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CROSS-DIFFUSION INDUCED INSTABILITY AND STABILITY IN REACTION-DIFFUSION SYSTEMS *

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Abstract In a reaction-diffusion system, diffusion can induce the instability of a uniform equilibrium which is stable with respect to a constant perturbation, as shown by Turing in 1950s. We show that cross-diffusion can destabilize a uniform equilibrium which is stable for the kinetic and self-diffusion reaction systems; on the other hand, cross-diffusion can also stabilize a uniform equilibrium which is stable for the kinetic system but unstable for the self-diffusion reaction system. Application is given to predator-prey system with preytaxis and vegetation pattern formation in a water-limited ecosystem.

Keywords Reaction-diffusion systems, instability, cross-diffusion, pattern formation.

MSC(2000) 92C15, 35K57, 37L15, 92D40.

1. Introduction

A pure diffusion process usually leads to a smoothering effect so that the system tends to a constant equilibrium state. However the combined effect of diffusion and chemical reaction may result in destabilizing the constant equilibrium. In 1952, Alan Turing published a paper "The chemical basis of morphogenesis" [31] which is now regarded as the foundation of basic chemical theory or reaction diffusion theory of morphogenesis. Turing suggested that, under certain conditions, chemicals can react and diffuse in such a way as to produce non-constant equilibrium solutions, which represent spatial patterns of chemical or morphogen concentration.

Turing's idea is a simple but profound one. He considered a reaction-diffusion system

$$\begin{cases} u_t = D_u \Delta u + f(u,v), & t > 0, \\ v_t = D_v \Delta v + g(u,v), & t > 0, \end{cases} \tag{1.1}$$

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and its corresponding kinetic equation

$$\begin{cases} u' = f(u, v), & t > 0, \\ v' = g(u, v), & t > 0. \end{cases} \tag{1.2}$$

He said that if, in the absence of the diffusion (considering (1.2)), u and v tend to a linearly stable uniform steady state, then, with the presence of diffusion and under certain conditions, the uniform steady state can become unstable, and spatial inhomogeneous patterns can evolve through bifurcations. In another word, a constant equilibrium can be asymptotically stable with respect to (1.2), but it is unstable with respect to (1.1). Therefore this constant equilibrium solution becomes unstable because of the diffusion, which is called *diffusion driven instability.*

Over the years, Turing's idea have attracted the attention of a great number of investigators and was successfully developed on the theoretical backgrounds. Not only it has been studied in biological and chemical fields, some investigations range as far as economics, semiconductor physics, and star formation. On the other hand, more realistic models of diffusion and reaction have been developed to accommodate pattern formation of biological systems. The attraction/repulsion between species can be modeled by cross-diffusion and self-diffusion, and the influence of advection on the spatiotemporal patterns have also been considered. Recently particular interests have been on the impact of environmental changes, such as climate, nutrient loading or biotic exploitation on the ecosystems. The response of ecosystems to most external conditions is in a smooth continuous way. However the existence of multiple stable states and threshold separation between them makes the catastrophic transition from one stable state to another possible. Such catastrophic shift occurs typically quite unannounced, and irreversible. Recent studies have provided a strong case for the existence of alternative stability domains in various important ecosystems, such as lakes, coral reef, woodlands, deserts and oceans, see Scheffer et. al. [24]. Moreover some stable states show spatial self-organized patchiness (see Rietkerk et. al. [21]), such as spots, stripes, labyrinths in arid and savanna ecosystems.

Some of these self-organized patterns have been attributed to the cross-diffusion and advection in the systems. The purpose of this article is to further explore Turing's diffusion-induced instability for the cross-diffusion systems. Our main results following Turing's idea can be summarized as follows: assume that in the absence of self-diffusion and cross-diffusion, there is a spatial homogeneous stable steady state; in the presence of self-diffusion but not cross-diffusion, this steady state remains stable hence it does not belong to the classical Turing instability scheme, but it could become unstable when cross-diffusion also comes to play a role in the system; thus it is a *cross-diffusion induced instability.* On the other hand, if Turing instability does occur, *i.e.* a spatial uniform steady state is stable with respect to the diffusion-free system, and it is unstable when diffusion (but not cross-diffusion) presents; this steady state could become stable with the inclusion of cross-diffusion influence, which represents a *cross-diffusion induced stability.* Moreover we show that such instability/stability driven by the cross-diffusion is usually induced by a pair of contradicting responses between the two species (see more details in Section 2).

We present a general instability analysis on cross-diffusion system in this paper. For the linearized system, the spatial non-homogeneous perturbation is in a form of $\exp(\lambda t + ikx)$, and k is the wave number and k^{-1} is proportional to the wavelength.

In Section 2 we assume the spatial domain to be the whole real line, and the wave number k can be any positive real number. Hence the resulting spatial patterns can be of any wave lengths. This is of particular interest for a large spatial ecosystem such as grassland or desert. A biological interpretation of the results following Segel and Jackson [25] and Edelstein-Keshet [4] is also given. In Section 3 we consider the instability on a bounded spatial domain $(0, L)$ with no-flux boundary condition. In this case, the perturbation must satisfy the boundary condition, thus the only eligible wave numbers are the eigenvalues of $-\phi_{xx}$ with no-flux boundary condition. This analysis can be applied to the pattern formation on a bounded region with the pattern wave length and the domain size being in the same order. The analysis in Section 2 is more suitable when the domain size is much larger than the pattern wave length. When the domain size L in Section 3 tends to infinity, then the asymptotic conditions of stability/instability is exactly that given in Section 2. Mathematical conditions for cross-diffusion induced instability have also been considered in Farkas [5], and Kovàcs [9], and Turing instability for reaction-diffusion model with more species is considered in Satnoianu, Menzinger and Maini [23], Dilão [3] and many others. In this paper we take a new angle of the problem and make an in-depth analysis of the parameter space for the stability/instability. For the simplicity of analysis, we consider a reaction-diffusion system on a one-dimensional spatial domain, and the extension to high spatial dimension case will be considered in the future. It would be interesting to see how the shape of the regions of instability depend on the shape of the spatial domains.

In Section 4 we apply our general analysis to a reaction-diffusion system modeling vegetation patterns and desertification introduced in [32] and [17]:

$$\begin{aligned} n_t &= \frac{\gamma w}{1+\sigma w} n - n^2 - \mu n + \Delta n, \\ w_t &= p - (1-\rho n)w - w^2 n + \delta \Delta (w - \beta n) - v(w - \alpha n)_x. \end{aligned} \tag{1.3}$$

where n is the vegetation biomass density and w is the soil water density, and the advection term indicates the water flowing downhill in a two-dimensional field. In this article we only consider the case without advection ($v = 0$) and we focus on the impact of cross-diffusion $-\delta\beta\Delta n$ in the second equation, which represents the absorption of water in the self-diffusion process of the water. We show that a uniform vegetation steady state is stable in the absence of self-diffusion and cross-diffusion, and it is still stable with self-diffusion only, but it is unstable with a strong cross-diffusion. The instability of uniform vegetation state implies the existence of non-uniform patterns, and numerical results of such kind have been found in [21, 32, 17]. Here we only find the conditions for instability but we do not prove the bifurcation of non-uniform steady state solutions due to the length of the paper. In [26], we sketch the bifurcation analysis for (1.3) at a bifurcation point induced by cross-diffusion, based on a global bifurcation theorem in [27].

In this paper, we consider the reaction-diffusion systems with cross-diffusion on bounded or unbounded domains, but our focus is on the linearized stability of a constant equilibrium. The global existence of solutions to cross-diffusion systems have been considered by [1, 2, 11, 12, 13, 16, 29, 30], and the existence of steady state solutions has been investigated in [10, 14, 15, 20, 19, 22, 33] and many others.

2. Stability analysis for cross-diffusion systems

We consider a reaction-diffusion system

$$\begin{cases} u_t = d_{11}u_{xx} + d_{12}v_{xx} + \alpha f(u,v), & t > 0,\ x \in \mathbf{R}, \\ v_t = d_{21}u_{xx} + d_{22}v_{xx} + \alpha g(u,v), & t > 0,\ x \in \mathbf{R}, \\ u(0,x) = h(x),\ \ v(0,x) = l(x), & x \in \mathbf{R}, \end{cases} \tag{2.1}$$

where $\alpha > 0$, f, g are smooth functions;

$$D = \begin{pmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{pmatrix} \tag{2.2}$$

is the diffusion matrix, and we always assume that $d_{11} > 0$, $d_{22} > 0$ and $Det(D) = d_{11}d_{22} - d_{12}d_{21} > 0$. In the following we refer d_{11} and d_{22} to be the self-diffusion coefficients of u and v respectively, and d_{12}, d_{21} to be the cross-diffusion coefficients. Suppose that (u_0, v_0) is a constant equilibrium solution, *i.e.*

$$f(u_0, v_0) = 0, \quad \text{and} \quad g(u_0, v_0) = 0. \tag{2.3}$$

Clearly (u_0, v_0) is also an equilibrium solution of a system of ordinary differential equations:

$$\begin{cases} u' = \alpha f(u,v), \quad v' = \alpha g(u,v), \quad t > 0, \\ u(0) = h, \quad v(0) = l. \end{cases} \tag{2.4}$$

Now we look for the conditions for the Turing instability described above. We always assume that (u_0, v_0) is linearly stable with respect to (2.4), then the eigenvalues of Jacobian

$$J = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} \tag{2.5}$$

at (u_0, v_0) must have negative real parts, which is equivalent to

$$Trace(J) = f_u + g_v < 0, \quad Det(J) = f_u g_v - f_v g_u > 0. \tag{2.6}$$

Linearizing the reaction-diffusion system (2.1) about the constant equilibrium (u_0, v_0) gives

$$\begin{cases} \phi_t = d_{11}\phi_{xx} + d_{12}\psi_{xx} + \alpha f_u(u_0,v_0)\phi + \alpha f_v(u_0,v_0)\psi, & t > 0,\ x \in \mathbf{R}, \\ \psi_t = d_{21}\phi_{xx} + d_{22}\psi_{xx} + \alpha g_u(u_0,v_0)\phi + \alpha g_v(u_0,v_0)\psi, & t > 0,\ x \in \mathbf{R}, \\ \phi(0,x) = c(x), \quad \psi(0,x) = d(x), & x \in \mathbf{R}, \end{cases} \tag{2.7}$$

or in matrix notation:

$$\mathbf{\Psi}_t = D\mathbf{\Psi}_{xx} + \alpha J \mathbf{\Psi}, \tag{2.8}$$

where

$$\mathbf{\Psi}(t,x) = \begin{pmatrix} \phi(t,x) \\ \psi(t,x) \end{pmatrix}, \quad \text{and } D = \begin{pmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{pmatrix}. \tag{2.9}$$

