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BIFURCATION ANALYSIS OF A DIFFUSIVE PLANT-WRACK MODEL WITH TIDE EFFECT ON THE WRACK

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ABSTRACT. This paper deals with the spatial, temporal and spatiotemporal dynamics of a spatial plant-wrack model. The parameter regions for the stability and instability of the unique positive constant steady state solution are derived, and the existence of time-periodic orbits and non-constant steady state solutions are proved by bifurcation method. The nonexistence of positive nonconstant steady state solutions are studied by energy method and Implicit Function Theorem. Numerical simulations are presented to verify and illustrate the theoretical results.

1. Introduction. More recently, many ecologists have paid more and more attention to the experimental investigation of regular spatial patterning in *Carex stricta*. *Carex stricta*, the tussock sedge, is a species with widespread distribution in freshwater marshes of North America. Spatial dispersals of vegetation (through tillers) and wrack (resulting from dead plant leaves dropping to the soil surface and movement by the tides) are modeled using a diffusion approximation. The model, which describes the interaction of the plant and wrack, is as follows [20]:

$$\begin{cases} \frac{\partial P}{\partial t} - d_1 \Delta \widetilde{P} = \widetilde{P}(1 - \widetilde{P})F(\widetilde{P}) - s\widetilde{P} - I(\widetilde{P},\widetilde{W}), & x \in \Omega, \ t > 0, \\ \frac{\partial \widetilde{W}}{\partial t} - d_2 \Delta \widetilde{W} = s\widetilde{P} - b\widetilde{W}, & x \in \Omega, \ t > 0, \end{cases}$$
(1)

where $\Omega \subset \mathbb{R}^N$ is a bounded domain, \widetilde{P} is the plant biomass, \widetilde{W} is the wrack biomass, $F(\widetilde{P})$ is a function describing the positive effect of plant biomass on its own growth, s is the specific rate of plant senescence, $I(\widetilde{P}, \widetilde{W})$ is a function describing the inhibiting effect of wrack on plant growth as a function of plant and the wrack biomass, b is the decay rate of wrack, and d_1 and d_2 are diffusion constants describing lateral movement of plants and wrack. Here, $\Delta = \frac{\partial^2}{\partial x_1^2} + \cdots + \frac{\partial^2}{\partial x_N^2}$ is the usual Laplacian operator in N-dimension space.

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In this paper, we focus on the following specific type with an indirect facilitation of growth by the root mound by lowering of inhibition by the wrack, which leads to

$$F(\widetilde{P}) = 1, \quad I(\widetilde{P}, \widetilde{W}) = \widetilde{a}\widetilde{P}\widetilde{W}\frac{K}{\widetilde{P} + K}$$

where $\frac{K}{\tilde{P}+K}$ is added to the inhibition term, lowering inhibition as \tilde{P} increases, K is the level of plant biomass where inhibition is lowered by half, and \tilde{a} is an inhibition coefficient [20]. As a result, model (1) with homogeneous Neumann boundary condition has the following from:

$$\begin{cases} \frac{\partial \widetilde{P}}{\partial t} - d_1 \Delta \widetilde{P} = \widetilde{P}(1 - \widetilde{P}) - s\widetilde{P} - \widetilde{a}\widetilde{P}\widetilde{W}\frac{K}{\widetilde{P} + K}, & x \in \Omega, \ t > 0, \\ \frac{\partial \widetilde{W}}{\partial t} - d_2 \Delta \widetilde{W} = s\widetilde{P} - b\widetilde{W}, & x \in \Omega, \ t > 0, \\ \frac{\partial \widetilde{P}}{\partial \nu} = \frac{\partial \widetilde{W}}{\partial \nu} = 0, & x \in \partial\Omega, \ t > 0, \\ \widetilde{P}(x, 0) = \widetilde{P}_0(x), \ \widetilde{W}(x, 0) = \widetilde{W}_0(x), & x \in \Omega, \end{cases}$$
(2)

where $\Omega \subset \mathbb{R}^N$ is a bounded domain with smooth boundary $\partial\Omega$, ν is the unit outward normal on $\partial\Omega$, and the homogeneous Neumann boundary conditions indicate that the system is self-contained with zero population flux across the boundary $\partial\Omega$. The constant $\tilde{a}, b, s, K, d_1, d_2$ are assumed to be positive. $\tilde{P}_0(x)$ and $\tilde{W}_0(x)$ are nonnegative nontrivial continuous functions.

For the sake of simplicity, we let $P = \widetilde{P}$, $W = b\widetilde{W}$, $a = \widetilde{a}/b$, then problem (2) becomes

$$\begin{cases} \frac{\partial P}{\partial t} - d_1 \Delta P = P(1-P) - sP - aPW \frac{K}{P+K}, & x \in \Omega, \ t > 0, \\ \frac{\partial W}{\partial t} - d_2 \Delta W = b(sP - W), & x \in \Omega, \ t > 0, \\ \frac{\partial P}{\partial \nu} = \frac{\partial W}{\partial \nu} = 0, & x \in \partial\Omega, \ t > 0, \\ \widetilde{P}(x,0) = P_0(x) = \widetilde{P}_0(x), \ W(x,0) = W_0(x) = b\widetilde{W}_0(x), & x \in \Omega. \end{cases}$$
(3)

In order to provide guidelines on the dynamics of the full reaction-diffusion system, it is important to consider the steady states corresponding to (3), which satisfies the following elliptic system:

$$\begin{cases} -d_1 \Delta P = P(1-P) - sP - aPW \frac{K}{p+K}, & x \in \Omega, \\ -d_2 \Delta W = b(sP - W), & x \in \Omega, \\ \frac{\partial P}{\partial \nu} = \frac{\partial W}{\partial \nu} = 0, & x \in \partial \Omega. \end{cases}$$
(4)

It is, naturally, the dynamics in the biologically meaningful region $\{(P, W) : P, W \ge 0\}$ are of interest. Furthermore, we want to find the positive steady state of the non-spatial model, (P_*, W_*) , which is corresponding to the coexistence of plant and wrack. By direct calculation, we find that if $s \ge 1$, problem (4) admits no positive constant solution. On the other hand, if

$$0 < s < 1,\tag{5}$$

problem (4) admits a unique positive constant solution (P_*, W_*) , where

$$P_* = \frac{-M + \sqrt{M^2 + 4(1-s)K}}{2}, \quad W_* = sP_*.$$
 (6)

Here,

$$M := (1+as)K - (1-s)$$
(7)

Spatial, temporal and spatiotemporal patterns could occur in the reaction-diffusion model (3) via three possible mechanisms: Turing instability, Hopf bifurcation, and positive non-constant steady states. There are a great deal of research have been devoted to the study of spatial, temporal and spatiotemporal patterns in chemical and biology contexts (see [1, 3, 9, 10, 11, 13, 19, 27, 32, 37, 53, 58, 59] for Brusselator model; [4, 6, 14, 23, 24, 30, 44, 54, 55, 57] for Gray-Scott model; [7, 17, 18, 25, 26, 50, 52] for Lengyel-Epstein model; [31, 48, 56] for Oregonator model, [12, 16, 34, 43, 45, 46, 49] for Schnakenberg model, [5, 8, 21, 28, 29, 33, 39] for Sel'klov model).

The goal of this article is to show that the diffusive plant-wrack model (2) exhibits various spatial, temporal and spatiotemporal patterns via the aforementioned three mechanisms. The organization of the remaining part of this paper is as follows. In Section 2, we investigate the asymptotic behavior of the positive equilibrium (P_*, W_*) and occurrence of Hopf bifurcation of the local system of (3). In section 3, we firstly consider the asymptotic behavior and Turing instability of the positive equilibrium (P_*, W_*) for the reaction-diffusion system (3), then we study the existence of Hopf bifurcation. In Section 4, we consider the existence and nonexistence of nonconstant positive solutions for problem (4) by bifurcation theory, energy method and Implicit Function Theorem. We end our study with numerical simulations in Section 5. Throughout this paper, \mathcal{N} is the set of natural numbers and $\mathcal{N}_0 = \mathcal{N} \cup \{0\}$. The eigenvalues of the operator $-\Delta$ with homogeneous Neumann boundary condition in Ω are denoted by $0 = \mu_0 < \mu_1 \le \mu_2 \le \cdots \le \mu_n \le \cdots$, and the eigenfunction corresponding to μ_n is $\phi_n(x)$.

2. Analysis of the local system. In this section, we mainly consider the following local system corresponding to problem (3):

$$\begin{cases} \dot{P} = P(1-P) - sP - aPW \frac{K}{P+K}, & t > 0, \\ \dot{W} = b(sP - W), & t > 0. \end{cases}$$

$$\tag{8}$$

The dynamical behavior of the solutions near the positive constant equilibrium (P_*, W_*) can be studied by computing the eigenvalues of the Jacobin matrix $L_0(b)$ of the system (8), namely,

$$L_{0}(b) = \begin{pmatrix} \frac{P_{*}}{P_{*}+K} (1-s-K-2P_{*}) & -\frac{aKP_{*}}{P_{*}+K} \\ bs & -b \end{pmatrix}$$

$$= \begin{pmatrix} \frac{P_{*}}{P_{*}+K} \left(asK - \sqrt{M^{2} + 4(1-s)K} \right) & -\frac{aKP_{*}}{P_{*}+K} \\ bs & -b \end{pmatrix}.$$
 (9)

The characteristic equation of $L_0(b)$ is

$$\xi^2 - T(b)\xi + D(b) = 0, \tag{10}$$

where

$$T(b) = \frac{P_*}{P_* + K} \left(asK - \sqrt{M^2 + 4(1-s)K} \right) - b, \tag{11}$$

$$D(b) = \frac{bP_*}{P_* + K}\sqrt{M^2 + 4(1-s)K} > 0.$$
 (12)

Then (u_*, v_*) is locally asymptotically stable if T(b) < 0 and it is unstable if T(b) > 0.

A series of calculations shows that

1. If $s + K \ge 1$ or s + K < 1 and

$$a \le \frac{(K+1-s)^2}{2sK(1-s-K)},\tag{13}$$

then $asK - \sqrt{M^2 + 4(1-s)K} \le 0$, which implies T(b) < 0 for all b > 0; 2. If

$$s + K < 1 \text{ and } a > \frac{(K+1-s)^2}{2sK(1-s-K)},$$
 (14)

then $asK - \sqrt{M^2 + 4(1-s)K} > 0$, which implies T(b) < 0 if $b > b_0$ and T(b) > 0 if $b < b_0$, where

$$b_0 := \frac{P_*}{P_* + K} \left(asK - \sqrt{M^2 + 4(1 - s)K} \right) > 0.$$
(15)

Theorem 2.1. Assume (5) holds. Let b_0 be the constant defined as (15). Then the positive equilibrium (P_*, W_*) of the local system (8) given as (6) is locally asymptotically stable if

(*i*): $s + K \ge 1$; or (*ii*): s + K < 1 and (13) holds; or (*iii*): (14) holds and $b > b_0$.

While the positive equilibrium (P_*, W_*) is unstable with respect to (8) if (14) holds and $b < b_0$. System (8) undergoes a Hopf bifurcation at (P_*, W_*) as b passes through b_0 .

Proof. (*i*), (*ii*), (*iii*) have been proved in the previous paragraphs. We only focus on the Hopf bifurcation occurring at (P_*, W_*) by using *b* as the bifurcation parameter. According to Poincaré-Andronov-Hopf Bifurcation Theorem [47, Theorem 3.1.3], system (8) has a small amplitude non-constant periodic solution bifurcating from (P_*, W_*) when *b* crosses through b_0 if the transversal condition is satisfied.

