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Reaction–diffusion equations of two species competing for two complementary resources with internal storage

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A B S T R A C T

This paper examines a system of reaction–diffusion equations arising from a mathematical model of two microbial species competing for two complementary resources with internal storage in an unstirred chemostat. The governing system can be reduced to a limiting system based on two uncoupled conservation principles. One of main technical difficulties in our analysis is the singularities in the reaction terms. Conditions for persistence of one population and coexistence of two competing populations are derived from eigenvalue problems, maximum principle and the theory of monotone dynamical systems.

1. Introduction

The understanding of competition between species for resources is one of the challenging aspects of mathematical ecology. The chemostat (see, e.g., [17]) is a piece of laboratory apparatus, yet it

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plays a central role in mathematical biology. The basic chemostat consists of three vessels. The first vessel, the feed bottle, contains all of the needed nutrients for growth. The nutrients are pumped at a constant rate into the second, called the culture vessel or bio-reactor. The culture vessel whose volume is constant contains microorganisms which compete for nutrient. The contents of the culture vessel are pumped at the same constant rate into the third vessel, called the overflow vessel. It is a model of a simple lake in which the competition is purely exploitative in the sense that organisms simply consume the nutrient, thereby making it unavailable for competitors.

The classical Monod model of microbial growth on a single limiting resource was proposed in [14]. In this model, the basic assumption is that the nutrient uptake rate is proportional to the reproductive rate, that is, growth is directly coupled to nutrient uptake. Since the constant of proportionality is usually called the yield constant, the classical Monod model is sometimes referred to as the "constant-yield model". In phytoplankton ecology, it has long been known that the yield is not a fixed constant. It can vary depending on the growth rate of species. This led to the formulation of the "variable-yield model" [4]. The second extension of the Monod model is to include multiple potentially limiting nutrients, such as nitrogen and phosphorus. When both nutrients are essential for growth, typically the nutrient in shortest supply limits growth, known as Liebig's law of the minimum [5].

The mathematical theory and biological implications of both modifications of the Monod model have been studied extensively for the cases of growth of a single species and competition between two species [12,13]. The authors in [13] investigated the following model for two phytoplankton species with variable internal stores of two essential resources:

$$
\begin{aligned}
\frac{dS}{dt} &= \big(S^{(0)} - S\big)D - f_{S1}(S, Q_{S1})u_1 - f_{S2}(S, Q_{S2})u_2, \\
\frac{dR}{dt} &= \big(R^{(0)} - R\big)D - f_{R1}(R, Q_{R1})u_1 - f_{R2}(R, Q_{R2})u_2, \\
\frac{dQ_{Si}}{dt} &= f_{Si}(S, Q_{Si}) - \min\big\{\mu_{Si}(Q_{Si}), \mu_{Ri}(Q_{Ri})\big\}Q_{Si}, \\
\frac{dQ_{Ri}}{dt} &= f_{Ri}(R, Q_{Ri}) - \min\big\{\mu_{Si}(Q_{Si}), \mu_{Ri}(Q_{Ri})\big\}Q_{Ri}, \\
\frac{du_i}{dt} &= \big[\min\big\{\mu_{Si}(Q_{Si}), \mu_{Ri}(Q_{Ri})\big\} - D\big]u_i, \\
S(0) \geqslant 0, \quad R(0) \geqslant 0, &\quad Q_{Si}(0) \geqslant 0, \quad Q_{Ri}(0) \geqslant 0, \quad u_i(0) \geqslant 0, \quad i = 1, 2.
\end{aligned}
\tag{1.1}
$$

Here $S(t)$ and $R(t)$ denote the concentrations of the limiting resources in the chemostat at time t. $u_i(t)$ denotes the concentration of species i at time t. Q_{Si} (Q_{Ri}) represents the amount of cell quota of resource S (R) per individual of species i at time t. $\mu_{Si}(Q_{Si})$ and $\mu_{Ri}(Q_{Ri})$ are the growth rates of species i as a function of cell quota Q_{Si} and Q_{Ri}, respectively. $f_{Si}(S, Q_{Si})$ ($f_{Ri}(R, Q_{Ri})$) is the per capita uptake rate of species i as a function of resource concentration S (R) and cell quota Q_{Si} (Q_{Ri}). D is the dilution rate of the chemostat. Each nutrient is supplied at the rate D, and both input concentrations are $S^{(0)}$ and $R^{(0)}$ respectively. $Q_{\min,Ni}$ denotes threshold cell quota below which no growth of species i occurs, where $N = S, R$. Growth rate for species is determined by the minimum of two Droop functions, that is, "Liebig's Law of the Minimum" is used to describe the dependence of species growth on cell quotas. This law reflects that the two resources are complementary, not substitutable.

According to [3–5], for $N = S, R$ and $i = 1, 2$, the growth rate $\mu_i(Q_{Ni})$ takes the forms:

$$
\mu_i(Q_{Ni}) = \mu_{\infty,Ni}\left(1 - \frac{Q_{\min,Ni}}{Q_{Ni}}\right),
$$

or

$$\mu_i(Q_{Ni}) = \mu_{\infty,Ni}\frac{(Q_{Ni} - Q_{\min,Ni})_+}{K_{Ni} + (Q_{Ni} - Q_{\min,Ni})_+}, \tag{1.2}$$

where $Q_{\min,Ni}$ is the minimum cell quota necessary to allow cell division and $(Q_{Ni} - Q_{\min,Ni})_+$ is the positive part of $(Q_{Ni} - Q_{\min,Ni})$ and $\mu_{\infty,Ni}$ is the maximal growth rate at infinite quotas (i.e., as $Q_{Ni} \to \infty$) of the species i.

According to Grover [6], for $N = S, R$ and $i = 1, 2$, the uptake rate $f_{Ni}(N, Q_{Ni})$ takes the form:

$$f_{Ni}(N, Q_{Ni}) = \rho_{Ni}(Q_{Ni})\frac{N}{k_{Ni} + N} \tag{1.3}$$

where $\rho_{Ni}(Q_{Ni})$ is defined as follows

$$\rho_{Ni}(Q_{Ni}) = \rho^{\text{high}}_{\max,Ni} - \left(\rho^{\text{high}}_{\max,Ni} - \rho^{\text{low}}_{\max,Ni}\right)\frac{Q_{Ni} - Q_{\min,Ni}}{Q_{\max,Ni} - Q_{\min,Ni}},$$

or

$$\rho_{Ni}(Q_{Ni}) = \rho_{\max,Ni}\frac{Q_{\max,Ni} - Q_{Ni}}{Q_{\max,Ni} - Q_{\min,Ni}}$$

here $Q_{\min,Ni} \leqslant Q_{Ni} \leqslant Q_{\max,Ni}$. Cunningham and Nisbet [1,2] took $\rho_{Ni}(Q_{Ni})$ to be a constant.

Motivated by the above classical models, we assume that for each $i = 1, 2$ and $N = S, R$, $\mu_{Ni}(Q_{Ni})$ is defined and continuously differentiable for $Q_{Ni} \geqslant Q_{\min,Ni} > 0$ and satisfies

(H_1) $\mu_{Ni}(Q_{Ni}) \geqslant 0$, $\mu'_{Ni}(Q_{Ni}) > 0$ and is continuous for $Q_{Ni} \geqslant Q_{\min,Ni}$, $\mu_{Ni}(Q_{\min,Ni}) = 0$.

We also assume that $f_{Ni}(N, Q_{Ni})$ is continuously differentiable for $N > 0$ and $Q_{Ni} \geqslant Q_{\min,Ni}$ and satisfies

(H_2) $$f_{Ni}(0, Q_{Ni}) = 0, \qquad \frac{\partial f_{Ni}}{\partial N} > 0, \qquad \frac{\partial f_{Ni}}{\partial Q_{Ni}} \leqslant 0.$$

Let $U_{Si} = u_i Q_{Si}$ and $U_{Ri} = u_i Q_{Ri}$ be the total amount of stored nutrient at time t for S and R, respectively, $i = 1, 2$ (see, e.g., [13]). Then system (1.1) can be rewritten as follows

$$\begin{gathered}
\frac{dS}{dt} = \left(S^{(0)} - S\right)D - f_{S1}\left(S, \frac{U_{S1}}{u_1}\right)u_1 - f_{S2}\left(S, \frac{U_{S2}}{u_2}\right)u_2, \\
\frac{dR}{dt} = \left(R^{(0)} - R\right)D - f_{R1}\left(R, \frac{U_{R1}}{u_1}\right)u_1 - f_{R2}\left(R, \frac{U_{R2}}{u_2}\right)u_2, \\
\frac{dU_{Si}}{dt} = -DU_{Si} + f_{Si}\left(S, \frac{U_{Si}}{u_i}\right)u_i, \\
\frac{dU_{Ri}}{dt} = -DU_{Ri} + f_{Ri}\left(R, \frac{U_{Ri}}{u_i}\right)u_i, \\
\frac{du_i}{dt} = \left[\min\left\{\mu_{Si}\left(\frac{U_{Si}}{u_i}\right), \mu_{Ri}\left(\frac{U_{Ri}}{u_i}\right)\right\} - D\right]u_i, \\
S(0) \geqslant 0, \qquad R(0) \geqslant 0, \qquad U_{Si}(0) \geqslant 0, \qquad U_{Ri}(0) \geqslant 0, \qquad u_i(0) \geqslant 0, \quad i = 1, 2.
\end{gathered} \tag{1.4}$$

It is not hard to see that the following conservation properties hold (see, e.g., [13, Eq. (2.4)]):

$$S + U_{S1} + U_{S2} = S^{(0)} + O\left(e^{-Dt}\right) \quad \text{as } t \to \infty,$$

and

$$R + U_{R1} + U_{R2} = R^{(0)} + O\left(e^{-Dt}\right) \quad \text{as } t \to \infty.$$

Thus, system (1.4) can be reduced into a limiting system which is a type-K monotone system (see, e.g., [13, Eq. (3.1)]).

Although the chemostat above provides us a simple model for the study of microbial growth, the assumption of "well-mixed" is often questionable, and several models have been introduced where the environment is partially mixed. In [11], the authors considered a constant-yield model in the unstirred chemostat, where flow enters at one boundary supplying nutrient, and exits at another, removing nutrients and organisms, while diffusion transports organisms and nutrient across the habitat domain. The specific question of how storage of nutrient resources affects competition in spatially variable habitats is challenging and very significant for mathematical ecology. Based on this motivation, Grover [7] did numerical simulations and obtained some interesting results in this topic. Note that Grover's model cannot be mathematically formulated and his results are numerical, not analytic. The authors in [9] investigated a mathematical model of two microbial species competing for a single-limited nutrient with internal storage in an unstirred chemostat and provided the results on washout, one species survival and the other washout and coexistence.