To examine the linear stability of (u_0, v_0), let

$$\mathbf{\Psi}(t,x) = \begin{pmatrix} \phi(t,x) \\ \psi(t,x) \end{pmatrix} = \begin{pmatrix} \rho_1 \\ \rho_2 \end{pmatrix} \exp(ikx + \lambda t), \tag{2.10}$$

where $\lambda \in \mathbf{R}$ and $k > 0$. Nontrivial solutions to (2.8) of this form are possible provided

$$\begin{aligned} Det(\lambda I - (\alpha J - k^2 D)) = \lambda^2 + (k^2(d_{11} + d_{22}) - \alpha(f_u + g_v))\lambda \\ +(k^2 d_{11} - \alpha f_u)(k^2 d_{22} - \alpha g_v) - (k^2 d_{21} - \alpha g_u)(k^2 d_{12} - \alpha f_v) = 0 \end{aligned} \tag{2.11}$$

where

$$\lambda I - (\alpha J - k^2 D) = \begin{pmatrix} \lambda + k^2 d_{11} - \alpha f_u & k^2 d_{12} - \alpha f_v \\ k^2 d_{21} - \alpha g_u & \lambda + k^2 d_{22} - \alpha g_v \end{pmatrix}. \tag{2.12}$$

If (2.7) is a linearly unstable system, then $\mathbf{\Psi}(t, x)$ would go to infinity as $t \to \infty$ for some $k \in \mathbf{R}^+$, *i.e.* one of the zeros λ in (2.11) has positive real part. Or equivalently, one of the eigenvalues of matrix $M_k = \alpha J - k^2 D$ has positive real part, which depends on the signs of its trace and determinant of M_k:

$$\begin{aligned} &Trace(M_k) = \alpha Trace(J) - k^2 Trace(D), \\ &Det(M_k) = k^4 Det(D) + k^2 F(J, D)\alpha + Det(J)\alpha^2, \end{aligned} \tag{2.13}$$

where

$$\begin{aligned} &Trace(D) = d_{11} + d_{22}, \ \ Det(D) = d_{11}d_{22} - d_{12}d_{21}, \\ &F(J, D) = -d_{22}f_u + d_{21}f_v + d_{12}g_u - d_{11}g_v. \end{aligned}$$

Since $Trace(J) < 0$, then $Trace(M_k) < 0$ is always true since we assume $d_{11} > 0$ and $d_{22} > 0$. Hence if M_k has an eigenvalue with positive real part, then it must be a real value one and the other eigenvalue must be a negative real one. A necessary condition is

$$F(J, D) < 0 \tag{2.14}$$

otherwise $Det(M_k) > 0$ for all $k > 0$ since $Det(D) > 0$ and $Det(J) > 0$. For instability we must have $Det(M_k) < 0$ for some $k > 0$, and we notice that $Det(M_k)$ achieves its minimum

$$\min_{k \in \mathbf{R}^+} Det(M_k) = \left[-\frac{F(J, D)^2}{4Det(D)} + Det(J) \right] \alpha^2 \tag{2.15}$$

at the critical value $k_* > 0$ where

$$k_*^2 = -\frac{F(J, D)\alpha}{2Det(D)}. \tag{2.16}$$

If (2.14) holds and $\min_k Det(M_k) < 0$, then (u_0, v_0) is an unstable equilibrium with respect to (2.7). Summarizing the above calculation, we conclude

Theorem 2.1. *Suppose that* (u_0, v_0) *is a constant equilibrium solution of* (2.1)*, and the matrices* J, D *are defined as above. Suppose that* $d_{11} > 0$*,* $d_{22} > 0$*,* $Det(D) > 0$*,* $\alpha > 0$*,* $Trace(J) < 0$ *and* $Det(J) > 0$*. If*

$$\min_{k \in \mathbf{R}^+} Det(M_k) = \left[-\frac{F(J, D)^2}{4Det(D)} + Det(J) \right] \alpha^2 < 0 \tag{2.17}$$

and

$$k_*^2 = -\frac{F(J, D)\alpha}{2Det(D)} > 0 \tag{2.18}$$

then (u_0, v_0) *is an unstable equilibrium solution with respect to the reaction-diffusion system* (2.1)*, but a stable equilibrium solution with respect to the ordinary differential equation system* (2.4)*.*

Theorem 2.1 gives a general criterion for the instability when self-diffusion and/or cross-diffusion is added to the system. We further investigate Theorem 2.1 and check the condition (2.17) and (2.18). From now on, we assume that D, J and α satisfy

$$\begin{aligned} &Det(D) = d_{11}d_{22} - d_{12}d_{21} > 0, d_{11} > 0, d_{22} > 0, \alpha > 0, \\ &f_u > 0,\ g_v < 0,\ f_u + g_v < 0,\ \ f_u g_v - f_v g_u > 0. \end{aligned} \tag{2.19}$$

When the cross-diffusion is absent ($d_{12} = d_{21} = 0$), the following result revisits the classical Turing instability:

Theorem 2.2. *Suppose that* (u_0, v_0) *is a constant stable equilibrium solution of* (2.1)*, and* (2.19) *holds. We further assume that* $d_{12} = d_{21} = 0$*, i.e., we consider*

$$\begin{cases} u_t = d_{11}u_{xx} + \alpha f(u, v), & t > 0,\ x \in \mathbf{R}, \\ v_t = d_{22}v_{xx} + \alpha g(u, v), & t > 0,\ x \in \mathbf{R}, \\ u(0, x) = h(x),\ \ v(0, x) = l(x), & x \in \mathbf{R}. \end{cases} \tag{2.20}$$

Then there exists an unbounded region $U_1 = \{(d_{11}, d_{22}) : d_{11} > 0, d_{22} > 0, d_{22} > \gamma_1 d_{11}\}$ *for some* $\gamma_1 > 0$*, such that for any* $(d_{11}, d_{22}) \in U_1$*,* (u_0, v_0) *is an unstable equilibrium solution with respect to* (2.20) *(see Figure 1.)*

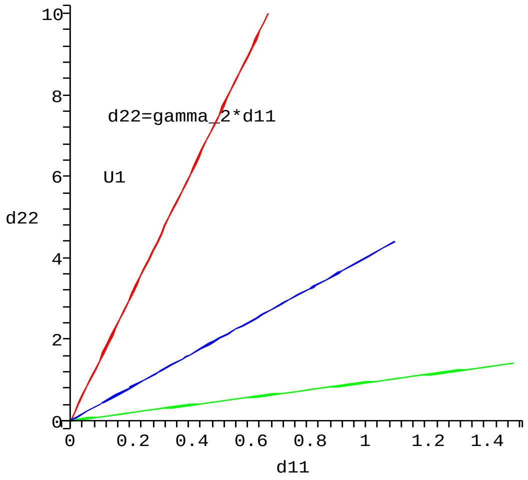

Figure 1. Parameter space for Turing instability. The parameter values are $f_u = 1, f_v = -3, g_u = 2, g_v = -4$ and $\alpha = 1$; the unstable region U_1 is the region between the line $d_{22} = \gamma_1 d_{11}$ and the d_{22}-axis; counterclockwisely the lines are $d_{22} = \gamma_1 d_{11}$, $d_{22} = \gamma_* d_{11}$ and $d_{22} = \gamma_2 d_{11}$ respectively.

Proof. Because $d_{12} = d_{21} = 0$, from (2.17), we obtain

$$\min_{k\in\mathbf{R}^+} Det(M_k) = -\frac{(d_{22}\, f_u + d_{11}\, g_v)^2\, \alpha^2}{4d_{11}\, d_{22}} + (f_u\, g_v - f_v\, g_u)\, \alpha^2,$$

$$\text{and} \quad k_*^2 = \frac{(d_{22} f_u + d_{11} g_v)\alpha}{2d_{11}d_{22}}.$$

Let

$$\begin{aligned} H(d_{11},d_{22}) &= -\left(d_{22}\,f_u + d_{11}\,g_v\right)^2 + 4d_{11}d_{22}\left(f_u\,g_v - f_v\,g_u\right), \\ &= -g_v^2 d_{11}^2 + 2(f_u g_v - 2f_v g_u)d_{11}d_{22} - f_u^2 d_{22}^2, \\ \text{and}\quad K(d_{11},d_{22}) &= f_u d_{22} + g_v d_{11}. \end{aligned}$$

Since $d_{11} > 0, d_{22} > 0$ and $\alpha > 0$, (2.17) and (2.18) are equivalent to $H(d_{11},d_{22}) < 0$ and $K(d_{11},d_{22}) > 0$. Define the ratio $\gamma = d_{22}/d_{11}$. Then

$$H(d_{11},d_{22}) = 0 \Leftrightarrow -g_v^2 + 2\gamma(f_u g_v - 2f_v g_u) - \gamma^2 f_u^2 = 0, \tag{2.21}$$

$$K(d_{11},d_{22}) = 0 \Leftrightarrow \gamma = -\frac{g_v}{f_u} \equiv \gamma_*, \tag{2.22}$$

Because $f_u > 0,\ g_v < 0,\ f_u + g_v < 0,\ \ f_u g_v - f_v g_u > 0$, then $0 > f_u g_v > f_v g_u$. It implies that $f_u g_v - 2f_v g_u > 0$, $-f_u f_v g_u g_v + f_v^2 g_u^2 = -f_v g_u(f_u g_v - f_v g_u) > 0$ and

$$4(f_u g_v - 2f_v g_u)^2 - 4f_u^2 g_v^2 = 16(-f_u f_v g_u g_v + f_v^2 g_u^2) > 0.$$

Therefore (2.21) has two positive roots

$$\gamma_1 = \frac{f_u g_v - 2f_v g_u + 2\sqrt{-f_u f_v g_u g_v + f_v^2 g_u^2}}{f_u^2}, \tag{2.23}$$

$$\text{and}\quad \gamma_2 = \frac{f_u g_v - 2f_v g_u - 2\sqrt{-f_u f_v g_u g_v + f_v^2 g_u^2}}{f_u^2}. \tag{2.24}$$