Let $\xi(b) = A(b) \pm iB(b)$ be the roots of (10). Then

$$A(b) = \frac{1}{2}T(b) = \frac{1}{2}(b_0 - b), \quad B(b) = \frac{1}{2}\sqrt{4D(b) - [T(b)]^2}.$$

Hence $A(b_0) = 0$, $A'(b_0) = -1/2$ and $B(b_0) = 2\sqrt{D(b_0)} > 0$ (see (12)). This shows that the transversal condition holds, and thus (8) undergoes a Hopf bifurcation at (P_*, W_*) as b passes through b_0 .

To illustrate the above result. We give an numerical example.

Example 2.2. Consider problem (8) with s = K = 0.25 and a = 25.6 such that (5) and (14) hold. Then we get the following system

$$\begin{cases} \dot{P} = P(1-P) - 0.25P - \frac{6.4PW}{P+0.25}, & t > 0, \\ \dot{W} = b(0.25P - W), & t > 0, \end{cases}$$
(16)

and the positive constant equilibrium is $(P_*, W_*) = (0.15, 0.0375)$, the constant



FIGURE 1. When $b = 0.085 > b_0 = 0.075$, the solution trajectories spiral toward the positive equilibrium (0.15, 0.0375) (left). When $b = 0.05 < b_0 = 0.075$, there is a limit cycle surrounding the positive equilibrium (0.15, 0.0375) (right).

 $b_0 = 0.075$. It follows from Theorem 2.1 that (0.15, 0.0375) is locally asymptotically stable when b > 0.075 and it is unstable when b < 0.075. Moreover when b passes through 0.075 from the right side of 0.075, (0.15, 0.0375) will lose its stability and Hopf bifurcation occurs, that is, a family of periodic solutions bifurcate from (0.15, 0.0375). Numerical simulations are presented in Fig. 1. The left of Fig. 1 shows the stable behavior when $b > b_0$. The right of Fig. 1 is the phase portrait of the problem (16) which depicts the limit cycle arising out of Hopf bifurcation around (0.15, 0.0375).

3. Analysis of the PDE model (3). In this section, we mainly consider the model (3), and the studies include the parameter regions for the stability and instability of the unique positive constant equilibrium (P_*, W_*) , the occurrence Turing instability and the existence of time periodic orbits.

3.1. Stability analysis. The local stability of (u_*, v_*) with respect to (3) is determined by the following eigenvalue problem which is got by linearizing the system (4) about the positive constant equilibrium (P_*, W_*)

$$\begin{cases} \begin{pmatrix} d_1 \Delta \phi \\ d_2 \Delta \psi \end{pmatrix} + L_0(b) \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \mu \begin{pmatrix} \phi \\ \psi \end{pmatrix}, \quad x \in \Omega, \\ \frac{\partial \phi}{\partial \nu} = \frac{\partial \psi}{\partial \nu} = 0, \quad x \in \partial\Omega, \end{cases}$$
(17)

where $L_0(b)$ is defined as (9). Denote

$$L(b) = \begin{pmatrix} d_1 \Delta & 0\\ 0 & d_2 \Delta \end{pmatrix} + L_0(b)$$

$$= \begin{pmatrix} d_1 \Delta + \frac{P_*}{P_* + K} \left(asK - \sqrt{M^2 + 4(1 - s)K} \right) & -\frac{aKP_*}{P_* + K} \\ bs & d_2 \Delta - b \end{pmatrix}.$$
 (18)

For each $n \in \mathcal{N}_0$, we define a 2×2 matrix

$$L_n(b) = \begin{pmatrix} -d_1\mu_n + \frac{P_*}{P_* + K} \left(asK - \sqrt{M^2 + 4(1 - s)K} \right) & -\frac{aKP_*}{P_* + K} \\ bs & -d_2\mu_n - b \end{pmatrix}.$$
 (19)

The following statements hold true by using Fourier decomposition:

- 1. If μ is an eigenvalue of (17), then there exists $n \in \mathcal{N}_0$ such that μ is an eigenvalue of $L_n(b)$.
- 2. The constant equilibrium (P_*, W_*) is locally asymptotically stable with respect to (3) if and only if for every $n \in \mathcal{N}_0$, all eigenvalues of $L_n(b)$ have negative real part.
- 3. The constant equilibrium (u_*, v_*) is unstable with respect to (3) if there exists an $n \in \mathcal{N}_0$ such that $L_n(b)$ has at least one eigenvalue with positive real part. The characteristic equation of $L_n(b)$ is

$$\mu^2 - T_n(b)\mu + D_n(b) = 0, \qquad (20)$$

where

$$T_n(b) = -(d_1 + d_2)\mu_n + T(b), \tag{21}$$

$$D_n(b) = d_1 d_2 \mu_n^2 + [d_1 b - d_2 (T(b) + b)] \mu_n + D(b).$$
(22)

Here, T(b) and D(b) are defined as (11) and (12) respectively. Then (P_*, W_*) is locally asymptotically stable if $T_n(b) < 0$ and $D_n(b) > 0$ for all $n \in \mathcal{N}_0$, and (P_*, W_*) is unstable if there exists $n \in \mathcal{N}_0$ such that $T_n(b) > 0$ or $D_n(b) < 0$.

Since D(b) > 0 and $\mu_n \ge 0$ for all $n \in \mathcal{N}_0$, a sufficient condition to ensure $T_n(b) < 0$ and $D_n(b) > 0$ is $T(b) \le -b$, which is equivalent to $asK \le \sqrt{M^2 + 4(1-s)K}$, i.e., $s + K \ge 1$ or s + K < 1 and (13) holds (see the analysis in Section 2).

In the following we consider the case that (14) holds, which implies b_0 , defined as (15), is positive. Then we have $T(b) = b_0 - b$, and then it follows from (12) that

$$T_n(b) = -(d_1 + d_2)\mu_n + b_0 - b,$$
(23)

$$D_n(b) = d_1 d_2 \mu_n^2 + (d_1 b - d_2 b_0) \mu_n + \chi b, \qquad (24)$$

where

$$\chi := \frac{P_*}{P_* + K} \sqrt{M^2 + 4(1 - s)K} > 0.$$
⁽²⁵⁾

We define

$$T(b,\mu) = -(d_1 + d_2)\mu + b_0 - b, \tag{26}$$

$$D(b,\mu) = d_1 d_2 \mu^2 + (d_1 b - d_2 b_0) \mu + \chi b, \qquad (27)$$

and

$$H = \{(b,\mu) \in (0,\infty) \times [0,\infty) : T(b,\mu) = 0\},$$
(28)

$$S = \{(b,\mu) \in (0,\infty) \times [0,\infty) : D(b,\mu) = 0\}.$$
(29)

Then H is the Hopf bifurcation curve and S is the steady state bifurcation curve. Furthermore, the sets H and S are graphs of functions defined as follows

$$b_H(\mu) = -(d_1 + d_2)\mu + b_0, \tag{30}$$

$$b_S(\mu) = \frac{-d_1 d_2 \mu^2 + d_2 b_0 \mu}{d_1 \mu + \chi}.$$
(31)



FIGURE 2. Illusion of Lemma 3.1. The curves are the graphs of $b_S(\mu)$ and the lines are graphs of $b_H(\mu)$. (a) is the case of $\frac{d_1}{d_2} < 1$; (b) is the case $\frac{d_1}{d_2} = 1$; (c) is the case $\frac{d_1}{d_2} > 1$; (d) is the case $\frac{d_1}{d_2} = D_1$; (e) is the case $\frac{d_1}{d_2} < D_1$. For all, the curves (1) represents $b_S^* < b_0$; the curves (2) represent $b_S^* = b_0$; the curves (3) represent $b_S^* > b_0$

Lemma 3.1. (see Fig. 2) Assume (5) and (14) hold. Let b_0 and χ be the two positive constants defined as (15) and (25) respectively. Let $b_H(\mu)$ and $b_S(\mu)$ be the two functions defined as (30) and (31) respectively.

(i): The function $b_H(\mu)$ is strictly decreasing for $\mu \in (0,\infty)$ such that

$$b_H(0) = b_H(\mu_2^*) = 0, \ b_H(\mu) > 0 \ for \ \mu \in [0, \mu_2^*)$$

$$b_H(\mu) < 0 \ for \ \mu > \mu_2^*, \ \lim_{\mu \to \infty} b_H(\mu) = -\infty,$$

where

$$\mu_2^* = \frac{b_0}{d_1 + d_2}.\tag{32}$$

(ii): Let

$$\mu_1^* := \frac{\sqrt{\chi^2 + b_0 \chi} - \chi}{d_1} < \mu_3^* := \frac{b_0}{d_1}.$$
(33)

Then $\mu = \mu_1^*$ is the unique critical value of $b_S(\mu)$, the function $b_S(\mu)$ is strictly increasing for $\mu \in (0, \mu_1^*)$, and it is strictly decreasing for $\mu > \mu_1^*$. $b_S(\mu) > 0$ for $\mu \in (0, \mu_3^*)$, $b_S(\mu) < 0$ for $\mu > \mu_3^*$, $b_S(0) = b_S(\mu_3^*) = 0$, and

$$\max_{\mu \in [0,\infty)} b_S(\mu) = b_S(\mu_1^*) = \frac{d_2}{d_1} \left(\sqrt{b_0 + \chi} - \sqrt{\chi} \right)^2 =: b_S^*$$
(34)

(iii): $b_H(\mu)$ and $b_S(\mu)$ cross at the point $(\mu_H, \lambda_H(\mu_H))$ and $b_H(\mu) > b_S(\mu)$ for $0 \le \mu < \mu_H, b_H(\mu) < b_S(\mu)$ for $\mu > \mu_H$, where

$$\mu_H := \frac{-[(d_2 - d_1)b_0 + (d_1 + d_2)\chi] + \sqrt{[(d_2 - d_1)b_0 + (d_1 + d_2)\chi]^2 + 4d_1^2 b_0 \chi}}{2d_1^2}.$$
 (35)

(iv):
$$\mu_1^* < \mu_2^* \text{ if } \frac{d_1}{d_2} > D_1, \ \mu_1^* = \mu_2^* \text{ if } \frac{d_1}{d_2} = D_1 \text{ and } \mu_1^* > \mu_2^* \text{ if } \frac{d_1}{d_2} < D_1, \text{ where}$$

$$D_1 := \sqrt{\frac{\chi}{b_0 + \chi}}.$$
(36)

(v): $\mu_H < \mu_1^*$ if and only if $b_H^* < b_S^*$ if and only if $\frac{d_1}{d_2} < 1$; $\mu_H = \mu_1^*$ if and only if $b_H^* = b_S^*$ if and only if $\frac{d_1}{d_2} = 1$; $\mu_H > \mu_1^*$ if and only if $b_H^* > b_S^*$ if and only if $\frac{d_1}{d_2} > 1$, where

$$b_H^* := b_H(\mu_1^*) = b_0 - \left(1 + \frac{d_2}{d_1}\right) \left(\sqrt{\chi^2 + b_0 \chi} - \chi\right).$$
(37)

(vi): Let

$$D_2 := \frac{\left(\sqrt{b_0 + \chi} - \sqrt{\chi}\right)^2}{b_0} < 1.$$
(38)

Then $b_{S}^{*} < b_{0}$ if $\frac{d_{1}}{d_{2}} > D_{2}$, $b_{S}^{*} = b_{0}$ if $\frac{d_{1}}{d_{2}} = D_{2}$, and $b_{S}^{*} > b_{0}$ if $\frac{d_{1}}{d_{2}} < D_{2}$. Moreover, if $\frac{d_{1}}{d_{2}} < D_{2}$, we have

1. there exist two positive constant μ_L and μ_R such that $0 < \mu_L < \mu_1^* < \mu_R$ and $b_S(\mu_L) = b_S(\mu_R) = b_0$, where

$$\mu_L := \frac{\left(1 - \frac{d_1}{d_2}\right)b_0 - \sqrt{\left(1 - \frac{d_1}{d_2}\right)^2 b_0^2 - 4b_0 \frac{d_1}{d_2}}}{2d_1},$$

$$\mu_R := \frac{\left(1 - \frac{d_1}{d_2}\right)b_0 + \sqrt{\left(1 - \frac{d_1}{d_2}\right)^2 b_0^2 - 4b_0 \frac{d_1}{d_2}}}{2d_1}.$$
(39)

2. $\lambda_S(\mu) > b_0 \text{ for } \mu_L < \mu < \mu_R \text{ and } 0 < \lambda_S(\mu) < b_0 \text{ for } \mu \in (0, \mu_L) \cup (\mu_R, \mu_3^*).$

Now we can give a stability result regarding the constant equilibrium (P_*, W_*) by the analysis above. To this end, we define

$$\bar{b} = \max_{n \in \mathcal{N}} b_S(\mu_n) \le b_S^*.$$
(40)

Theorem 3.2. Assume (5) holds. Then the constant equilibrium (P_*, W_*) of the system (3) given as (6) is locally asymptotically stable if

(*i*): $s + K \ge 1$; or

(*ii*): s + K < 1 and (13) holds; or

(iii): (14) holds and $b > \max\{b_0, \overline{b}\}$. In particular, $b > \max\{b_0, \overline{b}\}$ holds if

$$b > \max\{b_0, b_S^*\} = \begin{cases} b_0, & \text{if } \frac{d_1}{d_2} \ge D_2; \\ b_S^*, & \text{if } \frac{d_1}{d_2} < D_2, \end{cases}$$

where b_0 , \bar{b} , b_S^* and D_2 are positive constants defined as (15), (40), (34) and (38) respectively.

