



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]

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

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, equipped with priori bounds, energy estimates and Leray–Schauder degree theory in elliptic partial differential equations (PDEs)

$$\begin{cases} -D_1\Delta u = k_2u^2v - (c+r)u + k_1v, & x \in \Omega \\ -D_2\Delta v = -k_2u^2v + b - k_1v + cu, & x \in \Omega \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \end{cases} \quad (1.2)$$

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 $K = \frac{k_2b^2+k_1r^2}{k_2b^2-k_1r^2}$, then (u^*, v^*) is locally asymptotically stable as $K \leq 0$ or $\frac{v^*}{u^*} < \min\{1, \frac{D_1}{D_2}\}K$, and is unstable for $\frac{v^*}{u^*} > K > 0$.*

Proof. Initially, the linear operator at E is

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

implying a sequence of matrices

$$L_i := \begin{pmatrix} 2k_2u^*v^* - (c+r) - D_1\mu_i & k_2u^{*2} + k_1 \\ -2k_2u^*v^* + c & -k_2u^{*2} - k_1 - D_2\mu_i \end{pmatrix} \quad (2.2)$$

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

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

with

$$\begin{aligned} \text{tr}(L_i) &= -(D_1 + D_2)\mu_i + 2k_2u^*v^* - (c+r) - k_2u^{*2} - k_1, \\ \det(L_i) &= D_1D_2\mu_i^2 + [(c+r - 2k_2u^*v^*)D_2 + (k_2u^{*2} + k_1)D_1]\mu_i + r(k_2u^{*2} + k_1). \end{aligned} \quad (2.4)$$

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 $i \geq 0$, $\text{tr}(L_i) < 0$ and $\det(L_i) > 0$. Thus, (u^*, v^*) is locally asymptotically stable.
2. When $k_2b^2 > k_1r^2$, it is required that

$$\begin{aligned} 2k_2u^*v^* - (c+r) - k_2u^{*2} - k_1 &< 0 \\ (k_2u^{*2} + k_1)D_1 &> (2k_2u^*v^* - c - r)D_2 \end{aligned} \quad (2.5)$$

for $\text{tr}(L_i) < 0$ 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 $\text{tr}(L_0) > 0$ causes at least one eigenvalue with positive real part. As a result, we have an unstable equilibrium. \square

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 $u_0(x) \geq 0$ ($\neq 0$), $v_0(x) \geq 0$ ($\neq 0$), system (1.1) has a unique solution $(u(x, t), v(x, t))$ satisfying $0 < u(x, t) \leq u^*$, $0 < v(x, t) \leq v^*$, as $t > 0$ and $x \in \bar{\Omega}$.*
- (ii) *If $k_1r^2 > 4k_2b^2$ and $k_1 \geq (\max_{x \in \bar{\Omega}} u_0(x))^2$, then $\lim_{t \rightarrow \infty} (u(x, t), v(x, t)) = (u^*, v^*)$ with $(u_0(x), v_0(x)) \geq (\neq)(0, 0)$.*

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

$$f_1(u, v) = k_2u^2v - (c+r)u + k_1v, \quad f_2(u, v) = -k_2u^2v + b - k_1v + cu.$$

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

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

are, respectively, solutions of

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

and

$$\begin{cases} \frac{dv}{dt} = cu^* + b - k_1v, \\ v(0) = \sup_{x \in \bar{\Omega}} v_0(x). \end{cases} \quad (2.7)$$

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

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

and

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

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

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

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

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

$$v_t - D_2 \Delta v \leq cu^* + b - k_1 v.$$

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

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

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

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

for $x \in \bar{\Omega}$, $t \geq T_1^\varepsilon$ and $\varepsilon > 0$ small enough.

Because of $k_1 r^2 > 4k_2 b^2$, one should note that

$$(c+r)^2 - 4k_1 k_2 (\bar{v}_1 + \varepsilon)^2 > 0$$

with $\varepsilon > 0$.