By direct calculation, $\gamma_1 > \gamma_* > \gamma_2 > 0$. Then $H(d_{11},d_{22}) > 0$ between the line $d_{22} = \gamma_1 d_{11}$ and the line $d_{22} = \gamma_2 d_{11}$, and $K(d_{11},d_{22}) > 0$ between the line $d_{22} = \gamma_* d_{11}$ and the d_{22}-axis. Therefore the region U_1, between $d_{22} = \gamma_1 d_{11}$ the d_{22}-axis, is an unstable region, *i.e.*, for any $(d_{11},d_{22}) \in U_1$, (u_0,v_0) is an unstable equilibrium solution with respect to (2.1). ☐

In the case Turing instability does not occur, *i.e.* (u_0,v_0) is still stable with a diffusion matrix only $d_{11},d_{22} \neq 0$, we show that the addition of appropriate cross-diffusion could cause instability:

Theorem 2.3. *Suppose that (u_0,v_0) is a stable constant equilibrium of (2.1), and (2.19) holds. Moreover we assume that (u_0,v_0) is a stable equilibrium solution with respect to (2.20). Then for fixed $(d_{11},d_{22}) \in (\mathbf{R}^+ \times \mathbf{R}^+)\backslash\overline{U_1}$ (defined in Theorem 2.2), there exists an unbounded region U_2 in the (d_{21},d_{12})-plane (see Figure 2), defined by*

$$\begin{aligned} U_2 =&\{(d_{21},d_{12}) \in \mathbf{R}^2 : \\ &-(d_{21}f_v + d_{12}g_u) > -(d_{22}f_u + d_{11}g_v) + 2\sqrt{d_{11}d_{22} - d_{12}d_{21}}\sqrt{Det(J)}\} \end{aligned} \tag{2.25}$$

such that for any point $(d_{21},d_{12}) \in U_2$, (u_0,v_0) is an unstable equilibrium solution with respect to (2.1).

Proof. First $d_{21}d_{12} < d_{11}d_{22}$ follows from $Det(D) = d_{11}d_{22} - d_{12}d_{21} > 0$. Hence (d_{21},d_{12}) falls into the region between the two components of the hyperbola $d_{12}d_{21} = d_{11}d_{22}$.

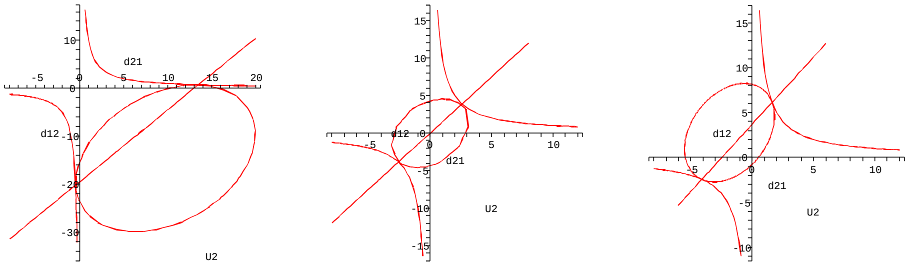

Figure 2. Parameter space for cross-diffusion induced instability. The parameter values are $f_u = 1, f_v = -3, g_u = 2, g_v = -4$, $\alpha = 1$, ($\gamma_1 = 8 + 4\sqrt{3} \approx 14.93$), and (left) $d_{11} = 10$, $d_{22} = 1$, ($\beta = -39$, $\gamma = 0.1$); (center) $d_{11} = \sqrt{10}/2$, $d_{22} = 2\sqrt{10}$, ($\beta = 0$, $\gamma = 4$); (right) $d_{11} = 10/11$, $d_{22} = 11$, ($\beta = 81/11$, $\gamma = 12.1$); The unstable region U_2 is the region between the two components of the hyperbola $d_{12}d_{21} = d_{11}d_{22}$, outside of the ellipse $H_1 = 0$, and on the right-lower side of the line $K_1 = 0$.

From Theorem 2.1, we obtain

$$\min_k Det(M_k) = -\frac{(-d_{22}f_u + d_{21}f_v + d_{12}g_u - d_{11}g_v)^2\alpha^2}{4(d_{11}d_{22} - d_{12}d_{21})} + (f_u g_v - f_v g_u)\alpha^2,$$
$$k_*^2 = -\frac{(-d_{22}f_u + d_{21}f_v + d_{12}g_u - d_{11}g_v)\alpha}{2(d_{11}d_{22} - d_{12}d_{21})}.$$

From (2.19), (2.17) and (2.18) are equivalent to $H_1(d_{21}, d_{12}) < 0$ and $K_1(d_{21}, d_{12}) > 0$, where

$$H_1(d_{21}, d_{12}) \equiv -(d_{21}f_v + d_{12}g_u - \beta)^2 + 4(d_{11}d_{22} - d_{12}d_{21})Det(J), \tag{2.26}$$
$$K_1(d_{21}, d_{12}) \equiv \beta - d_{21}f_v - d_{12}g_u, \tag{2.27}$$

and

$$\beta = d_{22}f_u + d_{11}g_v. \tag{2.28}$$

We prove that $H_1(d_{21}, d_{12}) = 0$ is an ellipse in $d_{21}d_{12}$-plane, and it is tangent to the hyperbola $d_{12}d_{21} = d_{11}d_{22}$; moreover the ellipse $H_1(d_{21}, d_{12}) = 0$, the line $K_1(d_{21}, d_{12}) = 0$ and the hyperbola $d_{12}d_{21} = d_{11}d_{22}$ meet at exactly the same two points. In fact, let

$$\Theta = d_{21}f_v + d_{12}g_u, \quad \Lambda = d_{21}f_v - d_{12}g_u, \tag{2.29}$$
$$d_{12} = \frac{\Theta - \Lambda}{2g_u}, \quad d_{21} = \frac{\Theta + \Lambda}{2f_v}. \tag{2.30}$$

Substituting (2.30) into $H_1(d_{21}, d_{12}) = 0$, we obtain

$$-\left(1 + \frac{Det(J)}{f_v g_u}\right)\Theta^2 + 2\beta\Theta + \frac{Det(J)}{f_v g_u}\Lambda^2 + 4d_{11}d_{22}Det(J) - \beta^2 = 0. \tag{2.31}$$

Since $Det(J) = f_u g_v - f_v g_u > 0$ and $f_u > 0$, $g_v < 0$, then $f_v g_u < 0$. Then

$\dfrac{Det(J)}{f_v g_u} < 0$ and $-\left(1 + \dfrac{Det(J)}{f_v g_u}\right) = -\dfrac{f_u g_v}{f_v g_u} < 0$. We rewrite (2.31) as follows

$$\frac{f_u g_v}{f_v g_u}\left(\Theta - \frac{f_v g_u \beta}{f_u g_v}\right)^2 + \frac{-Det(J)}{f_v g_u}\Lambda^2 = -\beta^2 \frac{Det(J)}{f_u g_v} + 4d_{11}d_{22}Det(J). \tag{2.32}$$

Note that the right hand side of (2.32) is positive, so $H_1(d_{21}, d_{12}) = 0$ gives rise to an ellipse in the $d_{21}d_{12}$-plane. Furthermore, if (d_{21}, d_{12}) is on the hyperbola $d_{12}d_{21} = d_{11}d_{22}$, $H_1(d_{21}, d_{12}) = 0$ if and only if $\beta - d_{21}f_v - d_{12}g_u = 0$. So the hyperbola $d_{12}d_{21} = d_{11}d_{22}$, the ellipse $H_1(d_{21}, d_{12}) = 0$ and the line $\beta - d_{21}f_v - d_{12}g_u = 0$ intersect at two points.

By direct calculation, if (d_{21}, d_{12}) is outside the ellipse, $H_1(d_{21}, d_{12}) < 0$. Taking the square root of the equation $H_1(d_{21}, d_{12}) < 0$ and using $K_1(d_{21}, d_{12}) > 0$, we obtain (2.25). ☐

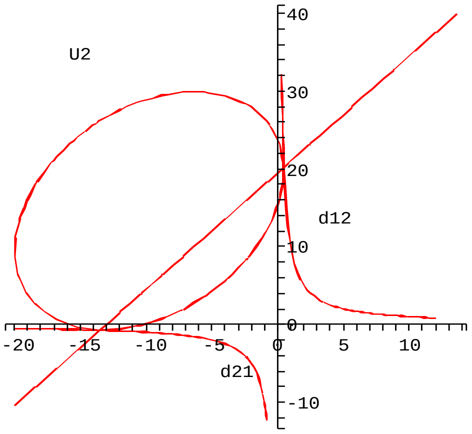

Figure 3. Parameter space for cross-diffusion induced instability. The parameter values are $f_u = 1, f_v = 3, g_u = -2, g_v = -4$, $d_{11} = 10, d_{22} = 1$ and $\alpha = 1$ ($\beta = -39$, $\gamma = 0.1 < \gamma_1 = 8 + 4\sqrt{3} \approx 14.93$); the unstable region U_2 is the region between the hyperbolas, outside of the ellipse $H_1 = 0$, and on the left-upper side of the line $K_1 = 0$.

Here we give a more geometrical description of U_2. The line $K_1(d_{21}, d_{12}) = 0$ has a positive slope since $f_v g_u < 0$, thus the intersection points of $K_1 = 0$ and the hyperbola $d_{12}d_{21} = d_{11}d_{22}$ are always in the first and the third quadrants. The line $K_1(d_{21}, d_{12}) = 0$ cuts through either the second or the fourth quadrant depending on the sign of β, f_v and g_u, and it can also go through exactly the origin if $\beta = 0$. The set of points between the two components of hyperbola and outside of the ellipse has two connected component, and U_2 is the component without the origin since the origin $(d_{21}, d_{12}) = (0, 0)$ is in stable range according to the assumptions. Therefore U_2 is always bordered by part of the ellipse and two adjacent hyperbola branches. Figure 2 shows three possible pictures with $f_v < 0$ and $g_u > 0$. In this case, the Jacobian is of activator-inhibitor type (see more discussion in the biological interpretation at the end of this section), and since the equilibrium is stable with respect to the self-diffusion system, the $\gamma = d_{22}/d_{11}$ satisfies $\gamma < \gamma_1$ where γ_1 is defined in (2.23). The three graphs in Figure 2 show the regions U_2 when $\beta < 0$, $\beta = 0$ and $\beta > 0$. In all cases, U_2 is the region at the lower-right corner. With β changing from negative to positive, the center of the ellipse $H_1 = 0$ moves from the fourth quadrant to the second quadrant; the size of the ellipse decreases for increasing $\beta < 0$, and the ellipse has the smallest size when $\beta = 0$ from (2.32). Another possible U_2 is seen in Figure 3 in which $f_v > 0$ and $g_u < 0$ (called the positive feedback system). Here the region U_2 is on the upper-right side of the line K_1. We shall explain more about this difference later in the biological interpretation at the end of this section.