The constant equilibrium (P_*, W_*) is unstable with respect to (3) if (14) holds and $b < \max\{b_0, \overline{b}\}.$

Next we consider the occurrence of Turing instability, which means the constant equilibrium (P_*, W_*) is stable with respect to the ODE model (8) while it is unstable with respect to the PDE model (3). Combining the Theorems 2.1 and 3.2, this can happen only if $b_0 < b < \overline{b}$.

Theorem 3.3. Assume (5) and (14) hold. Then Turing instability happens if

- (i): $\frac{d_1}{d_2} < D_2$; and (ii): there exists $j, k \in \mathcal{N}$ such that $\mu_{j-1} \leq \mu_L < \mu_j \leq \mu_k < \mu_R \leq \mu_{k+1}$ and

$$b_0 < b < \overline{b} = \begin{cases} b_S(\mu_j), & \text{if } j = k;\\ \max_{i \in [j,k] \cap \mathcal{N}} b_S(\mu_i), & \text{if } j < k, \end{cases}$$

where D_2 , μ_L , μ_R , b_0 and \overline{b} are positive constants defined as (38), (39), (15) and (40) respectively, $b_S(\mu)$ is the function given in (31).

3.2. Hopf bifurcation. In this part, we study the existence of periodic solutions of (3) by analyze the Hopf bifurcation from the constant equilibrium (P_*, W_*) under the assumption (5) and (14) since there is no change of stability for other cases. We assume that all eigenvalues μ_i are simple, and denote the corresponding eigenfunction by $\phi_i(x), i \in \mathcal{N}_0$. Note that this assumption always holds when N = 1 for $\Omega = (0, \ell \pi)$, as for $i \in \mathcal{N}_0$, $\mu_i = i^2/\ell^2$ and $\phi_i(x) = \cos(ix/\ell)$, where ℓ is a positive constant. We use b as the main bifurcation parameter. To identify possible Hopf bifurcation value b_H , we recall the following necessary and sufficient condition from [15, 50, 51].

(HS) There exists $i \in \mathcal{N}_0$ such that

$$T_i(b_H) = 0, \ D_i(b_H) > 0 \text{ and } T_j(b_H) \neq 0, \ D_j(b_H) \neq 0 \text{ for } j \in \mathcal{N}_0 \setminus \{i\},$$
(41)

where $T_i(b)$ and $D_i(b)$ are given in (23) and (24) respectively, and for the unique pair of complex eigenvalues $A(b) \pm iB(b)$ near the imaginary axis,

$$A'(b_H) \neq 0 \text{ and } B(b_H) > 0.$$
 (42)

For $i \in \mathcal{N}_0$, we define

$$b_{i,H} = b_H(\mu_i),\tag{43}$$

where the function $b_H(\mu)$ is given in (30). Then $T_i(b_{i,H}) = 0$ and $T_i(b_{i,H}) \neq 0$ for $j \neq i$. By (41), we need $D_i(b_{i,H}) > 0$ to make $b_{i,H}$ as a possible bifurcation value, which means $\mu_i < \mu_H$ by Lemma 3.1, where μ_H is given in (35). Let $n_0 \in \mathcal{N}_0$ such that $\mu_{n_0} < \mu_H \leq \mu_{n_0+1}$, then we can see (41) holds with $\lambda_H = \lambda_{i,H}$ for $i \in \{0, \dots, n_0\}$ (see Fig. 2). Finally, we consider the conditions in (42). Let the eigenvalues close to the pure imaginary one at $b = b_{i,H}$ be $A(b) \pm iB(b)$. Then

$$A'(b_{i,H}) = \frac{T'_i(b_{i,H})}{2} = -\frac{1}{2} < 0 \text{ and } B(b_{i,H}) = \sqrt{D_i(b_{i,H})} > 0 \text{ for } i = 0, \cdots, n_0$$

Then all conditions in (HS) are satisfied if $i \in \{0, \dots, n_0\}$. Now by using the Hopf bifurcation theorem in [51], we have

Theorem 3.4. Assume (5) and (14) hold. Let Ω be a smooth domain so that all eigenvalues μ_i , $i \in \mathcal{N}_0$, are simple. Then there exists a $n_0 \in \mathcal{N}_0$ such that $\mu_{n_0} < \mu_H \leq \mu_{n_0+1}$, and $b_{i,H}$, defined as (43), is a Hopf bifurcation value for $i \in \{0, \dots, n_0\}$, where μ_H is given in (35). At each $b_{i,H}$, the system (3) undergoes a Hopf bifurcation, and the bifurcation periodic orbits near $(b, P, W) = (b_{i,H}, P_*, W_*)$

can be parameterized as $(b_i(\tau), P_i(\tau), W_i(\tau))$, so that $b_i(\tau)$ is the form of $b_i(\tau) = b_{i,H} + o(\tau)$ for $\tau \in (0, \rho)$ for some constant $\rho > 0$, and

$$P_{i}(\tau)(x,t) = P_{*} + \tau a_{i} \cos(\omega(b_{i,H})t)\phi_{i}(x) + o(\tau),$$

$$W_{i}(\tau)(x,t) = W_{*} + \tau b_{i} \cos(\omega(b_{i,H})t)\phi_{i}(x) + o(\tau),$$

where $\omega(b_{i,H}) = \sqrt{D_i(b_{i,H})}$ with $D_i(b)$ given in (24) is the corresponding time frequency, $\phi_i(x)$ is the corresponding spatial eigenfunction, and (a_i, b_i) is the corresponding eigenvector, *i.e.*,

$$(L(b_{i,H}) - i\omega(b_{i,H})I) \begin{pmatrix} a_i\phi_i(x) \\ b_i\phi_i(x) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

where L(b) is given in (18). Moreover,

- 1. The bifurcation periodic orbit from $b_{0,H} = b_0$ are spatially homogeneous, where b_0 is given in (15);
- 2. The bifurcation periodic orbit from $b_{i,H}$, $i \in \{1, \dots, n_0\}$, are spatially nonhomogeneous.

Next we calculate the direction of Hopf bifurcation and the stability of the bifurcating periodic orbits bifurcating from $b = b_0$. We use the normal form method and center manifold theorem in [15] to study it. Let $L^*(b)$ be the conjugate operator of L(b) defined as (18) i.e.,

$$L^*(b) = \begin{pmatrix} d_1 \Delta + b_0 & bs \\ -\frac{aKP_*}{P_* + K} & d_2 \Delta - b \end{pmatrix},$$
(44)

with domain

$$D(L^*(b)) = D(L(b)) = \mathbf{X} \oplus i\mathbf{X} = \{x_1 + ix_2 : x_1, x_2 \in \mathbf{X}\},\$$

where b_0 is given in (15) and

$$\mathbf{X} := \left\{ (P, W) \in H^2(\Omega) \times H^2(\Omega) : \frac{\partial P}{\partial \nu} = \frac{\partial W}{\partial \nu} = 0 \text{ on } \partial \Omega \right\}.$$

Let

$$q = \begin{pmatrix} q_1 \\ q_2 \end{pmatrix} = \begin{pmatrix} 1 \\ \frac{P_* + K}{aKP_*} \left(b_0 - i\sqrt{\chi b_0}\right) \end{pmatrix},$$
$$q^* = \begin{pmatrix} q_1^* \\ q_2^* \end{pmatrix} = \frac{1}{2|\Omega|} \begin{pmatrix} 1 + i\sqrt{\frac{b_0}{\chi}} \\ -i\frac{aKP_*}{(P_* + K)\sqrt{\chi b_0}} \end{pmatrix},$$

and χ be the constants given in (25). It holds

- 1. $\langle L^*(b)\xi,\eta\rangle = \langle \xi, L(b)\eta\rangle$ for $\xi \in D(L^*(b))$ and $\eta \in D(L(b))$,
- 2. $L^*(b_0)q^* = -i\sqrt{\chi b_0}q^*$ and $L(b_0)q = i\sqrt{\chi b_0}q$,
- 3. $\langle q^*, q \rangle = 1$ and $\langle q^*, \overline{q} \rangle = 0$,

where

$$\langle \xi, \eta \rangle = \int_{\Omega} \overline{\xi}^T \eta dx$$

denotes the inner product in $L^2(\Omega) \times L^2(\Omega)$. According to [15], we decompose $\mathbf{X} = \mathbf{X}^C \oplus \mathbf{X}^S$ with

$$\mathbf{X}^C = \left\{ zq + \overline{zq} : z \in \mathbb{C} \right\}, \ \mathbf{X}^S = \left\{ \omega \in \mathbf{X} : \left\langle q^*, \omega \right\rangle = 0 \right\}.$$

For any $(P, W) \in \mathbf{X}$, there exists $z = \langle q^*, (P, W)^T \rangle \in \mathbb{C}$ and $\omega = (\omega_1, \omega_2) \in \mathbf{X}^S$ such that

$$(P,W)^T = zq + \overline{zq} + (\omega_1, \omega_2)^T.$$

Thus,

$$P = z + \overline{z} + \omega_1,$$

$$W = \frac{z(P_* + K)}{aKP_*} \left(b_0 - i\sqrt{\chi b_0} \right) + \frac{\overline{z}(P_* + K)}{aKP_*} \left(b_0 + i\sqrt{\chi b_0} \right) + \omega_2.$$