The current paper is a continuation of [9] and we shall consider *two complementary nutrients* rather than the single-limited nutrient. In other words, we will introduce the "spatially variable habitats" into system (1.1). Thus, we consider the following system of partial differential equations:

$$\begin{aligned}
S_t &= dS_{xx} - f_{S1}\left(S, \frac{U_{S1}}{u_1}\right)u_1 - f_{S2}\left(S, \frac{U_{S2}}{u_2}\right)u_2, \\
R_t &= dR_{xx} - f_{R1}\left(R, \frac{U_{R1}}{u_1}\right)u_1 - f_{R2}\left(R, \frac{U_{R2}}{u_2}\right)u_2, \\
(U_{Si})_t &= d(U_{Si})_{xx} + f_{Si}\left(S, \frac{U_{Si}}{u_i}\right)u_i, \\
(U_{Ri})_t &= d(U_{Ri})_{xx} + f_{Ri}\left(R, \frac{U_{Ri}}{u_i}\right)u_i, \\
(u_i)_t &= d(u_i)_{xx} + \min\left\{\mu_{Si}\left(\frac{U_{Si}}{u_i}\right), \mu_{Ri}\left(\frac{U_{Ri}}{u_i}\right)\right\}u_i, \quad i = 1, 2
\end{aligned} \tag{1.5}$$

in $(0, 1) \times (0, \infty)$ with boundary conditions

$$\begin{aligned}
S_x(0, t) &= -S^{(0)}, \qquad S_x(1, t) + \gamma S(1, t) = 0, \\
R_x(0, t) &= -R^{(0)}, \qquad R_x(1, t) + \gamma R(1, t) = 0, \\
(U_{Si})_x(0, t) &= 0, \qquad (U_{Si})_x(1, t) + \gamma U_{Si}(1, t) = 0, \\
(U_{Ri})_x(0, t) &= 0, \qquad (U_{Ri})_x(1, t) + \gamma U_{Ri}(1, t) = 0, \\
(u_i)_x(0, t) &= 0, \qquad (u_i)_x(1, t) + \gamma u_i(1, t) = 0, \quad i = 1, 2
\end{aligned} \tag{1.6}$$

and initial conditions

$$\begin{aligned}
&S(x,0)=S^0(x)\geqslant 0, \qquad R(x,0)=R^0(x)\geqslant 0,\\
&U_{Si}(x,0)=U_{Si}^0(x)\geqslant 0, \qquad U_{Si}^0(x)\not\equiv 0,\\
&U_{Ri}(x,0)=U_{Ri}^0(x)\geqslant 0, \qquad U_{Ri}^0(x)\not\equiv 0,\\
&u_i(x,0)=u_i^0(x)\geqslant 0, \qquad u_i^0(x)\not\equiv 0, \quad i=1,2.
\end{aligned} \tag{1.7}$$

Here the functions μ_{Ni} and f_{Ni} satisfy (H_1) and (H_2) respectively, for $N=S,R$; $i=1,2$. The constants d and γ represent the diffusion coefficient and the washout constant, respectively. $S^{(0)}$ and $R^{(0)}$ are the nutrient flux.

Let

$$z_S(x):=S^{(0)}\left(\frac{1+\gamma}{\gamma}-x\right), \qquad z_R(x):=R^{(0)}\left(\frac{1+\gamma}{\gamma}-x\right), \quad 0<x<1. \tag{1.8}$$

Introducing the new variable

$$\Lambda_N(x,t)=N+U_{N1}+U_{N2}, \quad \forall N=S,R$$

into (1.5)–(1.7), one shall have the following linear equation with boundary condition:

$$\begin{aligned}
&\frac{\partial \Lambda_N}{\partial t}=d\frac{\partial^2\Lambda_N}{\partial x^2}, \quad x\in(0,1),\ t>0,\\
&\frac{\partial \Lambda_N}{\partial x}(0,t)=-N^{(0)}, \qquad \frac{\partial \Lambda_N}{\partial x}(1,t)+\gamma\Lambda_N(1,t)=0.
\end{aligned}$$

Thus $\Lambda_N(x,t)$ satisfies $\lim_{t\to\infty}\Lambda_N(x,t)=z_N(x)$ uniformly in $x\in[0,1]$, $N=S,R$. Therefore, we conclude that the limiting system for (1.5)–(1.7) takes the form

$$\begin{aligned}
&(u_i)_t=d(u_i)_{xx}+\min\left\{\mu_{Si}\left(\frac{U_{Si}}{u_i}\right),\mu_{Ri}\left(\frac{U_{Ri}}{u_i}\right)\right\}u_i,\\
&(U_{Si})_t=d(U_{Si})_{xx}+f_{Si}\left(z_S(x)-U_{S1}-U_{S2},\frac{U_{Si}}{u_i}\right)u_i,\\
&(U_{Ri})_t=d(U_{Ri})_{xx}+f_{Ri}\left(z_R(x)-U_{R1}-U_{R2},\frac{U_{Ri}}{u_i}\right)u_i, \quad i=1,2
\end{aligned} \tag{1.9}$$

in $(0,1)\times(0,\infty)$ with boundary conditions

$$\begin{aligned}
&(u_i)_x(0,t)=0, \qquad (u_i)_x(1,t)+\gamma u_i(1,t)=0,\\
&(U_{Si})_x(0,t)=0, \qquad (U_{Si})_x(1,t)+\gamma U_{Si}(1,t)=0,\\
&(U_{Ri})_x(0,t)=0, \qquad (U_{Ri})_x(1,t)+\gamma U_{Ri}(1,t)=0, \quad i=1,2
\end{aligned} \tag{1.10}$$

and initial conditions

$$\begin{aligned}
&u_i(x,0)=u_i^0(x)\geqslant 0, \qquad u_i^0(x)\not\equiv 0,\\
&U_{Si}(x,0)=U_{Si}^0(x)\geqslant 0, \qquad U_{Si}^0(x)\not\equiv 0,\\
&U_{Ri}(x,0)=U_{Ri}^0(x)\geqslant 0, \qquad U_{Ri}^0(x)\not\equiv 0, \quad i=1,2.
\end{aligned} \tag{1.11}$$

In this paper, we will determine the global dynamics of the system (1.9)–(1.11). Since $\frac{U_{Ni}}{u_i}$ with $U_{Ni} = 0$ and $u_i = 0$ produces a singularity in the reaction terms, this makes the analysis more difficult and we are unable to do the bifurcation analysis and linearization at the origin. To overcome this difficulty, technical construction of suitable upper-lower solutions near the singularity is needed. Roughly speaking, we shall construct upper-lower solutions with those components sufficiently small, each of which has singularity at zero, and replace the linearization tool by the combination of the constructed upper-lower solutions, maximum principle and the theory of monotone dynamical system. These upper-lower solutions play a role of eigenfunctions in some extent.

The organization of the paper is as follows. In Section 2, we consider two invariant subsystems which describe the single population growth corresponding to the system (1.9)–(1.11). We can show uniqueness of the positive steady state. The results for the single population are almost sharp: either washout of the organism or survival of the organism occurs, as expected. We determine the conditions for both of the washout and survival of the organisms. Section 3 is devoted to the study of two competing species model. It is remarkable that some extinction results can be established based on the previous results in [9] and the comparison principle. We also prove the existence of coexistence for the model of two competing species. The main result is given in case both organisms are viable (able to survive in absence of competition) and this is a persistence result requiring that each single-species population can be invaded by its competitor. In this case, almost all solutions converge to a positive steady state although there may be several such steady states. What is achieved strongly depends on the construction of upper-lower solutions, the maximum principle and the theory of monotone dynamical systems. The routine proof about “the invariance of the feasible domain” is collected in Appendix A.

2. Single population growth

The system (1.9)–(1.11) has two invariant subsystems with respect to (u_1, U_{S1}, U_{R1}) and (u_2, U_{S2}, U_{R2}), respectively, which describe the growth of a single species on two essential resources based on internal storage. Both invariant subsystems have the following form:

$$\begin{aligned}
u_t &= du_{xx} + \min\left\{\mu_S\left(\frac{U_S}{u}\right), \mu_R\left(\frac{U_R}{u}\right)\right\}u, \\
(U_S)_t &= d(U_S)_{xx} + f_S\left(z_S(x) - U_S, \frac{U_S}{u}\right)u, \quad x \in (0,1),\ t > 0, \\
(U_R)_t &= d(U_R)_{xx} + f_R\left(z_R(x) - U_R, \frac{U_R}{u}\right)u
\end{aligned} \tag{2.1}$$

with boundary conditions

$$\begin{aligned}
u_x(0,t) = 0, &\qquad u_x(1,t) + \gamma u(1,t) = 0, \\
(U_S)_x(0,t) = 0, &\qquad (U_S)_x(1,t) + \gamma U_S(1,t) = 0, \\
(U_R)_x(0,t) = 0, &\qquad (U_R)_x(1,t) + \gamma U_R(1,t) = 0
\end{aligned} \tag{2.2}$$

and initial conditions

$$\begin{aligned}
u(x,0) = u^0(x) \geqslant 0, &\qquad u^0(x) \not\equiv 0, \\
U_S(x,0) = U_S^0(x) \geqslant 0, &\qquad U_S^0(x) \not\equiv 0, \\
U_R(x,0) = U_R^0(x) \geqslant 0, &\qquad U_R^0(x) \not\equiv 0.
\end{aligned} \tag{2.3}$$

Here μ_N and f_N satisfy (H_1) and (H_2) respectively, $N = S, R$.

The feasible domain for initial value functions should be

$$\Delta = \Big\{ \big(u^0, U_S^0, U_R^0\big) \in \big(C\big([0,1]\big)\big)^3 \ \big|\ u^0(x) > 0,\ 0 < U_N^0(x) \leqslant z_N(x),$$
$$\frac{U_N^0(x)}{u^0(x)} \geqslant Q_{\min,N} \text{ on } [0,1],\ N = S, R \Big\},$$

which is our phase space. It is easy to check by definition that Δ is convex. Denote by Φ_t the solution semiflow generated by (2.1)–(2.3). Then we have

Proposition 2.1. *The phase space Δ is positively invariant under the semiflow Φ_t.*

The proof of this proposition is contained in Appendix A.

