Pattern formation of a Schnakenberg-type plant root hair initiation model

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Abstract. This paper concentrates on the diversity of patterns in a quite general Schnakenberg-type model. We discuss existence and nonexistence of nonconstant positive steady state solutions as well as their bounds. By means of investigating Turing, steady state and Hopf bifurcations, pattern formation, including Turing patterns, nonconstant spatial patterns or time periodic orbits, is shown. Also, the global dynamics analysis is carried out.

Keywords: Schnakenberg-type model, pattern formation, global bifurcation, steady state solution, Hopf bifurcation, Turing bifurcation.

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1 Introduction

Reaction-diffusion systems have definitely become a powerful tool for explaining biochemical reactions and species diversity because of the incorporation of elements including interaction mechanism and spatiotemporal behavior. In this paper, our attention is paid to the following spatially homogeneous plant root hair initiation model proposed in [20] which is viewed as the generalisation of Schnakenberg system [25]

$$\begin{cases} \frac{\partial u}{\partial t} = D_1 \Delta u + k_2 u^2 v - (c+r)u + k_1 v, & x \in \Omega, \ t > 0, \\ \frac{\partial v}{\partial t} = D_2 \Delta v - k_2 u^2 v + cu - k_1 v + b, & x \in \Omega, \ t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \ t > 0, \\ u(x, 0) = u_0(x) \ge 0, & v(x, 0) = v_0(x) \ge 0, \ x \in \Omega, \end{cases}$$
(1.1)

where all parameters are positive and $\Omega \in \mathbb{R}^n$ is a bounded domain. From the perspective of biology, initiation and growth of root hair (RH) result from the accumulation of active small G-proteins ROPs (Rhos of plants). In fact, the active ROPs are derived both from the transformation of inactive ROP by guanine nucleotide exchange factors (GEF) and from the

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induction of auxins together with other substances. Based on the mechanism above, the model simulates the interactions between inactive and active ROP (the detailed modeling process is found in [1, 20]). u(x, t) and v(x, t) in (1.1) indicate concentrations of active and inactive ROP, respectively. $k_1 + k_2u^2$ is the rate of ROP activation, *c* is the unbinding rate of active ROP, *r* shows the removing rate of active ROP by degradation, recycling, or other irreversible binding, and the inactive ROP is produced at rate *b*.

Early in 1952, Alan M. Turing put forward a reaction-diffusion model in order to explain pattern formation in embryo. It is demonstrated that the diffusion can be considered as a spontaneous driving force for spatiotemporal structure of non-equilibrium states. His analysis not only contributed to experimental research [3, 6, 11, 18], but also greatly stimulated theoretical results on the mathematical models of pattern formation. For instance, (1.1) gives us several particular well-known models: Sel'kov model [26] as well as excellent related work [5, 13, 21, 24, 30, 37], Gray–Scott model [16, 23], Schnakenberg model [8, 14, 32, 34, 38], Sel'kov–Schnakenberg model [12, 28], Brusselator model [2, 4, 7, 10].

The extremely general model to include cases above is just the same as system (1.1), and we will continue to treat its patterns on the basis of previous extensive works. Our paper aims at pattern formation in the system (1.1). To explore existence and nonexistence of pattern formation, it is essential to discuss problems about steady states. In detail, by analyzing characteristic equation as well as some classical techniques (including comparison theorem, lower-upper solutions, priori estimate), constant bounds, existence and uniqueness of solutions in parabolic equation (1.1) are determined, also, another points are local and global asymptotically stability of constant equilibrium. Moreover, equiped with priori bounds, energy estimates and Leray–Schauder degree theory in elliptic partial differential equations (PDEs)

$$\begin{cases}
-D_{1}\Delta u = k_{2}u^{2}v - (c+r)u + k_{1}v, \ x \in \Omega \\
-D_{2}\Delta v = -k_{2}u^{2}v + b - k_{1}v + cu, \ x \in \Omega \\
\frac{\partial u}{\partial v} = \frac{\partial v}{\partial v} = 0, \quad x \in \partial\Omega,
\end{cases}$$
(1.2)

we prove existence together with nonexistence of nonconstant positive steady states, which explains whether system (1.1) processes spatial patterns. Moreover, by taking global dynamics of PDE system into consideration, the diversity of patterns is revealed. In detail, analysis for bifurcations indicates Turing, nonconstant spatial as well as time-periodic patterns.

2 Stability of equilibrium

2.1 Local stability

Obviously, we are able to find that system (1.1) has a unique equilibrium $E = (u^*, v^*) = (\frac{b}{r}, \frac{br(c+r)}{k_2b^2+k_1r^2})$. The locally asymptotical stability of *E* can be analyzed.

Theorem 2.1. Denote $K = \frac{k_2 b^2 + k_1 r^2}{k_2 b^2 - k_1 r^2}$, then (u^*, v^*) is locally asymptotically stable as $K \leq 0$ or $\frac{v^*}{u^*} < \min\left\{1, \frac{D_1}{D_2}\right\}K$, and is unstable for $\frac{v^*}{u^*} > K > 0$.

Proof. Initially, the linear operator at *E* is

$$L := \begin{pmatrix} 2k_2u^*v^* - (c+r) + D_1\Delta & k_2u^{*2} + k_1 \\ -2k_2u^*v^* + c & -k_2u^{*2} - k_1 + D_2\Delta \end{pmatrix}$$
(2.1)

implying a sequence of matrices

$$L_{i} := \begin{pmatrix} 2k_{2}u^{*}v^{*} - (c+r) - D_{1}\mu_{i} & k_{2}u^{*2} + k_{1} \\ -2k_{2}u^{*}v^{*} + c & -k_{2}u^{*2} - k_{1} - D_{2}\mu_{i} \end{pmatrix}$$
(2.2)

where μ_i is the *i*th eigenvalue of $-\Delta$ in $H^1(\Omega)$ corresponding to Neumann boundary condition satisfying $0 = \mu_0 < \mu_1 \leq \mu_2 \leq \cdots$ and $\lim_{i\to\infty} \mu_i = \infty$. Assume λ is the eigenvalue of *L*, and the characteristic equation is written as

$$\lambda^2 - \operatorname{tr}(L_i)\lambda + \operatorname{det}(L_i) = 0, \qquad i = 0, 1, 2, \dots$$
 (2.3)

with

$$\operatorname{tr}(L_i) = -(D_1 + D_2)\mu_i + 2k_2u^*v^* - (c+r) - k_2u^{*2} - k_1,$$

$$\operatorname{det}(L_i) = D_1 D_2 \mu_i^2 + [(c+r - 2k_2u^*v^*)D_2 + (k_2u^{*2} + k_1)D_1]\mu_i + r(k_2u^{*2} + k_1).$$
(2.4)

Next, it is essential to discuss the eigenvalues of (2.3) because all eigenvalues with negative real parts demonstrate that *E* is locally asymptotically stable, otherwise *E* is unstable.

1. If $2k_2u^*v^* \leq c + r$, i.e., $k_2b^2 \leq k_1r^2$, then for all $i \geq 0$, $tr(L_i) < 0$ and $det(L_i) > 0$. Thus, (u^*, v^*) is locally asymptotically stable.