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

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

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

$$u_2^\varepsilon = \frac{c + r + \sqrt{(c + r)^2 - 4k_1k_2(\bar{v}_1 + \varepsilon)^2}}{2k_2(\bar{v}_1 + \varepsilon)} > \sqrt{k_1}.$$

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

$$\begin{aligned} \limsup_{t \rightarrow \infty} \max_{x \in \bar{\Omega}} u(x, t) &\leq \frac{c + r - \sqrt{(c + r)^2 - 4k_1k_2\bar{v}_1^2}}{2k_2\bar{v}_1} \\ &= \frac{k_1r - \sqrt{k_1^2r^2 - 4k_1k_2b^2}}{2k_2b} =: \bar{u}_1. \end{aligned} \quad (2.8)$$

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

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

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

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

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

In the same manner above,

$$\liminf_{t \rightarrow \infty} \min_{x \in \bar{\Omega}} u(x, t) \geq \frac{c + r - \sqrt{(c + r)^2 - 4k_1k_2\bar{v}_1^2}}{2k_2\bar{v}_1} =: \underline{u}_1 \leq \bar{u}_1. \quad (2.10)$$

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

Also, one can get

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

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

$$\limsup_{t \rightarrow \infty} \max_{x \in \Omega} u(x, t) \leq \frac{c+r - \sqrt{(c+r)^2 - 4k_1k_2\bar{v}_2^2}}{2k_2\bar{v}_2} =: \bar{u}_2 \quad (2.12)$$

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

Now, denote

$$\begin{aligned} \varphi(s) &= \frac{b+cu^*}{k_1+k_2s^2}, \quad s > 0 \\ \psi(s) &= \frac{c+r - \sqrt{(c+r)^2 - 4k_1k_2s^2}}{2k_2s}, \quad 0 < s < \frac{c+r}{2\sqrt{k_1k_2}}. \end{aligned}$$

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

$$\begin{cases} \underline{v}_1 = \varphi(\bar{u}_1) \leq \varphi(\underline{u}_1) = \bar{v}_2 \leq \bar{v}_1 = \frac{b(c+r)}{k_1r}, \\ \underline{u}_1 = \psi(\bar{v}_1) \leq \psi(\bar{v}_2) = \bar{u}_2 \leq \bar{u}_1 = \psi(\bar{v}_1), \\ \underline{v}_1 \leq \liminf_{t \rightarrow \infty} \min_{x \in \Omega} v(x, t) \leq \limsup_{t \rightarrow \infty} \max_{x \in \Omega} v(x, t) \leq \bar{v}_2, \\ \underline{u}_1 \leq \liminf_{t \rightarrow \infty} \min_{x \in \Omega} u(x, t) \leq \limsup_{t \rightarrow \infty} \max_{x \in \Omega} u(x, t) \leq \bar{u}_2. \end{cases} \quad (2.13)$$

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

$$\bar{v}_1 = \frac{b(c+r)}{k_1r}, \quad \bar{u}_i = \psi(\bar{v}_i), \quad \underline{v}_i = \varphi(\bar{u}_i), \quad \underline{u}_i = \psi(\underline{v}_i), \quad \bar{v}_{i+1} = \varphi(\underline{u}_i), \quad (2.14)$$

such that

$$\begin{aligned} \underline{v}_i &\leq \liminf_{t \rightarrow \infty} \min_{x \in \Omega} v(x, t) \leq \limsup_{t \rightarrow \infty} \max_{x \in \Omega} v(x, t) \leq \bar{v}_i, \\ \underline{u}_i &\leq \liminf_{t \rightarrow \infty} \min_{x \in \Omega} u(x, t) \leq \limsup_{t \rightarrow \infty} \max_{x \in \Omega} u(x, t) \leq \bar{u}_i. \end{aligned} \quad (2.15)$$

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

$$\begin{aligned} \underline{v}_i &\leq \underline{v}_{i+1} = \varphi(\bar{u}_{i+1}) \leq \varphi(\underline{u}_i) = \bar{v}_{i+1} \leq \bar{v}_i, \\ \underline{u}_i &\leq \underline{u}_{i+1} = \psi(\underline{v}_{i+1}) \leq \psi(\bar{v}_{i+1}) = \bar{u}_{i+1} \leq \bar{u}_i. \end{aligned} \quad (2.16)$$