From now on, we restrict our attention to the system (2.1)–(2.3) with initial condition in the feasible set Δ. We show next that the system (2.1)–(2.3) is monotone. It is well known that [16] if Δ is convex, a sufficient condition for this to happen is that the system satisfies the Kamke condition. Denote the reaction terms in (2.1) by

$$H(u, U_S, U_R) = \big(H_1(u, U_S, U_R), H_2(u, U_S, U_R), H_3(u, U_S, U_R)\big),$$

where

$$H_1(u, U_S, U_R) = \min\left\{\mu_S\left(\frac{U_S}{u}\right), \mu_R\left(\frac{U_R}{u}\right)\right\}u,$$
$$H_2(u, U_S, U_R) = f_S\left(z_S(x) - U_S, \frac{U_S}{u}\right)u,$$
$$H_3(u, U_S, U_R) = f_R\left(z_R(x) - U_R, \frac{U_R}{u}\right)u.$$

By the monotonicity assumptions (H_1) and (H_2), H_i satisfies Kamke condition for each i. The Jacobian matrix of H at almost all points in the phase space Δ is cooperative, and irreducible at almost all interior points of Δ. Thus

Proposition 2.2. *The solution semiflow Φ_t is monotone on Δ, and strongly monotone in the interior of Δ.*

Let $\eta_0 > 0$ be the principal eigenvalue of the problem

$$d\phi_1''(x) + \eta_0\phi_1(x) = 0, \quad x \in (0,1),$$
$$\phi_1'(0) = \phi_1'(1) + \gamma\phi_1(1) = 0 \tag{2.4}$$

with the corresponding positive eigenfunction $\phi_1(x)$ uniquely determined by the normalization $\max_{[0,1]}\phi_1(x) = 1$. Suppose that there exists a unique constant number $Q_{c,S} \geqslant Q_{\min,S}$, $Q_{c,R} \geqslant Q_{\min,R}$ satisfying

$$\mu_S(Q_{c,S}) = \mu_R(Q_{c,R}) = \eta_0. \tag{2.5}$$

Remark 2.1. As in [9, Remark 2.1], if we choose the following functions $\mu(Q_N) = \mu_{\infty,N}(1 - \frac{Q_{\min,N}}{Q_N})$ as defined in (1.2), it is easy to see that (2.5) holds provided that the asymptotic growth rate $\mu_{\infty,N}$ is large enough, for either $N = S, R$.

In order to give a sufficient condition for the non-existence of a nontrivial steady state for (2.1)–(2.3), we need some results in [9]. In [9, Section 2], the authors considered the following system:

$$u_t = du_{xx} + \mu_N\left(\frac{U_N}{u}\right)u, \quad x \in (0,1),\ t > 0,$$
$$(U_N)_t = d(U_N)_{xx} + f_N\left(z_N(x) - U_N, \frac{U_N}{u}\right)u, \quad x \in (0,1),\ t > 0 \tag{2.6}$$

with boundary conditions

$$u_x(0,t) = 0, \qquad u_x(1,t) + \gamma u(1,t) = 0,$$
$$(U_N)_x(0,t) = 0, \qquad (U_N)_x(1,t) + \gamma U_N(1,t) = 0 \tag{2.7}$$

and initial conditions

$$u(x,0) = u^0(x) \geqslant 0, \qquad u^0(x) \not\equiv 0,$$
$$U_N(x,0) = U_N^0(x) \geqslant 0, \qquad U_N^0(x) \not\equiv 0, \tag{2.8}$$

where $z_N(x) = N^{(0)}(\frac{1+\gamma}{\gamma} - x)$.

Lemma 2.1. *(See [9, Theorem 2.1].) Suppose* η_0 *is defined in* (2.4) *and* $\mu_N(Q_{c,N}) = \eta_0$. *Then*:

(i) *If* $\min_{x\in[0,1]} f_N(z_N(x), Q_{c,N}) > \eta_0 Q_{c,N}$, *then the system* (2.6)–(2.8) *has a unique positive steady state which is globally asymptotically stable in its feasible set.*
(ii) *If* $\max_{x\in[0,1]} f_N(z_N(x), Q_{c,N}) \leqslant \eta_0 Q_{c,N}$, *then there is no steady state in its feasible set and every solution of the system* (2.6)–(2.8) *with initial condition in the feasible set satisfies* $(u(\cdot,t), U_N(\cdot,t)) \to (0,0)$ *as* $t \to \infty$.

Theorem 2.1. *Let* $\max_{x\in[0,1]} f_S(z_S(x), Q_{c,S}) \leqslant \eta_0 Q_{c,S}$ *or* $\max_{x\in[0,1]} f_R(z_R(x), Q_{c,R}) \leqslant \eta_0 Q_{c,R}$. *Then there is no steady state in* Δ *and every solution of the system* (2.1)–(2.3) *with initial condition in* Δ *satisfies* $(u(\cdot,t), U_S(\cdot,t), U_R(\cdot,t)) \to (0,0,0)$ *as* $t \to \infty$.

Proof. Without loss of generality, one may assume that $\max_{x\in[0,1]} f_S(z_S(x), Q_{c,S}) \leqslant \eta_0 Q_{c,S}$. From (2.1)–(2.3), we have the following inequalities

$$u_t = du_{xx} + \min\left\{\mu_S\left(\frac{U_S}{u}\right), \mu_R\left(\frac{U_R}{u}\right)\right\}u \leqslant du_{xx} + \mu_S\left(\frac{U_S}{u}\right)u,$$
$$(U_S)_t = d(U_S)_{xx} + f_S\left(z_S(x) - U_S, \frac{U_S}{u}\right)u,$$
$$(U_R)_t = d(U_R)_{xx} + f_R\left(z_R(x) - U_R, \frac{U_R}{u}\right)u.$$

By comparison theorem [16, p. 130, Theorem 3.4] and Lemma 2.1(ii) with $N = S$, we have $\lim_{t\to\infty}(u(x,t), U_S(x,t)) = (0,0)$ uniformly in $x \in [0,1]$. Therefore, the limiting equation for the third equation in (2.1) becomes

$$(U_R)_t = d(U_R)_{xx}$$

with the usual boundary condition (2.2) and initial condition (2.3). Hence,

$$\lim_{t\to\infty} U_R(x,t) = 0$$

uniformly in $x \in [0,1]$. We complete the proof. □

In the following, we shall construct upper and lower solutions for the elliptic equations associated with (2.1)–(2.3).

Lemma 2.2. *Suppose* $(\bar{u}, \bar{U}_S, \bar{U}_R) = (\min\{\frac{S^{(0)}}{Q_{\min,S}}, \frac{R^{(0)}}{Q_{\min,R}}\}(\frac{1+\gamma}{\gamma} - x), z_S(x), z_R(x))$. *Then* $(\bar{u}, \bar{U}_S, \bar{U}_R)$ *is a strict upper solution for the elliptic equations associated with the system* (2.1)–(2.3), *where* $z_S(x)$ *and* $z_R(x)$ *are defined in* (1.8).

Proof. Obviously, $\frac{\bar{U}_S}{\bar{u}} = \frac{S^{(0)}}{\min\{\frac{S^{(0)}}{Q_{\min,S}}, \frac{R^{(0)}}{Q_{\min,R}}\}} \geqslant Q_{\min,S}$ and $\frac{\bar{U}_R}{\bar{u}} = \frac{R^{(0)}}{\min\{\frac{S^{(0)}}{Q_{\min,S}}, \frac{R^{(0)}}{Q_{\min,R}}\}} \geqslant Q_{\min,R}$. This proves that

$$(\bar{u}, \bar{U}_S, \bar{U}_R) \in \Delta.$$

Clearly,

$$-\bar{u}'(0) = \min\left\{\frac{S^{(0)}}{Q_{\min,S}}, \frac{R^{(0)}}{Q_{\min,R}}\right\} > 0, \qquad \bar{u}'(1) + \gamma\bar{u}(1) = 0,$$
$$-\bar{U}_N'(0) = N^{(0)} > 0, \qquad \bar{U}_N'(1) + \gamma\bar{U}_N(1) = 0, \quad \forall N = S, R$$

where $\bar{u}'(0)$ is the outer normal derivative for $\bar{u}$ at 0, $\bar{u}'(1)$ et al. being similar. We note that if $\frac{S^{(0)}}{Q_{\min,S}} \leqslant \frac{R^{(0)}}{Q_{\min,R}}$ ($\frac{S^{(0)}}{Q_{\min,S}} \geqslant \frac{R^{(0)}}{Q_{\min,R}}$), then $\frac{\bar{U}_S}{\bar{u}} = Q_{\min,S}$ ($\frac{\bar{U}_R}{\bar{u}} = Q_{\min,R}$). This shows that $\min\{\mu_S(\frac{\bar{U}_S}{\bar{u}}), \mu_R(\frac{\bar{U}_R}{\bar{u}})\} = 0$. By calculation, we have

$$d\bar{u}'' + \min\left\{\mu_S\left(\frac{\bar{U}_S}{\bar{u}}\right), \mu_R\left(\frac{\bar{U}_R}{\bar{u}}\right)\right\}\bar{u} = 0 + 0 = 0,$$

and

$$d\bar{U}_N'' + f_N\left(z_N(x) - \bar{U}_N, \frac{\bar{U}_N}{\bar{u}}\right)\bar{u} = 0 + f_N\left(0, \frac{\bar{U}_N}{\bar{u}}\right)\bar{u} = 0, \quad \forall N = S, R,$$

which proves our lemma. □

Lemma 2.3. *Let* $\min_{x\in[0,1]} f_N(z_N(x), Q_{c,N}) > \eta_0 Q_{c,N}$ *with* $N = S, R$. *Then for* ϵ *sufficiently small,*

$$(\underline{u}, \underline{U}_S, \underline{U}_R) = (\epsilon\phi_1, \epsilon Q_{c,S}\phi_1, \epsilon Q_{c,R}\phi_1)$$

is a strict lower solution for the elliptic equations associated with the system (2.1)–(2.3).

Proof. Obviously, $(\underline{u}, \underline{U}_S, \underline{U}_R) \in \Delta$ satisfies the boundary conditions (2.2). It remains to show the following inequalities:

$$d\underline{u}'' + \min\left\{\mu_S\left(\frac{\underline{U}_S}{\underline{u}}\right), \mu_R\left(\frac{\underline{U}_R}{\underline{u}}\right)\right\}\underline{u} \geqslant 0, \tag{2.9a}$$

$$d\underline{U}_N'' + f_N\left(z_N(x) - \underline{U}_N, \frac{\underline{U}_N}{\underline{u}}\right)\underline{u} \geqslant 0, \quad \forall N = S, R. \tag{2.9b}$$

By calculation, we have

$$\begin{aligned} d\underline{u}'' + \min\left\{\mu_S\left(\frac{\underline{U}_S}{\underline{u}}\right), \mu_R\left(\frac{\underline{U}_R}{\underline{u}}\right)\right\}\underline{u} &= \epsilon d\phi_1'' + \min\{\mu_S(Q_{c,S}), \mu_R(Q_{c,R})\}\epsilon\phi_1 \\ &= \epsilon\left[d\phi_1''(x) + \eta_0\phi_1(x)\right] = 0, \end{aligned}$$

and

$$\begin{aligned} d\underline{U}_N'' + f_N\left(z_N(x) - \underline{U}_N, \frac{\underline{U}_N}{\underline{u}}\right)\underline{u} &= \epsilon Q_{c,N} d\phi_1'' + \epsilon f_N\big(z_N(x) - \epsilon Q_{c,N}\phi_1, Q_{c,N}\big)\phi_1 \\ &= \epsilon Q_{c,N}(-\eta_0\phi_1) + \epsilon f_N\big(z_N(x) - \epsilon Q_{c,N}\phi_1, Q_{c,N}\big)\phi_1 \\ &= \epsilon\big[-Q_{c,N}\eta_0 + f_N\big(z_N(x) - \epsilon Q_{c,N}\phi_1, Q_{c,N}\big)\big]\phi_1 > 0, \end{aligned}$$

provided that $\min_{x\in[0,1]} f_N(z_N(x), Q_{c,N}) > \eta_0 Q_{c,N}$ and $\epsilon > 0$ is small enough, for $N = S, R$. This proves (2.9a) and (2.9b). □