On the other hand, if the equilibrium is destabilized by self-diffusion as Turing has suggested, then for some appropriate cross-diffusion, the stability can be regained as we show in the next theorem. The proof is similar to that of Theorem 2.3, thus we omit it.

Theorem 2.4. *Suppose that* (u_0, v_0) *is a stable constant equilibrium solution of* (2.1), *but it is an unstable equilibrium solution with respect to* (2.20) *thus it is Turing unstable. Then for fixed* $(d_{11}, d_{22}) \in U_1$ *(defined in Theorem 2.2), there exists an unbounded region* S *in the* $d_{21}d_{12}$*-plane, defined by*

$$S = \left\{(d_{21}, d_{12}) \in \mathbf{R}^2 : d_{21}d_{12} < d_{11}d_{22}, H_1(d_{21}, d_{12}) > 0\right\} \tag{2.33}$$

$$\bigcup \left\{(d_{21}, d_{12}) \in \mathbf{R}^2 : d_{21}d_{12} < d_{11}d_{22}, K_1(d_{21}, d_{12}) < 0\right\}, \tag{2.34}$$

where H_1, K_1 *and* β *are defined in Theorem 2.3, such that for any point* $(d_{21}, d_{12}) \in S$, (u_0, v_0) *is a stable equilibrium solution with respect to* (2.1) *(see Figure 4.)*

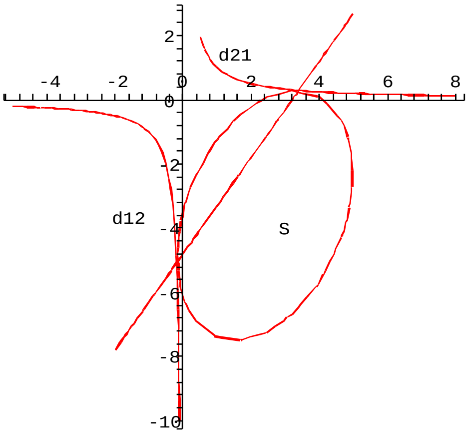

Figure 4. Parameter space for cross-diffusion induced instability. The parameter values are $f_u = 1, f_v = -3, g_u = 2, g_v = -4$, $d_{11} = 0.1, d_{22} = 10$ and $\alpha = 1$ ($\beta = 9.6$, $\gamma = 100 > \gamma_1 = 8 + 4\sqrt{3} \approx 14.93$); The region S is the union of the interior of the ellipse and the region on the left-upper side to the line.

Notice that we use the same Jacobian (activator-inhibitor type) in Figure 4 as the one in Figure 2, but the self-diffusion rate (d_{11}, d_{22}) are in different ranges. The region S is bordered by the short arc of the ellipse and the adjacent hyperbola branches, and it is on the upper-left side of the boundary.

Biological interpretation: In his 1952 seminal paper [31], Turing first introduce the idea of diffusion induced instability which leads to the "chemical morphogenesis". Segel and Jackson [25] derived necessary and sufficient conditions for diffusive instability (see also Edelstein-Keshet [4], Murray [18]), and they also explain the biological meaning in an elegant way. Here we follow the line of [25] and [4] to explain the instability or stability induced by cross-diffusion. We assume that $u(x,t)$ and $v(x,t)$ are the concentration of two chemical involved in this reaction-diffusion event.

As we have seen in the analysis above, the stability/instability is determined by the diffusion matrix

$$D = \begin{pmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{pmatrix}, \tag{2.35}$$

and the community matrix (Jacobian) at the equilibrium (u_0, v_0):

$$J = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}. \tag{2.36}$$

As above, we assume that (u_0, v_0) is stable for the ODE, hence $f_u + g_v < 0$ and $f_u g_v - f_v g_u > 0$. We also assume $d_{11} > 0$ and $d_{22} > 0$ for self-diffusion, and $Det(D) = d_{11}d_{22} - d_{12}d_{21} > 0$ so that cross-diffusion is not overpowering self-diffusion. Although we do not always have Turing instability in the cases considered, we assume $f_u g_v < 0$, and more specific we assume $f_u > 0$ and $g_v < 0$. Thus the chemical u is an activator as it promotes or activates its own formation; and v is an inhibitor which inhibits its own formation. (In [25] they are called stabilizer and destabilizer, but activator and inhibitor are apparently more widely used.) Now $f_u g_v - f_v g_u > 0$ and $f_u g_v < 0$ imply that $f_v g_u < 0$, thus f_v and g_u must have opposite signs. There are two possibilities which are best shown with the sign patterns of the Jacobian: ([4])

$$\text{activator-inhibitor} \ : \ f_v < 0, \ \ g_u > 0, \ \ J = \begin{pmatrix} + & - \\ + & - \end{pmatrix}; \tag{2.37}$$

and

$$\text{positive feedback (substrate depletion)} \ : \ f_v > 0, \ \ g_u < 0, \ \ J = \begin{pmatrix} + & + \\ - & - \end{pmatrix}. \tag{2.38}$$

First for the sake of completeness, we give the conditions for instability induced by self-diffusion (Turing instability), which was first introduced in [25]. From Theorem 2.2 and its proof, one necessary condition for instability is $\beta = f_u d_{22} + g_v d_{11} > 0$, or

$$\left| \frac{d_{22}}{g_v} \right| > \left| \frac{d_{11}}{f_u} \right|. \tag{2.39}$$

The quantities in (2.39) have the units of mean square displacement during the doubling time of the activator or the half-life of the inhibitor. $\sqrt{d_{22}/|g_v|}$ and $\sqrt{d_{11}/|f_u|}$ are the ranges of inhibition and activation respectively. Thus (2.39) can be restated as: the range of inhibition is larger than the range of activation. In connection to the proof of Theorem 2.2 and Figure 1, (2.39) is equivalent to (d_{11}, d_{22}) is above the line $d_{22} = \gamma_* d_{11}$ with $\gamma_* = -g_v/f_u$. However the sufficient condition for Turing instability is that (d_{11}, d_{22}) is above a steeper line $d_{22} = \gamma_1 d_{11}$ with $\gamma_1 > \gamma_*$, where

$$\gamma_1 = \frac{f_u g_v - 2f_v g_u + 2\sqrt{-f_u f_v g_u g_v + f_v^2 g_u^2}}{f_u^2}. \tag{2.40}$$

An equivalent sufficient condition (see the proof of Theorem 2.2 or [25]) is

$$f_u d_{22} + g_v d_{11} > 2(d_{11}d_{22})^{1/2}(f_u g_v - f_v g_u)^{1/2} > 0, \tag{2.41}$$

or in comparison with (2.39) and its interpretation: the range of inhibition is larger than a constant multiple of the range of activation, while the constant can be determined from (2.40).

Now we turn to the explanation of the main result of this paper about the cross-diffusion. In term of chemical reactions, the cross-diffusion terms appear in the equation to describe attraction and repulsion between the activator and inhibitor. The classical model of slim mold aggregation of Keller and Segel [7, 8] is the earliest one which includes cross-diffusion effect, and Shigesada, Kawasaki and Teramoto [28] introduced cross-diffusion system of interacting species. Notice that in these models, the diffusion matrix sometimes is also nonlinear which brings additional difficulties in mathematical analysis. Here we consider the constant diffusion matrix and linear analysis around the equilibrium, which are still valid for local analysis for nonlinear cross-diffusion. The cross-diffusion coefficient d_{12} indicate the influence of v density to u density. If $d_{12} > 0$, then u is repelled from v; and if $d_{12} < 0$, then u is attracted to v. d_{21} has the same meaning with the role of u and v switched. Mathematically we point out that the sufficient condition for the instability we obtain in Theorem 2.3 is

$$\begin{aligned} &2(d_{11}d_{22})^{1/2}(f_u g_v - f_v g_u)^{1/2} > f_u d_{22} + g_v d_{11} \\ &> f_v d_{21} + g_u d_{12} + 2(d_{11}d_{22} - d_{12}d_{21})^{1/2}(f_u g_v - f_v g_u)^{1/2}. \end{aligned} \tag{2.42}$$

Compared with (2.41), the first part of the inequality is just the opposite to (2.41) as we assume it is stable with respect to the self-diffusion system, and the second part of the inequality shows how the cross-diffusion plays into the instability problem.

In Theorem 2.3, the equilibrium (u_0, v_0) is stable with respect to both the kinetic and self-diffusion equations. The quantity $\beta = f_u d_{22} + g_v d_{11}$ could be either positive or negative: $\beta > 0$ implies the range of of inhibition is larger than the range of activation, while $\beta < 0$ implies the opposite. In the former case, $\gamma_1 > \gamma > \gamma_*$, where $\gamma = d_{22}/d_{11}$ is the ratio of the two self-diffusion coefficients. The sign choices of f_v and g_u makes it activator-inhibitor or positive feedback type systems. All together it gives four possibilities:

(A) $\beta > 0$ and $\gamma < \gamma_1$, $f_v > 0$ and $g_u < 0$;

(B) $\beta < 0$, $f_v < 0$ and $g_u > 0$;

(C) $\beta > 0$ and $\gamma < \gamma_1$, $f_v < 0$ and $g_u > 0$;

(D) $\beta < 0$, $f_v > 0$ and $g_u < 0$.

(A) and (B) both make the center of ellipse $H_1 = 0$ in the fourth quadrant, and (C) and (D) both make the center in the second quadrant. We use (C) to illustrate the ideas (see Figure 2 right). This is an activator-inhibitor system with activator u and inhibitor v. Here $\beta > 0$ but (u_0, v_0) is (self)-diffusively stable, thus $\gamma_1 > d_{22}/d_{11} > \gamma_*$: the range of of inhibition is larger than the range of activation but not large enough so that self-diffusion alone can generate concentration pattern. The instability can be induced by the cross-diffusion if (d_{21}, d_{12}) is in U_2, the lower-right portion of $\mathbf{R}^2$ bounded by an arc of the ellipse and adjacent hyperbolas (see Figure 2 right). U_2 consists of portions in 1st, 3rd, and 4th quadrants. When $d_{21} > 0$ and $d_{12} > 0$, u and v are repelled from each other; and when $d_{21} < 0$ and $d_{12} < 0$, they are attracted to each other. In these two cross-diffusion scenarios, instability is only possible when d_{12} is small and d_{21} is large (1st quadrant) or $-d_{12}$ is large and $-d_{21}$ is small (3rd quadrant), and the instability parameter regions are narrow stripes bounded by the hyperbolas.