Then system (3) in (z, ω) coordinates become

$$\begin{cases} \dot{z} = i\sqrt{\chi b_0} z + \langle q^*, \mathfrak{F} \rangle, \\ \dot{\omega} = L(b)\omega + H(z, \overline{z}, \omega), \end{cases}$$
(45)

where $H(z,\overline{z},\omega) = \mathfrak{F} - \langle q^*,\mathfrak{F} \rangle q - \langle \overline{q}^*,\mathfrak{F} \rangle \overline{q}$, $\mathfrak{F} = (f,g)^T$ and $f = P(1-P) - sP - aPW\frac{K}{P+K}$, g = b(sP - W) and so

$$\begin{split} \langle q^*, \mathfrak{F} \rangle &= \frac{1}{2} \left[\left(1 - i\sqrt{\frac{b_0}{\chi}} \right) f + i\frac{aKP_*}{(P_* + K)\sqrt{\chi b_0}} g \right], \\ \langle \overline{q}^*, \mathfrak{F} \rangle &= \frac{1}{2} \left[\left(1 + i\sqrt{\frac{b_0}{\chi}} \right) f - i\frac{aKP_*}{(P_* + K)\sqrt{\chi b_0}} g \right], \\ \langle q^*, \mathfrak{F} \rangle q &= \frac{1}{2} \left(\begin{array}{c} f + i\left(\sqrt{\frac{b_0}{\chi}} f - \frac{aKP_*}{(P_* + K)\sqrt{\chi b_0}} g\right) \\ g - i\left[\frac{P_* + K}{aKP_*} \left(\sqrt{\chi b_0} + b_0\sqrt{\frac{b_0}{\chi}} \right) f - \sqrt{\frac{b_0}{\chi}} g \right] \right), \\ \langle \overline{q}^*, \mathfrak{F} \rangle \overline{q} &= = \frac{1}{2} \left(\begin{array}{c} f - i\left(\sqrt{\frac{b_0}{\chi}} f - \frac{aKP_*}{(P_* + K)\sqrt{\chi b_0}} g\right) \\ g + i\left[\frac{P_* + K}{aKP_*} \left(\sqrt{\chi b_0} + b_0\sqrt{\frac{b_0}{\chi}} \right) f - \sqrt{\frac{b_0}{\chi}} g \right] \end{array} \right). \end{split}$$

A direct calculation shows that $H(z, \overline{z}, \omega) = (0, 0)^T$. Let

$$H(z,\overline{z},\omega) = \frac{1}{2}H_{20}z^2 + H_{11}z\overline{z} + \frac{1}{2}H_{02}\overline{z}^2 + O(|z|^3).$$

It follows [15, Appendix A] that the system (45) possesses a center manifold, then we can write ω in the form

$$\omega = \frac{1}{2}\omega_{20}z^2 + \omega_{11}z\overline{z} + \frac{1}{2}\omega_{02}\overline{z}^2 + O(|z|^3).$$

Thus we have

$$\overline{\omega}_{02} = \omega_{20} = \left(2i\sqrt{\chi b_0}I - L\right)^{-1}H_{20} = 0, \ \omega_{11} = (-L)^{-1}H_{11} = 0.$$

For later uses, we denote

$$\begin{split} c_0 &= f_{PP} q_1^2 + 2 f_{PW} q_1 q_2 + f_{WW} q_2^2 = -2 + 2 \frac{a s K^2 P_*}{(P_* + K)^3} - 2 \frac{a K^2}{(P_* + K)^2} q_2, \\ &= -2 + \frac{2 a s K^2 P_*}{(P_* + K)^3} - \frac{2 K b_0}{P_* (P_* + K)} + i \frac{2 K \sqrt{\chi b_0}}{P_* (P_* + K)}, \\ d_0 &= g_{PP} q_1^2 + 2 g_{PW} q_1 q_2 + g_{WW} q_2^2 = 0, \end{split}$$

$$\begin{split} e_0 &= f_{PP} |q_1|^2 + f_{PW} (q_1 \overline{q}_2 + \overline{q}_1 q_2) + f_{WW} |q_2|^2 \\ &= -2 + 2 \frac{asK^2 P_*}{(P_* + K)^3} - \frac{aK^2}{(P_* + K)^2} (\overline{q}_2 + q_2), \\ &= -2 + \frac{2asK^2 P_*}{(P_* + K)^3} - \frac{2Kb_0}{P_*(P_* + K)}, \\ f_0 &= g_{PP} |q_1|^2 + g_{PW} (q_1 \overline{q}_2 + \overline{q}_1 q_2) + g_{WW} |q_2|^2 = 0, \\ g_0 &= f_{PPP} |q_1|^2 q_1 + f_{PPW} (2|q_1|^2 q_2 + q_1^2 \overline{q}_2) \\ &+ f_{PWW} (2q_1 |q_2|^2 + \overline{q}_1 q_2^2) + f_{WWW} |q_2|^2 q_2 \\ &= -6 \frac{asK^2 P_*}{(P_* + K)^4} + 2 \frac{aK^2}{(P_* + K)^3} (2q_2 + \overline{q}_2), \\ &= -\frac{6asK^2 P_*}{(P_* + K)^4} + \frac{6Kb_0}{P_*(P_* + K)^2} - i \frac{2K\sqrt{\chi b_0}}{P_*(P_* + K)^2}, \\ h_0 &= g_{PPP} |q_1|^2 q_1 + g_{PPW} (2|q_1|^2 q_2 \\ &+ q_1^2 \overline{q}_2) + g_{PWW} (2q_1 |q_2|^2 + \overline{q}_1 q_2^2) + g_{WWW} |q_2|^2 q_2 \\ &= 0, \end{split}$$

with all the partial derivatives evaluated at the point $(P, W) = (P_*, W_*)$. Therefore, the model (3) restricted to the center manifold in z, \overline{z} coordinates is given by

$$\frac{dz}{dt} = i\sqrt{\chi b_0}z + \frac{1}{2}\phi_{20}z^2 + \phi_{11}z\overline{z} + \frac{1}{2}\phi_{02}\overline{z}^2 + \frac{1}{2}\phi_{21}z^2\overline{z} + O(|z|^4),$$

where

$$\begin{split} \phi_{20} &= \left\langle q^*, (c_0, d_0)^T \right\rangle \\ &= -1 + \frac{asK^2 P_*}{(P_* + K)^3} \\ &+ i \left[\frac{K\sqrt{\chi b_0}}{P_*(P_* + K)} + \sqrt{\frac{b_0}{\chi}} \left(1 - \frac{asK^2 P_*}{(P_* + K)^3} + \frac{Kb_0}{P_*(P_* + K)} \right) \right], \\ \phi_{11} &= \left\langle q^*, (e_0, f_0)^T \right\rangle \\ &= -1 + \frac{asK^2 P_*}{(P_* + K)^3} - \frac{Kb_0}{P_*(P_* + K)} \\ &+ i \sqrt{\frac{b_0}{\chi}} \left[1 - \frac{asK^2 P_*}{(P_* + K)^3} + \frac{Kb_0}{P_*(P_* + K)} \right], \end{split}$$

$$\begin{split} \phi_{21} &= \left\langle q^*, (g_0, h_0)^T \right\rangle \\ &= -\frac{3asK^2P_*}{(P_* + K)^4} + \frac{2Kb_0}{P_*(P_* + K)^2} \\ &+ i\left[\sqrt{\frac{b_0}{\chi}} \left(\frac{3asK^2P_*}{(P_* + K)^4} - \frac{3Kb_0}{P_*(P_* + K)^2} \right) - \frac{K\sqrt{\chi b_0}}{P_*(P_* + K)^2} \right]. \end{split}$$

According to [15], we have

$$\operatorname{Re}(c_1(b_0)) = \operatorname{Re}\left\{\frac{i}{2\sqrt{\chi b_0}} \left(\phi_{20}\phi_{11} - 2|\phi_{11}|^2 - \frac{1}{3}|\phi_{02}|^2\right) + \frac{1}{2}\phi_{21}\right\}$$

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$$= -\frac{1}{2\sqrt{\chi b_0}} \left[\operatorname{Re}(\phi_{20})\operatorname{Im}(\phi_{11}) + \operatorname{Im}(\phi_{20})\operatorname{Re}(\phi_{11}) \right] + \frac{1}{2}\operatorname{Re}(\phi_{21}).$$
(46)

Based on the above analysis, we give our results in the following theorem.

Theorem 3.5. Suppose the assumptions in Theorem 3.4 hold. Let $\operatorname{Re}(c_1(b_0))$ be the constant defined as (46). Then

- 1. if $\operatorname{Re}(c_1(b_0)) < 0$, the Hopf bifurcation at $b = b_0$ is subcritical and the bifurcating periodic solutions are orbitally asymptotical stable;
- 2. if $\operatorname{Re}(c_1(b_0)) > 0$, the Hopf bifurcation at $b = b_0$ is supercritical and the bifurcating periodic solutions are unstable.

4. Analysis of the PDE model (4). In this section, we study the model (4) by analyzing the existence and nonexistence of nonconstant positive solutions. We obtain existence/nonexistence results for by using energy estimates, Implicit Function Theorem and bifurcation methods.

4.1. A priori estimates. Firstly, we give some estimates for the positive solutions of (4), which will be used later. The following lemma is given in [22].

Lemma 4.1. Suppose that $g \in C(\overline{\Omega} \times \mathbb{R})$.

(i): Assume that $w \in C^2(\Omega) \cap C^1(\overline{\Omega})$ and satisfies

$$\Delta w(x) + g(x, w(x)) \ge 0 \text{ in } \Omega, \quad \frac{\partial w}{\partial \nu} \le 0 \text{ on } \partial \Omega.$$
(47)

If $w(x_0) = \max_{x \in \overline{\Omega}} w(x)$, then $g(x_0, w(x_0)) \ge 0$.

(ii): Assume that $w \in C^2(\Omega) \cap C^1(\overline{\Omega})$ and satisfies

$$\Delta w(x) + g(x, w(x)) \le 0 \text{ in } \Omega, \quad \frac{\partial w}{\partial \nu} \ge 0 \text{ on } \partial \Omega.$$
(48)

If $w(x_0) = \min_{x \in \overline{\Omega}} w(x)$, then $g(x_0, w(x_0)) \leq 0$.

Theorem 4.2. Assume

(i): $K \ge 1, \ 0 < s < \min\{1, \frac{1}{a}\}$; or (ii): $0 < K < 1, \ a(1-K) < 1 \ and \ 1-K \le s < \min\{1, \frac{1}{a}\}$; or (iii): $0 < K < 1, \ a(1-K) > 1 \ and \ \frac{1}{a} \le s < 1-K$.

Then any positive solution (P, W) of problem (4) satisfies

$$B < P(x) < A, sB < W(x) < sA, \ x \in \overline{\Omega},$$
(49)

where

$$B := \frac{1 - s - K + \sqrt{(1 - s - K)^2 + 4(1 - s)(1 - as)K}}{2} \in (0, 1 - s), \quad (50)$$

$$\frac{1 - s - K + \sqrt{(1 - s - K)^2 + 4(1 - s - asB)K}}{4(1 - s - asB)K}$$

$$A := \frac{1 - s - K + \sqrt{(1 - s - K)^2 + 4(1 - s - asB)K}}{2} \in (B, 1 - s).$$
(51)

Proof. Assume (P, W) is a positive solution of (4), and let

$$P(x_1) = \max_{x \in \overline{\Omega}} P(x), \ W(x_2) = \max_{x \in \overline{\Omega}} W(x), \ P(y_1) = \min_{x \in \overline{\Omega}} P(x), \ W(y_2) = \min_{x \in \overline{\Omega}} W(x).$$

Then it follows from Lemma 4.1 that

$$1 - s - P(x_1) - \frac{aKW(x_1)}{P(x_1) + K} \ge 0, \quad 1 - s - P(y_1) - \frac{aKW(y_1)}{P(y_1) + K} \le 0, \quad (52)$$

$$sP(x_2) - W(x_2) \ge 0,$$
 $sP(y_2) - W(y_2) \le 0.$ (53)

In view of the definitions of x_i and y_i , i = 1, 2, by (52) and (53), we get $P(x_1) < 1 - s$ and

$$P^{2}(x_{1}) - (1 - s - K)P(x_{1}) + asKP(y_{1}) - (1 - s)K \le 0,$$
(54)

$$P^{2}(y_{1}) - (1 - s - K)P(y_{1}) + asKP(x_{1}) - (1 - s)K \ge 0,$$
(55)

$$W(x_2) \le sP(x_1), \ W(y_2) \ge sP(y_1).$$
 (56)

It follows from $P(x_1) < 1 - s$ and (55) that

$$P^{2}(y_{1}) - (1 - s - K)P(y_{1}) - (1 - s)(1 - as)K > 0,$$

which implies $P(y_1) > B$ if (i) or (ii) or (iii) holds, where B is defined as (50). Then, by (54), we get

$$P^{2}(x_{1}) - (1 - s - K)P(x_{1}) + asKB - (1 - s)K < 0,$$

which implies $P(x_1) < A$. So B < P(x) < A, $x \in \overline{\Omega}$. By (56), we get sB < W(x) < sA, $x \in \overline{\Omega}$.