2. When $k_2b^2 > k_1r^2$, it is required that

$$2k_2u^*v^* - (c+r) - k_2u^{*2} - k_1 < 0$$

(k_2u^{*2} + k_1)D_1 > (2k_2u^*v^* - c - r)D_2
(2.5)

for tr(L_i) < 0 and det(L_i) > 0, that is, the equilibrium is stable. By some calculation, the condition is equivalent to $\frac{v^*}{u^*} < \min\{1, \frac{D_1}{D_2}\}\frac{k_2b^2 + k_1r^2}{k_2b^2 - k_1r^2}$.

3. Also for $k_2b^2 > k_1r^2$, if $\frac{v^*}{u^*} > \frac{k_2b^2 + k_1r^2}{k_2b^2 - k_1r^2}$, then tr(L_0) > 0 causes at least one eigenvalue with positive real part. As a result, we have an unstable equilibrium.

2.2 Global stability

The main conclusion about global stability of *E* in this subsection is demonstrated as follows.

Theorem 2.2. Suppose that the domain $\Omega \subset \mathbb{R}^n$ is bounded and the boundary $\partial \Omega$ is smooth.

- (*i*) For $u_0(x) \ge 0 \ (\neq 0)$, $v_0(x) \ge 0 \ (\neq 0)$, system (1.1) has a unique solution (u(x, t), v(x, t)) satisfying $0 < u(x, t) \le u^*$, $0 < v(x, t) \le v^*$, as t > 0 and $x \in \overline{\Omega}$.
- (ii) If $k_1r^2 > 4k_2b^2$ and $k_1 \ge (\max_{x \in \bar{\Omega}} u_0(x))^2$, then $\lim_{t \to \infty} (u(x, t), v(x, t)) = (u^*, v^*)$ with $(u_0(x), v_0(x)) \ge (\not\equiv)(0, 0)$.

Proof. (i) Follow the marks in [19] and denote

$$f_1(u, v) = k_2 u^2 v - (c+r)u + k_1 v, \ f_2(u, v) = -k_2 u^2 v + b - k_1 v + cu.$$

Apparently, (1.1) is a nonquasimonotone system. Let $(\hat{u}, \hat{v}) = (\bar{u}(t), 0)$ and $(\tilde{u}, \tilde{v}) = (u^*, \min\{v^*, \bar{v}(t)\})$, where

$$\bar{u}(t) = u(0)e^{-(c+r)t}$$
 and $\bar{v}(t) = \frac{b(c+r) - [b(c+r) - k_1rv(0)]e^{-k_1t}}{k_1r}$

are, respectively, solutions of

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$$\begin{cases} \frac{du}{dt} = -(c+r)u, \\ u(0) = \inf_{x \in \bar{\Omega}} u_0(x), \end{cases}$$
(2.6)

and

$$\begin{cases} \frac{dv}{dt} = cu^* + b - k_1 v, \\ v(0) = \sup_{x \in \bar{\Omega}} v_0(x). \end{cases}$$
(2.7)

Subsequently, we are dedicated to proving that (\hat{u}, \hat{v}) and (\tilde{u}, \tilde{v}) are lower and supper solutions of (1.1), respectively. In fact,

$$\begin{aligned} \frac{\partial u}{\partial t} - D_1 \Delta \hat{u} - f_1(\hat{u}, v) &= -(k_2 \hat{u}^2 v + k_1 v) < 0 = -f_1(u^*, v^*) \\ &\leq \frac{\partial \tilde{u}}{\partial t} - D_1 \Delta \tilde{u} - f_1(\tilde{u}, v), \quad \text{for all } v \in \langle \hat{v}, \, \tilde{v} \rangle, \end{aligned}$$

and

$$\begin{aligned} \frac{\partial \hat{v}}{\partial t} - D_2 \Delta \hat{v} - f_2(u, \, \hat{v}) &= -(cu+b) < 0 < c(u^*-u) + k_2 u^2 \bar{v} \\ &= \frac{\partial \bar{v}}{\partial t} - D_2 \Delta \bar{v} - f_2(u, \, \bar{v}), \quad \text{for all } u \in \langle \hat{u}, \, \tilde{u} \rangle. \end{aligned}$$

It is also easy to check the boundary-initial conditions are satisfied, so a pair of lower and upper solutions is definitely found.

In addition, one can get $f_i(u, v)$ (i = 1, 2) meet the Lipschitz condition. Theorem 8.9.3 in [19] implies that system (1.1) has a unique global solution (u(x, t), v(x, t)) and

$$\hat{u} \leq u(x, t) \leq \tilde{u}, \ \hat{v} \leq v(x, t) \leq \tilde{v}, \ t \geq 0.$$

Then u(x, t), v(x, t) > 0 as t > 0 for $x \in \overline{\Omega}$ by the strong maximum principle [35].

(ii) About the global stability of (u^*, v^*) , the second equation of system (1.1) admits that

$$v_t - D_2 \Delta v \le c u^* + b - k_1 v_2$$

Thus, Lemma A.1 in [39] and comparison principle show that

$$\limsup_{t\to\infty} \max_{x\in\bar{\Omega}} v(x, t) \le \frac{b(c+r)}{k_1 r} =: \bar{v}_1.$$

This yields that there exists a constant $T_1^{\varepsilon} \gg 1$ such that

$$v(x, t) \leq \bar{v}_1 + \varepsilon$$

for $x \in \overline{\Omega}$, $t \ge T_1^{\varepsilon}$ and $\varepsilon > 0$ small enough. Because of $k_1 r^2 > 4k_2 b^2$, one should note that

$$(c+r)^2 - 4k_1k_2(\bar{v}_1 + \varepsilon)^2 > 0$$

with $\varepsilon > 0$.

Now considering the first equation in (1.1), it is easy to conclude that for $x \in \overline{\Omega}$ and $t \ge T_1^{\varepsilon}$,

$$u_t - D_1 \Delta u \le k_2 (\bar{v}_1 + \varepsilon) u^2 - (c + r) u + k_1 (\bar{v}_1 + \varepsilon) =: \zeta_1(u).$$

The roots of $\zeta_1(u)$ then are u_1^{ε} and u_2^{ε} , where

$$u_1^{\varepsilon} = \frac{c + r - \sqrt{(c+r)^2 - 4k_1k_2(\bar{v}_1 + \varepsilon)^2}}{2k_2(\bar{v}_1 + \varepsilon)}$$

and

$$u_{2}^{\varepsilon} = \frac{c + r + \sqrt{(c + r)^{2} - 4k_{1}k_{2}(\bar{v}_{1} + \varepsilon)^{2}}}{2k_{2}(\bar{v}_{1} + \varepsilon)} > \sqrt{k_{1}}$$

It is derived from $\max_{x\in\bar{\Omega}} u_0(x) \leq \sqrt{k_1}$ that there is a constant $\sigma > 0$ such that $\zeta_1(u)$ has exactly one root $u_1^{\varepsilon} \in (0, \max_{x\in\bar{\Omega}} u_0(x) + \sigma]$. Notice $\zeta'_1(u_1^{\varepsilon}) < 0$ and again apply Lemma A.1 in [39] and comparison principle to get

$$\limsup_{t \to \infty} \max_{x \in \bar{\Omega}} u(x, t) \le \frac{c + r - \sqrt{(c + r)^2 - 4k_1 k_2 \bar{v}_1^2}}{2k_2 \bar{v}_1} = \frac{k_1 r - \sqrt{k_1^2 r^2 - 4k_1 k_2 b^2}}{2k_2 b} =: \bar{u}_1.$$
(2.8)