Theorem 2.2. *The system* (2.1)–(2.3) *has at most one nontrivial steady state in the phase space* Δ *which is globally asymptotically stable if it exists, otherwise, the origin is globally attractive. A sufficient condition for the existence of a nontrivial steady state is that*

$$\min_{x\in[0,1]} f_N\big(z_N(x), Q_{c,N}\big) > \eta_0 Q_{c,N}, \quad \textit{for } N = S, R.$$

Proof. Let $V = (u, U_S, U_R)$ and rewrite the system (2.1)–(2.3) in vector form:

$$\begin{aligned} G(V) &:= \big(G_1(V), G_2(V), G_3(V)\big) \\ &:= \left(\min\left\{\mu_S\left(\frac{U_S}{u}\right), \mu_R\left(\frac{U_R}{u}\right)\right\}u, f_S\left(z_S(x) - U_S, \frac{U_S}{u}\right)u, f_R\left(z_R(x) - U_R, \frac{U_R}{u}\right)u\right). \end{aligned}$$

Then (2.1)–(2.3) takes the form

$$\begin{aligned} &V_t = dV_{xx} + G(V), \quad 0 < x < 1,\ t > 0, \\ &V_x(0,t) = 0, \qquad V_x(1,t) + \gamma V(1,t) = 0. \end{aligned}$$

Next, we verify the following sublinear property of G: for any $0 < \alpha < 1$,

$$G(\alpha V) > \alpha G(V).$$

By calculation, we have

$$G_1(\alpha V) = \min\left\{\mu_S\left(\frac{\alpha U_S}{\alpha u}\right), \mu_R\left(\frac{\alpha U_R}{\alpha u}\right)\right\}(\alpha u) = \alpha G_1(V),$$

$$G_2(\alpha V) = f_S\left(z_S(x) - \alpha U_S, \frac{\alpha U_S}{\alpha u}\right)(\alpha u) > f_S\left(z_S(x) - U_S, \frac{U_S}{u}\right)(\alpha u) = \alpha G_2(V),$$

and

$$G_3(\alpha V) > \alpha G_3(V).$$

This shows that $G(\alpha V) > \alpha G(V)$ for any $0 < \alpha < 1$.

One can use the same arguments in [9] to show that the solution semiflow Φ_t has the property:

$$\Phi_t(\alpha P) > \alpha \Phi_t(P) \quad \text{for } 0 < \alpha < 1 \quad \text{and} \quad P := \left(u^0, U_S^0, U_R^0\right) \in \Delta. \tag{2.10}$$

(2.10) is a so-called sublinear property. Therefore, the system (2.1)–(2.3) has at most one positive steady-state solution (see, e.g., the proof of [9, Theorem 2.1]).

We note that the upper solution $(\bar{u}, \bar{U}_S, \bar{U}_R)$ in Lemma 2.2 is the greatest point in Δ with respect to the order $\leqslant$. So by the invariance of the solution semiflow, $\Phi_t(P) \leqslant (\bar{u}, \bar{U}_S, \bar{U}_R)$ for any $t > 0$ and $P \in \Delta$. Thus all solutions are bounded. Thus, P^* is globally asymptotically stable in Δ if a positive steady state P^* exists (see [10, Theorem D]). Otherwise, suppose that there is no steady state in Δ. Then we claim that every omega set from initial point in Δ is the origin. Let $P \in \Delta$ and $\omega(P)$ be its ω-limit set. Suppose that $\omega(P) \neq \{0\}$. Then since Δ is convex, $\omega(P)$ has the least upper bound $Q \in \Delta$. Thus $\Phi_t(\omega(P)) \leqslant \Phi_t(Q)$ for all t and $\omega(P) \leqslant \Phi_t(Q)$ by the invariance of ω-limit set. It follows that $Q \leqslant \Phi_t(Q)$. Therefore, by Convergence Criterion (see [16, p. 3, Theorem 2.1]), $\Phi_t(Q)$ converges to a steady state $P^* \gg 0$, contradicting the fact that there is no steady state in Δ.

Suppose that the conditions are true in the theorem. Then by Lemma 2.3, the system (2.1)–(2.3) has a lower solution $P(\epsilon) = (\underline{u}, \underline{U}_S, \underline{U}_R) = (\epsilon\phi_1, \epsilon Q_{c,S}\phi_1, \epsilon Q_{c,R}\phi_1)$ for sufficiently small ϵ. Thus $\Phi_t(P(\epsilon))$ increasingly tends to a unique steady state P^*. This completes the proof. □

Remark 2.2. Since $z_N(x) = N^{(0)}(\frac{1+\gamma}{\gamma} - x)$ and $f(N, Q_N)$ satisfies (H_2), it follows that $\min_{x\in[0,1]} f(z_N(x), Q_{c,N}) = f(z_N(1), Q_{c,N})$ and $\max_{x\in[0,1]} f(z_N(x), Q_{c,N}) = f(z_N(0), Q_{c,N})$.

Remark 2.3 *(Biological interpretation for Theorems 2.1–2.2).* As in [9, Remark 2.3], it is easy to see that $\eta_0 := \eta_0(d, \gamma)$ is increasing in d and γ respectively and $\eta_0(d, \gamma) \to 0$ as $d \to 0$ or $\gamma \to 0$. From (1.3), we assume $f(z_N(x), Q_N)$ takes the form

$$f\left(z_N(x), Q_N\right) = \rho_{\max,N} \frac{Q_{\max,N} - Q_N}{Q_{\max,N} - Q_{\min,N}} \frac{z_N(x)}{k_N + z_N(x)}.$$

Since $z_N(x) = N^{(0)}(\frac{1+\gamma}{\gamma} - x)$, it follows from Remark 2.2 that

$$\min_{x\in[0,1]} f\left(z_N(x), Q_{c,N}\right) = \rho_{\max,N} \frac{Q_{\max,N} - Q_{c,N}}{Q_{\max,N} - Q_{\min,N}} \frac{\frac{N^{(0)}}{\gamma}}{k_N + \frac{N^{(0)}}{\gamma}}$$

and

$$\max_{x\in[0,1]} f\left(z_N(x),\, Q_{c,N}\right) = \rho_{\max,N}\frac{Q_{\max,N}-Q_{c,N}}{Q_{\max,N}-Q_{\min,N}}\frac{N^{(0)}\frac{1+\gamma}{\gamma}}{k_N+N^{(0)}\frac{1+\gamma}{\gamma}}.$$

Thus, the condition for the existence of a nontrivial steady state in Theorem 2.2 is equivalent to

$$\rho_{\max,N}\frac{Q_{\max,N}-Q_{c,N}}{Q_{\max,N}-Q_{\min,N}}\frac{\frac{N^{(0)}}{\gamma}}{k_N+\frac{N^{(0)}}{\gamma}} > \eta_0(d,\gamma)Q_{c,N}, \quad \text{for } N=S,R,$$

it means that if the maximal uptake rates $\rho_{\max,S}$ and $\rho_{\max,R}$ are both larger, the diffusion coefficient d is smaller, the washout constant γ is smaller then the species survives.

Since $\max_{x\in[0,1]} f_N(z_N(x), Q_{c,N}) \leqslant \eta_0 Q_{c,N}$ is equivalent to

$$\rho_{\max,N}\frac{Q_{\max,N}-Q_{c,N}}{Q_{\max,N}-Q_{\min,N}}\frac{N^{(0)}\frac{1+\gamma}{\gamma}}{k_N+N^{(0)}\frac{1+\gamma}{\gamma}} \leqslant \eta_0(d,\gamma)Q_{c,N},$$

and hence, Theorem 2.1 means that if one of the maximal uptake rates $\rho_{\max,S}$ and $\rho_{\max,R}$ is smaller, one of the nutrient fluxes $S^{(0)}$ and $R^{(0)}$ is smaller, one of the half-saturation constants k_S and k_R is larger then the species goes to extinction.

3. Two species competition

The feasible domain for initial value functions of (1.9)–(1.11) is

$$\Sigma = \Bigg\{\left(u_1^0(x), U_{S1}^0(x), U_{R1}^0(x), u_2^0(x), U_{S2}^0(x), U_{R2}^0(x)\right) \in \left(C\left([0,1]\right)\right)^6 \;\Big|\; u_i^0(x)>0,\ U_{Ni}^0(x)>0,$$

$$U_{N1}^0(x)+U_{N2}^0(x) \leqslant z_N(x),\ \frac{U_{Ni}^0(x)}{u_i^0(x)} \geqslant Q_{\min,Ni},\ \text{on } [0,1],\ N=S,R,\ i=1,2\Bigg\}.$$

It is not difficult to examine by definition that Σ is convex. Denote by Ψ_t the solution semiflow generated by (1.9)–(1.11). Then we have

Proposition 3.1. *Σ is positively invariant under the semiflow Ψ_t.*

The proof of Proposition 3.1 is collected in Appendix A.

The assumptions (H_1) and (H_2) imply the Kamke condition holds for the system (1.9)–(1.11) in the sense of type-K order below. The Jacobian matrix of reaction terms at almost all points in the phase space Δ is cooperative, and irreducible at almost all interior points of Δ due to $\min\{\cdot,\cdot\}$ functions. The Jacobian of reaction terms in (1.9) with respect to $(u_1, U_{S1}, U_{R1}, u_2, U_{S2}, U_{R2})$ in Σ (if it exists) has the form

$$J = \begin{pmatrix} * & + & + & 0 & 0 & 0 \\ a_{S1} & * & 0 & 0 & - & 0 \\ a_{R1} & 0 & * & 0 & 0 & - \\ 0 & 0 & 0 & * & + & + \\ 0 & - & 0 & a_{S2} & * & 0 \\ 0 & 0 & - & a_{R2} & 0 & * \end{pmatrix}.$$

Note that for each $i = 1, 2$ and $N = S, R$, there holds

$$\begin{aligned} a_{Ni} &= f_{Ni}\left(z_N(x) - U_{N1} - U_{N2}, \frac{U_{Ni}}{u_i}\right) - \frac{U_{Ni}}{u_i}\frac{\partial f_{Ni}}{\partial Q_{Ni}}\left(z_N(x) - U_{N1} - U_{N2}, \frac{U_{Ni}}{u_i}\right) \\ &\geqq f_{Ni}\left(z_N(x) - U_{N1} - U_{N2}, \frac{U_{Ni}}{u_i}\right) \geqq 0. \end{aligned}$$