Based on the monotonicity of sequences, assume that

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

Thus, $\underline{u}, \bar{u}, \underline{v}, \bar{v}$ maintain the order $0 \leq \underline{u} \leq \bar{u}, 0 \leq \underline{v} \leq \bar{v}$ and satisfy

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

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

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

Combining the first and last two equations, respectively, gives us that

$$\begin{aligned} (c+r)\bar{u} - b - cu^* - k_2\bar{v}(\bar{u} - \underline{u})(\bar{u} + \underline{u}) &= 0, \\ (c+r)\underline{u} - b - cu^* + k_2\underline{v}(\bar{u} - \underline{u})(\bar{u} + \underline{u}) &= 0. \end{aligned} \quad (2.20)$$

Consider the equations above together, it follows that

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

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}, \bar{C} , depending on $k_1, k_2, c, r, b, \Omega$, such that*

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

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

$$\int_{\Omega} [k_2u^2v - (c+r)u + k_1v]dx = \int_{\Omega} [-k_2u^2v + cu - k_1v + b]dx = 0. \quad (3.1)$$

Adding the two equalities above, we obtain that

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

According to the first equation, the following relationship is satisfied

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

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

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

Adding the equations in (1.2), denoting $w = D_1u + D_2v$ and $w(x_0) = \max_{\bar{\Omega}} w(x)$, then

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

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

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

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

$$-k_2u^2(x_1)v(x_1) + cu(x_1) - k_1v(x_1) + b \geq 0, \quad (3.5)$$

and it is easy to see that

$$v(x_1) \leq \frac{b + cu(x_1)}{k_1 + k_2u^2(x_1)} \leq \frac{b(c+r)}{r(k_1 + k_2C^2)}. \quad (3.6)$$

Again because of Proposition 2.2 in [15],

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

produces

$$v(x_2) \geq \frac{b + cu(x_2)}{k_1 + k_2u^2(x_2)} \geq \frac{r^2(b + cC)}{k_1r^2 + k_2b^2}. \quad (3.7)$$

Therefore, it is concluded that

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

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

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 $D = \max \left\{ r + \frac{3c+k_1+7k_2\bar{C}^2}{2}, \frac{c+3k_1+5k_2\bar{C}^2}{2} \right\}$.*

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

$$\begin{aligned}
 D_1 \int_{\Omega} |\nabla(u - u_0)|^2 dx &= \int_{\Omega} [k_2 u^2 v - (c + r)u + k_1 v](u - u_0) dx \\
 &= \int_{\Omega} [k_2 u^2 v - k_2 u_0^2 v_0 + (c + r)u_0 - k_1 v_0 - (c + r)u + k_1 v](u - u_0) dx \\
 &= \int_{\Omega} [k_2 u^2 v - k_2 u_0^2 v_0 - (c + r)(u - u_0) - k_1(v - v_0)](u - u_0) dx \\
 &= k_2 \int_{\Omega} [v(u + u_0)(u - u_0) + u_0^2(v - v_0)](u - u_0) dx \\
 &\quad - (c + r) \int_{\Omega} (u - u_0)^2 dx - k_1 \int_{\Omega} (u - u_0)(v - v_0) dx \\
 &\leq (c + r + 2k_2 \bar{C}^2) \int_{\Omega} (u - u_0)^2 dx + (k_1 + k_2 \bar{C}^2) \int_{\Omega} (u - u_0)(v - v_0) dx \\
 &\leq \left(c + r + \frac{5}{2} k_2 \bar{C}^2 + \frac{k_1}{2} \right) \int_{\Omega} (u - u_0)^2 dx + \frac{k_1 + k_2 \bar{C}^2}{2} \int_{\Omega} (v - v_0)^2 dx.
 \end{aligned} \tag{3.8}$$