Also, for $\varepsilon > 0$ small enough, $\exists T_2^{\varepsilon} \gg 1$ guarantees that as $x \in \overline{\Omega}$ and $t \leq T_2^{\varepsilon}$,

$$u(x, t) \leq \bar{u}_1 + \varepsilon.$$

Let $\varepsilon \to 0$, and Lemma A.1 in [39] together with the second equation of (1.1) give us that

$$\liminf_{t \to \infty} \min_{x \in \bar{\Omega}} v(x, t) \ge \frac{b + cu^*}{k_1 + k_2 \bar{u}_1^2} =: \underline{v}_1 \le \bar{v}_1.$$
(2.9)

For $0 < \varepsilon < \underline{v}_1$, we have

$$(c+r)^2 - 4k_1k_2(\bar{v}_1 - \varepsilon)^2 > 0.$$

As a result, $\exists T_3^{\varepsilon} \gg 1$ makes sure that

$$v(x, t) \geq \underline{v}_1 - \varepsilon$$

for $x \in \overline{\Omega}$ and $t \geq T_3^{\varepsilon}$.

In the same manner above,

$$\liminf_{t \to \infty} \min_{x \in \bar{\Omega}} u(x, t) \ge \frac{c + r - \sqrt{(c+r)^2 - 4k_1 k_2 \underline{v}_1^2}}{2k_2 \underline{v}_1} =: \underline{u}_1 \le \bar{u}_1.$$
(2.10)

Thus, it is obtained that for $0 < \varepsilon < \underline{u}_1$, there exists $T_4^{\varepsilon} \gg 1$ such that

$$u(x, t) \geq \underline{u}_1 - \varepsilon$$

with $x \in \overline{\Omega}$ and $t \geq T_4^{\varepsilon}$.

Also, one can get

$$\limsup_{t \to \infty} \max_{x \in \bar{\Omega}} v(x, t) \le \frac{b + cu^*}{k_1 + k_2 \underline{u}_1^2} =: \bar{v}_2,$$
(2.11)

as well as $\underline{v}_1 \leq \overline{v}_2 \leq \overline{v}_1$. Similarly, it is correct that

$$\limsup_{t \to \infty} \max_{x \in \bar{\Omega}} u(x, t) \le \frac{c + r - \sqrt{(c + r)^2 - 4k_1 k_2 \bar{v}_2^2}}{2k_2 \bar{v}_2} =: \bar{u}_2$$
(2.12)

and $\underline{u}_1 \leq \overline{u}_2 \leq \overline{u}_1$.

Now, denote

$$\begin{split} \varphi(s) &= \frac{b + cu^*}{k_1 + k_2 s^2}, \ s > 0 \\ \psi(s) &= \frac{c + r - \sqrt{(c + r)^2 - 4k_1 k_2 s^2}}{2k_2 s}, \qquad 0 < s < \frac{c + r}{2\sqrt{k_1 k_2}} \end{split}$$

Obviously, φ , ψ are decreasing and increasing, respectively. \bar{u}_i , \bar{v}_i , \underline{u}_i , \underline{v}_i (i = 1, 2) above satisfy

$$\begin{cases} \underline{v}_{1} = \varphi(\bar{u}_{1}) \leq \varphi(\underline{u}_{1}) = \bar{v}_{2} \leq \bar{v}_{1} = \frac{b(c+r)}{k_{1}r}, \\ \underline{u}_{1} = \psi(\bar{v}_{1}) \leq \psi(\bar{v}_{2}) = \bar{u}_{2} \leq \bar{u}_{1} = \psi(\bar{v}_{1}), \\ \underline{v}_{1} \leq \liminf_{t \to \infty} \min_{x \in \bar{\Omega}} v(x, t) \leq \limsup_{t \to \infty} \max_{x \in \bar{\Omega}} v(x, t) \leq \bar{v}_{2}, \\ \underline{u}_{1} \leq \liminf_{t \to \infty} \min_{x \in \bar{\Omega}} u(x, t) \leq \limsup_{t \to \infty} \max_{x \in \bar{\Omega}} u(x, t) \leq \bar{u}_{2}. \end{cases}$$
(2.13)

That is to say, we construct four sequences $\{\overline{v}_i\}_{i=1}^{\infty}$, $\{\overline{u}_i\}_{i=1}^{\infty}$, $\{\underline{v}_i\}_{i=1}^{\infty}$, $\{\underline{u}_i\}_{i=1}^{\infty}$ with

$$\bar{v}_1 = \frac{b(c+r)}{k_1 r}, \quad \bar{u}_i = \psi(\bar{v}_i), \quad \underline{v}_i = \varphi(\bar{u}_i), \quad \underline{u}_i = \psi(\underline{v}_i), \quad \bar{v}_{i+1} = \varphi(\underline{u}_i), \quad (2.14)$$

such that

$$\underline{v}_{i} \leq \liminf_{t \to \infty} \min_{x \in \bar{\Omega}} v(x, t) \leq \limsup_{t \to \infty} \max_{x \in \bar{\Omega}} v(x, t) \leq \bar{v}_{i},$$

$$\underline{u}_{i} \leq \liminf_{t \to \infty} \min_{x \in \bar{\Omega}} u(x, t) \leq \limsup_{t \to \infty} \max_{x \in \bar{\Omega}} u(x, t) \leq \bar{u}_{i}.$$
(2.15)

Applying the monotonicity of φ and ψ and the relationship above, it follows

$$\underline{v}_{i} \leq \underline{v}_{i+1} = \varphi(\overline{u}_{i+1}) \leq \varphi(\underline{u}_{i}) = \overline{v}_{i+1} \leq \overline{v}_{i},$$

$$\underline{u}_{i} \leq \underline{u}_{i+1} = \psi(\underline{v}_{i+1}) \leq \psi(\overline{v}_{i+1}) = \overline{u}_{i+1} \leq \overline{u}_{i}.$$
(2.16)

Based on the monotonicity of sequences, assume that

$$\lim_{i \to \infty} \underline{u}_i = \underline{u}, \quad \lim_{i \to \infty} \bar{u}_i = \bar{u}, \quad \lim_{i \to \infty} \underline{v}_i = \underline{v}, \quad \lim_{i \to \infty} \bar{v}_i = \underline{v}.$$
(2.17)

Thus, \underline{u} , \overline{u} , \underline{v} , \overline{v} maintain the order $0 \le \underline{u} \le \overline{u}$, $0 \le \underline{v} \le \overline{v}$ and satisfy

$$\bar{u} = \psi(\bar{v}), \quad \bar{v} = \varphi(\underline{u}), \quad \underline{u} = \psi(\underline{v}), \quad \underline{v} = \varphi(\bar{u}).$$
 (2.18)

