1)} + f_3(\bar{w}^{(m-1)}, \bar{u}^{(m-1)}, \bar{v}^{(m-1)}), \\ -d_1\underline{u}_{xx}^{(m)} + K_1\underline{u}^{(m)} = K_1\underline{u}^{(m-1)} + f_1(\underline{u}^{(m-1)}, \underline{v}^{(m-1)}, \bar{w}^{(m-1)}), \\ -d_2\underline{v}_{xx}^{(m)} + K_2\underline{v}^{(m)} = K_2\underline{v}^{(m-1)} + f_2(\underline{v}^{(m-1)}, \bar{u}^{(m-1)}, \underline{w}^{(m-1)}), \\ -d_3\underline{w}_{xx}^{(m)} + K_3\underline{w}^{(m)} = K_3\underline{w}^{(m-1)} + f_3(\underline{w}^{(m-1)}, \underline{u}^{(m-1)}, \underline{v}^{(m-1)}), \\ \bar{u}_x^{((m))} = \bar{v}_x^{((m))} = \bar{w}_x^{((m))} = 0, \\ \underline{u}_x^{((m))} = \underline{v}_x^{((m))} = \underline{w}_x^{((m))} = 0, \end{cases}$$

$$\begin{cases} d_1u_{xx} + f_1(u, \underline{v}^{(\infty)}, \bar{w}^{(\infty)}) = 0, & x \in (0,L), \\ d_2v_{xx} + f_2(v, \bar{u}^{(\infty)}, \underline{w}^{(\infty)}) = 0, & x \in (0,L), \\ d_3w_{xx} + f_3(w, \underline{u}^{(\infty)}, \underline{v}^{(\infty)}) = 0, & x \in (0,L), \\ u_x = v_x = w_x = 0, & x = 0, L, \end{cases}$$

and

$$\begin{cases} d_1u_{xx} + f_1(u, \bar{v}^{(\infty)}, \underline{w}^{(\infty)}) = 0, & x \in (0,L), \\ d_2v_{xx} + f_2(v, \underline{u}^{(\infty)}, \bar{w}^{(\infty)}) = 0, & x \in (0,L), \\ d_3w_{xx} + f_3(w, \bar{u}^{(\infty)}, \bar{v}^{(\infty)}) = 0, & x \in (0,L), \\ u_x = v_x = w_x = 0, & x = 0, L, \end{cases}$$

respectively, we can get the desired results by the similar process. □

Theorem 3.2. *For Case II, the following statements are valid.*

(i) Suppose either (H1) *or* (H2) *holds, then there is an attractor for any any* $\mathrm{U}_0(x) \in \langle \Theta, \mathrm{S} \rangle$.

(ii) Suppose one of (H3)–(H5) *holds, then for any* $\mathrm{U}_0(x) \in \langle \underline{\mathrm{M}}, \tilde{\mathrm{M}} \rangle$*, the solution* $\mathrm{U}(x,t)$ *of (1.1) satisfies*

$$\underline{\mathrm{U}}^{(\infty)} \le \lim_{t\to\infty} \inf \mathrm{U}(t,x) \le \lim_{t\to\infty} \sup \mathrm{U} \le \bar{\mathrm{U}}^{(\infty)}, \tag{3.6}$$

where $\underline{\mathrm{U}}^{(\infty)} = (\underline{u}^{(\infty)}, \underline{v}^{(\infty)}, \underline{w}^{(\infty)})$ *and* $\bar{\mathrm{U}}^{(\infty)} = (\bar{u}^{(\infty)}, \bar{v}^{(\infty)}, \bar{w}^{(\infty)})$ *refer to (3.7) and satisfy* (3.8)*,* (3.9)*.*

Proof. Just choosing $(\bar{u}^0, \bar{v}^0, \bar{w}^0) = (\frac{Da_0}{n_s}, a_0, (n_p + r_mY_p)\frac{a_0}{n_s})$, one can verify part (i) by the similar process to the proof of Theorem 3.1.

Part (ii). By using $(\bar{u}^0,\bar{v}^0,\bar{w}^0)=(D\frac{a_0-s}{n_s+\frac{r_m}{Y_s}},a_0,\frac{a_0-s}{n_s+\frac{r_m}{Y_s}}(n_p+Y_p r_m))$ and $(\underline{u}^0,\underline{v}^0,\underline{w}^0)=(0,s,0)$, as a pair of coupled iterations in the iteration process

$$\begin{cases} -d_1\bar{u}^{(m)}_{xx}+\tilde{K}_1\bar{u}^{(m)}=\tilde{K}_1\bar{u}^{(m-1)}+f_1(\bar{u}^{(m-1)},\underline{v}^{(m-1)}),\\ -d_2\bar{v}^{(m)}_{xx}+\tilde{K}_2\bar{v}^{(m)}=\tilde{K}_2\bar{v}^{(m-1)}+f_2(\bar{v}^{(m-1)},\underline{u}^{(m-1)}),\\ -d_3\bar{w}^{(m)}_{xx}+\tilde{K}_3\bar{w}^{(m)}=\tilde{K}_3\bar{w}^{(m-1)}+f_3(\bar{w}^{(m-1)},\bar{u}^{(m-1)},\underline{v}^{(m-1)}),\\ -d_1\underline{u}^{(m)}_{xx}+\tilde{K}_1\underline{u}^{(m)}=\tilde{K}_1\underline{u}^{(m-1)}+f_1(\underline{u}^{(m-1)},\bar{v}^{(m-1)}),\\ -d_2\underline{v}^{(m)}_{xx}+\tilde{K}_2\underline{v}^{(m)}=\tilde{K}_2\underline{v}^{(m-1)}+f_2(\underline{v}^{(m-1)},\bar{u}^{(m-1)}),\\ -d_3\underline{w}^{(m)}_{xx}+\tilde{K}_3\underline{w}^{(m)}=\tilde{K}_3\underline{w}^{(m-1)}+f_3(\underline{w}^{(m-1)},\underline{u}^{(m-1)},\bar{v}^{(m-1)}),\\ \bar{u}^{((m))}_x=\bar{v}^{((m))}_x=\bar{w}^{((m))}_x=0,\\ \underline{u}^{((m))}_x=\underline{v}^{((m))}_x=\underline{w}^{((m))}_x=0, \end{cases}$$

where $\tilde{K}_i$ is a Lipschitz constant of $f_i(\cdot,\mathrm{U})$ in $\langle\underline{\mathrm{U}},\bar{\mathrm{U}}\rangle$. Then sequences $\bar{\mathrm{U}}^{(m)}\equiv\{\bar{u}^{(m)},\bar{v}^{(m)},\bar{u}^{(w)}\}$ and $\underline{\mathrm{U}}^{(m)}\equiv\{\underline{u}^{(m)},\underline{v}^{(m)},\underline{u}^{(w)}\}$ possess the monotone property

$$\underline{\mathrm{U}}\le\underline{\mathrm{U}}^{(m)}\le\underline{\mathrm{U}}^{(m+1)}\le\bar{\mathrm{U}}^{(m+1)}\le\bar{\mathrm{U}}^{(m)}\le\bar{\mathrm{U}},$$

and the limits

$$\lim_{m\to\infty}\underline{\mathrm{U}}^{(m)}=\underline{\mathrm{U}}^{(\infty)},\quad \lim_{m\to\infty}\bar{\mathrm{U}}^{(m)}=\bar{\mathrm{U}}^{(\infty)},\tag{3.7}$$

exist and satisfy

$$\begin{cases} d_1u_{xx}+f_1(u,\bar{v}^{(\infty)})=0, & x\in(0,L),\\ d_2v_{xx}+f_2(v,\bar{u}^{(\infty)})=0, & x\in(0,L),\\ d_3w_{xx}+f_3(w,\underline{u}^{(\infty)},\bar{v}^{(\infty)})=0, & x\in(0,L),\\ u_x=v_x=w_x=0, & x=0,L, \end{cases}\tag{3.8}$$

$$\begin{cases} d_1u_{xx}+f_1(u,\underline{v}^{(\infty)})=0, & x\in(0,L),\\ d_2v_{xx}+f_2(v,\underline{u}^{(\infty)})=0, & x\in(0,L),\\ d_3w_{xx}+f_3(w,\bar{u}^{(\infty)},\underline{v}^{(\infty)})=0, & x\in(0,L),\\ u_x=v_x=w_x=0, & x=0,L, \end{cases}\tag{3.9}$$

respectively.