The instability is more likely when $d_{21} > 0$ and $d_{12} < 0$, that is, the activator u is attracted to the inhibitor v but v is repelled from u. However this is a case biologically not very likely: in the context of predator-prey model, it requires the predator tries to evade the prey, but the prey chases the predator! On the other hand, the more reasonable signs $d_{21} < 0$ and $d_{12} > 0$ as in chemotaxis or preytaxis prohibit the instability. We will use en example of classical predator-prey model to illustrate this phenomenon. In the chemical context, such instability is possible but no example is known.

In conclusion, for activator-inhibitor systems, when the self-diffusion rates of the two chemical species are not different enough to cause the instability and consequent pattern formation, different types of attraction-repulsion between the species can do it. But we shall be cautious that the types depend not only on the nature of the chemical kinetics (activator-inhibitor or positive feedback) but also the ratio of the activation and inhibition ranges (β and γ). On the other hand, mutual attraction or repulsion usually will not lead to instability and pattern formation unless the rates are quite different.

We also comment that the pattern formation induced by cross-diffusion instability do not have to occur in activator-inhibitor system. The kinetic system could be a sink, and the condition (2.42) could still be satisfied. We will show the example of a water-limited ecosystem to demonstrate that possibility in Section 5.

Finally we discuss the mechanism of Theorem 2.4. In this scenario, Turing instability occurs when self-diffusion is added to the kinetic system, but the stability is regained when appropriate cross-diffusion is imposed. For the continuation of the discussion, we again use $f_v < 0$ and $g_u > 0$ as above, and $\beta > 0$ and $\gamma > \gamma_1$ holds since Turing instability occurs. From Figure 4, the parameter region of (d_{21}, d_{12}) which stabilizes the equilibrium is almost in the opposite part of $\mathbf{R}^2$ as in Fig 2. Again mutually attraction or repulsion unlikely stabilizes the self-diffusion induced instability, but if the activator u is repelled from the inhibitor v and v is attracted to u, then such a stabilization will be realized. Note that this response relation between the activator and the inhibitor is typically seen in the chemotaxis or preytaxis models. Together with discussion above, we can conclude that the chemotaxis or preytaxis is a stabilizing force for reaction-diffusion models. Application of Theorem 2.4 is given in Section 4 for a predator-prey model.

3. Cross-diffusion systems in finite domain

The analysis in Section 2 can be applied to the situation where the spatial domain is **R**, and a spatial non-homogeneous perturbation can cause instability. There is no constraint on such perturbation. But on the other hand, for some problems, the boundary conditions and the size of domain can both play roles in the process of pattern formation. Here we switch to the same reaction-diffusion model on an interval $(0, L)$ and no-flux boundary condition. Similar results can be obtained for high dimensional rectangular domains and periodic boundary conditions.

Consider the stability/instability of the constant solution (u_0, v_0) as an equilibrium of

$$\begin{cases} u_t = d_{11}u_{xx} + d_{12}v_{xx} + \alpha f(u,v), \;\; t > 0, \; x \in (0,L), \\ v_t = d_{21}u_{xx} + d_{22}v_{xx} + \alpha g(u,v), \;\; t > 0, \; x \in (0,L), \\ u_x(t,0) = u_x(t,L) = v_x(t,0) = v_x(t,L) = 0, \\ u(0,x) = h(x), \;\; v(0,x) = l(x), \;\; x \in (0,L), \end{cases} \tag{3.1}$$

where $L > 0$ is the length of interval. Again we start with the linearized system (2.8) and we look for solutions of (2.8) in the form (2.10), but now with $k^2 = (n\pi/L)^2$ being an eigenvalue of

$$w_{xx} + k^2 w = 0, \quad x \in (0,L), \;\; w_x(0) = w_x(L) = 0. \tag{3.2}$$

We require nontrivial solutions for $\mathbf{\Psi}(t,x)$, so the eigenvalues λ are the roots of the characteristic polynomial given by (2.11), *i.e.*,

$$Det(\lambda I - (\alpha J - k^2 D)) = \lambda^2 + (k^2(d_{11} + d_{22}) - \alpha(f_u + g_v))\lambda + Det(M_k) = 0, \tag{3.3}$$

where $M_k = \alpha J - k^2 D$ and

$$\lambda I - (\alpha J - k^2 D) = \begin{pmatrix} \lambda + k^2 d_{11} - \alpha f_u & k^2 d_{12} - \alpha f_v \\ k^2 d_{21} - \alpha g_u & \lambda + k^2 d_{22} - \alpha g_v \end{pmatrix}. \tag{3.4}$$

The equilibrium point (u_0, v_0) is linearly stable with respect to (3.1) if all eigenvalues of $\alpha J - k^2 D$ have negative real part for $k \in \mathbf{N}\pi/L$. We assume all conditions in (2.19) hold. Then $k^2(d_{11} + d_{22}) - \alpha(f_u + g_v) > 0$ for all real k. So the only way $Re(\lambda)$ can be positive is that $Det(M_k) < 0$ for some k, where

$$\begin{aligned} Det(M_k) &= k^4 Det(D) + k^2 F(J,D)\alpha + Det(J)\alpha^2 \\ &= k^4(d_{11}d_{22} - d_{12}d_{21}) + k^2(-d_{22}f_u + d_{21}f_v + d_{12}g_u - d_{11}g_v)\alpha + (f_u g_v - f_v g_u)\alpha^2, \end{aligned} \tag{3.5}$$

which achieves its minimum

$$\min_k Det(M_k) = -\frac{(F(J,D)\alpha)^2}{4Det(D)} + Det(J)\alpha^2 \tag{3.6}$$

at the critical point k_* defined by

$$k_*^2 = -\frac{F(J,D)\alpha}{2Det(D)}. \tag{3.7}$$

In order to have $Re(\lambda) > 0$, the following inequalities must hold:

$$\min_k Det(M_k) < 0, \qquad k_*^2 = -\frac{F(J,D)\alpha}{2Det(D)} > 0. \tag{3.8}$$

However the inequalities in (3.8) are necessary but not sufficient for instability in finite domain. The possible wave numbers k are discrete and depend in part on the boundary conditions. We must have $Det(M_k) < 0$ for some $k = n\pi/L$ where $n \in \mathbf{N}$. Let $k_1^2 < k_2^2$ be the zeros of $Det(M_k) = 0$, *i.e.*

$$\begin{aligned} k_1^2 &= \frac{\left(-F(J,D) - \sqrt{(F(J,D))^2 - 4Det(D)Det(J)}\right)\alpha}{2Det(D)} \le k_*^2 \\ \le k_2^2 &= \frac{\left(-F(J,D) + \sqrt{(F(J,D))^2 - 4Det(D)Det(J)}\right)\alpha}{2Det(D)}. \end{aligned} \tag{3.9}$$

When $0 < k_1^2 \le k^2 = \left(\frac{n\pi}{L}\right)^2 \le k_2^2$ for some $n \in \mathbf{N}$, $\alpha J - k^2 D$ has an eigenvalue which is positive for this n. Summarizing the above calculation, we have the following conclusion.

Theorem 3.1. *Suppose that* (u_0, v_0) *is a stable constant equilibrium solution of* (2.4)*. We assume* (2.19) *holds. If* (3.8) *is satisfied, and*

$$0 < k_1^2 \le k^2 = \left(\frac{n\pi}{L}\right)^2 \le k_2^2 \tag{3.10}$$

for some positive integer n*, where* k_1^2 *and* k_2^2 *are defined by* (3.9)*, then* (u_0, v_0) *is an unstable equilibrium solution with respect to* (3.1)*.*

Because the discrete wave number k increase π/L to wave number $k+1$, a sufficient condition, which guarantees that the interval $[k_1^2, k_2^2]$ includes at least one $k^2 = (n\pi/L)^2$ for some n, is that the length of the interval $[k_1, k_2]$ is larger than π/L, *i.e.*,

$$(k_2 - k_1)^2 = (k_1^2 + k_2^2) - 2\sqrt{k_1^2 k_2^2} \ge \left(\frac{\pi}{L}\right)^2,$$

which is equivalent to

$$-\frac{F(J,D)\alpha}{Det(D)} - 2\sqrt{\frac{Det(J)\alpha^2}{Det(D)}} \ge \left(\frac{\pi}{L}\right)^2, \tag{3.11}$$

or

$$-F(J,D) - 2\sqrt{Det(D)Det(J)} \ge \frac{Det(D)}{\alpha}\left(\frac{\pi}{L}\right)^2. \tag{3.12}$$

Replacing the conditions (3.8), (3.9) and (3.10), we have theorem 3.1$'$.

Theorem 3.1$'$. *Suppose that* (u_0, v_0) *is a stable constant equilibrium solution of* (2.4)*, and we assume* (2.19) *holds. If*

$$-F(J,D) - 2\sqrt{Det(D)Det(J)} \ge \frac{Det(D)}{\alpha}\left(\frac{\pi}{L}\right)^2. \tag{3.13}$$

then (u_0, v_0) *is an unstable equilibrium solution with respect to* (3.1)*.*

Remark. To compare Theorem 3.1′ with Theorem 2.1, we notice that the inequality (2.17) is equivalent to

$$-F(J,D) - 2\sqrt{Det(D)Det(J)} > 0 \tag{3.14}$$

Comparing (3.14) with (3.13), we conclude that the parameter α has no effect on the unstable region for the infinite domain $\mathbf{R}$ but it does have effect on the unstable region for finite domain $(0, L)$.

To consider the effect of bounded domain to the parameter range of instability, we develop results parallel to Theorems 2.2-2.4.