Plugging the functions into the equations, then it should be that

$$\begin{cases} (c+r)\bar{u} - k_2\bar{u}^2\bar{v} - k_1\bar{v} = 0, \\ k_1\bar{v} + k_2\underline{u}^2\bar{v} - b - cu^* = 0, \\ (c+r)\underline{u} - k_2\underline{u}^2\underline{v} - k_1\underline{v} = 0, \\ k_1\underline{v} + k_2\bar{u}^2\underline{v} - b - cu^* = 0. \end{cases}$$
(2.19)

$$(c+r)\bar{u} - b - cu^* - k_2\bar{v}(\bar{u} - \underline{u})(\bar{u} + \underline{u}) = 0,$$

(c+r)u - b - cu^* + k_2\underline{v}(\bar{u} - \underline{u})(\bar{u} + \underline{u}) = 0. (2.20)

Consider the equations above together, it follows that

$$(\bar{v}+\underline{v})(\bar{u}+\underline{u})(\bar{u}-\underline{u}) = 0 \tag{2.21}$$

implying $\bar{u} = \underline{u} = \frac{b}{r}$ and $\bar{v} = \underline{v} = \frac{br(c+r)}{k_1r^2 + k_2b^2}$.

3 Existence and nonexistence of nonconstant positive steady states

In this section, we investigate whether there exist nonconstant positive steady states for system (1.1). In other words, the solutions of (1.2) should be considered.

3.1 Nonexistence of nonconstant positive steady states

In the beginning, we focus on the priori estimate of positive solutions for (1.2). According to Proposition 2.2 in [15] and Theorem 8.18 in [9] (also see [13]), the following conclusion is demonstrated.

Theorem 3.1. For any solution (u(x), v(x)) of (1.2) and given positive constant $c^* > 0$, there exists two positive constant \underline{C} , \overline{C} , depending on k_1 , k_2 , c, r, b, Ω , such that

$$\underline{C} \leq u(x), \ v(x) \leq \overline{C} \text{ for any } x \in \overline{\Omega}$$

provided that $c \leq c^*$.

Proof. Let (u, v) is a solution of (1.2). First integrating both sides of (1.2) by parts gives that

$$\int_{\Omega} [k_2 u^2 v - (c+r)u + k_1 v] dx = \int_{\Omega} [-k_2 u^2 v + cu - k_1 v + b] dx = 0.$$
(3.1)

Adding the two equalities above, we obtain that

$$\int_{\Omega} u(x)dx = \frac{b}{r}|\Omega|.$$
(3.2)

According to the first equation, the following relationship is satisfied

$$-\Delta u + \frac{c^* + r}{D_1}u \ge -\Delta u + \frac{c + r}{D_1}u = \frac{1}{D_1}(k_2u^2v + k_1v) \ge 0.$$
(3.3)

Thus, Theorem 8.18 in [9] shows that there exists a positive constant C such that

$$u(x) \geq C, \qquad \forall x \in \bar{\Omega}.$$

Adding the equations in (1.2), denoting $w = D_1 u + D_2 v$ and $w(x_0) = \max_{\overline{\Omega}} w(x)$, then

$$-\Delta w = b - ru \quad \text{in } \Omega \quad \text{and} \quad \partial_{\nu} w = 0 \quad \text{on } \partial\Omega. \tag{3.4}$$

Applying Proposition 2.2 in [15] yields that

$$b-ru(x_0)\geq 0,$$

that is, $u(x_0) \leq \frac{b}{r}$.

As a result, we finally get that

$$C \le u(x) \le \frac{b}{r}.$$

Next, we discuss the priori estimate of v(x). As a detail, set $v(x_1) = \max_{\bar{\Omega}} v(x)$ and $v(x_2) = \min_{\bar{\Omega}} v(x)$.

Then it follows from Proposition 2.2 in [15] that

$$-k_2 u^2(x_1) v(x_1) + c u(x_1) - k_1 v(x_1) + b \ge 0,$$
(3.5)

and it is easy to see that

$$v(x_1) \le \frac{b + cu(x_1)}{k_1 + k_2 u^2(x_1)} \le \frac{b(c+r)}{r(k_1 + k_2 C^2)}.$$
(3.6)

Again because of Proposition 2.2 in [15],

$$-k_2u^2(x_2)v(x_2) + cu(x_2) - k_1v(x_2) + b \le 0$$

produces

$$v(x_2) \ge \frac{b + cu(x_2)}{k_1 + k_2 u^2(x_2)} \ge \frac{r^2(b + cC)}{k_1 r^2 + k_2 b^2}.$$
(3.7)

Therefore, it is concluded that

$$\frac{r^2(b+cC)}{k_1r^2+k_2b^2} \le v(x) \le \frac{b(c+r)}{r(k_1+k_2C^2)}.$$

Finally, it follows that $\underline{C} = \min \{C, \frac{r^2(b+cC)}{k_1r^2+k_2b^2}\}, \ \overline{C} = \max \{\frac{b}{r}, \frac{b(c+r)}{r(k_1+k_2C^2)}\}.$

With the help of Theorem 3.1 and methods together with results in [31], the nonexistence of nonconstant solutions is stated.

Theorem 3.2. For any fixed k_1 , k_2 , b, c, r, if $\min\{D_1, D_2\} > \frac{D}{\mu_1}$, then the only nonnegative solution to (1.2) is (u^*, v^*) , where μ_1 is the smallest positive eigenvalue corresponding to the operator $-\Delta$ and $D = \max\{r + \frac{3c+k_1+7k_2\bar{C}^2}{2}, \frac{c+3k_1+5k_2\bar{C}^2}{2}\}$.

Proof. Let (u, v) is a nonnegative solution of (1.2), $u_0 = \frac{1}{|\Omega|} \int_{\Omega} u dx$, and $v_0 = \frac{1}{|\Omega|} \int_{\Omega} v dx$. Consequently, $u_0 = \frac{b}{r}$ from (3.2), and

$$\int_{\Omega} (u-u_0) dx = \int_{\Omega} (v-v_0) dx = 0.$$

Multiplying the first equation by $u - u_0$ and using the integration by parts in Ω , we have

$$D_{1} \int_{\Omega} |\nabla(u - u_{0})|^{2} dx$$

$$= \int_{\Omega} [k_{2}u^{2}v - (c + r)u + k_{1}v](u - u_{0})dx$$

$$= \int_{\Omega} [k_{2}u^{2}v - k_{2}u_{0}^{2}v_{0} + (c + r)u_{0} - k_{1}v_{0} - (c + r)u + k_{1}v](u - u_{0})dx$$

$$= \int_{\Omega} [k_{2}u^{2}v - k_{2}u_{0}^{2}v_{0} - (c + r)(u - u_{0}) - k_{1}(v - v_{0})](u - u_{0})dx$$

$$= k_{2} \int_{\Omega} [v(u + u_{0})(u - u_{0}) + u_{0}^{2}(v - v_{0})](u - u_{0})dx$$

$$- (c + r) \int_{\Omega} (u - u_{0})^{2}dx - k_{1} \int_{\Omega} (u - u_{0})(v - v_{0})dx$$

$$\leq (c + r + 2k_{2}\bar{C}^{2}) \int_{\Omega} (u - u_{0})^{2}dx + (k_{1} + k_{2}\bar{C}^{2}) \int_{\Omega} (v - v_{0})^{2}dx.$$
(3.8)