Again by Theorem 2.1 in [18], for any $\mathrm{U}_0(x)\in\langle\underline{\mathrm{M}},\tilde{\mathrm{M}}\rangle$, the solution $\mathrm{U}(x,t)$ of (1.1) satisfies (3.6). $\square$

4. Stability and bifurcation analysis

This section is devoted to the stability and bifurcation analysis at the steady states. The steady state problem corresponding to (1.1) is considered as follows

$$\begin{cases} d_1 u_{xx} + u(r - D) = 0, & x \in (0, L), \\ d_2 v_{xx} + D(a_0 - v) - u(n_s + \frac{r}{Y_s}) = 0, & x \in (0, L), \\ d_3 w_{xx} + u(n_p + Y_p r) - Dw = 0, & x \in (0, L), \\ u_x = v_x = w_x = 0, & x = 0, L. \end{cases} \tag{4.1}$$

As noted in [9], the nonnegative solutions to (4.1) are classified by four types:

(i) trivial nonnegative solution: $(0, 0, 0)$, which is a trivial steady state of (1.1);
(ii) weak semitrivial solutions: $(\tilde{u}, 0, 0), (0, \tilde{v}, 0), (0, 0, \tilde{w})$, which are known as weak semitrivial steady states of (1.1);
(iii) strong semitrivial solutions: $(\breve{u}, \breve{v}, 0), (\hat{u}, 0, \hat{w}), (0, \grave{v}, \grave{w})$, which are referred to strong semitrivial steady states of (1.1);
(iv) positive solutions: (u^*, v^*, w^*), which is a positive steady state of (1.1).

The second and third types are collectively called semitrivial solutions. We stress that all of $\tilde{u}, \tilde{v}, \tilde{w}, \breve{u}, \breve{v}, u^*, v^*, w^*$ are nonnegative and not identically zero.

For semitrivial steady states, the following statements hold true.

Theorem 4.1. *For Case I- III, system (1.1) has no trivial steady state and admits the unique semitrivial steady state* $E = (0, a_0, 0)$.

Proof. It is clear that (1.1) has no trivial steady state, and easy to see that there are no such weak semitrivial solutions as $(0, 0, \tilde{w})$ and $(\tilde{u}, 0, 0)$. So we only determine the solution $(0, \tilde{v}, 0)$, which satisfies

$$\begin{cases} d_2 v_{xx} + D(a_0 - v) = 0, \ x \in (0, L), \\ v_x(0) = v_x(L) = 0. \end{cases} \tag{4.2}$$

Simple calculations yield that only $\tilde{v} = a_0$ solves (4.2), which indicates that $(0, a_0, 0)$ is one solution to (4.1). To determine the strong semitrivial solutions, we solve

$$\begin{cases} d_1 u_{xx} + r_m \frac{uv}{v+k} - Du = 0, & x \in (0, L), \\ d_2 v_{xx} + D(a_0 - v) - n_s u - \frac{r_m}{Y_s} \frac{uv}{v+K} = 0, & x \in (0, L), \\ n_p u + r_m Y_p \frac{uv}{v+k} = 0, & x \in (0, L), \\ u_x = v_x = 0, & x = 0, L, \end{cases} \tag{4.3}$$

$$\begin{cases} d_2 v_{xx} + D(a_0 - v) = 0, & x \in (0, L), \\ d_3 w_{xx} - Dw = 0, & x \in (0, L), \\ v_x = w_x = 0, & x = 0, L, \end{cases} \tag{4.4}$$

and

$$\begin{cases} d_1 u_{xx} - Du = 0, & x \in (0, L), \\ Da_0 - n_s u = 0, & x \in (0, L), \\ d_3 w_{xx} + n_p u - Dw = 0, & x \in (0, L), \\ u_x = w_x = 0, & x = 0, L, \end{cases} \tag{4.5}$$

respectively.

By some simple calculations, we get none of (4.3)–(4.5) has solution, which indicates that there is no strong semitrivial solution to (4.1). Therefore, system (1.1) has one and only one semitrivial steady state $E = (0, a_0, 0)$. □

Theorem 4.2. *For Case I or III, the following statements hold true.*

(i) Suppose $D > r_m \frac{a_0}{a_0+K}$, then E is locally asymptotically stable.

(ii) Suppose $D < r_m \frac{a_0}{a_0+K}$, then

(a) E is unstable if $d_1 \mu_1 > r_m \frac{a_0}{a_0+K} - D$;

(b) let N_1 be the largest integer such that $d_1 \mu_n \leq r_m \frac{a_0}{a_0+K} - D$, then for $n \geq N_1$, (1.1) undergoes the steady state bifurcation at E if $d_1 \mu_1 \leq r_m \frac{a_0}{a_0+K} - D$.

(iii) Suppose $D = r_m \frac{a_0}{a_0+K}$, then for $n = 0$, system (1.1) undergoes the steady state bifurcation at E.

Proof. The linearized operator of the steady state system (4.1) evaluated at E is

$$\mathcal{L}(E) = \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + f_{1u}(E) & f_{1v}(E) & f_{1w}(E) \\ f_{2u}(E) & d_2 \frac{\partial^2}{\partial x^2} + f_{2v}(E) & f_{2w}(E) \\ f_{3u}(E) & f_{3v}(E) & d_3 \frac{\partial^2}{\partial x^2} + f_{3w}(E) \end{pmatrix}, \tag{4.6}$$

where

$$\begin{aligned} &f_{1u}(E) = r_m \tfrac{a_0}{a_0+K} - D, \quad f_{1v}(E) = 0, \quad f_{1w}(E) = 0, \\ &f_{2u}(E) = -n_s - \tfrac{r_m}{Y_s} \tfrac{a_0}{a_0+K}, \ f_{2v}(E) = -D, \ f_{2w}(E) = 0, \\ &f_{3u}(E) = n_p + Y_p r_m \tfrac{a_0}{a_0+K}, \ f_{3v}(E) = 0, \quad f_{3w}(E) = -D. \end{aligned}$$

It is known that the eigenvalue problem

$$\begin{cases} \varphi_{xx} = -\mu\varphi, \ x \in (0, L), \\ \varphi_x = 0, \qquad x = 0, L, \end{cases} \tag{4.7}$$

has eigenvalues $\mu_n = (\frac{n\pi}{L})^2$ and $\varphi_n(x) = \cos \frac{n\pi}{L} x$ are the corresponding eigenfunctions, $n = 0, 1, 2, 3, \ldots$