In the same way, we can also get

$$\begin{aligned}
 D_2 \int_{\Omega} |\nabla(v - v_0)|^2 dx &= \int_{\Omega} [-k_2 u^2 v + cu - k_1 v + b](v - v_0) dx \\
 &= \int_{\Omega} [-k_2 u^2 v + k_2 u_0^2 v_0 + cu - k_1 v - cu_0 + k_1 v_0](v - v_0) dx \\
 &= \int_{\Omega} [-k_2 u^2 v + k_2 u_0^2 v_0](v - v_0) dx + c \int_{\Omega} (u - u_0)(v - v_0) dx - k_1 \int_{\Omega} (v - v_0)^2 dx \\
 &= -k_2 \int_{\Omega} [v(u + u_0)(u - u_0) + u_0^2(v - v_0)](v - v_0) dx \\
 &\quad + c \int_{\Omega} (u - u_0)(v - v_0) dx - k_1 \int_{\Omega} (v - v_0)^2 dx \\
 &\leq (k_1 + k_2 \bar{C}^2) \int_{\Omega} (v - v_0)^2 dx + (c + 2k_2 \bar{C}^2) \int_{\Omega} (u - u_0)(v - v_0) dx \\
 &\leq \left(\frac{c}{2} + k_2 \bar{C}^2 \right) \int_{\Omega} (u - u_0)^2 dx + \left(k_1 + 2k_2 \bar{C}^2 + \frac{c}{2} \right) \int_{\Omega} (v - v_0)^2 dx.
 \end{aligned} \tag{3.9}$$

In addition, based on the Poincaré inequality

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

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

$$\begin{aligned}
 D_1 \int_{\Omega} |\nabla(u - u_0)|^2 dx + D_2 \int_{\Omega} |\nabla(v - v_0)|^2 dx \\
 \leq \frac{1}{\mu_1} \left(A \int_{\Omega} |\nabla(u - u_0)|^2 dx + B \int_{\Omega} |\nabla(v - v_0)|^2 dx \right),
 \end{aligned} \tag{3.10}$$

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. \square

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

$$\begin{aligned} X &= \{(u, v) \in C^1(\bar{\Omega}) \times C^1(\bar{\Omega}) : \partial_\nu u = \partial_\nu v = 0 \text{ on } \partial\Omega\}, \\ X^+ &= \{(u, v) : u, v \geq 0, (u, v) \in X\}, \\ \Lambda &= \{(u, v) \in X : \underline{C} \leq u, v \leq \bar{C} \text{ for } x \in \bar{\Omega}\}, \\ E(\mu) &= \{\phi \mid -\Delta\phi = \mu\phi \text{ in } \Omega, \partial_\nu\phi = 0 \text{ on } \partial\Omega\}. \end{aligned} \quad (3.11)$$

If $E(\mu_i)$ is the eigenspace corresponding to μ_i , $\{\phi_{ij} \mid j = 1, \dots, \dim E(\mu_i)\}$ 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

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

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

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

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

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

where I is the identity operator. By calculation,

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

where

$$\mathcal{A} = D_U G(U^*) = \begin{pmatrix} D_1^{-1}(2k_2 u^* v^* - c - r) & D_1^{-1}(k_2 u^* + k_1) \\ D_2^{-1}(c - 2k_2 u^* v^*) & -D_2^{-1}(k_2 u^* + k_1) \end{pmatrix}.$$

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

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

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

To calculate γ , it is needed to define

$$\begin{aligned} H(\mu) &= \det(\mu I - \mathcal{A}) \\ &= \mu^2 + [D_2^{-1}(k_2 u^{*2} + k_1) + D_1^{-1}(c + r - 2k_2 u^* v^*)]\mu + D_1^{-1} D_2^{-1} r (k_2 u^{*2} + k_1). \end{aligned} \quad (3.13)$$

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 $\mu_i I - \mathcal{A}$. Theorem 6.1.1 in [29] tells us if $\mu_i I - \mathcal{A}$ is invertible for any $i \geq 0$, then it is correct that

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

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

Obviously, when

$$[D_2^{-1}(k_2 u^{*2} + k_1) + D_1^{-1}(c + r - 2k_2 u^* v^*)]^2 > 4D_1^{-1} D_2^{-1} r(k_2 u^{*2} + k_1), \quad (3.14)$$

$H(\mu) = 0$ 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 $0 \leq i < j$, such that $0 \leq \mu_i < \mu^- < \mu_{i+1} \leq \mu_j < \mu^+ < \mu_{j+1}$ 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 $\hat{H} : \Lambda \times [0, 1] \rightarrow X^+$ by

