

Linear Stability of Delayed Reaction-Diffusion Systems

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Abstract

A common feature of pattern formation in both space and time is the destabilization of a stable equilibrium solution of an ordinary differential equation by adding diffusion or delay, or both. Here we study linear stability of general reaction-diffusion systems with off-diagonal time delays. We show that a delay-stable system cannot be destabilized by diffusion, and that a diffusion stable system is also stable with respect to delay, if the diffusion is sufficiently fast. A system with direct negative feedback which is strongly stable with respect to diffusion can be destabilized by off-diagonal delay.

Keywords: Reaction-diffusion system with delays; linear stability; Turing instability

1. Introduction

Since the seminal work of Turing in 1952 [1] it has been known that stable equilibrium solutions of ordinary differential equations can be destabilized in a spatial setting by the introduction of diffusion with different diffusion constants for different species. Later works have proposed specific reaction mechanisms exhibiting Turing instability, for instance the well-known activator-inhibitor model introduced originally by Gierer and Meinhardt [2]. The mechanism for Turing instability in general

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systems for n interacting species has been studied in [3, 4, 5, 6]. The typical results are necessary or sufficient conditions for a change in the spectrum of a matrix with respect to the imaginary axis. For more examples of possible reaction kinetics and sample applications, see the book by Murray [7].

Instability caused by time delays has also been studied in some recent works such as [8] for neural networks, [9] for general chemical networks and [10] for a model of human respiration. Commonly, instabilities caused by delays are associated with oscillations of the solutions of a system of delay differential equations. The linear stability of general delay systems has been studied in [11], where the authors give necessary and sufficient conditions for the null solution of a linear delay system to be asymptotically stable for any choice of off-diagonal delays. The interaction of delay and diffusion effects often occurs simultaneously, in particular in models inspired by biological problems. For some recent works that investigate both diffusion and delay together we refer to [12, 13, 14, 15, 16, 17, 18]. These works exhibit many different techniques to derive results, such as the use of Lyapunov functions, and a large number of applications, such as modeling of infectious diseases.

In this paper, we investigate the relationship between different kinds of linear stability of reaction-diffusion systems with delays. Haderler and Ruan in [13] showed that for 2-dimensional systems, stability with respect to off-diagonal delay implies stability with respect to diffusion. We extend this result from two dimensional reaction-diffusion systems with off-diagonal delays to general n -dimensional systems. Our results apply to systems with non-negative diffusion coefficients and non-negative off-diagonal delays. The theory on linear stability for delay systems developed in [11] is instrumental in many of the proofs.

In Section 2, we review some definitions of matrix stability. In Sections 3 and 4, we discuss stability and instability results for general reaction-diffusion systems and delay systems, respectively. Section 5 is devoted to the study of reaction-diffusion systems with delays. There we prove the main results of this paper about the relationships between the different stability concepts. Finally, in Section 6, we present an example illustrating the main results.

2. Matrix definitions and stability

The stability of equilibrium solutions of differential equations can often be described in terms of matrix stability. In this section we give the relevant definitions and review some results on matrix stability. Let $D = \text{diag}(d_1, \dots, d_n)$ be a diagonal matrix with entries d_i , $i = 1, 2, \dots, n$. We will write $D \geq 0$ if all $d_i \geq 0$ and $D > 0$ if all $d_i > 0$. We use the common notations like $x > 0$ to indicate inequalities for all components of a vector or a matrix.

Definition 1. A matrix $A \in \mathbb{R}^{n \times n}$ is called

- (a) *stable* if all eigenvalues of A have negative real part,
- (b) *strongly stable with respect to diffusion* if $A - D$ is stable for every non-negative diagonal matrix D ,
- (c) *excitable with respect to diffusion* if it is stable, but not strongly stable with respect to diffusion.

Matrices that are strongly stable with respect to diffusion have been characterized up to order $n = 3$ in [19].