Let

$$\begin{pmatrix} \phi \\ \psi \\ \zeta \end{pmatrix} = \sum_{n=0}^{n=\infty} \cos \frac{n\pi}{L} x \begin{pmatrix} a_n \\ b_n \\ c_n \end{pmatrix}, \tag{4.8}$$

be the eigenvalue function for $\mathcal{L}$ with eigenvalue λ, that is

$$\mathcal{L}\begin{pmatrix}\phi\\ \psi\\ \zeta\end{pmatrix}=\lambda\begin{pmatrix}\phi\\ \psi\\ \zeta\end{pmatrix}. \tag{4.9}$$

Employing some straightforward analysis, one can get

$$\mathcal{L}_n\begin{pmatrix}a_n\\ b_n\\ c_n\end{pmatrix}=\lambda\begin{pmatrix}a_n\\ b_n\\ c_n\end{pmatrix}, \tag{4.10}$$

where

$$\mathcal{L}_n(E)=\begin{pmatrix}-d_1\mu_n+r_m\frac{a_0}{a_0+K}-D & 0 & 0\\ n_s+\frac{r_m}{Y_s}\frac{a_0}{a_0+K} & -d_2\mu_n-D & 0\\ n_p+Y_pr_m\frac{a_0}{a_0+K} & 0 & -d_3\mu_n-D\end{pmatrix}. \tag{4.11}$$

Thus the eigenvalues of $\mathcal{L}(E)$ are given by the eigenvalues of $\mathcal{L}_n(E)$, and the characteristic matrix of $\mathcal{L}_n(E)$ is

$$\lambda I-\mathcal{L}_n(E)=\begin{pmatrix}\lambda+d_1\mu_n-r_m\frac{a_0}{a_0+K}+D & 0 & 0\\ -(n_s+\frac{r_m}{Y_s}\frac{a_0}{a_0+K}) & \lambda+d_2\mu_n+D & 0\\ -(n_p+Y_pr_m\frac{a_0}{a_0+K}) & 0 & \lambda+d_3\mu_n+D\end{pmatrix}, \tag{4.12}$$

where I is the identity matrix. Then the corresponding characteristic equation is

$$(\lambda+d_3\mu_n+D)(\lambda+d_1\mu_n-r_m\frac{a_0}{a_0+K}+D)(\lambda+d_2\mu_n+D)=0. \tag{4.13}$$

It is easy to find $\lambda_1=-(d_2\mu_n+D)<0$, $\lambda_2=-(d_3\mu_n+D)<0$ for $n\geq 0$. We discuss $\lambda_3=-d_1\mu_n+r_m\frac{a_0}{a_0+K}-D$ in the following three cases.

(I) $D>r_m\frac{a_0}{a_0+K}$, it is clear that $\lambda_3<0$ for any $n\geq 0$.

(II) $D<r_m\frac{a_0}{a_0+K}$, if $d_1\mu_1>r_m\frac{a_0}{a_0+K}-D$, then $\lambda_3<0$ for any $n\geq 1$, but $\lambda_3>0$ for $n=0$; if $d_1\mu_1\leq r_m\frac{a_0}{a_0+K}-D$, let N_1 be the largest integer such that $d_1\mu_n\leq r_m\frac{a_0}{a_0+K}-D$, then for $n\geq N_1$, one can well define

$$d_1^n=\frac{r_m\frac{a_0}{a_0+K}-D}{\mu_n},$$

such that $\lambda_3=0$ for $d_1=d_1^n$.

(III) $D=r_m\frac{a_0}{a_0+K}$, it is obvious $\lambda_3=0$ for $n=0$.

Finally we get the desired results by [25] and Theorem 5.1.1 in [13]. □

According to the similar process to Theorem 4.2, the following statements can be achieved.

Theorem 4.3. *For Case II, the following statements hold true.*

(i) *Suppose* $D > r_m \frac{a_0}{a_0+K}(1-\frac{a_0}{c})$, *then* E *is locally asymptotically stable.*

(ii) *Suppose* $D < r_m \frac{a_0}{a_0+K}(1-\frac{a_0}{c})$, *then*

(a) E *is unstable if* $d_1\mu_1 > r_m \frac{a_0}{a_0+K}(1-\frac{a_0}{c}) - D$;

(b) *let* N_2 *be the largest integer such that* $d_1\mu_n \le r_m \frac{a_0}{a_0+K}(1-\frac{a_0}{c}) - D$, *then for* $n \ge N_2$, *system (1.1) undergoes the steady state bifurcation at* E *if* $d_1\mu_1 \le r_m \frac{a_0}{a_0+K}(1-\frac{a_0}{c}) - D$.

(iii) *Suppose* $D = r_m \frac{a_0}{a_0+K}(1-\frac{a_0}{c})$, *for* $n = 0$, *system (1.1) undergoes the steady state bifurcation at* E.

Next we concentrate on the constant positive steady states of (1.1). It is obvious that $r_m > D$ and $v < a_0$ are necessary if (1.1) has constant positive steady states.

4.1. Case I

Theorem 4.4. *If* $r_m > D$ *and* $a_0 > \frac{DK}{r_m-D}$, *then (1.1) has only one constant positive steady state* $E_0 = (u^*, v^*, w^*)$, *and* E_0 *is locally asymptotically stable, where*

$$u^* = \frac{D(a_0 - v^*)}{n_s + \frac{D}{Y_s}}, v^* = \frac{DK}{r_m - D}, w^* = (\frac{n_p}{D} + Y_p)u^*. \tag{4.14}$$

Proof. Solving the following equations

$$\begin{cases} r_m \frac{v}{v+k} - D = 0, \\ D(a_0 - v) - n_s u - \frac{r_m}{Y_s}\frac{uv}{v+K} = 0, \\ n_p u + Y_p r_m \frac{uv}{v+k} - Dw = 0, \end{cases} \tag{4.15}$$

we can get $E_0 = (u^*, v^*, w^*)$ is the only constant positive solution to (4.1) if $r_m > D$ and $a_0 > \frac{DK}{r_m-D}$.

Now we show the stability of E_0. The linearized operator of the steady state system (4.1) evaluated at E_0 is

$$\mathcal{L}(E_0) = \begin{pmatrix} d_1\frac{\partial^2}{\partial x^2} + f_{1u}(E_0) & f_{1v}(E_0) & f_{1w}(E_0) \\ f_{2u}(E_0) & d_2\frac{\partial^2}{\partial x^2} + f_{2v}(E_0) & f_{2w}(E_0) \\ f_{3u}(E_0) & f_{3v}(E_0) & d_3\frac{\partial^2}{\partial x^2} + f_{3w}(E_0) \end{pmatrix}, \tag{4.16}$$

where

$$\begin{aligned} &f_{1u}(E_0) = 0, && f_{1v}(E_0) = r_m K\frac{u^*}{(v^*+K)^2}, \ f_{1w}(E_0) = 0, \\ &f_{2u}(E_0) = -n_s - \frac{D}{Y_s}, && f_{2v}(E_0) = -D - \frac{f_{1v}(E_0)}{Y_s}, \ f_{2w}(E_0) = 0, \\ &f_{3u}(E_0) = n_p + Y_p D, && f_{3v}(E_0) = Y_p f_{1v}(E_0), \quad f_{3w}(E_0) = -D. \end{aligned}$$

By the proof of Theorem 4.2, one can see the eigenvalues of $\mathcal{L}(E_0)$ can be given by the eigenvalues of the following matrix

$$\mathcal{L}_n(E_0) = \begin{pmatrix} -d_1\mu_n & r_m K\frac{u^*}{(v^*+K)^2} & 0 \\ -n_s - \frac{D}{Y_s} & -d_2\mu_n - D - r_m K\frac{u^*}{Y_s(v^*+K)^2} & 0 \\ n_p + Y_p D & Y_p r_m K\frac{u^*}{(v^*+K)^2} & -d_3\mu_n - D \end{pmatrix}.$$