Theorem 3.2. *Suppose that* (u_0, v_0) *is a stable constant equilibrium solution of the reaction-diffusion system* (3.1). *We further assume that* $d_{12} = d_{21} = 0$, *i.e., we consider*

$$\begin{cases} u_t = d_{11}u_{xx} + \alpha f(u,v), & t > 0,\ 0 < x < L, \\ v_t = d_{22}v_{xx} + \alpha g(u,v), & t > 0,\ 0 < x < L, \\ u_x(t,0) = u_x(t,L) = v_x(t,0) = v_x(t,L) = 0, \\ u(0,x) = h(x),\ \ v(0,x) = l(x), & 0 < x < L. \end{cases} \tag{3.15}$$

Then there exists an unbounded region $U_3 = \{(d_{11}, d_{22}) : d_{11} > 0, d_{22} > 0, d_{22}f_u + d_{11}g_v - 2\sqrt{d_{11}d_{22}(f_u g_v - f_v g_u)} > d_{11}d_{22}\pi^2(\alpha L^2)^{-1}\}$, *such that for any* $(d_{11}, d_{22}) \in U_3$, (u_0, v_0) *is an unstable equilibrium solution with respect to* (3.15) *(see Figure 5.)*

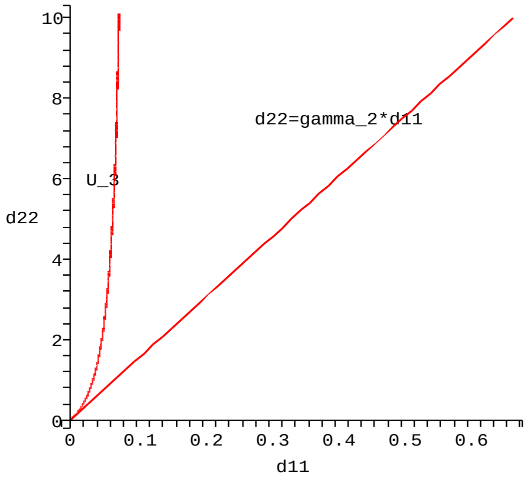

Figure 5. The parameter values are $f_u = 1, f_v = -3, g_u = 2, g_v = -4, \alpha = 1, L = 1, d_{12} = 0, d_{21} = 0$; The region U_3 is the region between d_{22}-axis and the curve implicitly defined by (3.13): $d_{22} - 4d_{11} - 2\sqrt{2d_{11}d_{22}} = d_{11}d_{22}\pi^2$. Note that the line in the graph is $d_{22} - 4d_{11} - 2\sqrt{2d_{11}d_{22}} = 0$.

Because the analysis and proof of Theorem 3.2 are similar to the proof of Theorem 2.1, we omit its proof. The instability parameter region in figure 5 is smaller than the one in figure 1, which reflects that the inequality (3.13) is more restrictive that (3.14). Corresponding results can also be proved for the ones in Theorem 2.3.

While we do not formulate the details, we point out that the cross-diffusion induced instability holds for (3.1) if d_{12}, d_{21} satisfy

$$-(d_{21}f_v+d_{12}g_u) \geq -(d_{22}f_u+d_{11}g_v)+2\sqrt{d_{11}d_{22}-d_{12}d_{21}}\sqrt{Det(J)}+\frac{Det(D)}{\alpha}\left(\frac{\pi}{L}\right)^2, \tag{3.16}$$

while we point out the condition in Theorem 2.3 for the case of without boundary conditions is

$$-(d_{21}f_v+d_{12}g_u) > -(d_{22}f_u+d_{11}g_v)+2\sqrt{d_{11}d_{22}-d_{12}d_{21}}\sqrt{Det(J)}. \tag{3.17}$$

We implicitly assume that $d_{11}d_{22} - d_{12}d_{21} > 0$ in (3.16) and (3.17). In this case (u_0, v_0) is an unstable equilibrium solution with respect to (3.1), but it is stable for (3.15) or the ODE system.

The possible spatial patterns for the bounded domain are tied to the domain length. For each positive integer k, the characteristic function $exp(ikx)$ can be the unstable mode if

$$\frac{\pi^2}{f_2(D)} \leq \frac{\alpha L^2}{k^2} \leq \frac{\pi^2}{f_1(D)}, \tag{3.18}$$

where

$$f_1(D) = \frac{-F(J,D) - \sqrt{(F(J,D))^2 - 4Det(D)Det(J)}}{2Det(D)},$$

$$f_2(D) = \frac{-F(J,D) + \sqrt{(F(J,D))^2 - 4Det(D)Det(J)}}{2Det(D)}.$$

For fixed J and D, if $(F(J,D))^2 - 4Det(D)Det(J) > 0$, there is a range of the scale α and L such that (3.18) holds for the given unstable mode $exp(ikx)$. Conversely, for fixed J, D and L, if α is sufficiently small, there is no integer k such that (3.18) holds, hence the equilibrium solution is always stable. Same is true if L is too small for fixed α. The parameter α can be understood as the reverse of the diffusion coefficient of the whole system with the same relative self-diffusion constant d_{22}/d_{11}. This just recovers the well-known fact that no pattern exists when the diffusion coefficient is too large or the spatial domain is too small. Indeed (3.18) with $k = 1$ gives the minimum domain size for pattern generation. Bounded domains also have impact on the result in Theorem 2.4, and we leave the details to the readers.

4. Stability of coexistence state in predator-prey system

Here we revisit a predator-prey model discussed in Segel and Jackson [25]. They proposed predator-prey system with diffusion:

$$v_t = (1+\kappa v)v - aev + \delta^2 \Delta v, \quad e_t = ev - e^2 + \Delta e. \tag{4.1}$$

Here the equations have been rescaled to a dimensionless form; $v(x,t)$ and $e(x,t)$ are the density function of prey (victims) and predator (exploiters); the nonlinearities are in the classical Lotka-Volterra form, where the prey reproduction rate exhibiting cooperativity, and the predator mortality is primarily due to the interspecies competition. More realistic model perhaps takes the reproduction rate per capita to be1 $+ \kappa v - \kappa_1 v^2$ to incorporate the crowding effect, and the mortality rate to be $-\kappa_1 e - e^2$ to include the random death. But as pointed out in [25], neglecting these terms do not alter the instability results, thus we take the simplified form.

We assume $a > \kappa$, then (4.1) has a unique coexistence equilibrium point $(e, v) = (L, L)$ where $L = (a - \kappa)^{-1}$. We also have the diffusion matrix and Jacobian to be

$$D = \begin{pmatrix} \delta^2 & 0 \\ 0 & 1 \end{pmatrix}, \quad J = \begin{pmatrix} \kappa L & -aL \\ L & -L \end{pmatrix}. \tag{4.2}$$

We assume that $(e, v) = (L, L)$ is stable for the ODE, which gives conditions:

$$0 < \kappa < 1, \quad 0 < \kappa < a. \tag{4.3}$$

This equilibrium is Turing unstable if

$$\kappa - \delta^2 > 2\delta(a - \kappa)^{1/2}, \tag{4.4}$$

or equivalently

$$0 < \delta < \frac{(-\kappa + 2a + 2\sqrt{a^2 - \kappa a})^{1/2}}{k}. \tag{4.5}$$

Note that (4.4) follows from (2.41) and (4.5) is from Theorem 2.2.

Now we consider a modified version of (4.1):

$$v_t = (1 + \kappa v)v - aev + \delta^2 \Delta v + d_{12} \Delta e, \quad e_t = ev - e^2 + \Delta e - d_{21} \Delta v. \tag{4.6}$$

The additional cross-diffusion is due to "preytaxis": the predator is attracted to the prey, thus the movement of predator also follows the gradient of prey density function. This effect is described by the $-d_{21}\Delta v$ term in the predator equation. We also add a term $d_{12}\Delta e$ in the prey equation to assume that the prey is repelled from predator. The prey species can evade from predator if they have information about the location of the predator. The two responses between the predator and prey have the similar effect on the dynamics, and our analysis below allows one of d_{12} and d_{21} to be zero. Now we have the diffusion matrix

$$D = \begin{pmatrix} \delta^2 & d_{12} \\ -d_{21} & 1 \end{pmatrix}, \tag{4.7}$$

with $d_{12} \geq 0$ and $d_{21} \geq 0$. First we point out that if δ satisfies (4.3) and

$$\kappa - \delta^2 < 2\delta(a - \kappa)^{1/2}, \tag{4.8}$$

i.e. Turing instability does not occur, then for any (d_{21}, d_{12}) such that $d_{12} \geq 0$ and $d_{21} \geq 0$, the coexistence equilibrium remains stable. In fact, the instability (2.42) becomes

$$2\delta(a - \kappa)^{1/2} > \kappa - \delta^2 > ad_{21} + d_{12} + 2(\delta^2 + d_{12}d_{21})^{1/2}(a - \kappa)^{1/2}. \tag{4.9}$$

But (4.9) is contradictory since the last expression is apparently larger than the first one. This shows the preytaxis is indeed is a stabilizing force which will not cause instability of the coexistence. On the other hand, if Turing instability occurs from the presence of the self-diffusion, *i.e.* (4.3) and (4.4) are satisfied, then the preytaxis again is a stabilizing force. Indeed, Theorem 2.4 implies that if (d_{12}, d_{21}) satisfies $d_{12} \geq 0$ and $d_{21} \geq 0$, and

$$d_{12} + ad_{21} - \kappa + \delta^2 < 2(\delta^2 + d_{12}d_{21})^{1/2}(a - \kappa)^{1/2}, \tag{4.10}$$

then the coexistence equilibrium is stable for ODE, unstable for self-diffusion system, but stable for cross-diffusion system as long as (4.10) is satisfied. In particular, if one of d_{21} or d_{12} is large, then (4.10) holds.

From these two demonstrations of our main results, one can see the preytaxis and chemotaxis usually have stabilizing effects on an equilibrium. However the cross-diffusion induced instability described in Theorem 2.3 is still possible if the equilibrium in the kinetic system is a sink, as we shall show in the next section's example.

5. Vegetation pattern formation

In this section, we apply general results in Section 2 and Section 3 to a reaction-diffusion model set forth by von Hardenberg, Meron, et. al. [32, 17], which gives a theoretical explanation of desertification phenomena in water limited systems. The model predicts no vegetation at low water levels and homogeneous vegetation at high water levels, with intermediate states of spots, stripes, and labyrinths. These patterns have all been documented in desert systems. The model also predicts the coexistence of steady states for several precipitation ranges. The non-dimensional form of the equations is

$$\begin{aligned} n_t &= \frac{\gamma w}{1 + \sigma w} n - n^2 - \mu n + \Delta n, \\ w_t &= p - (1 - \rho n)w - w^2 n + \delta \Delta(w - \beta n) - v(w - \alpha n)_x, \end{aligned} \tag{5.1}$$

where $n(x, t)$ is the vegetation biomass density and $w(x, t)$ is the soil water density. The plant growth is linear in n but the growth rate saturates when the water amount is more than adequate, that is shown in the term $\gamma wn/(1 + \sigma w)$; μ is the mortality rate of plant, and the quadratic term $-n^2$ represents saturation due to limited nutrients; spatial dispersal of the plants is modeled by the diffusion term Δn, here Δ is the Laplacian operator. In the equation of soil water density, p is the precipitation, and the loss term $-(1 - \rho n)w$ represents the evaporation; the uptake of water by the plants is modeled by the term $-w^2 n$; the transport of the water in the soil is modeled by Darcy's law, but the water matric potential $\phi = w - \beta n$ to take account of the suction of water by the roots; finally the water downhill runoff is described in the term $v(w - \alpha n)_x$ assuming that x is the direction that altitude drops. In the paper we shall only consider the case of $v = 0$, but concentrate on the impact of cross-diffusion term $-\beta \Delta n$ on the stability of equilibrium solutions.