In the same way, we can also get

$$D_{2} \int_{\Omega} |\nabla(v-v_{0})|^{2} dx$$

$$= \int_{\Omega} [-k_{2}u^{2}v + cu - k_{1}v + b](v-v_{0})dx$$

$$= \int_{\Omega} [-k_{2}u^{2}v + k_{2}u_{0}^{2}v_{0} + cu - k_{1}v - cu_{0} + k_{1}v_{0}](v-v_{0})dx$$

$$= \int_{\Omega} [-k_{2}u^{2}v + k_{2}u_{0}^{2}v_{0}](v-v_{0})dx + c \int_{\Omega} (u-u_{0})(v-v_{0})dx - k_{1} \int_{\Omega} (v-v_{0})^{2}dx$$

$$= -k_{2} \int_{\Omega} [v(u+u_{0})(u-u_{0}) + u_{0}^{2}(v-v_{0})](v-v_{0})dx$$

$$+ c \int_{\Omega} (u-u_{0})(v-v_{0})dx - k_{1} \int_{\Omega} (v-v_{0})^{2}dx$$

$$\leq (k_{1}+k_{2}\bar{C}^{2}) \int_{\Omega} (v-v_{0})^{2}dx + (c+2k_{2}\bar{C}^{2}) \int_{\Omega} (u-u_{0})(v-v_{0})dx$$

$$\leq \left(\frac{c}{2}+k_{2}\bar{C}^{2}\right) \int_{\Omega} (u-u_{0})^{2}dx + \left(k_{1}+2k_{2}\bar{C}^{2}+\frac{c}{2}\right) \int_{\Omega} (v-v_{0})^{2}dx.$$
(3.9)

In addition, based on the Poincaré inequality

$$\mu_1 \int_{\Omega} (u - u_0)^2 dx \le \int_{\Omega} |\nabla (u - u_0)|^2 dx, \ \mu_1 \int_{\Omega} (v - v_0)^2 dx \le \int_{\Omega} |\nabla (v - v_0)|^2 dx,$$

where μ_1 is the smallest positive eigenvalue of $-\Delta$. The results above lead to

$$D_{1} \int_{\Omega} |\nabla (u - u_{0})^{2}| dx + D_{2} \int_{\Omega} |\nabla (v - v_{0})^{2}| dx$$

$$\leq \frac{1}{\mu_{1}} \left(A \int_{\Omega} |\nabla (u - u_{0})^{2}| dx + B \int_{\Omega} |\nabla (v - v_{0})^{2}| dx \right),$$
(3.10)

where $A = r + \frac{3c + k_1 + 7k_2\bar{C}^2}{2}$, $B = \frac{c + 3k_1 + 5k_2\bar{C}^2}{2}$. This shows that if

$$\min\{D_1, D_2\} > \frac{1}{\mu_1}\max\{A, B\},$$

then

$$\nabla(u-u_0) = \nabla(v-v_0) = 0,$$

and (u, v) must be a constant solution.

3.2 Existence of nonconstant positive steady states

We intend to indicate the existence of nonconstant steady states in this subsection. Set the following function spaces

$$X = \{(u, v) \in C^{1}(\bar{\Omega}) \times C^{1}(\bar{\Omega}) : \partial_{\nu}u = \partial_{\nu}v = 0 \text{ on } \partial\Omega\},\$$

$$X^{+} = \{(u, v) : u, v \ge 0, (u, v) \in X\},\$$

$$\Lambda = \{(u, v) \in X : \underline{C} \le u, v \le \bar{C} \text{ for } x \in \bar{\Omega}\},\$$

$$E(\mu) = \{\phi | -\Delta\phi = \mu\phi \text{ in } \Omega, \ \partial_{\nu}\phi = 0 \text{ on } \partial\Omega\}.$$
(3.11)

If $E(\mu_i)$ is the eigenspace corresponding to μ_i , $\{\phi_{ij} \mid j = 1, ..., \dim E(\mu_i)\}$ are the orthogonal bases of $E(\mu_i)$ and $X_{ij} = \{c\phi_{ij} \mid c \in \mathbb{R}^2\}$, then X can be separated into

$$X = \bigoplus_{i=1}^{\infty} X_i$$
, $X_i = \bigoplus_{j=1}^{\dim E(\mu_i)} X_{ij}$.

According to the Leray–Schauder topological degree theory, transfer (1.2) into

 $-\Delta U = G(U) \quad \text{in } \Omega, \quad \partial_{\nu} U = 0 \quad \text{on } \partial \Omega$ (3.12)

where

$$G(U) = \begin{pmatrix} \frac{1}{D_1} (k_2 u^2 v - (c+r)u + k_1 v) \\ \frac{1}{D_2} (-k_2 u^2 v + cu - k_1 v + b) \end{pmatrix}.$$

Then U is a positive solution of (2.7) if and only if

$$\Gamma(U) \doteq U - (-\Delta + I)^{-1} \{ G(U) + U \} = 0$$
 in X^+ ,

where I is the identity operator. By calculation,

$$D_U \Gamma(U^*) = \mathbf{I} - (-\Delta + \mathbf{I})^{-1} (\mathbf{I} + \mathcal{A}),$$

where

$$\mathcal{A} = D_U G(U^*) = \begin{pmatrix} D_1^{-1}(2k_2u^*v^* - c - r) & D_1^{-1}(k_2u^* + k_1) \\ D_2^{-1}(c - 2k_2u^*v^*) & -D_2^{-1}(k_2u^* + k_1) \end{pmatrix}$$

If $D_U\Gamma(U^*)$ is invertible, then the Leray–Schauder Theorem (see [15,17,22,29,30]) demonstrates that

index(
$$\Gamma(\cdot)$$
, U^*) = $(-1)^{\gamma}$,

where γ is the algebraic sum of negative eigenvalues of $D_U \Gamma(U^*)$.

To calculate γ , it is needed to define

$$H(\mu) = \det(\mu I - \mathcal{A})$$

= $\mu^2 + [D_2^{-1}(k_2u^{*2} + k_1) + D_1^{-1}(c + r - 2k_2u^*v^*)]\mu + D_1^{-1}D_2^{-1}r(k_2u^{*2} + k_1).$ (3.13)

The previous works [22, 29] imply that β is an eigenvalue of $D_U \Gamma(U^*)$ on X_i if and only if $\beta(1 + \mu_i)$ is an eigenvalue of $\mu_i I - A$. Theorem 6.1.1 in [29] tells us if $\mu_i I - A$ is invertible for any $i \ge 0$, then it is correct that

$$\operatorname{index}(\Gamma(\cdot), U^*) = (-1)^{\gamma}, \ \gamma = \sum_{i \ge 0, \ H(\mu_i) < 0} m(\mu_i),$$

where $m(\mu_i)$ is the algebraic multiplicity of μ_i .