Obviously, J has the block structure characteristic of type K monotone system [16], consisting of diagonal 3×3 blocks with nonnegative off-diagonal entries and off-diagonal 3×3 non-positive blocks, where $K = \{(u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0) \in (C([0,1]))^6 \mid u_1^0 \geqslant 0,\ U_{S1}^0 \geqslant 0,\ U_{R1}^0 \geqslant 0;\ u_2^0 \leqslant 0,\ U_{S2}^0 \leqslant 0,\ U_{R2}^0 \leqslant 0\}$. Thus, the semiflow generated by the system (1.9)–(1.11) is monotone [16] under the partial order $\leqslant_K$. Furthermore, if

$$U_{S1} + U_{S2} < z_S(x) \quad \text{and} \quad U_{R1} + U_{R2} < z_R(x) \quad \text{for } x \in [0,1],$$

then J is irreducible (there is a simple test to show J is irreducible (see, e.g., [17, p. 256])), which implies that such a semiflow is strongly monotone in the interior of Σ. Thus, we have

Lemma 3.1. *Σ is convex, and $\Psi_t : \Sigma \to \Sigma$ is strongly monotone in the type K-order.*

Proof. From the above discussion, it suffices to show that for any initial data $P = (u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0) \in \Sigma$ with $U_{S1}^0(x_0) + U_{S2}^0(x_0) = z_S(x_0)$ for some $x_0 \in [0,1]$, we have

$$U_{S1}(x,t,P) + U_{S2}(x,t,P) < z_S(x) \quad \text{for any } t > 0,\ x \in [0,1].$$

If not, then there is a $\bar{t} > 0$, and $\bar{x} \in [0,1]$ such that

$$U_{S1}(\bar{x},\bar{t},P) + U_{S2}(\bar{x},\bar{t},P) = z_S(\bar{x}).$$

Let $Y_S(x,t) = z_S(x) - U_{S1}(x,t,P) - U_{S2}(x,t,P)$. Then

$$d(Y_S)_{xx} - (Y_S)_t = f_{S1}\left(Y_S(x,t), \frac{U_{S1}(x,t)}{u_1(x,t)}\right)u_1(x,t) + f_{S2}\left(Y_S(x,t), \frac{U_{S2}(x,t)}{u_2(x,t)}\right)u_2(x,t)$$

on $\Omega_{\bar{t}}$, where $\Omega_t \triangleq (0,1) \times (0,t]$. Denote

$$h(x,t) = u_1 \int_0^1 \frac{\partial f_{S1}}{\partial S}\left(\tau Y_S, \frac{U_{S1}}{u_1}\right) d\tau + u_2 \int_0^1 \frac{\partial f_{S2}}{\partial S}\left(\tau Y_S, \frac{U_{S2}}{u_2}\right) d\tau.$$

Then $h(x,t) \geqslant 0$. By the invariance of the solution semiflow on Σ (see Proposition 3.1), zero is the minimum value for $Y_S(x,t)$ on $\bar{\Omega}_{\bar{t}}$ at $(\bar{x},\bar{t})$, and

$$d(Y_S)_{xx} - (Y_S)_t - h(x,t)Y_S = 0 \quad \text{on } \Omega_{\bar{t}}.$$

Applying maximum principle, we obtain a contradiction. Similarly, for any initial data $P = (u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0) \in \Sigma$ with $U_{R1}^0(\tilde{x}_0) + U_{R2}^0(\tilde{x}_0) = z_R(\tilde{x}_0)$ for some $\tilde{x}_0 \in [0,1]$, we have

$$U_{R1}(x,t,P) + U_{R2}(x,t,P) < z_R(x) \quad \text{for any } x \in [0,1] \text{ and } t > 0.$$

Thus we conclude that $\Psi_t : \Sigma \to \Sigma$ is strongly monotone.

Suppose that there exists a unique constant number $Q_{c,Si} \geqslant Q_{\min,Si}$, $Q_{c,Ri} \geqslant Q_{\min,Ri}$ satisfying

$$\mu_{Si}(Q_{c,Si}) = \mu_{Ri}(Q_{c,Ri}) = \eta_0, \quad i = 1, 2,$$

where $\eta_0 > 0$ is the principal eigenvalue of the problem (2.4). In order to state our results, we require the following conditions:

(A) $$\min_{x\in[0,1]} f_{S1}\big(z_S(x), Q_{c,S1}\big) > \eta_0 Q_{c,S1} \quad \text{and} \quad \min_{x\in[0,1]} f_{R1}\big(z_R(x), Q_{c,R1}\big) > \eta_0 Q_{c,R1};$$

(A′) $$\max_{x\in[0,1]} f_{S1}\big(z_S(x), Q_{c,S1}\big) \leqslant \eta_0 Q_{c,S1} \quad \text{or} \quad \max_{x\in[0,1]} f_{R1}\big(z_R(x), Q_{c,R1}\big) \leqslant \eta_0 Q_{c,R1};$$

(B) $$\min_{x\in[0,1]} f_{S2}\big(z_S(x), Q_{c,S2}\big) > \eta_0 Q_{c,S2} \quad \text{and} \quad \min_{x\in[0,1]} f_{R2}\big(z_R(x), Q_{c,R2}\big) > \eta_0 Q_{c,R2};$$

(B′) $$\max_{x\in[0,1]} f_{S2}\big(z_S(x), Q_{c,S2}\big) \leqslant \eta_0 Q_{c,S2} \quad \text{or} \quad \max_{x\in[0,1]} f_{R1}\big(z_R(x), Q_{c,R2}\big) \leqslant \eta_0 Q_{c,R2}. \qquad \Box$$

Let the condition (A) hold. Then from Theorem 2.2, the system (2.1)–(2.3) with $\mu_N = \mu_{N1}$ and $f_N = f_{N1}$ for $N = S, R$ has a unique positive steady state $(u_1^*, U_{S1}^*, U_{R1}^*)$ which is globally asymptotically stable in its feasible region. Similarly, if the condition (B) holds, then the system (2.1)–(2.3) with $\mu_N = \mu_{N2}$ and $f_N = f_{N2}$ for $N = S, R$ has a unique positive steady state $(u_2^*, U_{S2}^*, U_{R2}^*)$ which is globally asymptotically stable in its feasible region. In the following, we will use the notations for both steady states.

Theorem 3.1. *The following statements hold*:

(i) *if the conditions* (A′) *and* (B′) *hold, then every solution* $(u_1, U_{S1}, U_{R1}, u_2, U_{S2}, U_{R2})$ *for the system* (1.9)–(1.11) *with initial data in* Σ *satisfies*

$$\lim_{t\to\infty} \big(u_1(x,t), U_{S1}(x,t), U_{R1}(x,t), u_2(x,t), U_{S2}(x,t), U_{R2}(x,t)\big) = (0,0,0,0,0,0)$$

uniformly in $x \in [0,1]$;

(ii) *if the conditions* (A) *and* (B′) *hold, then there is a semi-trivial solution* $(u_1^*, U_{S1}^*, U_{R1}^*, 0, 0, 0)$ *for the system* (1.9)–(1.11) *which is globally attractive in* Σ;

(iii) *if the conditions* (A′) *and* (B) *hold, then there is a semi-trivial solution* $(0, 0, 0, u_2^*, U_{S2}^*, U_{R2}^*)$ *for the system* (1.9)–(1.11) *which is globally attractive in* Σ.

Proof. (i) Suppose that the condition (B′) holds. From (1.9), we have the following inequalities

$$\begin{aligned}
(u_2)_t &= d(u_2)_{xx} + \min\left\{\mu_{S2}\left(\frac{U_{S2}}{u_2}\right), \mu_{R2}\left(\frac{U_{R2}}{u_2}\right)\right\}u_2, \\
(U_{S2})_t &= d(U_{S2})_{xx} + f_{S2}\left(z_S(x) - U_{S1} - U_{S2}, \frac{U_{S2}}{u_2}\right)u_2 \\
&\leqslant d(U_{S2})_{xx} + f_{S2}\left(z_S(x) - U_{S2}, \frac{U_{S2}}{u_2}\right)u_2, \\
(U_{R2})_t &= d(U_{R2})_{xx} + f_{R2}\left(z_R(x) - U_{R1} - U_{R2}, \frac{U_{R2}}{u_2}\right)u_2 \\
&\leqslant d(U_{R2})_{xx} + f_{R2}\left(z_R(x) - U_{R2}, \frac{U_{R2}}{u_2}\right)u_2.
\end{aligned}$$

By comparison theorem and Theorem 2.1, $\lim_{t\to\infty}(u_2(x,t), U_{S2}(x,t), U_{R2}(x,t)) = 0$ uniformly in $x \in [0,1]$. Similarly, $\lim_{t\to\infty}(u_1(x,t), U_{S1}(x,t), U_{R1}(x,t)) = (0,0,0)$ uniformly in $x \in [0,1]$ if the condition (A′) holds.

(ii) Obviously, from the condition (B′) and the proof of (i), (u_2, U_{S2}, U_{R2}) goes to extinction, and therefore, the limiting equations for the first three equations in (1.9) become

$$\begin{aligned}
(u_1)_t &= d(u_1)_{xx} + \min\left\{\mu_{S1}\left(\frac{U_{S1}}{u_1}\right), \mu_{R1}\left(\frac{U_{R1}}{u_1}\right)\right\}u_1,\\
(U_{S1})_t &= d(U_{S1})_{xx} + f_{S1}\left(z_S(x) - U_{S1}, \frac{U_{S1}}{u_1}\right)u_1, \quad x \in (0,1),\ t > 0,\\
(U_{R1})_t &= d(U_{R1})_{xx} + f_{R1}\left(z_R(x) - U_{R1}, \frac{U_{R1}}{u_1}\right)u_1
\end{aligned}$$

with the usual boundary conditions and initial conditions. By the condition (A) and Theorem 2.2, the above system has a unique steady state $(u_1^*, U_{S1}^*, U_{R1}^*)$ which is globally asymptotically stable in its feasible domain. Thus, $(u_1^*, U_{S1}^*, U_{R1}^*, 0, 0, 0)$ is a semi-trivial solution for system (1.9)–(1.11). The global attraction for the semi-trivial steady state $(u_1^*, U_{S1}^*, U_{R1}^*, 0, 0, 0)$ follows from the limiting equation theory.

(iii) The proof for (iii) is similar. □

In order to present our final result on coexistence or persistence, we need some notations and preliminary results.