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

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

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

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

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

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

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

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

Corollary 3.4. *If $K > 0$, $\mu_j < \frac{c+r}{KD_1} < \mu_{j+1}$ for some integer $j \geq 1$ 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

$$\mu^- \rightarrow 0 \quad \text{and} \quad \mu^+ \rightarrow \frac{2k_2 u^* v^* - c - r}{D_1} = \frac{c+r}{KD_1} \quad \text{as } D_2 \rightarrow \infty. \quad (3.19)$$

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

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 $\text{tr}(L_0) < 0$ and $\text{det}(L_0) > 0$, which is equivalent to

$$(H_1) \quad K > \frac{(c+r)r^2}{k_2b^2+k_1r^2}.$$

If the condition (H_1) is satisfied, then for all $i \geq 0$, $\text{tr}(L_i) < 0$. So as long as $\exists i \in \mathbb{N}$ such that $\text{det}(L_i) < 0$, (1.1) experiences Turing instability. Noticing that $\text{det}(L_i)$ is a quadratic function about μ_i , (3.14) and

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

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

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

and

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

is the ultimate condition. \square

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 $j \geq 1$ 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. \square

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

$$\begin{aligned} T_i(c) &= -(D_1 + D_2)\mu_i + \frac{c+r}{K} - k_2u^{*2} - k_1, \\ D_i(c) &= D_1D_2\mu_i^2 + \left[-\frac{c+r}{K}D_2 + (k_2u^{*2} + k_1)D_1 \right] \mu_i + r(k_2u^{*2} + k_1). \end{aligned} \quad (4.4)$$

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

(H₂) there exists an $i \in \mathbb{N}_0$ such that

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

and

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

Indeed, $D_0(c) = r(k_2 u^{*2} + k_1) > 0$ 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

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

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

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

to be potential steady state bifurcation points.

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

$$\begin{aligned} p = p_{\pm}(c) &:= \frac{\frac{c+r}{K} D_2 - (k_2 u^{*2} + k_1) D_1}{2 D_1 D_2} \\ &\pm \frac{\sqrt{\left[\frac{c+r}{K} D_2 - (k_2 u^{*2} + k_1) D_1 \right]^2 - 4 D_1 D_2 r (k_2 u^{*2} + k_1)}}{2 D_1 D_2} \end{aligned} \quad (4.7)$$

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

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

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

$$2D_1 K - p c''(p) = 0,$$

leading to

$$c''(p) = \frac{2D_1 K}{p} > 0.$$

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 $\lim_{p \rightarrow 0^+} c(p) = \lim_{p \rightarrow +\infty} c(p) = +\infty$, 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. \square

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 $S = \{\mu_i : i \geq 0\}$ maintains*

(i) *All eigenvalues μ_i ($i \geq 0$) are simple;*

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

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

1. *There exists a smooth curve Γ_j of positive solutions of (1.2) bifurcation from $(c, u, v) = (c_j^S, u_{c_j^S}, v_{c_j^S})$, Γ_j contained in a global branch \mathcal{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 $u_j(s) = c_j^S + sa_j\phi_j(s) + s\psi_{1,j}(s)$, $v_j(s) = c_j^S + sb_j\phi_j(s) + s\psi_{2,j}(s)$ 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*

$$L(c_j^S)[(a_j, b_j)^T \phi_j(x)] = (0, 0)^T.$$

3. *Either \mathcal{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 \mathcal{C}_j onto c -axis contains the interval (c_j^S, c^*) .*

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

$$\frac{dD_j}{dc}(c_j^S) = -\frac{D_2}{K}\mu_j < 0$$

which proves that a steady state bifurcation occurs from c_j^S . From the global bifurcation theorem in reference [27], Γ_j is included in a global branch of \mathcal{C}_j of solutions.