Obviously, when

$$[D_2^{-1}(k_2u^{*2}+k_1)+D_1^{-1}(c+r-2k_2u^*v^*)]^2 > 4D_1^{-1}D_2^{-1}r(k_2u^{*2}+k_1),$$
(3.14)

 $H(\mu) = 0$ has two different positive roots μ^{\pm} with $\mu^{+} > \mu^{-}$. Thus, $H(\mu) < 0$ if and only if $\mu \in (\mu^{-}, \mu^{+})$.

Consequently, the following result describing the existence of nonconstant steady states of (1.2) is derived.

Theorem 3.3. Assume that (3.14) is satisfied, and there exists integers $0 \le i < j$, such that $0 \le \mu_i < \mu^- < \mu_{i+1} \le \mu_j < \mu^+ < \mu_{j+1}$ and $\sum_{k=i+1}^j m(\mu_k)$ is odd, then (1.2) has at least one nonconstant solution in Λ .

Proof. Define a mapping $\hat{H} : \Lambda \times [0, 1] \longrightarrow X^+$ by

$$\hat{H}(U, t) = (-\Delta + I)^{-1} \left(u + (\frac{1-t}{D} + \frac{t}{D_1})(k_2 u^2 v - (c+r)u + k_1 v) \\ v + (\frac{1-t}{D} + \frac{t}{D_2})(-k_2 u^2 v + cu - k_1 v + b) \right)$$
(3.15)

where *D* is defined in Theorem 3.2.

It is easy to obtain that solving (1.2) is equivalent to finding the fixed points of $\hat{H}(\cdot, 1)$ in Λ . From the definitions of D and Λ , we easily get that $\hat{H}(\cdot, 0)$ has the only fixed point (u^*, v^*) in Λ .

On the one hand, we deduce that

$$\deg(\mathbf{I} - \hat{H}(\cdot, 0), \Lambda) = \operatorname{index}(\mathbf{I} - \hat{H}(\cdot, 0), (u^*, v^*)) = 1.$$
(3.16)

Suppose that (1.2) has no other solutions except the constant one (u^*, v^*) , then

$$\deg(\mathbf{I} - \hat{H}(\cdot, 1), \Lambda) = \operatorname{index}(\Gamma, (u^*, v^*)) = (-1)^{\sum_{k=i+1}^{j} m(\mu_k)} = -1.$$
(3.17)

On the other hand, from the homotopic invariance of Leray–Schauder degree, it is reasonable that

$$1 = \deg(I - \hat{H}(\cdot, 0), \Lambda) = \deg(I - \hat{H}(\cdot, 1), \Lambda) = -1,$$
(3.18)

leading to a contradiction. Therefore, this shows that there exists at least one nonconstant solution of (1.2). \Box

Corollary 3.4. If K > 0, $\mu_j < \frac{c+r}{KD_1} < \mu_{j+1}$ for some integer $j \ge 1$ and $\sum_{k=1}^{j} m(\mu_k)$ is odd, where K is defined in Theorem 2.1. Then there exists a large positive number D^* such that (1.2) has at least one nonconstant solution as $D_2 > D^*$.

Proof. Looking for the explicit expression of $H(\mu)$, it is clear that (3.14) holds for sufficient large D_2 . Besides, K > 0 gives that

$$\mu^{-} \to 0 \text{ and } \mu^{+} \to \frac{2k_{2}u^{*}v^{*} - c - r}{D_{1}} = \frac{c + r}{KD_{1}} \text{ as } D_{2} \to \infty.$$
 (3.19)

As a result, i = 1 in Theorem 3.3 implies this corollary.

4 Bifurcation analysis

In order to better understand patterns of system (1.1), we consider bifurcations from the positive constant equilibrium, such as Turing, steady state and Hopf bifurcations.

4.1 Turing bifurcation

Several theorems could answer the existence of Turing bifurcation. In this section, we still employ quantity *K* in Theorem 2.1 to give our results.

Theorem 4.1. Assume that $\frac{D_1}{D_2} < \frac{(c+r)r^2}{K(k_2b^2+k_1r^2)} < 1$ and $\frac{c+r}{K}D_2 - \frac{k_2b^2+k_1r^2}{r^2}D_1 > 2\sqrt{\frac{D_1D_2(k_2b^2+k_1r^2)}{r}}$, then Turing bifurcation occurs in PDE system (1.1).

Proof. Once more, we study the characteristic equation (2.3). First, without diffusion term, sufficient conditions for locally asymptotically stable equilibrium *E* in ordinary differential equation (ODE) are $tr(L_0) < 0$ and $det(L_0) > 0$, which is equivalent to

(H₁)
$$K > \frac{(c+r)r^2}{k_2b^2 + k_1r^2}$$

If the condition (**H**₁) is satisfied, then for all $i \ge 0$, tr(L_i) < 0. So as long as $\exists i \in \mathbb{N}$ such that det(L_i) < 0, (1.1) experiences Turing instability. Noticing that det(L_i) is a quadratic function about μ_i , (3.14) and

$$(c+r-2k_2u^*v^*)D_2 + (k_2u^{*2}+k_1)D_1 < 0$$
(4.1)

can confirm that (2.3) has at least one root with positive real part. Simple calculation suggests that

$$\frac{D_1}{D_2} < \frac{(c+r)r^2}{K(k_2b^2 + k_1r^2)} < 1$$
(4.2)

and

$$\frac{c+r}{K}D_2 - \frac{k_2b^2 + k_1r^2}{r^2}D_1 > 2\sqrt{\frac{D_1D_2(k_2b^2 + k_1r^2)}{r}}$$
(4.3)

is the ultimate condition.

Theorem 4.2. Suppose that $0 < \frac{(c+r)r^2}{K(k_2b^2+k_1r^2)} < 1$, $\mu_j < \frac{c+r}{KD_1} < \mu_{j+1}$ for some integer $j \ge 1$ and $\sum_{k=1}^{j} m(\mu_k)$ is odd. Then there exists a large positive number D^* such that Turing pattern of (1.1) occurs as $D_2 > D^*$.

Proof. Under the assumption in this theorem, conditions in Theorem 4.1 hold and (1.1) experiences the Turing instability. In addition, Corollary 3.4 guarantees the existence of nonconstant solutions in (1.2) provided that $D_2 > D^*$. That is to say, the nonconstant solutions are generated by Turing instability and Turing patterns follow.

4.2 Steady state bifurcation

In this subsection and in next one, we assume that all eigenvalues μ_i of $-\Delta$ are simple. Choose c as the bifurcation parameter and rewrite (2.4) into

$$T_{i}(c) = -(D_{1} + D_{2})\mu_{i} + \frac{c+r}{K} - k_{2}u^{*2} - k_{1},$$

$$D_{i}(c) = D_{1}D_{2}\mu_{i}^{2} + \left[-\frac{c+r}{K}D_{2} + (k_{2}u^{*2} + k_{1})D_{1}\right]\mu_{i} + r(k_{2}u^{*2} + k_{1}).$$
(4.4)

It is well known from [36] that the bifurcation point c^{S} of steady state bifurcation satisfies

(*H*₂) there exists an $i \in \mathbb{N}_0$ such that

$$D_i(c^S) = 0, \ T_i(c^S) \neq 0, \ \text{ and } \ D_j(c^S) \neq 0, \ T_j(c^S) \neq 0 \ \text{ for } j \neq i;$$

and

$$\frac{\mathrm{d}}{\mathrm{d}c}D_i(c^S)\neq 0$$

Indeed, $D_0(c) = r(k_2u^{*2} + k_1) > 0$ for any c > 0, so we just check $i \in \mathbb{N}$.