Some calculations yield the characteristic equation

$$(\lambda + d_3\mu_n + D)(\lambda^2 + A_n(E)\lambda + B_n(E)) = 0, \tag{4.17}$$

where

$$\begin{cases} A_n(E) = d_1\mu_n + d_2\mu_n + D + r_m K \frac{u^*}{Y_s(v^*+K)^2}, \\ B_n(E) = d_1\mu_n(d_2\mu_n + D + r_m K \frac{u^*}{Y_s(v^*+K)^2}) + r_m K \frac{u^*}{(v^*+K)^2}(n_s + \frac{D}{Y_s}). \end{cases} \tag{4.18}$$

One can find $\lambda_1 = -(d_3\mu_n + D) < 0$, and the other two eigenvalues of $\mathcal{L}_n(E_0)$ are the roots of $\lambda^2 + A_n(E)\lambda + B_n(E) = 0$. It follows from $\mu_n \geq 0$ that

$$A_n(E) > 0, B_n(E) > 0,$$

if $r_m > D$ and $a_0 > \frac{DK}{r_m - D}$. Therefore, three eigenvalues all have negative real parts, which leads to the desired results by Theorem 5.1.1 in [13]. □

4.2. Case II

Lemma 4.1. *System (1.1) has two constant positive steady states $E_1 = (u_1^*, v_1^*, w_1^*)$ and $E_2 = (u_2^*, v_2^*, w_2^*)$ if $r_m > D$, $a_0 > \max\{v_1^*, v_2^*\}$ and*

$$(r_m - D)^2 \geq \frac{4r_m DK}{c}, \tag{4.19}$$

where

$$u_1^* = \frac{D(a_0 - v_1^*)}{n_s + \frac{D}{Y_s}}, v_1^* = \frac{c(r_m - D + \sqrt{\Delta})}{2r_m}, w_1^* = (n_p + Y_p D)\frac{a_0 - v_1^*}{n_s + \frac{D}{Y_s}}, \tag{4.20}$$

$$u_2^* = \frac{D(a_0 - v_2^*)}{n_s + \frac{D}{Y_s}}, v_2^* = \frac{c(r_m - D - \sqrt{\Delta})}{2r_m}, w_2^* = (n_p + Y_p D)\frac{a_0 - v_2^*}{n_s + \frac{D}{Y_s}}, \tag{4.21}$$

$$\Delta = (r_m - D)^2 - \frac{4r_m DK}{c}.$$

Particularly, $E_1 = E_2$ for $(r_m - D)^2 = \frac{4r_m DK}{c}$.

Proof. Suppose (u^*, v^*, w^*) is a constant positive solution of (4.1), then it satisfies

$$\begin{cases} r_m \frac{v}{v+K}(1 - \frac{v}{c}) = D, \\ D(a_0 - v) - u(n_s + \frac{D}{Y_s}) = 0, \\ u(n_p + Y_p D) - Dw = 0. \end{cases} \tag{4.22}$$

It follows from straightforward calculations that, for $r_m > D$ and $(r_m - D)^2 \geq \frac{4r_m DK}{c}$, the first equation of (4.22) has two positive solutions

$$v_{1,2} = \frac{c(r_m - D \pm \sqrt{\Delta})}{2r_m}, \tag{4.23}$$

where $\Delta = (r_m - D)^2 - \frac{4r_m DK}{c}$.

Combining (4.23) with (4.22), one get the constant positive solution $E_i = (u^*, v^*, w^*)$ to (4.1) if $a_0 > v_i^*$, where

$$u_i^* = \frac{D(a_0 - v_i^*)}{n_s + \frac{D}{Y_s}}, v_i^* = \frac{c(r_m - D \pm \sqrt{\Delta})}{2r_m}, w_i^* = (n_p + Y_p D)\frac{a_0 - v_i^*}{n_s + \frac{D}{Y_s}}, \quad i = 1, 2,$$

which completes the proof of part (ii) in Lemma 4.1. □

Lemma 4.2. *r_v is monotone decrease strictly with respect to v, and*

$$\begin{cases} 0 < r_v < \frac{r_m}{K}, & 0 < v < s, \\ r_v = 0, & v = s, \\ r_v < 0, & v > s, \end{cases} \tag{4.24}$$

where s is in the form of (2.1).

Proof. It follows from $r = r_m \frac{v}{v+K}(1 - \frac{v}{c})$ that

$$r_v = \frac{r_m}{c(v+K)^2}(-v^2 - 2vK + cK), \tag{4.25}$$

and

$$r_{vv} = -\frac{2r_m(cK + K^2)}{c(v+K)^3} < 0. \tag{4.26}$$

Therefore, r_v is monotone decrease strictly for $v \geq 0$, and (4.24) can be verified directly. □

Theorem 4.5. *For $i = 1, 2$, the following statements are valid.*

(i) If $0 < v_i^* < s$, then E_i is locally asymptotically stable.

(ii) If $v_i^* > s$, choosing d_2 as the bifurcation parameter, then

(a) for any $d_2 \geq 0$, system (1.1) *doesn't undergo Hopf bifurcation at E_i,*

(b) for $Y_s D > -u_i^* r_v(E_i)$, let N be the largest positive integer such that

$$d_1[Y_s D + u_i^* r_v(E_i)]\mu_n < -u_i^* r_v(E_i)(Y_s n_s + D). \tag{4.27}$$

Assume $d_2^{n_1} \neq d_2^{n_2}$ whenever $n_1 \neq n_2$, $1 \leq n_1, n_2 \leq N$, then for $1 \leq n \leq N$, system (1.1) *undergoes the steady state bifurcation at E_i, where*

$$d_2^n = \frac{-u_i^* r_v(E_i)(Y_s n_s + D) - [Y_s D + u_i^* r_v(E_i)]d_1\mu_n}{Y_s d_1 \mu_n^2}, \tag{4.28}$$

(c) for $Y_s D \leq -u_i^* r_v(E_i)$, assume $d_2^{n_1} \neq d_2^{n_2}$ whenever $n_1 \neq n_2$, $n_1, n_2 \geq 1$, then for $n \geq 1$, system (1.1) *undergoes the steady state bifurcation at E_i, where d_2^n is given by* (4.28),

(iii) If $v_i^* = s$, then the steady state bifurcation occurs for $n = 0$.

Proof. Part (i). Since $r = r_m \frac{v}{v+K}(1 - \frac{v}{c})$, the linearized operator of system (4.1) evaluated at $E_i = (u_i^*, v_i^*, w_i^*)$ is

$$\mathcal{L}(E_i) = \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + f_{1u}(E_i) & f_{1v}(E_i) & f_{1w}(E_i) \\ f_{2u}(E_i) & d_2 \frac{\partial^2}{\partial x^2} + f_{2v}(E_i) & f_{2w}(E_i) \\ f_{3u}(E_i) & f_{3v}(E_i) & d_3 \frac{\partial^2}{\partial x^2} + f_{3w}(E_i) \end{pmatrix}, \tag{4.29}$$

where

$$\begin{aligned}
&f_{1u}(E_i)=0, && f_{1v}(E_i)=u_i^* r_v(E_i), && f_{1w}(E_i)=0,\\
&f_{2u}(E_i)=-n_s-\tfrac{D}{Y_s}, && f_{2v}(E_i)=-D-u_i^*\tfrac{r_v(E_i)}{Y_s}, && f_{2w}(E_i^*)=0,\\
&f_{3u}(E_i)=n_p+Y_pD, && f_{3v}(E_i)=u_i^*Y_pr_v(E_i), && f_{3w}(E_i)=-D,\\
&r_v(E_i)=r_m\tfrac{(-(v_i^*)^2-2v_i^*K+cK)}{c(v_i^*+K)^2}.
\end{aligned}$$