Remark 4.3. Assume (P(x), W(x)) is the positive of problem (4).

(1): For fixing $K \ge 1$ and 0 < s < 1, the condition (i) holds when a is small enough. Similarly, for fixing 0 < K < 1 and 1 - K < s < 1, the condition (ii) holds when a is small enough. Furthermore, we have

$$\lim_{a \to 0} A = \lim_{a \to 0} B = 1 - s = P_* \Big|_{a=0}$$

where P_* is given in (6). Then it follows from Theorem 4.2 that $(P(x), W(x)) \rightarrow (1 - s, s(1 - s))$ uniformly on $\overline{\Omega}$ as $a \rightarrow 0$, where (1 - s, s(1 - s)) is the unique solution of (4) with a = 0. These facts intrigue us to consider the nonexistence of nonconstant positive solutions of (4) if

1. $K \ge 1$ and 0 < s < 1 are fixed and a is small enough; or

2. 0 < K < 1 and 1 - K < s < 1 are fixed and a is small enough (see (III) of Remark 4.8).

(2): For fixing $K \ge 1$ and a > 0, the condition (i) holds when s is small enough. Furthermore, we have

$$\lim_{s \to 0} A = \lim_{s \to 0} B = 1 = P_* \Big|_{s=0}$$

Then it follows from Theorem 4.2 that $(P(x), W(x)) \to (1, 0)$ uniformly on $\overline{\Omega}$ as $s \to 0$, where (1, 0) is the unique solution of (4) with s = 0. These facts intrigue us to consider the nonexistence of nonconstant positive solutions of (4) if $K \ge 1$ and a > 0 are fixed and s is small enough (see (IV) of Remark 4.8).

(3): For fixing a > 1 and $\frac{1}{a} \le s < 1$, the condition (*iii*) holds when K is small enough. Furthermore, we have

$$\lim_{K \to 0} A = \lim_{K \to 0} B = 1 - s = P_* \Big|_{K=0}.$$

Then it follows from Theorem 4.2 that $(P(x), W(x)) \to (1 - s, s(1 - s))$ uniformly on $\overline{\Omega}$ as $a \to 0$, where (1 - s, s(1 - s)) is the unique solution of (4) with K = 0. These facts intrigue us to consider the nonexistence of nonconstant positive solutions of (4) if a > 1 and $\frac{1}{a} \leq s < 1$ are fixed and K is small enough (see (V) of Remark 4.8).

Remark 4.4. Let $\rho(t) := -t^2 + (1 - s - K)t + (1 - s)K$. Then we can rewrite (55) as $asKP(x_1) \ge \rho(P(y_1))$. Since $0 \le P(y_1) \le P(x_1)$, we get

$$asKP(x_1) \ge \min\{\rho(0), \rho(P(x_1))\} = \min\{(1-s)K, \rho(P(x_1))\}.$$
(57)

If $(1-s)K \leq \rho(P(x_1))$, then we get from (57) that $P(x_1) \geq \frac{1-s}{as}$. On the other hand, if $(1-s)K > \rho(P(x_1))$, it follows from (57) that

$$-P^{2}(x_{1}) + (1 - s - K - asK)P(x_{1}) + (1 - s)K \le 0,$$

which means

$$P(x_1) \ge \frac{1 - s - K - asK + \sqrt{(1 - s - K - asK)^2 + 4(1 - s)K}}{2} > 0$$

In all, without the assumptions in Theorem 49, there exists a positive constant C_1 depending on $s \in (0, 1)$ and $a, K \in (0, \infty)$ such that the positive solution (P, W) of problem (4) satisfies

$$\max_{x\in\overline{\Omega}}P(x) \ge C_1. \tag{58}$$

Now we introduce a Harnack inequality derived in [36].

Lemma 4.5. Let $w \in C^2(\Omega) \cap C^1(\overline{\Omega})$ be a positive solution to

$$\Delta w(x) + c(x)w(x) = 0 \text{ in } \Omega, \ \frac{\partial w}{\partial \nu} = 0 \text{ on } \partial \Omega,$$

where c(x) is a continuous function on $\overline{\Omega}$. Then there exists a positive constant C, depending only on $\|c\|_{\infty} := \max_{x \in \overline{\Omega}} |c(x)|$ and Ω , such that $\max_{x \in \overline{\Omega}} w(x) \leq C \min_{x \in \overline{\Omega}} w(x)$.

Upon (58) and above lemma, we can discard the assumptions in Theorem 4.2 and get the following results.

Theorem 4.6. Suppose (5) holds. Let d be any positive constant. Then there exists a positive constant θ depending only on a, s, K, d and Ω such that when $d_1 \ge d$ and $d_2 > 0$, the positive solution (P, W) of problem (4) satisfies

$$\theta \le P(x) < 1-s, \ \theta \le W(x) < s(1-s), \ x \in \overline{\Omega}.$$

Proof. By the proof of Theorem 4.2, we get

$$P(x) < 1 - s, \ W(x) < s(1 - s), \ x \in \overline{\Omega},$$

$$(59)$$

$$s\min_{x\in\overline{\Omega}}P(x) \le \min_{x\in\overline{\Omega}}W(x).$$
(60)

Let's rewrite the first equation of (4) as $\Delta P(x) + c(x)P(x) = 0$ with

$$c(x) := \frac{1}{d_1} \left(1 - s - P - \frac{aKW}{P + K} \right).$$

Furthermore,

$$||c||_{\infty} \le \frac{1}{d} \left(1 - s + ||P||_{\infty} + a||W||_{\infty}\right) \le \frac{1}{d} (1 - s)(2 + as).$$

Then it follows from Lemma 4.5 and Remark 4.4 that there exists a positive constant C, depending only on a, s, d and Ω such that

$$C_1 \le \max_{x \in \overline{\Omega}} P(x) \le C \min_{x \in \overline{\Omega}} P(x),$$

which combining with (60) implies

$$P(x) \ge \frac{C_1}{C}, \ W(x) \ge s\frac{C_1}{C}, \ x \in \overline{\Omega}.$$

Since 0 < s < 1, the conclusion holds for $\theta = sC_1/C$.

4.2. Nonexistence of positive nonconstant steady state solutions.

Theorem 4.7. Let assumptions in Theorem 4.2 hold. Let A and B be the two positive constants given in (51) and (50) respectively. If μ_1 is large enough such that

$$\mu_1 > M := \frac{1 - s - B}{d_1} + \frac{abAKs}{d_1(A + K)(d_2\mu_1 + b)},\tag{61}$$

then (4) admits no positive nonconstant solutions.

Before giving the proof, we firstly make some remarks on above theorem.

- **Remark 4.8.** (*I*): It is clear that (61) holds if μ_1 is large enough. Note that large μ_1 is reflected by small "size" of the domain Ω (see [2, 40] for precise explanation of "size").
 - (II): Obviously, (61) holds if d_1 is large enough.
 - (III): For fixing $K \ge 1$ and 0 < s < 1, the condition (i) of Theorem 4.2 holds when a is small enough. Similarly, for fixing 0 < K < 1 and 1 - K < s < 1, the condition (ii) of Theorem 4.2 holds when a is small enough. Furthermore, since $\lim_{a\to 0} M = 0$, (61) holds for a is small enough. So problem (4) admits no positive nonconstant solutions if
 - 1. $K \ge 1$ and 0 < s < 1 are fixed and a is small enough; or
 - 2. 0 < K < 1 and 1 K < s < 1 are fixed and a is small enough.
 - (*IV*): For fixing $K \ge 1$ and a > 0, the condition (*i*) of Theorem 4.2 holds when s is small enough. Furthermore, since $\lim_{s\to 0} M = 0$, (61) holds for s is small enough. So problem (4) admits no positive nonconstant solutions if $K \ge 1$ and a > 0 are fixed and s is small enough.
 - (V): For fixing a > 1 and $\frac{1}{a} \le s < 1$, the condition (*iii*) of Theorem 4.2 holds when K is small enough. Furthermore, since $\lim_{K\to 0} M = 0$, (61) holds for K is small enough. So problem (4) admits no positive nonconstant solutions if a > 1 and $\frac{1}{a} \le s < 1$ are fixed and K is small enough.

Proof of Theorem 4.7. In the proof we denote $|\Omega|^{-1} \int_{\Omega} \xi(x) dx$ by $\overline{\xi}$ for $\xi \in L^{1}(\Omega)$. Let (P, W) be a positive solution of (4), then it is obvious that $\int_{\Omega} (P - \overline{P}) dx = \int_{\Omega} (W - \overline{W}) dx = 0$.

Multiplying the first equation of (4) by $P - \overline{P}$, by (49), we obtain

$$d_{1} \int_{\Omega} \left| \nabla \left(P - \overline{P} \right) \right|^{2} dx = \int_{\Omega} \left((1 - s)P - P^{2} - \frac{aKPW}{P + K} \right) \left(P - \overline{P} \right) dx$$

$$= \int_{\Omega} \left[(1 - s) \left(P - \overline{P} \right) - \left(P^{2} - \overline{P}^{2} \right) - aK \left(\frac{PW}{P + K} - \frac{\overline{PW}}{\overline{P} + K} \right) \right] \left(P - \overline{P} \right) dx$$

$$= \int_{\Omega} \left[(1 - s) - \left(P + \overline{P} \right) - \frac{aK^{2}W}{(P + K)(\overline{P} + K)} \right] \left(P - \overline{P} \right)^{2} dx \qquad (62)$$

$$- \int_{\Omega} \frac{aK\overline{P}}{(\overline{P} + K)} \left(P - \overline{P} \right) \left(W - \overline{W} \right) dx$$

$$\leq (1 - s - B) \int_{\Omega} \left(P - \overline{P} \right)^{2} dx + \frac{aAK}{A + K} \int_{\Omega} \left| P - \overline{P} \right| \left| W - \overline{W} \right| dx.$$

Similarly, multiplying the first equation of (4) by $W - \overline{W}$, by (49), we obtain

$$d_2 \int_{\Omega} \left| \nabla \left(W - \overline{W} \right) \right|^2 dx \le bs \int_{\Omega} \left| P - \overline{P} \right| \left| W - \overline{W} \right| dx - b \int_{\Omega} \left(W - \overline{W} \right)^2 dx.$$
(63)

Thus, thanks to the well-known Poincaré's inequality,

$$\mu_1 \int_{\Omega} \left(\xi - \overline{\xi}\right)^2 dx \le \int_{\Omega} \left|\nabla\left(\xi - \overline{\xi}\right)\right|^2 dx, \ \xi \in H^1(\Omega),$$

we find from (63) that

$$(d_{2}\mu_{1}+b)\int_{\Omega} \left(W-\overline{W}\right)^{2} dx \leq bs \int_{\Omega} \left|P-\overline{P}\right| \left|W-\overline{W}\right| dx$$
$$\leq bs \left[\int_{\Omega} \left|P-\overline{P}\right|^{2} dx\right]^{\frac{1}{2}} \left[\int_{\Omega} \left|W-\overline{W}\right|^{2} dx\right]^{\frac{1}{2}}.$$
 (64)

If $W = \overline{W}$ on $\overline{\Omega}$, the second equation of (4) shows $P = \overline{W}/s$, so P and W are both constants. Next we assume that $W \not\equiv \overline{W}$. Then (64) leads to

$$(d_2\mu_1 + b) \left[\int_{\Omega} \left| W - \overline{W} \right|^2 dx \right]^{\frac{1}{2}} \le bs \left[\int_{\Omega} \left| P - \overline{P} \right|^2 dx \right]^{\frac{1}{2}}$$

which together with (64), infers

$$\int_{\Omega} \left| P - \overline{P} \right| \left| W - \overline{W} \right| dx \le \frac{bs}{d_2 \mu_1 + b} \int_{\Omega} \left| P - \overline{P} \right|^2 dx.$$
(65)

By virtue of (62), (65) and Poincaré's inequality, we get

$$d_{1}\mu_{1}\int_{\Omega}\left|P-\overline{P}\right|^{2}dx \leq \left(1-s-B+\frac{abAKs}{(A+K)(d_{2}\mu_{1}+b)}\right)\int_{\Omega}\left|P-\overline{P}\right|^{2}dx,$$

which combining with (61) implies $P \equiv \overline{P}$, and then it follows from the second equation of (4) that $W \equiv s\overline{P}$.