Recall that a submatrix of a matrix is called a *principal submatrix* if rows and columns with the same indices are deleted. The determinant of a submatrix is called a *minor*, thus the determinant of a principal submatrix is a *principal minor*. If $I \subset \{1, \dots, n\}$ is a subset of indices, then $\det A[I]$ denotes the corresponding principal minor, which is formed by the rows and columns with indices in I . Let the complementary set to I be $I^c = \{1, \dots, n\} \setminus I$. Then $\det A[I^c]$ denotes the corresponding *complementary* principal minor, where the rows and columns with indices in I have been removed. The empty matrix is defined to have determinant 1. The quantity $(-1)^{|I|} \det A[I]$ where $|I|$ is the number of indices in I is called the *signed* principal minor.

The *companion matrix* of a matrix A is defined as in [20],

$$\mathcal{M}(A) = \begin{cases} -|a_{ij}| & \text{if } i \neq j \\ |a_{ii}| & \text{otherwise} \end{cases}.$$

We will need the following definitions throughout the paper. The second set of definitions is taken from [20].

Definition 2.

- (a) A $n \times n$ -matrix is called *irreducible*, if the directed graph of the corresponding adjacency matrix is strongly connected, that is, every vertex can be reached from every other vertex along a directed path.
- (b) A matrix A is called a *Z-matrix* if $a_{ij} \leq 0$ for $i \neq j$.
- (c) A matrix A is called a *M-matrix* if it is of the form $A = sI - B$ where $s \geq \varrho(B)$ and $B \geq 0$, [21]. Here ϱ denotes the spectral radius.
- (d) A matrix A is called an *H-matrix* if the companion matrix $\mathcal{M}(A)$ is an *M-matrix*.

- (e) A matrix A is called a *P-matrix* if all principal minors are positive. A matrix A is of class P_0 if all its principal minors are non-negative.

We note that the labeling of the matrix classes is not uniform across the literature. A Z -matrix for which all eigenvalues have positive real part is indeed a nonsingular M -matrix. We refer to the book by Fiedler [22] for many equivalent conditions for a matrix with non-positive off-diagonal entries to have only positive, respectively only non-negative principal minors, where these classes are denoted by \mathbf{K} , respectively \mathbf{K}_0 . The \mathbf{K} -matrices are also known as nonsingular M -matrices (see Definition 2 (c) above).

3. Reaction-diffusion systems and Turing Instability

Let $u = (u_1, \dots, u_n)$ denote, for example, the vector of non-negative species concentrations or populations. If variations in the concentration in space are neglected, the species interactions are given by the ordinary differential equation

$$\frac{du}{dt} = f(u), \quad (1)$$

where $f(u)$ is a smooth function. Let $A = \frac{\partial f_i}{\partial u_j}(u^*)$ be the Jacobi matrix of f , evaluated at the equilibrium point u^* . We assume that u^* is a hyperbolic equilibrium of (1), that is, A has only eigenvalues with nonzero real part. By linearizing (1) at u^* we obtain

$$\frac{du}{dt} = Au.$$

Now we assume that species concentrations $u_i(x, t)$, $i = 1, \dots, n$ vary within a bounded domain $\Omega \subset \mathbb{R}^k$ with smooth boundary, and that species i diffuses with rate constant $\tilde{d}_i \geq 0$. The reaction-diffusion system with the same dynamics as in equation (1) becomes

$$\frac{\partial u}{\partial t} = f(u) + \tilde{D}\Delta u, \quad x \in \Omega, \quad t \geq 0. \quad (2)$$

The system (2) has to be supplied with initial and boundary conditions. The initial conditions in applications are usually nonnegative $u(x, 0) = u_0(x) \geq 0$. For the latter, most often the flux across the boundary $\partial\Omega$ is prescribed. In the simplest case, there is no flux across the boundary. We will work with homogeneous Neumann boundary conditions,

$$\frac{\partial u}{\partial \nu} = 0, \quad \text{on } \partial\Omega,$$

where ν denotes the outward unit normal. The system corresponding to (2), linearized at the same equilibrium u^* of (1), is

$$\frac{\partial u}{\partial t} = Au + \tilde{D}\Delta u.$$

Using the Fourier ansatz [23], the characteristic equation becomes

$$\det(A - \mu\tilde{D} - \lambda I) = 0,$$

where $\mu > 0$ is an eigenvalue of the negative Laplacian with homogeneous Neumann boundary conditions. From now on we let $D = \mu\tilde{D}$ for fixed $\mu > 0$, where $d_i = \mu\tilde{d}_i$ for each i , for convenience. We say that a *Turing instability* occurs, if A is excitable with respect to diffusion.