First we study the corresponding ordinary differential equation system:

$$\begin{aligned} n_t &= \frac{\gamma w}{1 + \sigma w} n - n^2 - \mu n, \\ w_t &= p - (1 - \rho n)w - w^2 n. \end{aligned} \tag{5.2}$$

The nullclines are given by:

$$n\text{-nullcline} : n = 0, \quad n = \frac{\gamma w}{1+\sigma w} - \mu, \tag{5.3}$$

$$w\text{-nullcline} : n = \frac{w-p}{w(\rho - w)}. \tag{5.4}$$

Apparently $(n, w) = (0, p)$ is an equilibrium point, which corresponds to bare state (no vegetation); other possible equilibrium points are the intersections of $n_1(w) = \dfrac{\gamma w}{1+\sigma w} - \mu$ and $n_2(w) = \dfrac{w-p}{w(\rho-w)}$. For $n_1(w)$, we have $n_1(0) = -\mu$, $\lim_{w\to\infty} n_1(w) = \gamma/\sigma - \mu$, and $n_1'(w) > 0$ for $w > 0$. Hence to have an intersection in the positive quarter, we must have $\gamma/\sigma - \mu > 0$. In the case that $\gamma/\sigma - \mu \le 0$, $(n, w) = (0, p)$ is the unique equilibrium point. Hence we assume $\gamma/\sigma - \mu > 0$ in the following.

Following [32], we use p (the precipitation level) as a bifurcation parameter, and fix all other parameters. Setting $n_1(w) = n_2(w)$, we can solve for the bifurcation parameter p in terms of w.

$$p(w) = \frac{-\gamma w^2}{1+\sigma w}(\rho - w) + \mu w(\rho - w) + w. \tag{5.5}$$

$\Sigma_0 = \{(p, n, w) = (p, 0, p) : p > 0\}$ is a line of trivial equilibrium solutions of (5.2). At the bifurcation point $(p, n, w) = (w_0, 0, w_0)$ where $w_0 = \mu/(\gamma - \mu\sigma)$, another curve Σ_1 of positive equilibrium solutions emerges from the trivial branch, and Σ_1 can be parameterized by w thus Σ_1 can be written as $\{(p, n, w) = (p(w), n_1(w), w) : w > w_0\}$, where $p(w)$ is given by (5.5). Notice that $n_1(w)$ is increasing in w, thus the properties of this positive equilibrium branch are mainly determined by the function $p(w)$. From the algebraic form of $p(w)$, we can find that $p(w)$ has at most two critical points for $w > 0$. We also notice that as $w \to \infty$, $p(w)/w^2 \to \gamma/\sigma - \mu > 0$ which implies $p(w) \to \infty$ when $w \to \infty$, or equivalently when $p \to \infty$, the unique positive equilibrium $(n(p), w(p))$ satisfies $w(p) \approx \sqrt{\frac{\sigma}{\gamma - \mu\sigma} p}$, *i.e.* $w(p)$ has a growth rate of $p^{1/2}$. On the other hand $p(w)$ may not be always positive when $w > w_0$ for some parameter choices, but here we are only interested in the part when w is large. See Figure 6 for some possible bifurcation diagrams of $(p(w), w)$ when $w > w_0$.

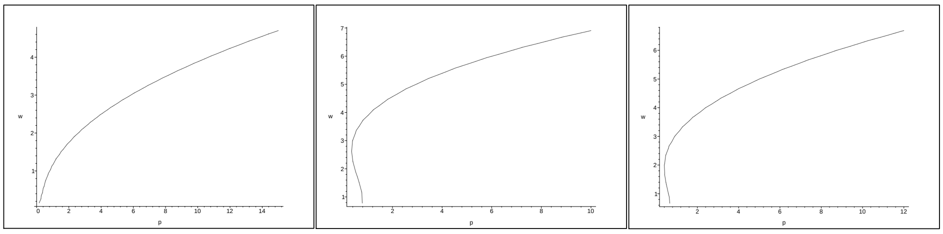

Figure 6. Bifurcation diagrams. horizontal axis is p, and vertical axis is w; (A) monotone $\gamma = 1.6$, $\sigma = 1.6$, $\mu = 0.2$ and $\rho = 1.5$; (B) two turning points $\gamma = 0.32$, $\sigma = 0.32$, $\mu = 0.2$ and $\rho = 6$; (C) one turning points $\gamma = 1$, $\sigma = 1$, $\mu = 0.4$ and $\rho = 5$.

We also point out that not all of the above bifurcation diagrams are physically realizable for the original system (5.2). Recall that the term $1-\rho n$ models evaporation. Since the evaporation cannot be negative, it is reasonable to assume $n \le \rho^{-1}$ in addition to $n > 0$ and $w > 0$. At equilibrium, n is given by $n_2(w) = (w-p)/(w(\rho-w))$. As a result, $\dfrac{w-p}{w(\rho-w)} \le \dfrac{1}{\rho}$ implies $p \le w^2\rho^{-1}$. So the solutions on curves in Figure 6 are only valid for when $p \le w^2\rho^{-1}$. In Figure 7, we plot both $p(w)$ in (5.5) and $p_2(w) = \rho^{-1}w^2$. Now only those points under the parabola $p_2(w)$ are valid. But if we assume that $\gamma/\sigma - \mu < \rho^{-1}$, or

$$\gamma - \mu\sigma < \frac{\sigma}{\rho}, \tag{5.6}$$

then when $w \to \infty$ (or $p \to \infty$), the unique equilibrium is a valid one as shown in Figure 7.

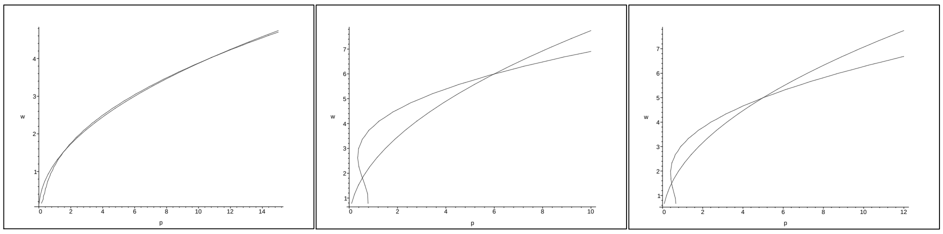

Figure 7. Bifurcation diagrams with additional condition $p \le w^2\rho^{-1}$. horizontal axis is p, and vertical axis is w; (A) monotone $\gamma = 1.6$, $\sigma = 1.6$, $\mu = 0.2$ and $\rho = 1.5$; (B) two turning points $\gamma = 0.32$, $\sigma = 0.32$, $\mu = 0.2$ and $\rho = 6$; (C) one turning points $\gamma = 1$, $\sigma = 1$, $\mu = 0.4$ and $\rho = 5$.

Next we turn to the stability of the equilibrium point with respect to the ODE system (5.2). The Jacobian of the system is

$$J = \begin{pmatrix} \dfrac{\gamma w}{1+\sigma w} - 2n - \mu & \dfrac{\gamma n}{(1+\sigma w)^2} \\ \rho w - w^2 & -(1-\rho n) - 2wn \end{pmatrix} \tag{5.7}$$

and at $(n, w) = (0, p)$, the Jacobian becomes

$$J(0,p) = \begin{pmatrix} \dfrac{\gamma p}{1+\sigma p} - \mu & 0 \\ \rho p - p^2 & -1 \end{pmatrix} \tag{5.8}$$

so the stability depends on its two eigenvalues, $\lambda_1 = \dfrac{\gamma p}{1+\sigma p} - \mu$ and $\lambda_2 = -1$. For the equilibrium to be stable, both eigenvalues must be less than zero. This is true for $\lambda_1 < 0$ when $p < \dfrac{\mu}{\gamma - \mu\sigma}$. Note that when $p < \dfrac{\mu}{\gamma-\mu\sigma}$, $(0, p)$ is the sole equilibrium point.

At $(n, w) = (\dfrac{\gamma w}{1+\sigma w} - \mu, w)$, the Jacobian becomes

$$J(\frac{\gamma w}{1+\sigma w} - \mu, w) = \begin{pmatrix} -n & \dfrac{\gamma n}{(1+\sigma w)^2} \\ \rho w - w^2 & -1 + \rho n - 2wn \end{pmatrix} \tag{5.9}$$

and by using $n = \dfrac{w-p}{w(\rho-w)}$, we obtain

$$Tr(J) = -n - (1-\rho n) - 2wn = -n - \frac{p}{w} - wn < 0, \tag{5.10}$$

and

$$Det(J) = n - \rho n^2 + 2wn^2 - \frac{\gamma(\rho-w)wn}{(1+\sigma w)^2} = n\left[\frac{p}{w} + wn - \frac{(\rho-w)n^2}{1+\sigma w}\right]. \tag{5.11}$$

Thus $Det(J) > 0$ if $w > \rho$. We summarize the above discussions to have

Theorem 5.1. *Suppose that*

$$0 < \gamma - \mu\sigma < \frac{\sigma}{\rho}, \text{ and } w > \rho, \tag{5.12}$$

then $(n, w) = (\dfrac{\gamma w}{1+\sigma w} - \mu, w)$ *is an equilibrium point of* (5.2) *satisfying* $1 - \rho n > 0$. *Moreover this equilibrium is linearly stable with respect to* (5.2).