Next we will discard the assumptions in Theorem 4.7 and study the nonexistence of positive nonconstant solutions of (4) as $d_1 \to \infty$ or $d_2 \to \infty$. To this end, we firstly introduce the following lemma.

Lemma 4.9. Let a, b, K > 0, 0 < s < 1 be fixed and (P_*, W_*) be the unique constant equilibrium defined as (6), then the following statements hold.

- (i): Let $d_2 > 0$ be fixed. Assume (P_i, W_i) is the positive solution of (4) with $(d_1, d_2) = (d_{1,i}, d_2)$, where $d_{1,i} \to \infty$ as $i \to \infty$, then $(P_i, W_i) \to (P_*, W_*)$ in $C^2(\overline{\Omega}) \times C^2(\overline{\Omega})$ as $i \to \infty$.
- (ii): Let $d_1 > 0$ be fixed. Assume (P_i, W_i) is the positive solution of (4) with $(d_1, d_2) = (d_1, d_{2,i})$, where $d_{2,i} \to \infty$ as $i \to \infty$, then $(P_i, W_i) \to (P_*, W_*)$ in $C^2(\overline{\Omega}) \times C^2(\overline{\Omega})$ as $i \to \infty$.
- (iii): Assume (P_i, W_i) is the positive solution of (4) with $(d_1, d_2) = (d_{1,i}, d_{2,i})$, where $d_{1,i} \to \infty$ and $d_{1,i} \to \infty$ as $i \to \infty$, then $(P_i, W_i) \to (P_*, W_*)$ in $C^2(\overline{\Omega}) \times C^2(\overline{\Omega})$ as $i \to \infty$.

Proof. (i) Without losing generality, we assume $d_{1,i} \ge 1$ for $i = 1, 2, \cdots$. By Theorem 4.6, there exists a positive constant θ depending only on a, s, K and Ω such that

$$\theta \le P_i(x) < 1-s, \ \theta \le W_i(x) < s(1-s), \ x \in \overline{\Omega}, \ i=1,2,\cdots$$

By Sobolev embedding theory and standard regularity theory of elliptic equations, there exists a subsequence of (P_i, W_i) , relabeled as itself, and $(P, W) \in C^2(\overline{\Omega}) \times C^2(\overline{\Omega})$ such that $(P_i, W_i) \to (P, W)$ in $C^2(\overline{\Omega}) \times C^2(\overline{\Omega})$ as $i \to \infty$. Furthermore, (P, W) satisfies the following relations

$$\begin{cases}
-\Delta P = 0, & x \in \Omega, \\
-d_2 \Delta W = b(sP - W), & x \in \Omega, \\
\frac{\partial P}{\partial \nu} = \frac{\partial W}{\partial \nu} = 0, & x \in \partial \Omega, \\
\int_{\Omega} \left[P(1 - P) - sP - aPW \frac{K}{p + K} \right] dx = 0.
\end{cases}$$
(66)

From the first and the third relations in (66), we know that $P \equiv c \geq \theta > 0$, where c is constant. Then W satisfies

$$\begin{cases} -d_2 \Delta W + bW = bsc, & x \in \Omega, \\ \frac{\partial W}{\partial \nu} = 0, & x \in \partial \Omega, \end{cases}$$
(67)

and the unique solution of (67) is W = sc. Then it follows the forth relation of (66) that c > 0 satisfies

$$1 - c - s - \frac{asKc}{c+k} = 0, (68)$$

i.e., $c = P_*$, where P_* is given in (6), which in turn implies $P = P_*$ and $W = W_*$. Then (i) holds. The proof of (ii) is similar to the proof of (i).

(*iii*) Similar arguments as above imply that there exists a subsequence of (P_i, W_i) , relabeled as itself, and $(P, W) \in C^2(\overline{\Omega}) \times C^2(\overline{\Omega})$ such that $(P_i, W_i) \to (P, W)$ in $C^2(\overline{\Omega}) \times C^2(\overline{\Omega})$ as $i \to \infty$. Furthermore, (P, W) satisfies the following relations

$$\begin{cases}
-\Delta P = 0, & x \in \Omega, \\
-\Delta W = 0, & x \in \Omega, \\
\frac{\partial P}{\partial \nu} = \frac{\partial W}{\partial \nu} = 0, & x \in \partial \Omega, \\
\int_{\Omega} \left[P(1-P) - sP - aPW \frac{K}{p+K} \right] dx = 0, \\
\int_{\Omega} sP - W dx = 0.
\end{cases}$$
(69)

Then $P \equiv c > 0$ and $W \equiv \tilde{c} > 0$, where c and \tilde{c} are constants. By the fifth relation of (69), we get $\tilde{c} = sc$, and then c satisfies (68). So as above we get $P = P_*$ and $W = W_*$.

Based on Lemma 4.9, we can obtain the following result by using Implicit Function Theorem.

Theorem 4.10. Let a, b, K > 0, 0 < s < 1 be fixed, then the following statements hold.

- (i): Let $d_2 > 0$ be fixed, then there exists a positive constant d_1^* depending on a, b, s, K, d_2 and Ω such that (4) admits no positive nonconstant solution when $d_1 > d_1^*$.
- (ii): Let $d_1 > 0$ be fixed, then there exists a positive constant d_2^* depending on a, b, s, K, d_1 and Ω such that (4) admits no positive nonconstant solution when $d_1 > d_2^*$.

(iii): There exists a positive constant d* depending on a, b, s, K and Ω such that
(4) admits no positive nonconstant solution when d₁ > d* and d₂ > d*.

Proof. (i) We write P as $P = U + \xi$ with $\xi = |\Omega|^{-1} \int_{\Omega} P dx$ such that $\int_{\Omega} U dx = 0$. Then we observe that finding solutions of (4) is equivalent to solving the following problem

$$\begin{cases} \Delta U + \sigma(U+\xi) \left[1 - s - (U+\xi) - \frac{aKW}{U+\xi+K} \right] = 0, & x \in \Omega, \\ d_2 \Delta W + b \left[s(U+\xi) - W \right] = 0, & x \in \Omega, \\ \frac{\partial U}{\partial \nu} = \frac{\partial W}{\partial \nu} = 0, & x \in \partial \Omega, \\ \int_{\Omega} (U+\xi) \left[1 - s - (U+\xi) - \frac{aKW}{U+\xi+K} \right] dx = 0, \end{cases}$$
(70)

where $\sigma = 1/d_1$. Clearly, $(U, W, \xi) = (0, W_*, P_*)$ is a solution of (70).

From above analysis, to verify our assertion, we only need to prove there exists a positive constant σ_0 which depends only on a, b, s, K, d_2 and Ω such that $(U, W, \xi) = (0, W_*, P_*)$ is the unique solution of (70) when $\sigma < \sigma_0$. For this, we define

$$W_{\nu}^{2,2} = \left\{ \omega \in W^{2,2}(\Omega) : \left. \frac{\partial \omega}{\partial \nu} \right|_{\partial \Omega} = 0 \right\},\tag{71}$$

$$L_0^2 = \left\{ \omega \in L^2(\Omega) : \int_{\Omega} \omega dx = 0 \right\},$$

$$F(\sigma, U, W, \xi) = (f_1, f_2, f_3)(\sigma, U, W, \xi),$$
(72)

where

$$\begin{aligned} f_1(\sigma, U, W, \xi) &= \Delta U + \sigma (U + \xi) \left[1 - s - (U + \xi) - \frac{aKW}{U + \xi + K} \right] \\ f_2(\sigma, U, W, \xi) &= d_2 \Delta W + b \left[s(U + \xi) - W \right], \\ f_3(\sigma, U, W, \xi) &= \int_{\Omega} (U + \xi) \left[1 - s - (U + \xi) - \frac{aKW}{U + \xi + K} \right] dx. \end{aligned}$$

Then

$$F: \mathbb{R}^1_+ \times \left(L^2_0 \cap W^{2,2}_\nu \right) \times W^{2,2}_\nu \times \mathbb{R}^1_+ \to L^2_0 \times L^2 \times \mathbb{R}^1,$$

and (70) is equivalent to solving $F(\sigma, U, W, \xi) = 0$. Moreover, similar to the proof of Lemma 4.9, (70) admits a unique solution $(U, W, \xi) = (0, W_*, P_*)$ when $\sigma = 0$. By simple computations, we have

$$\begin{split} \Phi(y,z,\tau) &:= D_{(U,W,\xi)} F(0,0,W_*,P_*,)(y,z,\tau) \\ &= \begin{pmatrix} \Delta y \\ d_2 \Delta z + b(sy-z+s\tau) \\ \int_{\Omega} \left[\left(1-s-2P_* - \frac{aK^2 W_*}{(P_*+K)^2}\right)(y+\tau) - \frac{aKP_*}{P_*+K}z \right] dx \end{pmatrix}, \end{split}$$

then

$$\Phi: \left(L_0^2 \cap W_{\nu}^{2,2}\right) \times W_{\nu}^{2,2} \times \mathbb{R}^1_+ \to L_0^2 \times L^2 \times \mathbb{R}^1.$$

In order to use Implicit Function Theorem, we need to prove Φ is invertible, that is Φ one-to one and onto. It is easy to see that Φ is a surjection. So we only need to prove the homogeneous equation $\Phi(y, z, \tau) = 0$ has unique solution $y = z = \tau = 0$.

,

Firstly, it follows from $\Phi(y, z, \tau) = 0$ that y satisfies

$$\begin{cases} \Delta y = 0, & x \in \Omega, \\ \frac{\partial y}{\partial \nu} = 0, & x \in \partial \Omega, \\ \int_{\Omega} y dx = 0. \end{cases}$$

Then $y \equiv 0$.

Secondly, it follows from $\Phi(y, z, \tau) = 0$ and $y \equiv 0$ that z satisfies

$$\begin{cases} -d_2\Delta z + bz = bs\tau, & x \in \Omega, \\ \frac{\partial z}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases}$$

Since b > 0, the above equation admits a unique constant solution $z = s\tau$.

Finally, since (P_*, W_*) satisfies

$$1 - 2 - P_* - \frac{aKW_*}{P_* + K} = 0, \quad W_* = sP_*, \tag{73}$$

it follows from y = 0 and $z = s\tau$ that

$$\begin{split} 0 &= \int_{\Omega} \left[\left(1 - s - 2P_* - \frac{aK^2 W_*}{(P_* + K)^2} \right) (y + \tau) - \frac{aKP_*}{P_* + K} z \right] dx \\ &= - \left(P_* + \frac{aK^2 W_*}{(P_* + K)^2} \right) |\Omega| \tau, \end{split}$$

i.e., $\tau = 0$, and then $z = s\tau = 0$.