Next, we are going to prove that any solution on \mathcal{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 \mathcal{C}_j but not positive. Because of the continuity of \mathcal{C}_j , an element $(c_e, u_e, v_e) \in \mathcal{C}_j$ with $c_e \in (0, c^*]$, $u_e \geq 0, v_e \geq 0$ for $x \in \bar{\Omega}$, that is to say, we can find $x_0 \in \bar{\Omega}$ 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 $\partial_\nu v_e(x_0) < 0$ not agreeing with Neumann boundary condition. Thus $v_e(x_0) = 0$ is impossible. In the same way, it must be $u(x) \geq 0$ for $x \in \bar{\Omega}$. We get that any solution of (1.2) on \mathcal{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 \mathcal{C}_j onto c -axis has a lower bound. Theorem 3.1 reports that all positive solutions of (1.2) are uniformly bounded for $c \leq c^*$. This tells us that \mathcal{C}_j must be bounded for $c \leq c^*$. Again by global bifurcation theorem, either \mathcal{C}_j contains another $(c_i^S, u_{c_i^S}, v_{c_i^S})$ ($i \neq j$), or \mathcal{C}_j is unbounded, or \mathcal{C}_j intersects the boundary of $(0, c^*] \times X \times X$. However, these cases all can demonstrate our results. \square

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

(H₃) there exists $i \in \mathbb{N}_0$ such that

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

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

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

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 $j \geq 1$ and

$$D_j(c_0^H) = D_1D_2\mu_j^2 + (k_2u^{*2} + k_1)(D_1 - D_2)\mu_j + r(k_2u^{*2} + k_1) > 0$$

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

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

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

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

$$0 < c_0^H < c_1^H < \cdots < c_n^H \leq c^*. \quad (4.9)$$

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

$$D_i(c_i^H, p) = -D_2^2p^2 + (k_2u^{*2} + k_1)(D_1 - D_2)p + r(k_2u^{*2} + k_1). \quad (4.10)$$

$D_i(c_i^H, p)$ 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 $k + 1 \leq j \leq m$. 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 $S = \{\mu_i : i \geq 0\}$ maintains*

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

Then we find $n + 1$ Hopf bifurcation points c_i^H ($0 \leq i \leq n$) 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 $(c, u, v) = (c_i^H, u_{c_i^H}, v_{c_i^H})$, Ξ_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 $D_1 \geq D_2$; 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 ($1 \leq i \leq n$) either contains another bifurcation point $(c_j^H, u_{c_j^H}, v_{c_j^H})$ ($j \neq i$) or contains a spatially homogeneous periodic orbit on \mathcal{P}_0 , or the projection $\text{Proj}_c \mathcal{P}_i$ contains the interval $(0, c_i^H)$ or (c_i^H, c^*) , or there is $\bar{c} \in (0, c^* - \delta)$ such that for a sequence of periodic orbits $(c_s, u_s, v_s) \in \mathcal{P}_i$, $c_s \rightarrow \bar{c}$ and $T_s \rightarrow \infty$ as $s \rightarrow \infty$, 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. \square

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

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References

- [1] V. BREÑA-MEDINA, A. R. CHAMPNEYS, C. GRIERSON, M. J. WARD, Mathematical modeling of plant root hair initiation: Dynamics of localized patches, *SIAM J. Appl. Dyn. Syst.* **13**(2014), 210–248. <https://doi.org/10.1137/120902264>
- [2] K. J. BROWN, F. A. DAVIDSON, Global bifurcation in the Brusselator system, *Nonlinear Anal.* **24**(1995), 1713–1725. [https://doi.org/10.1016/0362-546X\(94\)00218-7](https://doi.org/10.1016/0362-546X(94)00218-7)
- [3] V. V. CASTETS, E. DULOS, J. BOISSONADE, P. DE KEPPEL, Experimental evidence of a sustained standing Turing-type nonequilibrium chemical pattern, *Phys. Rev. Lett.* **64**(1990), 2953–2956. <https://doi.org/10.1103/PhysRevLett.64.2953>