Next, we are devoted to finding c which satisfies (H₂). Let us define

$$T(c, p) := -(D_1 + D_2)p + \frac{c+r}{K} - k_2 u^{*2} - k_1,$$

$$D(c, p) := D_1 D_2 p^2 + \left[-\frac{c+r}{K} D_2 + (k_2 u^{*2} + k_1) D_1 \right] p + r(k_2 u^{*2} + k_1).$$
(4.5)

Then $D_i(c) = 0$ is equivalent to D(c, p) = 0, that is, $\{(c, p) \in \mathbb{R}^2_+ : D(c, p) = 0\}$ is the steady state bifurcation curve. Solving this equation demonstrates

$$c = c(p) := \frac{D_1 D_2 K p^2 + (D_1 K k_2 u^{*2} + D_1 K k_1 - r D_2) p + r K (k_1 u^{*2} + k_1)}{D_2 p}$$
(4.6)

to be potential steady state bifurcation points.

In order to determine possible bifurcation points, we again solve D(c, p) = 0 and have

$$p = p_{\pm}(c) := \frac{\frac{c+r}{K}D_2 - (k_2u^{*2} + k_1)D_1}{2D_1D_2}$$

$$\pm \frac{\sqrt{[\frac{c+r}{K}D_2 - (k_2u^{*2} + k_1)D_1]^2 - 4D_1D_2r(k_2u^{*2} + k_1)}}{2D_1D_2}$$
(4.7)

with K > 0. To reach our goal, the following lemma is important.

Lemma 4.3. The function c = c(p): $(0, +\infty) \to \mathbb{R}^+$ decided by (4.6) has a unique critical point $p_* \in (0, +\infty)$, being the global minimum of c(p), and $\lim_{p\to 0^+} c(p) = \lim_{p\to +\infty} c(p) = +\infty$. As a result, for $c \ge c_* := c(p_*)$, $p_{\pm}(c)$ is well defined in (4.7), $p_{+}(c)$ is strictly increasing and $p_{-}(c)$ is strictly decreasing, and $p_{+}(c_*) = p_{-}(c_*) = p_*$, $\lim_{c\to +\infty} p_{+}(c) = +\infty$, $\lim_{c\to +\infty} p_{-}(c) = 0$.

Proof. Remembering c = c(p), differentiate D(c(p), p) = 0 twice and let c'(p) = 0, we then get that

$$2D_1K - pc''(p) = 0,$$

leading to

$$c''(p) = \frac{2D_1K}{p} > 0$$

This shows us that for any critical point p of c(p), c''(p) > 0, therefore, the critical point must be unique and a local minimum point.

On the other hand, it is easy to check $\lim_{p\to 0^+} c(p) = \lim_{p\to +\infty} c(p) = +\infty$, thus, the unique critical point p_* is the global minimum point. Furthermore, because of the similarity between curves $\{(c(p), p)\}$ and $\{(c, p_{\pm}(c))\}$, the properties about $p_{\pm}(c)$ are obtained. \Box

According to Lemma 4.3, it may happen that $c(p_i) = c(p_j)$ and $p_-(c_i^S) = p_+(c_j^S)$ for some i < j. Then for $c = c_i^S = c_j^S$, 0 is not a simple eigenvalue of L := L(c) defined by (2.1) and such Bogdanov–Takens bifurcation points are not under our consideration. To our surprise, [36] have implied that for n = 1 and $\Omega = (0, l\pi)$, there are only countably many l leading to case above. For general bounded domains in \mathbb{R}^n , that case does not occur.

Summarizing the discussion above and utilizing a general bifurcation theorem in [27], a main theorem about global bifurcation of steady states is as follows.

Theorem 4.4. Suppose that Ω is a bounded smooth domain so that its spectral set $S = \{\mu_i : i \ge 0\}$ maintains

- (i) All eigenvalues μ_i $(i \ge 0)$ are simple;
- (*ii*) there exists k, l, $m \in \mathbb{N}$ with $0 = \mu_0 < \cdots < \mu_k < p_- < \mu_{k+1} < \cdots < \mu_l < p^* < \mu_{l+1} < \cdots < \mu_m < p_+ < \mu_{m+1}$, where p^* , p_- , p_+ are defined in Lemma 4.3 and (4.7).

Then $c_j^S = c(\mu_j)$ $(k+1 \le j \le m)$ with $c_* < c_j^S \le c^*$ are bifurcation points for system (1.1). *Furthermore,*

- 1. There exists a smooth curve Γ_j of positive solutions of (1.2) bifurcation from $(c, u, v) = (c_j^S, u_{c_i^S}, v_{c_i^S}), \Gamma_j$ contained in a global branch C_j of positive solutions of (1.2).
- 2. Near $(c, u, v) = (c_j^S, u_{c_j^S}, v_{c_j^S}), \Gamma_j = \{c_j(s), u_j(s), v_j(s) : s \in (-\varepsilon, \varepsilon)\}, where <math>u_j(s) = c_j^S + sa_j\phi_j(s) + s\psi_{1,j}(s), v_j(s) = c_j^S + sb_j\phi_j(s) + s\psi_{2,j}(s) \text{ for smooth functions } c_j, \psi_{1,j}, \psi_{2,j}$ such that $c_j(0) = c_j^S, \psi_{1,j}(0) = \psi_{2,j}(0) = 0$. Here (a_j, b_j) satisfies

$$L(c_i^S)[(a_i, b_i)^T \phi_i(x)] = (0, 0)^T$$

3. Either C_j contains another $(c_i^S, u_{c_i^S}, v_{c_i^S})$ for $i \neq j$ and $k+1 \leq i \leq m$, or the projection of C_j onto *c*-axis contains the interval (c_i^S, c^*) .

Proof. In the beginning, it is trivial to calculate that

$$\frac{\mathrm{d}D_j}{\mathrm{d}c}(c_j^S) = -\frac{D_2}{K}\mu_j < 0$$

which proves that a steady state bifurcation occurs from c_j^S . From the global bifurcation theorem in reference [27], Γ_i is included in a global branch of C_i of solutions.

Next, we are going to prove that any solution on C_j is positive for $c \in (0, c^*]$. Indeed, it is true for solutions on Γ_j . Let us use the proof by contradiction, thus assume that there is a solution on C_j but not positive. Because of the continuity of C_j , an element $(c_e, u_e, v_e) \in C_j$ with $c_e \in (0, c^*]$, $u_e \ge 0$, $v_e \ge 0$ for $x \in \overline{\Omega}$, that is to say, we can find $x_0 \in \overline{\Omega}$ such that $u_e(x_0) = 0$ or $v_e(x_0) = 0$. If $v_e(x_0) = 0$, then v_e reaches its minimum at x_0 . $x_0 \in \Omega$ contradicts with $-D_2\Delta v_e(x_0) = cu(x_0) + b > 0$. In addition, if $x_0 \in \partial\Omega$, then $-D_2\Delta v_e(x_0) > 0$ near $x = x_0$ and x_0 is the local minimum, which implies $\partial_v v_e(x_0) < 0$ not agreeing with Neumann boundary condition. Thus $v_e(x_0) = 0$ is impossible. In the same way, it must be $u(x) \ge 0$ for $x \in \overline{\Omega}$. We get that any solution of (1.2) on C_j is positive as $c \in (0, c^*]$.