By the Implicit function Theorem, there exists positive constants σ_0 and ϵ_0 such that for each $\sigma \in (0, \sigma_0)$, $(0, W_*, P_*)$ is the unique solution of $F(\sigma, U, W, \xi) = 0$ in $B_{\epsilon_0}(0, W_*, P_*)$, where $B_{\epsilon_0}(0, W_*, P_*)$ is the ball in $(L_0^2 \cap W_{\nu}^{2,2}) \times W_{\nu}^{2,2} \times \mathbb{R}^1$ centered at $(0, W_*, P_*)$ with radius ϵ_0 . Taking smaller σ_0 and ϵ_0 smaller if necessary, we can conclude the proof by using the first conclusion of Lemma 4.9. Then (i) holds. The proof of (ii) is similar to the proof of (i).

(*iii*) We write P and W as $P = U + \xi$ and $W = V + \eta$ with $\xi = |\Omega|^{-1} \int_{\Omega} P dx$ and $\eta = |\Omega|^{-1} \int_{\Omega} W dx$ such that $\int_{\Omega} U dx = 0$ and $\int_{\Omega} V dx = 0$. Then we observe that finding solutions of (4) is equivalent to solving the following problem

$$\begin{cases} \Delta U + \sigma_1(U+\xi) \left[1 - s - (U+\xi) - \frac{aK(V+\eta)}{U+\xi+K} \right] = 0, & x \in \Omega, \\ \Delta V + \sigma_2 b \left[s(U+\xi) - (V+\eta) \right] = 0, & x \in \Omega, \\ \frac{\partial U}{\partial \nu} = \frac{\partial V}{\partial \nu} = 0, & x \in \partial \Omega, \\ \int_{\Omega} (U+\xi) \left[1 - s - (U+\xi) - \frac{aK(V+\eta)}{U+\xi+K} \right] dx = 0, \\ \int_{\Omega} \left[s(U+\xi) - (V+\eta) \right] = 0 \end{cases}$$
(74)

where $\sigma_1 = 1/d_1$ and $\sigma_2 = 1/d_2$. Clearly, $(U, V, \xi, \eta) = (0, 0, P_*, W_*)$ is a solution of (74).

From above analysis, to verify our assertion, we only need to prove there exists a positive constant σ_0 which depends only on a, b, s, K and Ω such that $(U, W, \xi, \eta) =$

 $(0,0,P_*,W_*)$ in the unique solution of (74) when $\sigma_1 < \sigma_0$ and $\sigma_2 < \sigma_0$. For this, we define

$$F(\sigma_1, \sigma_2, U, V, \xi, \eta) = (f_1, f_2, f_3, f_4)(\sigma_1, \sigma_2, U, V, \xi, \eta),$$

where

$$\begin{split} f_1(\sigma_1, \sigma_2, U, V, \xi, \eta) &= \Delta U + \sigma_1(U + \xi) \left[1 - s - (U + \xi) - \frac{aK(V + \eta)}{U + \xi + K} \right] \\ f_2(\sigma_1, \sigma_2, U, V, \xi, \eta) &= \Delta V + \sigma_2 b \left[s(U + \xi) - (V + \eta) \right], \\ f_3(\sigma_1, \sigma_2, U, V, \xi, \eta) &= \int_{\Omega} (U + \xi) \left[1 - s - (U + \xi) - \frac{aK(V + \eta)}{U + \xi + K} \right], \\ f_4(\sigma_1, \sigma_2, U, V, \xi, \eta) &= \int_{\Omega} \left[s(U + \xi) - (V + \eta) \right]. \end{split}$$

Then

$$F: \mathbb{R}^1_+ \times \mathbb{R}^1_+ \times \left(L^2_0 \cap W^{2,2}_\nu\right) \times \left(L^2_0 \cap W^{2,2}_\nu\right) \times \mathbb{R}^1_+ \times \mathbb{R}^1_+ \to L^2_0 \times L^2_0 \times \mathbb{R}^1 \times \mathbb{R}^1,$$

and (74) is equivalent to solving $F(\sigma_1, \sigma_2, U, V, \xi, \eta) = 0$. Moreover, similar to the proof of Lemma 4.9, (74) admits a unique solution $(U, W, \xi, \eta) = (0, 0, P_*, W_*)$ when $\sigma_1 = \sigma_2 = 0$. By simple computations, we have

$$\begin{split} \Phi(y,z,\tau,\varrho) &:= D_{(U,V,\xi,\eta)} F(0,0,0,0,P_*,W_*,)(y,z,\tau,\varrho) \\ &= \begin{pmatrix} \Delta y \\ \Delta z \\ \int_{\Omega} \left[\left(1 - s - 2P_* - \frac{aK^2 W_*}{(P_* + K)^2} \right) (y+\tau) - \frac{aKP_*}{P_* + K} (z+\varrho) \right] dx \\ &\int_{\Omega} [s(y+\tau) - (z+\varrho)] dx \end{split} \right), \end{split}$$

then

$$\Phi: \left(L_0^2 \cap W_{\nu}^{2,2}\right) \times \left(L_0^2 \cap W_{\nu}^{2,2}\right) \times \mathbb{R}^1_+ \times \mathbb{R}^1_+ \to L_0^2 \times L_0^2 \times \mathbb{R}^1 \times \mathbb{R}^1.$$

In order to use Implicit Function Theorem, we need to prove Φ is invertible, that is Φ one-to one and onto. It is easy to see that Φ is a surjection. So we only need to prove the homogeneous equation $\Phi(y, z, \tau, \varrho) = 0$ has unique solution $y = z = \tau = \varrho = 0$. It follows from $\Phi(y, z, \tau, \varrho) = 0$ that y and z satisfy

$$\begin{cases} \Delta y = 0, & x \in \Omega, \\ \frac{\partial y}{\partial \nu} = 0, & x \in \partial \Omega, \\ \int_{\Omega} y dx = 0, & & \\ \end{bmatrix} \begin{pmatrix} \Delta z = 0, & x \in \Omega, \\ \frac{\partial z}{\partial \nu} = 0, & x \in \partial \Omega, \\ \int_{\Omega} z dx = 0. & & \\ \end{cases}$$

Then $y \equiv z \equiv 0$, and so

$$0 = \int_{\Omega} [s(y+\tau) - (z+\varrho)] = (s\tau - \varrho)|\Omega$$

i.e., $\rho = s\tau$. Furthermore, since (P_*, W_*) satisfies (73), we get

$$\begin{split} 0 &= \int_{\Omega} \left[\left(1 - s - 2P_* - \frac{aK^2 W_*}{(P_* + K)^2} \right) (y + \tau) - \frac{aKP_*}{P_* + K} (z + \varrho) \right] dx \\ &= - \left(P_* + \frac{aK^2 W_*}{(P_* + K)^2} \right) |\Omega| \tau, \end{split}$$

i.e., $\tau = 0$, and then $\varrho = s\tau = 0$.

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By the Implicit function Theorem, there exists positive constants σ_0 and ϵ_0 such that for each $\sigma_1, \sigma_2 \in (0, \sigma_0), (0, 0, P_*, W_*)$ is the unique solution of

$$F(\sigma_1, \sigma_2, U, V, \xi, \eta) = 0$$

in $B_{\epsilon_0}(0, 0, P_*, W_*)$, where $B_{\epsilon_0}(0, 0, P_*, W_*)$ is the ball in $(L_0^2 \cap W_{\nu}^{2,2}) \times (L_0^2 \cap W_{\nu}^{2,2}) \times \mathbb{R}^1 \times \mathbb{R}^1$ centered at $(0, 0, P_*, W_*)$ with radius ϵ_0 . Taking smaller σ_0 and ϵ_0 smaller if necessary, we can conclude the proof by using the third conclusion of Lemma 4.9.

Note the relationship between b and d_2 in the second equation (4), we get $d_2 \to \infty$ is equivalent to $b \to 0$. Then we get the following corollary from (*ii*) of Lemma 4.9 and (*ii*) of Theorem 4.10.

Corollary 4.11. Let $a, b, d_1, d_2, K > 0$, 0 < s < 1 be fixed, then there exists a positive constant b^* depending on a, b, s, d_1, d_2, K and Ω such that (4) admits no positive nonconstant solution when $b < b^*$.

4.3. Existence of positive nonconstant steady state solutions. In this part, we analyze model (4) by bifurcation theory with b as the bifurcation parameter. As in Section 3, we assume (5) and (14) hold, and all eigenvalues μ_i are simple, and denote the corresponding eigenfunction by $\phi_i(x)$, $i \in \mathcal{N}_0$. We identify state bifurcation value b_S of (4), which satisfies the following conditions [51].

(SS) There exists $i \in \mathcal{N}_0$ such that

$$D_i(b_S) = 0, \ D'_i(b_S) \neq 0, \ T_i(b_S) \neq 0, \ D_j(b_S) \neq 0 \ \text{and} \ T_j(b_S) \neq 0 \ \text{for} \ j \in \mathcal{N}_0 \setminus \{i\},$$

where $D_i(b)$ and $T_i(b)$ are given in (24) and (23) respectively.

Since $D_0(b) = \chi b > 0$, where χ is defined as (25), we only consider $i \in \mathcal{N}$. In the following, we determine *b*-values satisfying (SS). We notice that $D_i(b) = 0$ is equivalent to $b = b_S(\mu_i)$, where $b_S(\mu)$ is defined as (31). Hence we make the following additional assumption on the spectral set $\{\mu_n\}_{n \in \mathcal{N}_0}$.

(SP) There exist $p \in \mathcal{N}$ such that $\mu_p < \mu_3^* \leq \mu_{p+1}$ and $\mu_H \neq \mu_i$ for $i = 1, \dots, p$, where μ_3^* and μ_H are given in (33) and (35) respectively.

In the following, for p satisfy (SP), we denote

$$b_{i,S} = b_S(\mu_i) \text{ for } i = 1, \cdots, p.$$
 (75)

The points $b_{i,S}$ defined above are potential steady state bifurcation points. In follows from Lemma 3.1 that for each $i = 1, \dots, p$, $D_i(b_{i,S}) = 0$, $D'_i(b_{i,S}) = d_1\mu_i + \chi > 0$ and $T_i(b_{i,S}) \neq 0$. On the other hand, it is possible that for some $\tilde{b} \in (0, b_S^*)$ with b_S^* defined as (34) such that

(SQ) $b_{i,S} = b_{j,S} = \tilde{b}$ for some $i, j \in \{1, \dots, p\}$ and $i \neq j$, i.e., $D_i(\tilde{b}) = D_j(\tilde{b})$.

(SS) is not satisfied if (SQ) holds, and we shall not consider bifurcations at such a point. On the other hand, it is also possible that

(SR) $b_{i,S} = b_{j,H}$ for some $i, j \in \{1, \dots, p\}$ and $i \neq j$, where $b_{j,H}$ is a Hopf bifurcation value defined as (43).

However, from an argument in [51], for $\mathcal{N} = 1$ and $\Omega = (\ell \pi)$, there are only countably many ℓ , such that (SQ) or (SP) occurs. One also can show that (SQ) or (SP) does not occur for generic domains in $\mathbb{R}^{\mathcal{N}}$ (see [42]).

Summarizing the above discussion, we obtain the main result of this part on bifurcation of steady state solutions.

Theorem 4.12. Assume (5) and (14) hold. Let Ω be a bounded smooth domain so that all eigenvalues μ_i , $i \in \mathcal{N}_0$, are simple, and satisfy (SP). Then for any

 $i \in \{1, \dots, p\}$, there exists a unique $b_{i,S}$ defined as (75) such that $D_i(b_{i,S}) = 0$, $D'_i(b_{i,S}) \neq 0$ and $T_i(b_{i,S}) \neq 0$. If in addition, we assume that

$$b_{i,S} \neq b_{j,S}, \ b_{i,S} \neq b_{j,H} \ for \ any \ j \in \{1, \cdots, p\} \ and \ i \neq j,$$

$$(76)$$

where $b_{j,H}$ is defined as (43). Then the following conclusions hold.