By the similar process to the proof of Theorem 4.2, the eigenvalues of $\mathcal{L}(E_i)$ are given by the eigenvalues of the following matrix

$$\mathcal{L}_n(E_i)=\begin{pmatrix} -d_1\mu_n & u_i^*r_v(E_i) & 0\\ -n_s-\frac{D}{Y_s} & -d_2\mu_n-D-u_i^*\frac{r_v(E_i)}{Y_s} & 0\\ n_p+Y_pD & u_i^*Y_pr_v(E_i) & -d_3\mu_n-D \end{pmatrix}, \tag{4.30}$$

and the characteristic equation is

$$(\lambda+d_3\mu_n+D)(\lambda^2+A_n(E_i^*)\lambda+B_n(E_i))=0, \tag{4.31}$$

where

$$\begin{cases} A_n(E_i)=d_1\mu_n+d_2\mu_n+D+\frac{u_i^*r_v(E_i)}{Y_s},\\ B_n(E_i)=d_1\mu_n(d_2\mu_n+D)+u_i^*r_v(E_i)(\frac{d_1\mu_n}{Y_s}+n_s+\frac{D}{Y_s}). \end{cases} \tag{4.32}$$

It is easy to see $\lambda_1=-(d_3\mu_n+D)<0$, and the other two eigenvalues are determined by $\lambda^2+A_n(E_i)\lambda+B_n(E_i)=0$. Then for $n\geq 0$, in view to part (ii) of Lemma 4.2, it is clear that

$$A_n(E_i)>0, B_n(E_i)>0,$$

if $0<v_i^*<s$, which ends the proof of Part (i).

Part (ii). (a). By an indirect argument, we suppose there exists some $d_2^H\geq 0$ such that system (1.1) undergoes the Hopf bifurcation at (d_2^H,E_i). Then we have

$$A_n(d_2^H,E_i)=d_1\mu_n+d_2^H\mu_n+D+\frac{u_i^*r_v(E_i)}{Y_s}=0, \tag{4.33}$$

$$B_n(d_2^H,E_i)=d_1\mu_n(d_2^H\mu_n+D+\frac{u_i^*r_v(E_i)}{Y_s})+u_i^*r_v(E_i)(n_s+\frac{D}{Y_s})>0. \tag{4.34}$$

It directly follows from (4.33) that

$$d_2^H=\frac{u_i^*(-r_v(E_i))-Y_sD-d_1Y_s\mu_n}{Y_s\mu_n}. \tag{4.35}$$

Now we continue the proof in the following two cases.

I. $-u_i^*r_v(E_i)\leq Y_sD$; II. $-u_i^*r_v(E_i)>Y_sD$.

For $-u_i^*r_v(E_i)\leq Y_sD$, one can find $d_2^H<0$ from (4.35), which results in a contradiction with $d_2^H\geq 0$.

For $-u_i^*r_v(E_i)>Y_sD$, we show the contradict in the either case

$$\mu_1\geq\frac{-u_i^*r_v(E_1)-Y_sD}{d_1Y_s}\quad\text{or}\quad \mu_1<\frac{-u_i^*r_v(E_1)-Y_sD}{d_1Y_s}.$$

If $\mu_1 \geq \frac{-u_i^* r_v(E_i) - Y_s D}{d_1 Y_s}$, then $d_2^H \leq 0$ from (4.35), contradicting $d_2^H > 0$.

If $\mu_1 < \frac{-u_i^* r_v(E_i) - Y_s D}{d_1 Y_s}$, denote N_3 as the largest integer such that

$$\mu_n \leq \frac{-u_i^* r_v(E_i) - Y_s D}{d_1 Y_s},$$

which implies $d_2^H \geq 0$. Then according to (4.33), for $1 \leq n \leq N_3$, (4.34) is equivalent to

$$Y_s[(d_1 + d_2^H)\mu_n + D] < \frac{Y_s d_1 \mu_n (d_2^H \mu_n + D)}{d_1 \mu_n + Y_s n_s + D},$$

that is

$$d_1 \mu_n (d_1 \mu_n + Y_s n_s + D) + (d_2^H \mu_n + D)(Y_s n_s + D) < 0. \tag{4.36}$$

It is clear that (4.36) contradicts the assumptions.

Consequently, for any $d_2 > 0$, system (1.1) doesn't undergo Hopf bifurcation at E_i.

(b). Since $Y_s D > -u_i^* r_v(E_i)$, there must exist the largest integer N such that (4.27) holds. Hence, for any $1 \leq n \leq N$, $d_2^n > 0$ is well defined as (4.28), which directly deduces

$$B_n(d_2^n, E_i) = 0. \tag{4.37}$$

According to the assumption, $d_2^{n_1} \neq d_2^{n_2}$ whenever $n_1 \neq n_2$, $1 \leq n_1, n_2 \leq N$, one get

$$B_m(d_2^n, E_i) \neq 0, \quad \text{for} \quad m, n \geq 1,\ m \neq n. \tag{4.38}$$

Moreover, for $1 \leq n \leq N$, there holds

$$B_n'(d_2^n) = d_1 \mu_n^2. \tag{4.39}$$

Therefore, by (4.37), (4.38) and (4.39), we deduce that system (1.1) undergoes the steady state bifurcation at (d_2^n, E_i).

(c). For any $n \geq 1$, (4.27) holds if $Y_s D \leq -u_1^* r_v(E_1)$. Then by the similar process to part (b), one can verify part (c).

Part (iii). Suppose $v_i^* = s$, we get $B_0(E_i) = 0$ and $B_n(E_i) \neq 0$ for $n \geq 1$, which leads to Part (iii) by [25] and Theorem 5.1.1 in [13]. □

4.3. Case III

Lemma 4.3. *System (1.1) only has one constant positive steady state E_3=(u_3^*,v_3^*,w_3^*) if $r_m > D$, where $E_3 = (u_3^*, v_3^*, w_3^*)$ will be given in the proof.*

Proof. Again suppose (u^*, v^*, w^*) is a constant positive solution of (4.1), then it satisfies

$$\begin{cases} r_m \frac{v}{v+K}(1 - \frac{w}{d}) = D, \\ D(a_0 - v) - u(n_s + \frac{D}{Y_s}) = 0, \\ u(n_p + Y_p D) - Dw = 0. \end{cases} \tag{4.40}$$

Some direct calculations yiled,

$$r_m(n_p + Y_p D)(v^*)^2 + [d(n_s + \frac{D}{Y_s})(r_m - D) - r_m(n_p + Y_p D)a_0]v^* - DdK(n_s + \frac{D}{Y_s}) = 0. \tag{4.41}$$

It is easy to check (4.41) has one positive root

$$v_3^* = \frac{a_0}{2} - \frac{d(n_s + \frac{D}{Y_s})(r_m - D)}{2r_m(n_p + Y_p D)} + \frac{\sqrt{\Delta}}{2r_m(n_p + Y_p D)},$$

where $\Delta = [d(n_s + \frac{D}{Y_s})(r_m - D) - r_m(n_p + Y_p D)a_0]^2 + 4r_m(n_p + Y_p D)DdK(n_s + \frac{D}{Y_s})$.