Set $C := (C([0,1]))^6$. For $P, Q \in C$ with $P \ll_K Q$, define type-K order intervals

$$[P, Q]_K = \{R \in C \mid P \leqslant_K R \leqslant_K Q\},$$

and

$$\big[[P, Q]\big]_K = \{R \in C \mid P \ll_K R \ll_K Q\}.$$

Let $P^* = (0, 0, 0, u_2^*, U_{S2}^*, U_{R2}^*)$ and $Q^* = (u_1^*, U_{S1}^*, U_{R1}^*, 0, 0, 0)$. Then

Lemma 3.2. *$\omega(P) \subset [P^*, Q^*]_K$ for any $P \in \Sigma$.*

Proof. Fix a point $P = (u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0) \in \Sigma$. Let

$$\Psi_t(P) = \big(u_1(.,t,P), U_{S1}(.,t,P), U_{R1}(.,t,P), u_2(.,t,P), U_{S2}(.,t,P), U_{R2}(.,t,P)\big)$$

be the solution with initial data P. For $i = 1, 2$, it follows that

$$\big(u_i(.,t,P), U_{Si}(.,t,P), U_{Ri}(.,t,P)\big)$$

satisfies

$$\begin{aligned}
(u_i)_t &= d(u_i)_{xx} + \min\left\{\mu_{Si}\left(\frac{U_{Si}}{u_i}\right), \mu_{Ri}\left(\frac{U_{Ri}}{u_i}\right)\right\}u_i,\\
(U_{Si})_t &\leqslant d(U_{Si})_{xx} + f_{Si}\left(z_S(x) - U_{Si}, \frac{U_{Si}}{u_i}\right)u_i, \quad x \in (0,1),\ t > 0,
\end{aligned}$$

$$(U_{Ri})_t \leqslant d(U_{Ri})_{xx} + f_{Ri}\left(z_R(x) - U_{Ri}, \frac{U_{Ri}}{u_i}\right)u_i,$$
$$(u_i)_x(0,t) = 0, \qquad (u_i)_x(1,t) + \gamma u_i(1,t) = 0,$$
$$(U_{Si})_x(0,t) = 0, \qquad (U_{Si})_x(1,t) + \gamma U_{Si}(1,t) = 0,$$
$$(U_{Ri})_x(0,t) = 0, \qquad (U_{Ri})_x(1,t) + \gamma U_{Ri}(1,t) = 0,$$
$$u_i(.,0) = u_i^0, \qquad U_{Si}(.,0) = U_{Si}^0, \qquad U_{Ri}(.,0) = U_{Ri}^0.$$

From [16, p. 130, Theorem 3.4] it follows that for any $t > 0$

$$\big(u_i(.,t,P), U_{Si}(.,t,P), U_{Ri}(.,t,P)\big) \leqslant \Psi_t^{(i)}\big(u_i^0, U_{Si}^0, U_{Ri}^0\big),$$

where $\Psi_t^{(i)}(u_i^0, U_{Si}^0, U_{Ri}^0)$ $(i = 1,2)$ is the solutions for (2.1)–(2.3) resulting from putting $\mu_N = \mu_{Ni}$ and $f_N = f_{Ni}$, for $N = S, R$. Thus, applying Theorem 2.2, we obtain that

$$P^{(i)}\omega(P) \leqslant \big(u_i^*, U_{Si}^*, U_{Ri}^*\big),$$

where

$$P^{(i)}\big(u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0\big) = \big(u_i^0, U_{Si}^0, U_{Ri}^0\big), \quad i = 1,2$$

are projection mappings, that is,

$$\omega(P) \subset \big[P^*, Q^*\big]_K. \qquad \square$$

Lemma 3.3. *The following statements hold.*

(i) *Suppose that the condition* (B) *holds,* $\min_{x\in[0,1]} f_{N1}(z_N(x) - U_{N2}^*, Q_{c,N1}) > \eta_0 Q_{c,N1}$ *for* $N = S, R$ *and let*

$$\bar{P}(\epsilon) := (\underline{u}_1, \underline{U}_{S1}, \underline{U}_{R1}, \bar{u}_2, \bar{U}_{S2}, \bar{U}_{R2}) = \big(\epsilon\phi_1, \epsilon Q_{c,S1}\phi_1, \epsilon Q_{c,R1}\phi_1, u_2^*, U_{S2}^*, U_{R2}^*\big).$$

Then for $\varepsilon > 0$ *sufficiently small,* $\bar{P}(\epsilon)$ *is a strict lower solution for the elliptic system associated with* (1.9)–(1.11) *in the type* K*-order.*

(ii) *Suppose that the condition* (A) *holds,* $\min_{x\in[0,1]} f_{N2}(z_N(x) - U_{N1}^*, Q_{c,N2}) > \eta_0 Q_{c,N2}$ *for* $N = S, R$ *and let*

$$\bar{Q}(\epsilon) := (\bar{u}_1, \bar{U}_{S1}, \bar{U}_{R1}, \underline{u}_2, \underline{U}_{S2}, \underline{U}_{R2}) = \big(u_1^*, U_{S1}^*, U_{R1}^*, \epsilon\phi_1, \epsilon Q_{c,S2}\phi_1, \epsilon Q_{c,R2}\phi_1\big).$$

Then for $\varepsilon > 0$ *sufficiently small,* $\bar{Q}(\epsilon)$ *is a strict upper solution for the elliptic system associated with* (1.9)–(1.11) *in the type* K*-order.*

Proof. It is not difficult to show that $\underline{P}(\epsilon) \in \Sigma$ for $\epsilon > 0$ sufficiently small. Obviously, $\underline{P}(\epsilon)$ satisfies the boundary conditions. It remains to show the following inequalities:

$$
\begin{aligned}
d\underline{u}_1'' + \min\left\{\mu_{S1}\left(\frac{\underline{U}_{S1}}{\underline{u}_1}\right), \mu_{R1}\left(\frac{\underline{U}_{R1}}{\underline{u}_1}\right)\right\}\underline{u}_1 = 0 \geqslant 0,\\
d\underline{U}_{N1}'' + f_{N1}\left(z_N(x) - \underline{U}_{N1} - \bar{U}_{N2}, \frac{\underline{U}_{N1}}{\underline{u}_1}\right)\underline{u}_1 \geqslant 0, \quad \forall N = S, R,\\
d\bar{u}_2'' + \min\left\{\mu_{S2}\left(\frac{\bar{U}_{S2}}{\bar{u}_2}\right), \mu_{R2}\left(\frac{\bar{U}_{R2}}{\bar{u}_2}\right)\right\}\bar{u}_2 = 0 \leqslant 0,\\
d\bar{U}_{N2}'' + f_{N2}\left(z_N(x) - \underline{U}_{N1} - \bar{U}_{N2}, \frac{\bar{U}_{N2}}{\bar{u}_2}\right)\bar{u}_2 < 0, \quad \forall N = S, R.
\end{aligned} \tag{3.1}
$$

By calculation, we have

$$
d\underline{u}_1'' + \min\left\{\mu_{S1}\left(\frac{\underline{U}_{S1}}{\underline{u}_1}\right), \mu_{R1}\left(\frac{\underline{U}_{R1}}{\underline{u}_1}\right)\right\}\underline{u}_1 = \epsilon\left[d\phi_1'' + \min\left\{\mu_{S1}(Q_{c,S1}), \mu_{R1}(Q_{c,R1})\right\}\phi_1\right] = 0,
$$

and

$$
\begin{aligned}
& d\underline{U}_{N1}'' + f_{N1}\left(z_N(x) - \underline{U}_{N1} - \bar{U}_{N2}, \frac{\underline{U}_{N1}}{\underline{u}_1}\right)\underline{u}_1\\
&= \epsilon Q_{c,N1} d\phi_1'' + f_{N1}\left(z_N(x) - \epsilon Q_{c,N1}\phi_1 - U_{N2}^*, Q_{c,N1}\right)\epsilon\phi_1\\
&= \epsilon\phi_1\left[f_{N1}\left(z_N(x) - \epsilon Q_{c,N1}\phi_1 - U_{N2}^*, Q_{c,N1}\right) - \eta_0 Q_{c,N1}\right] > 0,
\end{aligned}
$$

provided that $f_{N1}(z_N(x) - U_{N2}^*, Q_{c,N1}) > \eta_0 Q_{c,N1}$ and $\epsilon > 0$ is small enough for $N = S, R$. Furthermore,

$$
d\bar{u}_2'' + \min\left\{\mu_{S2}\left(\frac{\bar{U}_{S2}}{\bar{u}_2}\right), \mu_{R2}\left(\frac{\bar{U}_{R2}}{\bar{u}_2}\right)\right\}\bar{u}_2 = d\left(u_2^*\right)'' + \min\left\{\mu_{S2}\left(\frac{U_{S2}^*}{u_2^*}\right), \mu_{R2}\left(\frac{U_{R2}^*}{u_2^*}\right)\right\}u_2^* = 0,
$$

and

$$
d\bar{U}_{N2}'' + f_{N2}\left(z_N(x) - \underline{U}_{N1} - \bar{U}_{N2}, \frac{\bar{U}_{N2}}{\bar{u}_2}\right)\bar{u}_2 < d\left(U_{N2}^*\right)'' + f_{N2}\left(z_N(x) - U_{N2}^*, \frac{U_{N2}^*}{u_2^*}\right)u_2^* = 0
$$

for either $N = S, R$. Thus, $\underline{P}(\epsilon)$ is a strict lower solution for the elliptic system associated with (1.9)–(1.11) in the type K-order. We have proved (3.1) and then complete the proof of part (i). Part (ii) can be proved in a similar way and we omit it. □

The following results show that coexistence of two competing species occurs if each can be invaded by its competitor.

Theorem 3.2. *Suppose that the conditions* (A), (B) *and*

$$
\min_{x\in[0,1]} f_{Ni}\left(z_N(x) - U_{Nj}^*, Q_{c,Ni}\right) > \eta_0 Q_{c,Ni}, \quad \text{for } i \neq j,\ i, j = 1, 2;\ N = S, R
$$

hold. Then there are a minimal steady state $E^- \in \Sigma$ which is lower asymptotically stable and a maximal steady state $E^+ \in \Sigma$ which is upper asymptotically stable such that

$$
\omega(P) \subset \left[E^-, E^+\right]_K \cap \Sigma \quad \text{for any } P \in \Sigma.
$$

The system (1.9)–(1.11) *is uniformly persistent and* $\Psi_t(P)$ *tends to a steady state for* P *in an open and dense subset in* Σ.

Proof. Combining Lemma 3.3, [16, Theorem 3.4], Lemma 3.2 and strong monotonicity for Ψ_t, one gets the results from the theory of strongly monotone dynamical systems (see, e.g., [16] and the proof of [9, Theorem 3.2]). □

Remark 3.1. We note that one can use the similar argument as that in [9, Theorem 3.3] to lift the dynamics of the limiting system (1.9)–(1.11) to the full system (1.5)–(1.7).

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Appendix A. The invariance on the feasible domains

In this appendix, we will prove the positive invariance for the solution semiflows of (2.1)–(2.3) and (1.9)–(1.11) on their feasible domains. Because the proofs of both positive invariance results are exactly the same, we only give the proof of Proposition 3.1 which is more complicated.

In order to give rigorous proof of the positive invariance, we need to extend definition for related functions involving in (1.9)–(1.11).