Now we look for whether Turing instability (self-diffusion induced instability) occurs for the non-trivial equilibrium. We consider the system with no advection term:

$$\begin{aligned} n_t &= \frac{\gamma w}{1+\sigma w} n - n^2 - \mu n + \Delta n, \quad t > 0, \ x \in \mathbf{R}, \\ w_t &= p - (1-\rho n)w - w^2 n + \delta\Delta(w - \beta n), \quad t > 0, \ x \in \mathbf{R}, \end{aligned} \tag{5.13}$$

and we have the diffusion matrix

$$D = \begin{pmatrix} 1 & 0 \\ -\beta\delta & \delta \end{pmatrix}. \tag{5.14}$$

For the equilibrium point $(n, w) = (\dfrac{\gamma w}{1+\sigma w} - \mu, w)$, J is given by (5.9). From Theorem 2.1, we have

$$\begin{aligned} F(J, D) &= \delta n + (-\beta\delta)(\frac{\gamma n}{(1+\sigma w)^2}) - (-1 + \rho n - 2wn) \\ &= \delta n - \frac{\beta\delta\gamma n}{(1+\sigma w)^2} + \frac{p}{w} + wn. \end{aligned}$$

If there is no cross-diffusion, *i.e.* $\beta = 0$, then $F(J, D) = \delta n + wn + p/w > 0$. So the equilibrium state is still stable with self-diffusion but not cross-diffusion as long as it is stable with respect to the ODE.

But if $\beta > 0$ large enough, $F(J, D) < 0$ is possible. Here we apply Theorems 2.1 and 2.3 to obtain the exact lower bound of β. Here we have $d_{12} = 0$ and $d_{21} = -\beta\delta$, from Theorem 2.3, $K_1 > 0$ if

$$\beta > \frac{(\delta n + pw^{-1} + wn)(1+\sigma w)^2}{\delta\gamma n}, \tag{5.15}$$

and $H_1 < 0$ is equivalent to

$$\beta > \frac{(\delta n + pw^{-1} + wn + 2\sqrt{\delta Det(J)})(1+\sigma w)^2}{\delta\gamma n}, \tag{5.16}$$

where $w > \rho$, $n = \dfrac{\gamma w}{1+\sigma w} - \mu$, $p = p(w)$ is given by (5.5) and $Det(J)$ is given by (5.11) Clearly (5.16) implies (5.15), hence we obtain

Theorem 5.2. *If* (5.12) *is satisfied, then* $(n, w) = (\dfrac{\gamma w}{1+\sigma w} - \mu, w)$ *is a constant equilibrium of* (5.13)*; it is stable with respect to the ODE system* (5.2)*, and it is also stable with respect to self-diffusion reaction system* (5.13) *with* $\beta = 0$*. If the cross-diffusion parameter* β *satisfies the inequality* (5.16)*, then the equilibrium point is unstable with respect to* (5.13)*.*

The cross-diffusion here is due to the suction of water by the roots of plant in the diffusive transport of the water. Our result here implies that the uniform vegetated state is stable without the dispersal of plant and the diffusion of water, and it is still stable with the dispersal of plant and the diffusion of water but the roots have only weak ability of sucking water (small β). However if the roots have strong ability of absorbing the soil water, the uniform vegetated state becomes unstable, and it implies the existence of non-uniform spatiotemporal patterns. Notice this result holds for the flat ground case with $v = 0$ in (5.1).

Given the parameters put forth in [32] ($\gamma = 1.6$, $\sigma = 1.6$, $\mu = 0.2$, $\rho = 1.5$, $\delta = 100$, $p = 1$), the equilibrium is $n = 0.4524689714$, $w = 1.173400570$, and the Jacobian and the diffusion matrix are

$$J = \begin{pmatrix} -.4524689714 & 0.0874371426 \\ 0.383231957 & -1.383151241 \end{pmatrix}$$

and

$$D = \begin{pmatrix} 1 & 0 \\ -100\beta & 100 \end{pmatrix}$$

respectively. The critical value in (5.16) is $\beta_* = 7.093389407$. Therefore with reasonable parameters in [32] except β (which is $\beta = 3$ in simulation of [32]), if $\beta > \beta_*$, a stripe pattern can occur and the uniform vegetated state is destabilized. If we choose $\beta = \beta_* + 1 = 8.093389407$, we can approximate the critical wave length of the pattern by using $k^* = 0.1206811798$.

6. Conclusions

We follow the ideas of Turing about diffusive instability but to consider the impact of cross-diffusion on the stability of a spatially uniform equilibrium in a biological or biochemical system. Cross-diffusion has been one of drivers of pattern formation in the biological systems. Examples are chemotaxis models [7, 8], preytaxis in predator-prey systems [6], and the vegetation-soil water interaction system considered in Section 4 [17, 32].

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References

[1] Y. S. Choi, Roger Lui and Yoshio Yamada, *Existence of global solutions for the Shigesada-Kawasaki-Teramoto model with weak cross-diffusion,* Discrete Contin. Dyn. Syst., 9(2003), 1193-1200.

[2] Y. S. Choi, Roger Lui and Yoshio Yamada, *Existence of global solutions for the Shigesada-Kawasaki-Teramoto model with strongly coupled cross-diffusion,* Discrete Contin. Dyn. Syst., 10(2004), 719-730.

[3] Rui Dilão, *Turing instabilities and patterns near a Hopf bifurcation,* Appl. Math. Comput., 164(2005), 391-414.

[4] Leah Edelstein-Keshet, *Mathematical models in biology,* The Random House/Birkhäuser Mathematics Series, Random House, Inc., New York, 1988.

[5] M. Farkas, *Two ways of modelling cross-diffusion. Proceedings of the Second World Congress of Nonlinear Analysts, Part 2 (Athens, 1996),* Nonlinear Anal., 30(1997), 1225-1233.

[6] Peter Kareiva and Garrett Odell, *Swarms of Predators Exhibit "Preytaxis " if Individual Predators Use Area-Restricted Search,* Amer. Naturalist, 130(1987), 233-270.

[7] E. F. Keller and L. A. Segel, *Initiation of slime mold aggregation viewed as an instability,* Jour. Theor. Biol., 26(1970), 399-415.

[8] E. F. Keller and L. A. Segel, *Model for chemotaxis,* Jour. Theor. Biol., 30(1971), 225-234.

[9] Sándor Kovàcs, *Turing bifurcation in a system with cross diffusion,* Nonlinear Anal., 59(2004), 567-581.

[10] Kousuke Kuto and Yoshio Yamada, *Multiple coexistence states for a prey-predator system with cross-diffusion,* J. Differential Equations, 197(2004), 315-348.

[11] Dung Le, *Cross diffusion systems on n spatial dimensional domains,* Indiana Univ. Math. J., 51(2002), 625-643.

[12] Dung Le, *Global existence for a class of strongly coupled parabolic systems,* Ann. Mat. Pura Appl., 185(2006), 133-154.

[13] Yi Li and Chunshan Zhao, *Global existence of solutions to a cross-diffusion system in higher dimensional domains,* Discrete Contin. Dyn. Syst., 12(2005), 185-192.

[14] Yuan Lou and Wei-Ming Ni, *Diffusion, self-diffusion and cross-diffusion,* J. Differential Equations, 131(1996), 79-131.

[15] Yuan Lou and Wei-Ming Ni, *Diffusion vs cross-diffusion: an elliptic approach,* J. Differential Equations, 154(1999), 157-190.

[16] Yuan Lou, Wei-Ming Ni and Yaping Wu, *On the global existence of a cross-diffusion system,* Discrete Contin. Dynam. Systems, 4(1998), 193-203.

[17] E. Meron, E. Gilad, J. von Hardenberg and M. Shachak, *Zarmi, Y., Vegetation Patterns along a rainfall gradient,* Chaos Solitons Fractals, 19(2004), 367-376.

[18] J. D. Murray, *Mathematical biology, Third edition. I. An introduction. Interdisciplinary Applied Mathematics,* 17, Springer-Verlag, New York, 2002; *II.*

Spatial models and biomedical applications, Interdisciplinary Applied Mathematics, 18, Springer-Verlag, New York, 2003.

[19] Kimie Nakashima and Yoshio Yamada, *Positive steady states for prey-predator models with cross-diffusion,* Adv. Differential Equations, 1(1996), 1099-1122.

[20] Wei-Ming Ni, *Diffusion, cross-diffusion, and their spike-layer steady states,* Notices Amer. Math. Soc., 45(1998), 9-18.

[21] Max Rietkerk, Stefan C. Dekker, Peter C. de Ruiter and Johan van de Koppel, *Self-Organized Patchiness and Catastrophic Shifts in Ecosystems,* Science, 305(2004), 1926-1929.

[22] Kimun Ryu and Inkyung Ahn, *Positive steady-states for two interacting species models with linear self-cross diffusions,* Discrete Contin. Dyn. Syst., 9(2003), 1049-1061.

[23] Razvan A. Satnoianu, Michael Menzinger and Philip K. Maini, *Turing instabilities in general systems,* J. Math. Biol., 41(2000), 493-512.

[24] Marten Scheffer, Steve Carpenter, Jonathan A. Foley, Carl Folke, and Brian Walkerk, *Catastrophic shifts in ecosystems,* Nature, 413(2001), 591-596.

[25] L.A. Segel and J.L. Jackson, *Dissipative structure: An explaination and an ecological example,* J. Theor. Biol., 37(1972), 545-559.

[26] Junping Shi, *Bifurcation in infinite dimensional spaces and applications in spatiotemporal biological and chemical models,* Front. Math. China, 4(2009), 407-424.

[27] Junping Shi and Xuefeng Wang, *On global bifurcation for quasilinear elliptic systems on bounded domains,* J. Differential Equations, 246(2009), 2788-2812.

[28] Nanako Shigesada, Kohkichi Kawasaki and Teramoto, Ei, *Spatial segregation of interacting species,* J. Theoret. Biol., 79(1979), 83-99.

[29] Phan Van Tuoc *Global existence of solutions to Shigesada-Kawasaki-Teramoto cross-diffusion systems on domains of arbitrary dimensions,* Proc. Amer. Math. Soc., 135(2007), 3933-3941.

[30] Phan Van Tuoc, *On global existence of solutions to a cross-diffusion system,* J. Math. Anal. Appl., 343(2008), 826-834.

[31] A.M. Turing, *The chemical basis of morphogenesis,* Phil. Trans. Royal Soc. London, B237(1952), 37-2.

[32] J. von Hardenberg, E. Meron, M. Shachak and Y. Zarmi, *Diversity of Vegetation Patterns and Desertification,* Phys. Rev. Lett., 87(2001), 198101.

[33] Xuefeng Wang, *Qualitative behavior of solutions of chemotactic diffusion systems: effects of motility and chemotaxis and dynamics,* SIAM J. Math. Anal., 31(2000), 535-560.