(i): There is a smooth curve Γ_i of positive solutions of (4) bifurcating from

 $(b, P, W) = (b_{i,S}, P_*, W_*), \text{ where } (P_*, W_*) \text{ is the positive constant solution of}$ (4) defined as (6). Near $(b, P, W) = (b_{i,S}, P_*, W_*), \Gamma_i = \{(b_i(\tau)), P_i(\tau), W_i(\tau) :$

 $|\tau| < \epsilon$, where ϵ is a small positive constant and

$$\begin{cases} P_i(\tau)(x) = P_* + \tau l_i \phi_i(x) + \tau \psi_{1,i}(\tau), \\ W_i(\tau)(x) = W_* + \tau m_i \phi_i(x) + \tau \psi_{2,i}(\tau) \end{cases}$$

for some smooth functions b_i , $\psi_{1,i}$ and $\psi_{2,i}$ such that $b_i(0) = b_{i,S}$ and $\psi_{1,i}(0) = \psi_{2,i}(0) = 0$, and (l_i, m_i) satisfies

$$L(b_{i,S})\left[(l_i, m_i)^T \phi_i(x)\right] = (0, 0)^T,$$

here L is the operator defined in (18).

- (ii): Γ_i is contained a global branch Σ_i of positive nontrivial solution of problem (4) and
 - 1. $\overline{\Sigma}_i$ connects another bifurcation point $(b_{j,S}, P_*, W_*)$ for some $j \in \{1, \dots, p\}$ and $j \neq i$; or
 - 2. the projection of Σ_i on to b-axis contains the interval $(b_{i,S}, \infty)$, and then for $b \in (b_{i,S}, \infty) \setminus (\bigcup_{k=1}^p b_{k,S})$, problem (4) admits at least one positive nonconstant solution.

Remark 4.13. If p = 1, i.e., $\mu_1 < \mu_3^* \leq \mu_2$, then the first conclusion of (*ii*) can not happen, and then for $b \in (b_{1,S}, \infty)$, problem (4) admits at least one positive nonconstant solution.

Proof. The condition (SS) has been proved in the previous paragraphs, and the bifurcation of solutions to (4) occur at $b = b_{i,S}$. Note that we assume (SQ) and (SR) hold, so $b = b_{i,S}$ ia always a bifurcating from simple eigenvalue point, then by using the general bifurcation theorem in [51], we know the conclusion (i) holds. Moreover, similar to the proof of Theorem 4.6, there exists a positive constant θ independent of $b_i(\tau)$ such that

$$\theta \le P_i(\tau)(x) < 1 - s, \quad \theta \le Q_i(\tau)(x) < s(1 - s), \quad x \in \overline{\Omega}.$$
(77)

From the global bifurcation in [35] and (77), Γ_i is contained in a global branch Σ_i of positive solutions. Furthermore, Σ_i must satisfy

- (1): $\overline{\Sigma}_i$ connects to another bifurcation point $(b_{j,S}, P_*, W_*)$ for some $j \in \{1, \dots, p\}$ and $j \neq i$; or
- (2): $\overline{\Sigma}_i$ in not compact in $\mathbb{R}^+ \times \mathbb{E}$, where $\mathbb{E} = W_{\nu}^{2,2} \times W_{\nu}^{2,2}$ with $W_{\nu}^{2,2}$ given in (71).

Assume (1) does not happen, then (2) occurs. By (77), we know the projection of $\overline{\Sigma}_i$ on to *b*-axis is not compact. Furthermore, by Corollary 4.11, we know that the projection of $\overline{\Sigma}_i$ on to *b*-axis can not extend to $-\infty$, and so the projection of Σ_i on to *b*-axis contains the interval $(b_{i,S}, \infty)$. The conclusion (*ii*) holds.

5. Numerical simulations. To visualize the cascade of Turing instability, Hopf bifurcation and steady state bifurcation described in Theorems 3.3, 3.4 and 4.12, we consider two numerical examples.

Example 5.1. We consider problem (3) with $\Omega = (0, 3\pi)$, s = K = 0.25 and a = 25.6 such that (5) and (14) hold, i.e.,

$$\begin{cases}
P_t - d_1 \Delta P = P(1 - P) - 0.25P - \frac{6.4PW}{P + 0.25}, & x \in (0, 3\pi), \ t > 0, \\
W_t - d_2 \Delta W = b(0.25P - W), & x \in (0, 3\pi), \ t > 0, \\
\frac{\partial P}{\partial \nu} = \frac{\partial W}{\partial \nu} = 0, & x = 0, 3\pi, \ t > 0, \\
P(x, 0) = P_0(x), \ W(x, 0) = W_0(x), & x \in (0, 3\pi).
\end{cases}$$
(78)



FIGURE 3. Graphs of Hopf bifurcation curve Γ_H : $b = b_H(\mu) = -1.01\mu + 0.075$ and steady state bifurcation curve Γ_H : $b = b_H(\mu) = \frac{-0.01\mu^2 + 0.075\mu}{0.01\mu + 0.525}$ when $(a, s, K, d_1, d_2) = (25.6, 0.25, 0.25, 0.01, 1)$.

Then $\mu_i = i^2/9, i \in \mathcal{N}_0$, and the positive constant equilibrium is $(P_*, W_*) = (0.15, 0.0375)$. Let b_0, χ and D_2 be the constants defined as (15), (25) and (38) respectively, then $b_0 = 0.075, \chi = 0.525, D_2 \approx 0.03337$. We choose $d_1 = 0.01$ and $d_2 = 1$ such that $\frac{d_1}{d_2} = 0.01 < D_2$. Then we can compute $\mu_3^* = 7.5$ and find that

$$\mu_1 = \frac{1}{9} < \mu_2 = \frac{4}{9} < \mu_3 = 1 < \mu_4 = \frac{16}{9} < \mu_5 = \frac{25}{9}$$
$$< \mu_6 = 4 < \mu_7 = \frac{49}{9} < \mu_8 = \frac{64}{9} < \mu_3^* < \mu_9 = 9.$$

This gives possible steady state bifurcation values

$$\begin{split} b_{6,S} &\approx 0.28866 > b_{5,S} \approx 0.23730 > b_{7,S} \approx 0.19314 > b_{4,S} \approx 0.18742 \\ &> b_{3,S} \approx 0.12150 > b_{2,S} \approx 0.05923 > b_{8,S} \approx 0.04639 > b_{1,S} \approx 0.0156053 \end{split}$$

while the largest Hopf bifurcation value $b_{0,H}$ defined as (43) is $b_0 = 0.075$, which is much smaller than $b_{i,S}$, i = 3, 4, 5, 6, 7. Hence for this parameter set (a, s, K, d_1, d_2) = (25.6, 0.25, 0.25, 0.01, 1), when b decreases, the first bifurcation point encountered is $b_{6,S} \approx 0.28866$, and a steady state bifurcation occurs there. Fig. 3 show the curves Γ_H and Γ_S in the case. Let \bar{b} be the constant defined in (40), then $\bar{b} = b_S(\mu_6) \approx$ 0.28866. Then for $b_0 < b < \bar{b}$ all conditions in Theorem 3.3 are satisfied and Turing instability happens.



FIGURE 4. Numerical simulation of problem (78). When $d_1 = d_2 = 0$, i.e., the ODE corresponding to (78), and $b_0 = 0.2$, the solution trajectories spiral toward the positive equilibrium (0.15, 0.0375) (see(1)). When $d_1 = 0.01$, $d_2 = 1$, b = 0.2, $P_0(x) = 0.15 + 0.05 \cos x$, $W_0(x) = 0.0375 + 0.05 \cos x$, then the solution converges to a spatially nonhomogeneous steady state solution (see (2) for P and (3) for W)

We choose b = 0.2, $P_0(x) = 0.15 + 0.05 \cos x$ and $W_0(x) = 0.0375 + 0.05 \cos x$. The solution trajectories of the corresponding ODE spiral toward the positive equilibrium (0.15, 0.0375) (see(1) of Fig. 4), while the solution of the PDE (78) converges to a spatially nonhomogeneous steady state solution (see (2) for P and (3) for W in Fig. 4).

Example 5.2. We consider problem (3) with $\Omega = (0, 9\pi)$, s = K = 0.25 and a = 25.6 such that (5) and (14) hold, i.e.,

$$\begin{cases} P_t - d_1 \Delta P = P(1-P) - 0.25P - \frac{6.4PW}{P+0.25}, & x \in (0,9\pi), \ t > 0, \\ W_t - d_2 \Delta W = b(0.25P - W), & x \in (0,9\pi), \ t > 0, \\ \frac{\partial P}{\partial \nu} = \frac{\partial W}{\partial \nu} = 0, & x = 0,9\pi, \ t > 0, \\ P(x,0) = P_0(x), \ W(x,0) = W_0(x), & x \in (0,9\pi). \end{cases}$$
(79)



FIGURE 5. Graphs of Hopf bifurcation curve $\Gamma_H: b = b_H(\mu) = -1.1\mu + 0.075$ and steady state bifurcation curve $\Gamma_S: b = b_S(\mu) = \frac{-0.1\mu^2 + 0.075\mu}{0.1\mu + 0.525}$ when $(a, s, K, d_1, d_2) = (25.6, 0.25, 0.25, 0.1, 1)$.



FIGURE 6. Numerical simulation of problem (79) with $d_1 = 0.1$, $d_2 = 1$, $b_0 = 0.05$, $P_0(x) = 0.15 + 0.1 \cos x$ and $W_0(x) = 0.0375 + 0.1 \cos x$. The solution converges to a spatially homogeneous periodic orbit.

Then $\mu_i = i^2/81, i \in \mathcal{N}_0$, and the positive constant equilibrium is $(P_*, W_*) = (0.15, 0.0375)$. Let b_0, χ and D_2 be the constants defined as (15), (25) and (38) respectively, then $b_0 = 0.075, \chi = 0.525, D_2 \approx 0.03337$. We choose $d_1 = 0.1$ and $d_2 = 1$ such that $\frac{d_1}{d_2} = 0.1 > D_2$. Then we can compute $\mu_H = 0.06$ and find that

$$\mu_0 = 0 < \mu_1 = \frac{1}{81} < \mu_2 = \frac{4}{81} < \mu_H < \mu_3 = \frac{1}{9}.$$

This gives possible Hopf bifurcation values

$$b_{0,H} = b_0 = 0.075 > b_{1,H} \approx 0.06142 > b_{2,H} \approx 0.02068,$$

while the largest state bifurcation value $\bar{b} = \max\{b_{1,S}, \cdots, b_{7,S}\} = b_{5,S} \approx 0.02451$ since $\mu_7 \approx 0.60494 < \mu_3^* = 0.075 < \mu_8 \approx 0.79012$, which is much smaller than $b_{i,H}$, i = 0, 1. Hence for this parameter set $(a, s, K, d_1, d_2) = (25.6, 0.25, 0.25, 0.1, 1)$, when b decreases, the first bifurcation point encountered is $b_{0,H} = 0.075$, and a Hopf bifurcation occurs there. We compute $\operatorname{Rec}_1(b_0) \approx -2.57812 < 0$, which indicates that the bifurcating temporal periodic solutions are orbitally asymptotically stable (see Theorem 3.5). Fig. 5 show the curves Γ_H and Γ_S in the case.

We choose b = 0.05, $P_0(x) = 0.15 + 0.1 \cos x$ and $W_0(x) = 0.0375 + 0.1 \cos x$, and the solution converges to a spatially homogeneous periodic orbit. (see Fig. 6).

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