For $i = 1, 2$ and $N = S, R$, define

$$F_{Ni}(N, Q_{Ni}) = \begin{cases} f_{Ni}(N, Q_{Ni}) & \text{for } N \geqslant 0,\ Q_{Ni} \geqslant Q_{\min,Ni}, \\ -f_{Ni}(|\,N\,|, Q_{Ni}) & \text{for } N < 0,\ Q_{Ni} \geqslant Q_{\min,Ni}, \\ f_{Ni}(N, Q_{\min,Ni}) & \text{for } N \geqslant 0,\ Q_{Ni} < Q_{\min,Ni}, \\ -f_{Ni}(|\,N\,|, Q_{\min,Ni}) & \text{for } N < 0,\ Q_N < Q_{\min,Ni} \end{cases}$$

and

$$\tilde{\mu}_{Ni}(Q_{Ni}) = \begin{cases} \mu_{Ni}(Q_{Ni}) & \text{for } Q_{Ni} \geqslant Q_{\min,Ni}, \\ \mu'_{Ni}(Q_{\min,Ni})(Q_{Ni} - Q_{\min,Ni}) & \text{for } Q_{Ni} < Q_{\min,Ni}. \end{cases}$$

Hence,

$$\tilde{\mu}_{Ni}(Q_{Ni}) = G_{Ni}(Q_{Ni})(Q_{Ni} - Q_{\min,Ni}),$$

where $G_{Ni}(Q_{Ni}) = \int_0^1 \tilde{\mu}'_{Ni}(\tau Q_{Ni} + (1-\tau)Q_{\min,Ni})\,d\tau > 0$.

For $i = 1, 2$ and $N = S, R$, we introduce

$$W_{Ni} = U_{Ni} - Q_{\min,Ni} u_i,$$

and we get that

$$\tilde{\mu}_{Ni}\left(\frac{U_{Ni}}{u_i}\right) = G_{Ni}\left(\frac{U_{Ni}}{u_i}\right)\frac{W_{Ni}}{u_i}.$$

Now, we consider the extended system

$$(u_i)_t = d(u_i)_{xx} + \min\left\{\tilde{\mu}_{Si}\left(\frac{U_{Si}}{u_i}\right), \tilde{\mu}_{Ri}\left(\frac{U_{Ri}}{u_i}\right)\right\}u_i,$$

$$(U_{Si})_t = d(U_{Si})_{xx} + F_{Si}\left(z_S(x) - U_{S1} - U_{S2}, \frac{U_{Si}}{u_i}\right)u_i, \quad x \in (0,1),\ t > 0,$$

$$(U_{Ri})_t = d(U_{Ri})_{xx} + F_{Ri}\left(z_R(x) - U_{R1} - U_{R2}, \frac{U_{Ri}}{u_i}\right)u_i, \quad i = 1,2 \tag{A.1}$$

with the usual boundary conditions (1.10) and initial conditions (1.11).

Without causing confusion, we drop the notation tilde in the following. Furthermore, we introduce

$$Y_N = z_N(x) - U_{N1} - U_{N2}, \quad N = S, R.$$

Proof of Proposition 3.1. By the theory of semilinear parabolic differential equations (see [8]), it follows that for every initial value data

$$P_0 = \left(u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0\right) \in \Sigma,$$

the system (A.1) has a unique regular solution

$$\left(u_1(x,t,P_0), U_{S1}(x,t,P_0), U_{R1}(x,t,P_0), u_2(x,t,P_0), U_{S2}(x,t,P_0), U_{R2}(x,t,P_0)\right)$$

with the maximal interval of existence $[0, \tau(P_0))$ and $\tau(P_0) = \infty$ provided

$$\left(u_1(x,t,P_0), U_{S1}(x,t,P_0), U_{R1}(x,t,P_0), u_2(x,t,P_0), U_{S2}(x,t,P_0), U_{R2}(x,t,P_0)\right)$$

has an L^∞-bound on $[0, \tau(P_0))$. The solution semiflow is defined by

$$\Psi_t(P_0) = \left(u_1(.,t,P_0), U_{S1}(.,t,P_0), U_{R1}(.,t,P_0), u_2(.,t,P_0), U_{S2}(.,t,P_0), U_{R2}(.,t,P_0)\right).$$

It suffices to show that Σ is positively invariant under the semiflow Ψ_t generated by the system (A.1).

We first notice that if $\Psi_t(u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0) \in \Sigma$ $(t > 0)$ for any initial data $P_0 = (u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0)$ in $\operatorname{Int}\Sigma$ satisfying $U_{S1}^0(x) + U_{S2}^0(x) < z_S(x)$, $U_{R1}^0(x) + U_{R2}^0(x) < z_R(x)$, $\frac{U_{Si}^0(x)}{u_i^0(x)} > Q_{\min,Si}$ and $\frac{U_{Ri}^0(x)}{u_i^0(x)} > Q_{\min,Ri}$ for $0 \leqslant x \leqslant 1$ and $i = 1,2$ then the conclusion of Proposition 3.1 holds. Suppose not. Then there is a point $P_0 = (u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0) \in \partial\Sigma$ so that at least one of the above inequalities become equal and a $\tau > 0$ such that $\Psi_\tau(u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0) \notin \Sigma$. Thus, by the continuity of solutions with respect to initial points, one can finds a point $\tilde{P}_0 = (\tilde{u}_1^0, \tilde{U}_{S1}^0, \tilde{U}_{R1}^0, \tilde{u}_2^0, \tilde{U}_{S2}^0, \tilde{U}_{R2}^0) \in \operatorname{Int}\Sigma$ such that $\Psi_\tau(\tilde{P}_0)$ goes out of Σ, a contradiction. Therefore, without loss of generality, we may assume that $P_0 = (u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0) \in \operatorname{Int}\Sigma$.

Suppose that the proposition is false. Let

$$t^* = \sup\left\{\tau \;\middle|\; \Psi_t\left(u_1^0, U_{S1}^0, U_{R1}^0, u_2^0, U_{S2}^0, U_{R2}^0\right) \in \Sigma \text{ on } [0,\tau]\right\}.$$

Then $0 < t^* < \tau(P_0)$. This implies that one of the following twelve cases must occur:

(I) $U_{S1}(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$ with $U_{S1}(x^*,t^*) = 0$ for some x^* in $[0,1]$, and $U_{R1}(x,t) \geqslant 0$, $u_1(x,t) \geqslant 0$, $U_{S2}(x,t) \geqslant 0$, $U_{R2}(x,t) \geqslant 0$, $u_2(x,t) \geqslant 0$, $Y_S(x,t) \geqslant 0$, $Y_R(x,t) \geqslant 0$, $W_{S1}(x,t) \geqslant 0$, $W_{S2}(x,t) \geqslant 0$, $W_{R1}(x,t) \geqslant 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(II) $U_{R1}(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$ with $U_{R1}(x^*,t^*) = 0$ for some x^* in $[0,1]$, and $U_{S1}(x,t) > 0$, $u_1(x,t) \geqslant 0$, $U_{S2}(x,t) \geqslant 0$, $U_{R2}(x,t) \geqslant 0$, $u_2(x,t) \geqslant 0$, $Y_S(x,t) \geqslant 0$, $Y_R(x,t) \geqslant 0$, $W_{S1}(x,t) \geqslant 0$, $W_{S2}(x,t) \geqslant 0$, $W_{R1}(x,t) \geqslant 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(III) $u_1(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$ with $u_1(x^*,t^*) = 0$ for some x^* in $[0,1]$, and $U_{S1}(x,t) > 0$, $U_{R1}(x,t) > 0$, $U_{S2}(x,t) \geqslant 0$, $U_{R2}(x,t) \geqslant 0$, $u_2(x,t) \geqslant 0$, $Y_S(x,t) \geqslant 0$, $Y_R(x,t) \geqslant 0$, $W_{S1}(x,t) \geqslant 0$, $W_{S2}(x,t) \geqslant 0$, $W_{R1}(x,t) \geqslant 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(IV) $U_{S2}(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$ with $U_{S2}(x^*,t^*) = 0$ for some x^* in $[0,1]$, and $U_{S1}(x,t) > 0$, $U_{R1}(x,t) > 0$, $u_1(x,t) > 0$, $U_{R2}(x,t) \geqslant 0$, $u_2(x,t) \geqslant 0$, $Y_S(x,t) \geqslant 0$, $Y_R(x,t) \geqslant 0$, $W_{S1}(x,t) \geqslant 0$, $W_{S2}(x,t) \geqslant 0$, $W_{R1}(x,t) \geqslant 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(V) $U_{R2}(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$ with $U_{R2}(x^*,t^*) = 0$ for some x^* in $[0,1]$, and $U_{S1}(x,t) > 0$, $U_{R1}(x,t) > 0$, $u_1(x,t) > 0$, $U_{S2}(x,t) > 0$, $u_2(x,t) \geqslant 0$, $Y_S(x,t) \geqslant 0$, $Y_R(x,t) \geqslant 0$, $W_{S1}(x,t) \geqslant 0$, $W_{S2}(x,t) \geqslant 0$, $W_{R1}(x,t) \geqslant 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(VI) $u_2(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$ with $u_2(x^*,t^*) = 0$ for some x^* in $[0,1]$, and $U_{S1}(x,t) > 0$, $U_{R1}(x,t) > 0$, $u_1(x,t) > 0$, $U_{S2}(x,t) > 0$, $U_{R2}(x,t) > 0$, $Y_S(x,t) \geqslant 0$, $Y_R(x,t) \geqslant 0$, $W_{S1}(x,t) \geqslant 0$, $W_{S2}(x,t) \geqslant 0$, $W_{R1}(x,t) \geqslant 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(VII) $Y_S(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x},\bar{t}) \in [0,1] \times (t^*,t)$ such that $Y_S(\bar{x},\bar{t}) < 0$, and $U_{S1}(x,t) > 0$, $U_{R1}(x,t) > 0$, $u_1(x,t) > 0$, $U_{S2}(x,t) > 0$, $U_{R2}(x,t) > 0$, $u_2(x,t) > 0$, $Y_R(x,t) \geqslant 0$, $W_{S1}(x,t) \geqslant 0$, $W_{S2}(x,t) \geqslant 0$, $W_{R1}(x,t) \geqslant 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(VIII) $Y_R(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x},\bar{t}) \in [0,1] \times (t^*,t)$ such that $Y_R(\bar{x},\bar{t}) < 0$, and $U_{S1}(x,t) > 0$, $U_{R1}(x,t) > 0$, $u_1(x,t) > 0$, $U_{S2}(x,t) > 0$, $U_{R2}(x,t) > 0$, $u_2(x,t) > 0$, $Y_S(x,t) > 0$, $W_{S1}(x,t) \geqslant 0$, $W_{S2}(x,t) \geqslant 0$, $W_{R1}(x,t) \geqslant 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(IX) $W_{S1}(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x},\bar{t}) \in [0,1] \times (t^*,t)$ such that $W_{S1}(\bar{x},\bar{t}) < 0$, and $U_{S1}(x,t) > 0$, $U_{R1}(x,t) > 0$, $u_1(x,t) > 0$, $U_{S2}(x,t) > 0$, $U_{R2}(x,t) > 0$, $u_2(x,t) > 0$, $Y_S(x,t) > 0$, $Y_R(x,t) > 0$, $W_{S2}(x,t) \geqslant 0$, $W_{R1}(x,t) \geqslant 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(X) $W_{S2}(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x},\bar{t}) \in [0,1] \times (t^*,t)$ such that $W_{S2}(\bar{x},\bar{t}) < 0$, and $U_{S1}(x,t) > 0$, $U_{R1}(x,t) > 0$, $u_1(x,t) > 0$, $U_{S2}(x,t) > 0$, $U_{R2}(x,t) > 0$, $u_2(x,t) > 0$, $Y_S(x,t) > 0$, $Y_R(x,t) > 0$, $W_{S1}(x,t) > 0$, $W_{R1}(x,t) \geqslant 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(XI) $W_{R1}(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x},\bar{t}) \in [0,1] \times (t^*,t)$ such that $W_{R1}(\bar{x},\bar{t}) < 0$, and $U_{S1}(x,t) > 0$, $U_{R1}(x,t) > 0$, $u_1(x,t) > 0$, $U_{S2}(x,t) > 0$, $U_{R2}(x,t) > 0$, $u_2(x,t) > 0$, $Y_S(x,t) > 0$, $Y_R(x,t) > 0$, $W_{S1}(x,t) > 0$, $W_{S2}(x,t) > 0$, $W_{R2}(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(XII) $W_{R2}(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x},\bar{t}) \in [0,1] \times (t^*,t)$ such that $W_{R2}(\bar{x},\bar{t}) < 0$, and $U_{S1}(x,t) > 0$, $U_{R1}(x,t) > 0$, $u_1(x,t) > 0$, $U_{S2}(x,t) > 0$, $U_{R2}(x,t) > 0$, $u_2(x,t) > 0$, $Y_S(x,t) > 0$, $Y_R(x,t) > 0$, $W_{S1}(x,t) > 0$, $W_{S2}(x,t) > 0$, $W_{R1}(x,t) > 0$ on $[0,1] \times [0,t^*]$.