Due to (4.40), there holds

$$u_3^* = \frac{D(a_0 - v_3^*)}{n_s + \frac{D}{Y_s}}, w_3^* = (n_p + Y_p D)\frac{a_0 - v_3^*}{n_s + \frac{D}{Y_s}},$$

which finishes the proof. □

Theorem 4.6. *For $r_m > D$, E_3 is locally asymptotically stable.*

Proof. Since $r = r_m \frac{v}{v+K}(1 - \frac{w}{d})$, then the linearized operator of system (4.1) evaluated at $E_3 = (u_3^*, v_3^*, w_3^*)$ is

$$\mathcal{L}(E_3) = \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + f_{1u}(E_3) & f_{1v}(E_3) & f_{1w}(E_3) \\ f_{2u}(E_3) & d_2 \frac{\partial^2}{\partial x^2} + f_{2v}(E_3) & f_{2w}(E_3) \\ f_{3u}(E_3) & f_{3v}(E_3) & d_3 \frac{\partial^2}{\partial x^2} + f_{3w}(E_3) \end{pmatrix}, \tag{4.42}$$

where

$$f_{1u}(E_3) = 0,\ f_{1v}(E_3) = u_3^* r_v(E_3),\ f_{1w}(E_3) = u_3^* r_w(E_3),$$
$$f_{2u}(E_3) = -n_s - \frac{D}{Y_s},\ f_{2v}(E_3) = -D - u_3^* \frac{r_v(E_3)}{Y_s},\ f_{2w}(E_3) = -u_3^* \frac{r_w(E_3)}{Y_s},$$
$$f_{3u}(E_3) = n_p + Y_p D,\ f_{3v}(E_3) = u_3^* Y_p r_v(E_3),\ f_{3w}(E_3) = -D + u_3^* Y_p r_w(E_3),$$
$$r_v(E_3) = r_m(1 - \frac{w^*}{d})\frac{K}{(v^* + K)^2},\ r_w(E_3) = -\frac{r_m v^*}{d(v^* + K)}.$$

Similarly, the eigenvalues of $\mathcal{L}(E_3)$ are given by the eigenvalues of the following matrix

$$\mathcal{L}_n(E_3) = \begin{pmatrix} -d_1\mu_n & u_3^* r_v(E_3) & u_3^* r_w(E_3) \\ -n_s - \frac{D}{Y_s} & -d_2\mu_n - D - u_3^* \frac{r_v(E_3)}{Y_s} & -u_3^* \frac{r_w(E_3)}{Y_s} \\ n_p + Y_p D & u_3^* Y_p r_v(E_3) & -d_3\mu_n - D + u_3^* Y_p r_w(E_3) \end{pmatrix}. \tag{4.43}$$

Then the characteristic equation is

$$\lambda^3 + B_{n2}(E_3)\lambda^2 + B_{n1}(E_3)\lambda + B_{n0}(E_3) = 0, \tag{4.44}$$

where

$$B_{n2}(E_3) = d_3\mu_n + D + d_1\mu_n + d_2\mu_n + D + \frac{u_3^* r_v(E_3)}{Y_s} - u_3^* Y_p r_w(E_3), \tag{4.45}$$

$$\begin{aligned} B_{n1}(E_3) = &(d_3\mu_n + D)(d_1\mu_n + d_2\mu_n + D + \frac{u_3^* r_v(E_3)}{Y_s}) \\ &+ d_1\mu_n(d_2\mu_n + D) + u_3^* r_v(E_3^*)(n_s + \frac{D + d_1\mu_n}{Y_s}) \\ &- u_3^* r_w(E_3)[Y_p(d_2\mu + D) + n_p + Y_p D + Y_p d_1\mu_n], \end{aligned} \tag{4.46}$$

$$\begin{aligned} B_{n0}(E_3) &= (d_3\mu_n + D)[d_1\mu_n(d_2\mu_n + D) + u_3^* r_v(E_3)(n_s + \frac{D + d_1\mu_n}{Y_s})] \\ &\quad - (d_2\mu_n + D)u_3^* r_w(E_3)(n_p + Y_p D + Y_p d_1\mu_n). \end{aligned} \tag{4.47}$$

It follows from $r = r_m \frac{v}{v+K}(1 - \frac{w}{d})$ that

$$r_v(E_3) = r_m(1 - \frac{w_3^*}{d})\frac{K}{(v_3^* + K)^2} > 0, \quad r_w(E_3) = -\frac{r_m}{d}\frac{v_3^*}{v_3^* + K} < 0.$$

Some direct calculations deduce

$$B_{ni} > 0, B_{n1}B_{n2} - B_{n3} > 0, \quad i = 0, 1, 2.$$

According to Routh-Hurwitz criterion, three eigenvalues of $\mathcal{L}(E_3)$ all have negative real parts, which leads to Theorem 4.6. $\square$

5. Numerical simulations

In this section, some numerical simulations are given to show our results above. Furthermore, it is illustrated that lager a_0 can induce system (1.1) to stabilize to the weak semitrivial steady state $(0, a_0, 0)$ as time proceeds, and the spatialtemporal patterns of $u(x,t)$, $v(x,t)$ and $w(x,t)$ are provided to exhibit the microorganism culture process.

Throughout this part, the following initial functions are used.

$$u_0(x) = 0.1 - 0.1\cos\frac{2\pi x}{L}, v_0(x) = 1 - 0.1\cos\frac{2\pi x}{L}, w_0(x) = 2 - 0.1\cos\frac{2\pi x}{L}, \tag{5.1}$$

$$u_0(x) = 0.1 - 0.1\cos\frac{2\pi x}{L}, v_0(x) = 6, w_0(x) = 2 - 0.1\cos\frac{2\pi x}{L}. \tag{5.2}$$

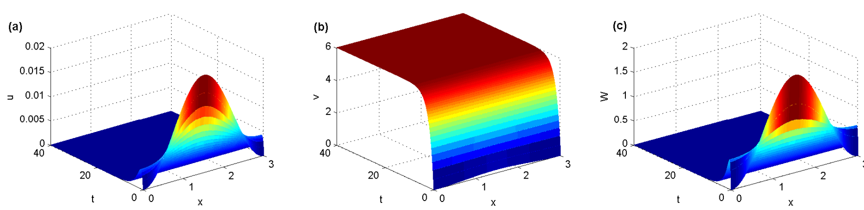

Figure 1. The asymptotic behaviors of $u(x,t)$ in (a), $v(x,t)$ in (b) and $w(x,t)$ in (c). Here $r_m = 0.01$, $D = 0.55$, $a_0 = 6$, $d_1 = 0.3$, $d_2 = 1.1$, $d_3 = 1$, $n_s = 1$, $Y_s = 0.4$, $K = 0.28$, $n_p = 0.8$, $Y_p = 50$; initial function (5.1) is chosen.

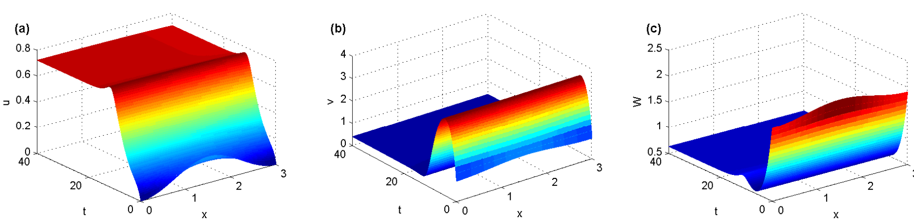

Figure 2. The asymptotic behaviors of $u(x,t)$ in (a), $v(x,t)$ in (b) and $w(x,t)$ in (c). Here $r_m = 0.6$, $D = 0.35$, $a_0 = 6$, $d_1 = 0.3$, $d_2 = 1.1$, $d_3 = 1.1$, $n_s = 1$, $Y_s = 0.2$, $r_m = 0.6$, $K = 0.28$, $n_p = 0.05$, $Y_p = 0.8$; initial function (5.1) is used.