In the previous paragraphs, we have shown that bifurcation points for steady state solutions are just $c = c_j^S > c_*$, thus the projection of C_j onto *c*-axis has a lower bound. Theorem 3.1 reports that all positive solutions of (1.2) are uniformly bounded for $c \le c^*$. This tells us that C_j must be bounded for $c \le c^*$. Again by global bifurcation theorem, either C_j contains another $(c_i^S, u_{c_i^S}, v_{c_i^S} \ (i \ne j)$, or C_j is unbounded, or C_j intersects the boundary of $(0, c^*] \times X \times X$. However, these cases all can demonstrate our results.

4.3 Hopf bifurcation

In this part, spatially homogeneous and nonhomogeneous periodic solutions of (1.1) are focused. Inspecting $T_i(c)$ and $D_i(c)$ in (4.4), a Hopf bifurcation point c^H should meet

(*H*₃) there exists $i \in \mathbb{N}_0$ such that

$$T_i(c^H) = 0, \ D_i(c^H) > 0, \ \text{ and } \ T_j(c^H) \neq 0, \ D_j(c^H) \neq 0 \ \text{ for } j \neq i;$$

and the unique pair of complex eigenvalues near the imaginary axis $\alpha(c) \pm i\omega(c)$ maintains

$$\alpha'(c^H) \neq 0, \qquad \omega(c^H) > 0.$$

Firstly, $T_0(c_0^H) = 0$ as $c_0^H = K(k_2u^{*2} + k_1) - r$ with K > 0, $T_j(c_0^H) = -(D_1 + D_2)\mu_j < 0$ for any $j \ge 1$ and

$$D_j(c_0^H) = D_1 D_2 \mu_j^2 + (k_2 u^{*2} + k_1)(D_1 - D_2)\mu_j + r(k_2 u^{*2} + k_1) > 0$$

for $j \in \mathbb{N}_0$ provided that $D_1 \ge D_2$. Consequently, c_0^H is a Hopf bifurcation point for spatially homogeneous periodic solutions.

Hereafter, we intend to investigate spatially nonhomogeneous Hopf bifurcation for $i \ge 1$. If c_i^H for some $i \in \mathbb{N}$ is a Hopf bifurcation point, then

$$c_i^H = K[(D_1 + D_2)\mu_i + k_2u^{*2} + k_1] - r.$$
(4.8)

This gives that there is $n \in \mathbb{N}$ such that possible bifurcation points c_i^H $(1 \le i \le n)$ satisfying

$$0 < c_0^H < c_1^H < \dots < c_n^H \le c^*.$$
(4.9)

Clearly, $T_i(c_i^H) = 0$ and $T_j(c_i^H) \neq 0$ for $j \neq i$. And another thing is to verify that $D_i(c_i^H) > 0$. Plugging (4.8) into $D_i(c)$ and still denoting μ_i to p, we have

$$D_i(c_i^H, p) = -D_2^2 p^2 + (k_2 u^{*2} + k_1)(D_1 - D_2)p + r(k_2 u^{*2} + k_1).$$
(4.10)

 $D_i(c_i^H, p)$ is a quadratic polynomial about p and its discriminant is $(k_2u^{*2} + k_1)^2[(D_1 - D_2)^2 + 4rD_2^2] > 0$, hence there should be two roots $p^- < 0 < p^+$ of $D_i(c_i^H, p)$ combining with primary analysis. This produces that as long as $0 < \mu_i < p^+$ we get $D_i(c_i^H) > 0$. Furthermore, $D_j(c_i^H) \neq 0$ if $c_i^H \neq c_j^S$ for $k + 1 \le j \le m$. We then have, making use of simple calculation,

$$\alpha'(c_i^H) = \frac{1}{2K} \neq 0.$$

According to previous discussion, we show the following Hopf bifurcation theorem.

Theorem 4.5. Suppose that Ω is a bounded smooth domain so that its spectral set $S = \{\mu_i : i \ge 0\}$ maintains

- (i) All eigenvalues μ_i $(i \ge 0)$ are simple;
- (ii) There exists $n \in \mathbb{N}$ such that $0 < \mu_i < p^+$ $(1 \le i \le n)$, where p^+ is defined above.
- (iii) $c_i^H \neq c_i^S$ for any $1 \le i \le n$ and $k+1 \le j \le m$, where c_i^S are defined in Theorem 4.4.

Then we find n + 1 Hopf bifurcation points c_i^H ($0 \le i \le n$) of (1.1) satisfying (4.9). In addition,

- 1. There is a smooth curve Ξ_i of positive periodic orbits of (1.1) bifurcating from $(c, u, v) = (c_i^H, u_{c^H}, v_{c^H}), \Xi_i$ contained in a global branch \mathcal{P}_i of positive periodic orbits of (1.1).
- 2. Occurrence of Hopf bifurcation at $c = c_0^H$ also needs $D_1 \ge D_2$; the bifurcating periodic orbits from $c = c_0^H$ are spatially homogeneous.
- 3. The bifurcating periodic orbits from $c = c_i^H$ $(i \neq 1)$ are spatially nonhomogeneous, which have the form of
 - $(c, u, v) = (c_i^H + o(s), u_{c_i^H} + sk_i \cos(\omega(c_i^H)t)\phi_i(x) + o(s), v_{c_i^H} + sl_i \cos(\omega(c_i^H)t)\phi_i(x) + o(s)),$

for $s \in (0, \epsilon)$ near c_i^H , where $\omega(c_i^H) = \sqrt{D_i(c_i^H)}$, is the corresponding frequency, and $\phi_i(x)$ together with (k_i, l_i) are the corresponding spatial eigenfunction and eigenvector, respectively.

4. The global branch of spatially nonhomogeneous periodic orbits \mathcal{P}_i $(1 \le i \le n)$ either contains another bifurcation point $(c_j^H, u_{c_j^H}, v_{c_j^H})$ $(j \ne i)$ or contains a spatially homogeneous periodic orbit on \mathcal{P}_0 , or the projection $\operatorname{Proj}_c \mathcal{P}_i$ contains the interval $(0, c_i^H)$ or (c_i^H, c^*) , or there is $\overline{c} \in (0, c^* - \delta)$ such that for a sequence of periodic orbits $(c_s, u_s, v_s) \in \mathcal{P}_i, c_s \to \overline{c}$ and $T_s \to \infty$ as $s \to \infty$, where T_s is the period of (c_s, u_s, v_s) .

Proof. Theorem 3.3 in [33] linking with general version of global bifurcation theorem similar to global steady state bifurcation in [27] give us the results about global Hopf bifurcation. \Box

Remark 4.6. Certainly, $c_i^H = c_j^S$ for some $1 \le i \le n$ and $k + 1 \le j \le m$ may lead Hopf-zero bifurcation, which is not in our scope.

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