- [4] A. J. CATLLÁ, A. MCNAMARA, C. M. TOPAZ, Instabilities and patterns in coupled reaction-diffusion layers, *Phys. Rev. E* **85**(2012), 026215. <https://doi.org/10.1103/PhysRevE.85.026215>
- [5] F. A. DAVIDSON, B. P. RYNNE, A priori bounds and global existence of solutions of the steady-state Sel'kov model, *Proc. Roy. Soc. Edinburgh Sect. A* **130**(2000), 507–516. <https://doi.org/10.1017/S0308210500000275>
- [6] A. D. ECONOMOU, A. OHAZAMA, T. PORNTAVEETUS, P. T. SHARPE, S. KONDO, M. A. BASSON, A. GRITLI-LINDE, M. T. COBOURNE, J. B. A. GREEN, Periodic stripe formation by a Turing mechanism operating at growth zones in the mammalian palate, *Nature Genetics* **44**(2012), 348–351. <https://doi.org/10.1038/ng.1090>
- [7] M. GHERGU, Non-constant steady-state solutions for Brusselator type systems, *Nonlinearity* **21**(2008), 2331–2345. <https://doi.org/10.1088/0951-7715/21/10/007>
- [8] M. GHERGU, V. D. RĂDULESCU, *Nonlinear PDEs. Mathematical models in biology, chemistry and population genetics*, Springer Monographs in Mathematics, Springer, Heidelberg, 2012. <https://doi.org/10.1007/978-3-642-22664-9>
- [9] D. GILBARG, N. S. TRUDINGER, *Elliptic partial differential equation of second order*, Springer-Verlag, Berlin, 2001. <https://doi.org/10.1007/978-3-642-61798-0>
- [10] T. KOLOKOLNIKOV, T. ERNEUX, J. WEI, Mesa-type patterns in the one-dimensional Brusselator and their stability, *Phys. D* **214**(2006), 63–77. <https://doi.org/10.1016/j.physd.2005.12.005>
- [11] J. LI, H. WANG, Q. OUYANG, Square Turing patterns in reaction-diffusion systems with coupled layers, *Chaos* **24**(2014), 023115. <https://doi.org/10.1063/1.4875262>
- [12] B. LI, X. ZHANG, Steady states of a Sel'kov–Schnakenberg reaction-diffusion system, *Discrete Contin. Dyn. Syst. Ser. S* **10**(2017), 1009–1023. <https://doi.org/10.3934/dcdss.2017053>
- [13] G. M. LIEBERMAN, Bounds for the steady-state Sel'kov model for arbitrary p in any number of dimensions, *SIAM J. Math. Anal.* **36**(2005), 1400–1406. <https://doi.org/10.1137/S003614100343651X>
- [14] P. LIU, J. SHI, Y. WANG, X. FENG, Bifurcation analysis of reaction-diffusion Schnakenberg model, *J. Math. Chem.* **51**(2013), 2001–2019. <https://doi.org/10.1007/s10910-013-0196-x>
- [15] Y. LOU, W. M. NI, Diffusion, self-diffusion and cross-diffusion, *J. Differential Equations* **131**(1996), 79–131. <https://doi.org/10.1006/jdeq.1996.0157>
- [16] J. S. MCGOUGH, K. RILEY, Pattern formation in the Gray–Scott model, *Nonlinear Anal. Real World Appl.* **5**(2004), 105–121. [https://doi.org/10.1016/S1468-1218\(03\)00020-8](https://doi.org/10.1016/S1468-1218(03)00020-8)
- [17] L. NIRENBERG, *Topics in nonlinear functional analysis*, Courant Institute of Mathematical Sciences, New York University, New York, 1974, Lecture Notes, 1974. <https://doi.org/10.1090/cIn/006>; MR0488102