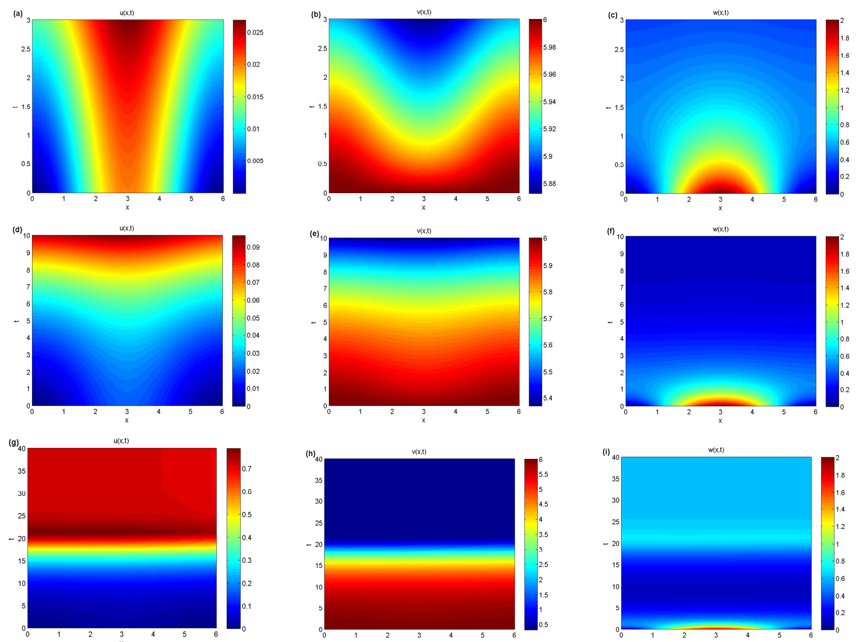

Figure 3. The spatiotemporal patterns of $u(x,t)$ in (a,d,g), $v(x,t)$ in (b,e,h) and $w(x,t)$ in (c,f,i). Here, $L=6$, all the other parameters take the same values as them in Figure 2; initial function (5.2) is used.

Example 5.1. Under the the conditions in part (i) of Theorem 2.1, for Case I, the asymptotic behaviors of $u(x,t), v(x,t), w(x,t)$ are described in Figure 1. Further let $c=30$ (resp. $d=20$), the numerical results for Case II (resp. Case III) are similar to Figure 1, where $u(x,t)$ in (a) and $w(x,t)$ in (b) decay to zero and $v(x,t)$ stabilizes to a_0 in the long run. In addition, if we choose initial function (5.2), Figure 1 can still show the tendency of $u(x,t), v(x,t), w(x,t)$.

Example 5.2. For Case I, the numerical solution to system (1.1) is illustrated by Figure 2. We obtain that $(u(x,t), v(x,t), w(x,t))$ stabilizes to the constant positive state $(0.7167, 0.3964, 0.6149)$, which is close to $(0.7137, 0.3920, 0.6730)$ computed by (4.14). Furthermore, the spatiotemporal patterns of $u(x,t)$, $v(x,t)$, $w(x,t)$ are given in Figure 3 to exhibit the microorganism culture process. In the initial stage, culture time $T=3$, see $(a-c)$: the concentration of substrate on the both ends of the tubular vessel is higher than that in the center, while the concentrations of biomass and product on the ends are lower than those in the middle; after a while, $T=10$, concentrations of biomass, substrate and product are still heterogeneous in general, see $(d-f)$; as time goes on, $T=40$, they all tend to homogeneous states, see $(g-i)$.

Example 5.3. For Case II and Case III, let $c=30, d=20$, keeping the other parameters same as them in Figure 2, and fix the initial function as (5.1), we get similar figures to Figure 2. Therefore, system (1.1) can stabilize to constant positive steady state under three cases. However, for Case II, if we only change $a_0=6$ as $a_0=20$, keeping all other parameters the same, then the numerical results can be illustrated by Figure 4. It is observed that $u(x,t)$ decays to zero in Figure 4 as time goes on but it stabilizes to a positive state in Figure 2. This implies that the lager

a_0 induce microorganisms to be extinct due to substrate inhibition, and the system stabilizes to $(0, a_0, 0)$ as time goes on, which is agree with Theorem 4.3.

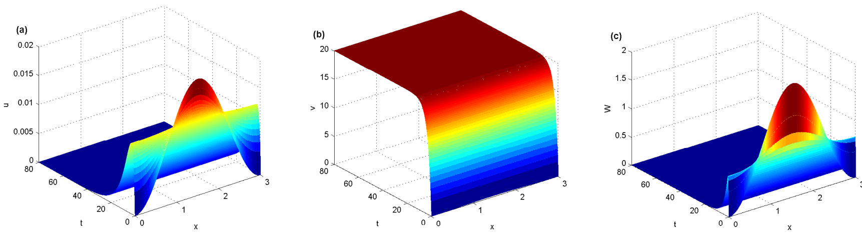

Figure 4. The asymptotic behaviors of $u(x,t)$ in (a), $v(x,t)$ in (b) and $w(x,t)$ in (c). Here $a_0 = 20$, $c = 30$ and all the other parameters take the same values as them in Figure 2; initial function (5.1) is chosen.

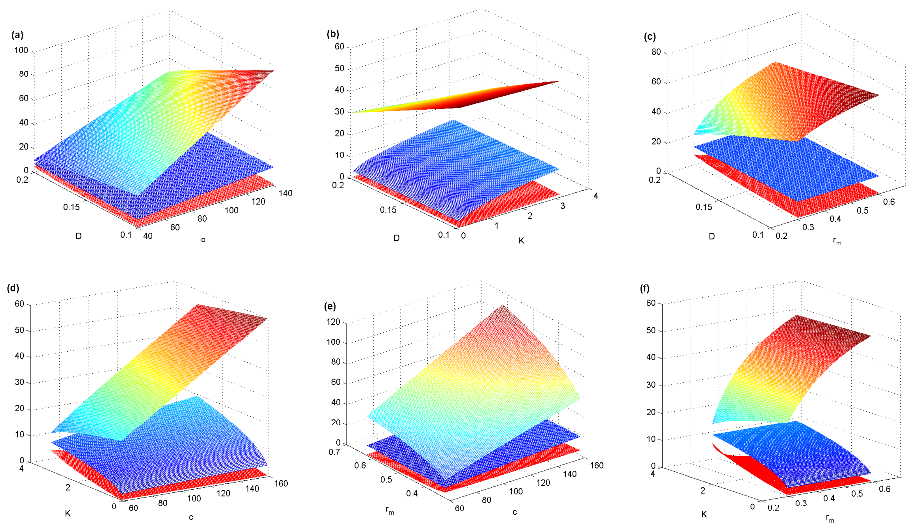

Figure 5. The graphs of v_1^*, s and v_2^* with respect to parameters c and D in (a), K and D in (b), r_m and D in (c), c and K in (d), c and r_m in (e), r_m and K in (f).