Let $\Omega_t = (0,1) \times (0,t]$. In each case, we shall deduce a contradiction via various maximum principles as follows.

Suppose that the case I occurs. Then

$$Y_S(x,t) = z_S(x) - U_{S1}(x,t) - U_{S2}(x,t) \geqslant 0 \quad \text{in } \bar{\Omega}_{t^*},$$

and

$$d(U_{S1})_{xx} - (U_{S1})_t = -F_{S1}\left(z_S(x) - U_{S1} - U_{S2}, \frac{U_{S1}}{u_1}\right)u_1(x,t)$$
$$= -F_{S1}\left(Y_S(x,t), \frac{U_{S1}(x,t)}{u_1(x,t)}\right)u_1(x,t) \leqslant 0 \quad \text{on } \Omega_{t^*}.$$

If $0 < x^* < 1$, then from the strong maximum principle (see [15, pp. 168–169, Theorem 2]), we obtain that $U_{S1}(x,t) \equiv 0$ on $\bar{\Omega}_{t^*}$ which is impossible because $U_{S1}(x,0) = U^0_{S1}(x) > 0$ on $[0,1]$. Thus $x^* = 0$ or 1. If $x^* = 0$, then $(U_{S1})_x(0,t^*) > 0$ [15, p. 170, Theorem 3], contradicting the boundary condition (1.10). If $x^* = 1$, that is, $U_{S1}(1,t^*) = 0$, then $(U_{S1})_x(1,t^*) < 0$ by the same theorem in [15]. However, from the boundary condition $(U_{S1})_x(1,t^*) + \gamma U_{S1}(1,t^*) = 0$, we deduce that $(U_{S1})_x(1,t^*) = 0$, a contradiction. The cases II, IV, V can be treated analogously.

Suppose the case III occurs. Then

$$\frac{U_{S1}(x,t)}{u_1(x,t)} \geqslant Q_{\min,S1}, \qquad \frac{U_{R1}(x,t)}{u_1(x,t)} \geqslant Q_{\min,R1} \quad \text{on } \Omega_{t^*},$$

and

$$d(u_1)_{xx} - (u_1)_t = -\min\left\{\mu_{S1}\left(\frac{U_{S1}(x,t)}{u_1(x,t)}\right), \mu_{R1}\left(\frac{U_{R1}(x,t)}{u_1(x,t)}\right)\right\}u_1(x,t) \leqslant 0 \quad \text{on } \Omega_{t^*}.$$

From the strong maximum principle and Hopf boundary lemma, one obtains contradictions again. The case VI can be treated analogously.

Suppose the case VII occurs. Then

$$d(Y_S)_{xx} - (Y_S)_t = \left[-d(U_{S1})_{xx} + (U_{S1})_t\right] + \left[-d(U_{S2})_{xx} + (U_{S2})_t\right]$$
$$= F_{S1}\left(Y_S(x,t), \frac{U_{S1}(x,t)}{u_1(x,t)}\right)u_1(x,t) + F_{S2}\left(Y_S(x,t), \frac{U_{S2}(x,t)}{u_2(x,t)}\right)u_2(x,t)$$
$$= \left[u_1\int_0^1 \frac{\partial F_{S1}}{\partial S}\left(\tau Y_S, \frac{U_{S1}}{u_1}\right)d\tau + u_2\int_0^1 \frac{\partial F_{S2}}{\partial S}\left(\tau Y_S, \frac{U_{S2}}{u_2}\right)d\tau\right]Y_S \quad \text{on } \Omega_{\tilde{t}}.$$

Let $h(x,t) \triangleq u_1\int_0^1 \frac{\partial F_{S1}}{\partial S}(\tau Y_S, \frac{U_{S1}}{u_1})\,d\tau + u_2\int_0^1 \frac{\partial F_{S2}}{\partial S}(\tau Y_S, \frac{U_{S2}}{u_2})\,d\tau$. Then $h(x,t) \geqslant 0$ on $\Omega_{\tilde{t}}$ and $Y_S(x,t)$ satisfies

$$d(Y_S)_{xx} - (Y_S)_t - h(x,t)Y_S = 0 \quad \text{on } \Omega_{\tilde{t}}.$$

Suppose $Y_S(x,t)$ gets the minimum at the point $\tilde{P} = (\tilde{x},\tilde{t})$ on $\bar{\Omega}_{\tilde{t}}$. If $0 < \tilde{x} < 1$, then the maximum principle in [15, p. 172, Theorem 4] implies that $Y_S(x,t) \equiv Y_S(\tilde{P})$ for $t \leqslant \tilde{t}$ and $x \in [0,1]$, which contradicts the boundary condition of U_{S1} and U_{S2} at $x = 0$. If $\tilde{x} = 0$, then by the boundary conditions (1.10), $(Y_S)_x(0,\tilde{t}) = -S^{(0)} - (U_{S1})_x(0,\tilde{t}) - (U_{S2})_x(0,\tilde{t}) = -S^{(0)} < 0$. Therefore, $Y_S(x,\tilde{t})$ is strictly decreasing as $0 < x \ll 1$, contradicting that Y_S attains a minimum at $(0,\tilde{t})$. If $\tilde{x} = 1$, then $(Y_S)_x(1,\tilde{t}) = -S^{(0)} - (U_{S1})_x(1,\tilde{t}) - (U_{S2})_x(1,\tilde{t}) = -S^{(0)} + \gamma U_{S1}(1,\tilde{t}) + \gamma U_{S2}(1,\tilde{t}) \leqslant 0$. But $0 > Y_S(1,\tilde{t}) = \frac{S^{(0)}}{\gamma} - U_{S1}(1,\tilde{t}) - U_{S2}(1,\tilde{t})$, equivalently, $-S^{(0)} + \gamma U_{S1}(1,\tilde{t}) + \gamma U_{S2}(1,\tilde{t}) > 0$, a contradiction the above inequality. The case VIII can be treated analogously.

We consider the case IX. From the assumptions of case IX, we may assume that $Y_S(x,t) > 0$ on $[0,1] \times [0,t^* + \epsilon]$ with $\epsilon > 0$ sufficiently small. We fix $t^* < t < t^* + \epsilon$ and the corresponding $\bar{t}$ is given in the assumptions. By calculation,

$$
\begin{aligned}
&d(W_{S1})_{xx} - (W_{S1})_t \\
&\quad = -F_{S1}\left(Y_S(x,t), \frac{U_{S1}(x,t)}{u_1(x,t)}\right)u_1(x,t) + Q_{\min,S1}\min\left\{G_{S1}\left(\frac{U_{S1}}{u_1}\right)\frac{W_{S1}}{u_1}, G_{R1}\left(\frac{U_{R1}}{u_1}\right)\frac{W_{R1}}{u_1}\right\}u_1 \\
&\quad \leqslant -F_{S1}\left(Y_S(x,t), \frac{U_{S1}(x,t)}{u_1(x,t)}\right)u_1(x,t) + Q_{\min,S1}G_{S1}\left(\frac{U_{S1}}{u_1}\right)W_{S1} \quad \text{on } \Omega_{\bar{t}},
\end{aligned}
$$

that is,

$$
\begin{aligned}
&d(W_{S1})_{xx} - (W_{S1})_t - Q_{\min,S1}G_{S1}\left(\frac{U_{S1}}{u_1}\right)W_{S1} \\
&\quad \leqslant -F_{S1}\left(Y_S(x,t), \frac{U_{S1}(x,t)}{u_1(x,t)}\right)u_1(x,t) \leqslant 0 \quad \text{on } \Omega_{\bar{t}},
\end{aligned}
$$

with the boundary conditions

$$(W_{S1})_x(0,t) = 0, \qquad (W_{S1})_x(1,t) + \gamma W_{S1}(1,t) = 0.$$

The assumptions for case IX imply that $W_{S1}(x,t)$ attains a negative minimum at a point $\tilde{P} = (\tilde{x}, \tilde{t})$ on $\bar{\Omega}_{\bar{t}}$. If $0 < \tilde{x} < 1$, then due to $h = -Q_{\min,S1}G_{S1}(\frac{U_{S1}}{u_1}) < 0$ by assumptions in case IX, a maximum principle in [15, p. 174, Theorem 7] is applied to this case to conclude that

$$W_{S1}(x,t) \equiv W_{S1}(\tilde{P}) < 0 \quad \text{on } \bar{\Omega}_{\bar{t}}$$

which leads to a contradiction that

$$W_{S1}(x,0) = U_{S1}^0(x) - Q_{\min,S1}u_1^0(x) > 0 \quad \text{on } [0,1].$$

If $\tilde{x} = 0$, then again using [15, p. 174, Theorem 7], we have $(W_{S1})_x(0,\tilde{t}) > 0$, contradicting to the boundary condition $(W_{S1})_x(0,t) = 0$. If $\tilde{x} = 1$, then [15, p. 174, Theorem 7] implies that $(W_{S1})_x(1,\tilde{t}) < 0$. But $W_{S1}(1,\tilde{t}) < 0$, it follows from the boundary condition for W_{S1} that

$$(W_{S1})_x(1,\tilde{t}) = -\gamma W_{S1}(1,\tilde{t}) > 0,$$

a contradiction. The cases X, XI, XII can be treated analogously. Thus we complete the proof of Proposition 3.1. □

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