- [18] Q. OUYANG, H. L. SWINNEY, Transition from a uniform state to hexagonal and striped Turing patterns, *Nature* **352**(1991), 610–612. <https://doi.org/10.1038/352610a0>
- [19] C. V. PAO, *Nonlinear parabolic and elliptic equations*, Springer Science & Business Media, 2012. <https://doi.org/10.1007/978-1-4615-3034-3>
- [20] R. J. H. PAYNE, C. S. GRIERSON, A theoretical model for ROP localisation by auxin in *Arabidopsis* root hair cells, *PLoS One* **4**(2009), e8337. <https://doi.org/10.1371/journal.pone.0008337>
- [21] R. PENG, Qualitative analysis of steady states to the Sel'kov model, *J. Differential Equations* **241**(2007), 386–398. <https://doi.org/10.1016/j.jde.2007.06.005>
- [22] R. PENG, J. SHI, M. WANG, On stationary patterns of a reaction-diffusion model with autocatalysis and saturation law, *Nonlinearity* **21**(2008), 1471–1488. <https://doi.org/10.1088/0951-7715/21/7/006>
- [23] R. PENG, M. X. WANG, Some nonexistence results for nonconstant stationary solutions to the Gray-Scott model in a bounded domain, *Appl. Math. Lett.* **22**(2009), 569–573. <https://doi.org/10.1016/j.aml.2008.06.032>
- [24] R. PENG, M. X. WANG, M. YANG, Positive steady-state solutions of the Sel'kov model, *Math. Comput. Model.* **44**(2006), 945–951. <https://doi.org/10.1016/j.mcm.2006.03.001>
- [25] J. SCHNAKENBERG, Simple chemical reaction systems with limit cycle behaviour, *J. Theor. Biol.* **81**(1979), 389–400. [https://doi.org/10.1016/0022-5193\(79\)90042-0](https://doi.org/10.1016/0022-5193(79)90042-0)
- [26] E. E. SEL'KOV, Self-oscillations in glycolysis, *Eur. J. Biochem.* **4**(1968), 79–86. <https://doi.org/10.1111/j.1432-1033.1968.tb00175.x>
- [27] J. SHI, X. WANG, On global bifurcation for quasilinear elliptic systems on bounded domains, *J. Differential Equations* **246**(2009), 2788–2812. <https://doi.org/10.1016/j.jde.2008.09.009>
- [28] H. UECKER, D. WETZEL, Numerical results for snaking of patterns over patterns in Some 2D Selkov–Schnakenberg reaction-diffusion systems, *SIAM J. Appl. Dyn. Syst.* **13**(2014), 94–128. <https://doi.org/10.1137/130918484>
- [29] M. WANG, *Nonlinear elliptic equation*, Science Press, Beijing, 2010.
- [30] M. X. WANG, Non-constant positive steady states of the Sel'kov model, *J. Differential Equations* **190**(2003), 600–620. [https://doi.org/10.1016/S0022-0396\(02\)00100-6](https://doi.org/10.1016/S0022-0396(02)00100-6)
- [31] J. WANG, J. WEI, J. SHI, Global bifurcation analysis and pattern formation in homogeneous diffusive predator–prey systems, *J. Differential Equations* **260**(2016), 3495–3523. <https://doi.org/10.1016/j.jde.2015.10.036>
- [32] M. J. WARD, J. C. WEI, The existence and stability of asymmetric spike patterns for the Schnakenberg model, *Stud. Appl. Math.* **109**(2002), 229–264. <https://doi.org/10.1111/1467-9590.00223>
- [33] J. WU, *Theory and applications of partial functional-differential equations*, Applied Mathematical Sciences, Vol. 119, Springer-Verlag, New York, 1996. <https://doi.org/10.1007/978-1-4612-4050-1>

- [34] C. XU, J. WEI, Hopf bifurcation analysis in a one-dimensional Schnakenberg reaction-diffusion model, *Nonlinear Anal. Real World Appl.* **13**(2012), 1961–1977. <https://doi.org/10.1016/j.nonrwa.2012.01.001>
- [35] Q. YE, Z. LI, M. WANG, Y. WU, *Introduction to reaction-diffusion equations*, Science Press, Beijing, 2011.
- [36] F. YI, J. WEI, J. SHI, Bifurcation and spatiotemporal patterns in a homogeneous diffusive predator–prey system, *J. Differential Equations* **246**(2009), 1944–1977. <https://doi.org/10.1016/j.jde.2008.10.024>
- [37] Y. YOU, Asymptotical dynamics of Selkov equations, *Discrete Contin. Dyn. Syst. Ser. S* **2**(2009), 193–219. <https://doi.org/10.3934/dcdss.2009.2.193>
- [38] Y. YOU, Upper-semicontinuity of global attractors for reversible Schnakenberg equations, *Stud. Appl. Math.* **130**(2013), 232–263. <https://doi.org/j.1467-9590.2012.00565.x>
- [39] J. ZHOU, J. P. SHI, Pattern formation in a general glycolysis reaction-diffusion system, *IMA J. Appl. Math.* **80**(2015), 1703–1738. <https://doi.org/10.1093/imamat/hxv013>