6. Discussion

A diffusive microbial continuous culture model is presented and studied under three growth conditions– Case I no inhibition, Case II only substrate inhibition and Case III only product inhibition. It shows that the proposed system with any growth function can finally stabilize to constant positive steady state, i.e., homogeneous state. But the dynamics of the microorganism culture process varies with different growth functions. The outcome of the system with Case I is similar to that for Case III: there is one positive constant steady state which is stable. Whereas the system subject to Case II have two positive constant steady states E_1 and E_2 with conditions of $r_m > D$, $a_0 > v_i^*$ and (4.19). E_i is stable if $v_i^* < s$, and there undergoes the steady state bifurcation if $v_i^* \geq s$, $i = 1, 2$. However, based on $r_m > D$, $a_0 > v_i^*$ and (4.19), it is observed that $v_2^* < s < v_1^*$ from Figure 5. Thus we conjecture that E_2 is stable and the steady state bifurcation occurs at E_1. Particularly in the absence of diffusion, we find that E_2 is stable but E_1 is unstable, which is an agreement with some arguments in [22]. In addition, it is illustrated that larger a_0 can induce system (1.1) with substrate inhibition to stabilize to the washout state $E = (0, a_0, 0)$. Then we may conclude that a_0 plays an important role in the outcome of the proposed system, which is in accordance with some results in [8]. Consequently, our results may be helpful in choosing appropriate experimental operating conditions to avoid the stability of washout state and something else unexpected in the actual microbial culture.

Example 6.1. Based on $r_m > D$ and $(r_m - D)^2 - \frac{4r_m DK}{c} > 0$, the graphs of v_1^*, s and v_2^* are presented in Figure 5. Let $r_m = 0.32, K = 2$, one get the surfaces of $v_1^*(c, D)$, $s(c, D)$ and $v_2^*(c, D)$ in Figure 5 (a), where the multi-colored one at the top, the blue one in the middle and the red one at the bottom display the trends of v_1^*, s and v_2^*, respectively. In turn, fix $r_m = 0.32, c = 80$; $K = 2.5, c = 80$; $D = 0.2, r_m = 0.32$; $D = 0.2, K = 2.5$; $D = 0.2, c = 80$, one can obtain the surfaces of v_1^*, v_2^* and s with respect to parameters K and D; r_m and D; c and K; c and r_m; r_m and K in Figure 5 $(b - f)$, respectively.

Acknowledgements. The authors thank the referees and the editors for their useful comments which helped to improve the paper.

References

[1] K. J. Appeldoorn, A. J. Boom, G. J. J. Kortstee, A. J. B. Zehnder, *Contribution of precipitated phosphates and acid-soluble polyphosphate to enhanced biological phosphate removal*, Water Res., 1992, 26(7), 937–943.

[2] J. F. Andrews, *A mathematical model for the continuous culture of microorganisms utilizing inhibitory substrates*, Biotechnol. Bioeng., 1968, 10(6), 707–723.

[3] F. W. Bai, L. J. Chen, W. A. Anderson, M. Moo-Young, *Parameter oscillations in a very high gravity medium continuous ethanol fermentation and their attenuation on a multistage packed column bioreactor system*, Biotechnol. Bioeng., 2004, 88(5), 558–566.

[4] M. Balat, *Production of bioethanol from lignocellulosic materials via the biochemical pathway: A review*, Energ. Convers. Manage., 2011, 52(2), 858–875.

[5] H. Biebl, *Glycerol fermentation of 1,3-propanediol by Clostridium butyricum. Measurement of product inhibition by use of a pH-auxostat*, Appl. Microbiol. Biot., 1991, 35(6), 701–705.

[6] E. A. Buehler, A. Mesbah, *Kinetic study of Acetone-Butanol-Ethanol fermentation in continuous culture*, Plos One, 2016, 11(8), 1932–6203.

[7] A. Carruthers, *Mechanisms for the facilitated diffusion of substrates across cell membranes*, Biochemistry, 1991, 30(16), 3898–3906.

[8] D. E. Contois, *Kinetics of bacterial growth: relationship between population density and specific growth rate of continuous cultures*, J. Gen. Microbiol., 1959, 21(1), 40–50.

[9] E. N. Dancer, Y. H. Du, *Positive solutions for a three-species competition system with diffusion-I. General existence results*, Nonlinear Anal., 1995, 24(3), 337–357.

[10] V. H. Edwards, R. C. Ko, S. A. Balogh, *Dynamics and control of continuous microbial propagators to subject substrate inhibition*, Biotechnol. Bioeng., 1972, 14(6), 939–974.

[11] M. Esfandyari, M. A. Fanaei, R. Gheshlaghi, M. A. Mahdavi, *Mathematical modeling of two-chamber batch microbial fuel cell with pure culture of Shewanella*, Chem. Eng. Res. Des., 2017, 117, 34–42.

[12] C. X. Gao, E. M. Feng, Z. T. Wang, Z. L. Xiu, *Parameters identification problem of the nonlinear dynamical system in microbial continuous cultures*, Appl. Math. Comput., 2005, 169(1), 476–484.

[13] D. Henry, *Geometric Theory of Semilinear Parabolic Equations, Lecture Notes in Mathematics*, Springer-Verlag, Berlin, 1981.

[14] E. Krichen, J. Harmand, M. Torrijos, J. J. Godon, N. Bernet, A. Rapaport, *High biomass density promotes density-dependent microbial growth rate*, Biochem. Eng. J., 2018, 130, 66–75.

[15] O. Levenspiel, *The Monod equation: A revisit and a generalization to product inhibition situations*, Biotechnol, Bioeng., 1980, 22(8), 1671–1687.

[16] J. H. T. Luong, *Kinetics of ethanol inhibition in alcohol fermentation*, Biotechnol. Bioeng., 1985, 27(3), 280–285.

[17] C. V. Pao, *Nonlinear Parabolic and Elliptic Equations*, Springer Science & Business Media, New York, 1992.

[18] C. V. Pao, *Quasisolutions and global attactor of reaction-diffusion systems*, Nonlinear Anal., 1996, 26(12), 1889–1903.

[19] J. L. Ren and Q. G. Yuan, *Bifurcations of a periodically forced microbial continuous culture model with restrained growth rate*, Chaos, 2017, 27(8), 083124.

[20] Y. Shen, X. Q. Zhao, X. M. Ge, F. W. Bai, *Metabolic flux and cell cycle analysis indicating new mechanism underlying process oscillation in continuous ethanol fermentation with Saccharomyces cerevisiae under VHG conditions*, Biotechnol. Adv., 2009, 27(6), 1118–1123.

[21] P. Skupin, M. Metzger, *Stability analysis of the continuous ethanol fermentation process with a delayed product inhibition*, Appl. Math. Model., 2017, 49, 48–58.

[22] Z. L. Xiu, A. P. Zeng, W. D. Deckwer, *Multiplicity and stability analysis of microorganisms in continuous culture: effects of metabolic overflow and growth inhibition*, Biotechnol. Bioeng., 1998, 57(3), 251–261.

[23] T. Yano, S. Koga, *Dynamic behavior of the chemostat subject to substrate inhibition*, Biotechnol. Bioeng., 1969, 11(2), 139–153.

[24] J. X. Ye, E. M. Feng, H. S. Lian, Z. L. Xiu, *Existence of equilibrium points and stability of the nonlinear dynamical system in microbial continuous cultures*, Appl. Math. Comput., 2009, 207(2), 307–318.

[25] F. Yi, J. Wei, J. Shi, *Bifurcation and spatiotemporal patterns in a homogeneous diffusive predatorCprey system*, J. Differ. Equations, 2009, 246(5), 1944–1977.

[26] A. P. Zeng, A. Ross, H. Biebl, C. Tag, B. Gunzel, W. D. Deckwer, *Multiple product inhibition and growth modeling of clostridium butyricum and klebsiella pneumoniae in glycerol fermentation*, Biotechnol. Bioeng., 1994, 44(8), 902–911.