The following is a sufficient condition for excitability with respect to diffusion and is proved in [6, Theorem 3.1].

Proposition 1. Let $A \in \mathbb{R}^{n \times n}$ be stable and suppose that A has a negative signed principal minor. Then A is excitable with respect to diffusion.

Proof. The result follows from the linearity of the determinant. First observe that

$$(-1)^n \det(A - D) = (-1)^n \det(A) + \sum_{k=1}^n (-1)^{n-k} \sum_{|I|=k} \left(\det A[I^c] \prod_{i \in I} d_i \right). \quad (3)$$

Let I be a set of indices for which $(-1)^{|I|} \det A[I] < 0$ (there could be more than one such set). We set the diffusion constants $d_i = 0$ for $i \in I$ and $d_i = d > 0$ for $i \in I^c$. Then

$$(-1)^n \det(A - D) = (-1)^n \det(A) + (-1)^{|I|} \det A[I] d^{n-|I|} + \text{lower powers of } d.$$

Note that since A is a (Hurwitz) stable matrix, $(-1)^n \det(A) > 0$ as the determinant is the product of the eigenvalues. Thus for d sufficiently large we can achieve $(-1)^n \det(A - D) < 0$, implying that the real part of an eigenvalue has moved into the right half plane. \square

It is further shown in [6, Theorem 3.2] that the complementary condition, namely that all signed principal minors are non-negative is necessary and sufficient for strong stability with respect to diffusion for $n \times n$ -matrices with $n \leq 3$. Satnoianu and van den Driessche [4] provide an example of a 4×4 -matrix with all signed principal minors positive that is excitable with respect to diffusion through a Hopf bifurcation.

The following proposition is a necessary condition for Turing instability arising from a zero eigenvalue of the matrix $A - D$ where $D \geq 0$ and D is not the zero matrix.

Proposition 2. Let $A \in \mathbb{R}^{n \times n}$ be a stable matrix. If $A - D$ has a zero eigenvalue for some $D \geq 0$, where at least one $d_i > 0$, then A has a negative signed principal minor of order $k < n$.

Proof. We use again (3). If $A - D$ has a zero eigenvalue for some $D \geq 0$ then $\det(A - D) = 0$. Since $(-1)^n \det(A) > 0$, it must be the case that at least one signed principal minor $(-1)^k \det A[I^c] < 0$ where $k < n$ for some choice of $d_i > 0$ for $i \in I$. \square

The following proposition shows that a Turing instability arising from a zero eigenvalue requires that the diffusion coefficients are not all equal. The result extends similar results on Turing instability from [7] to the case of $n > 2$, see also [3].

Proposition 3. If A is stable, then $A - dI$ has no zero eigenvalue for all $d \geq 0$.

Proof. This follows immediately from the fact that the characteristic polynomial of A , $\det(A - dI) = 0$ must have all its roots in the left half plane, while $d \geq 0$. \square

4. Stability and instability of delay differential equations

We now turn to the delay differential equation

$$\frac{du_i}{dt} = f_i(u_1(t - \tau_{i1}), \dots, u_n(t - \tau_{in})) \quad i = 1, 2, \dots, n \quad (4)$$

where $\tau_{ij} \geq 0$ are the delays $1 \leq i \neq j \leq n$ and $\tau_{ii} = 0$ for all i . After linearization at the equilibrium $u = u^*$, we obtain the linear system as in [11],

$$\frac{du_i}{dt} = \sum_{j=1}^n a_{ij} u_j(t - \tau_{ij}) \quad i = 1, \dots, n \quad (5)$$

where $a_{ij} = \frac{\partial f_i}{\partial u_j}(u^*)$. The corresponding characteristic polynomial to (5) is

$$\det \begin{bmatrix} a_{11} - \lambda & a_{12}e^{-\lambda\tau_{12}} & \dots \\ a_{21}e^{-\lambda\tau_{21}} & a_{22} - \lambda & \dots \\ \dots & \dots & \dots \end{bmatrix} = 0. \quad (6)$$

Definition 3. A matrix $A \in \mathbb{R}^{n \times n}$ is called *strongly stable with respect to delay* if the characteristic polynomial (6) has only roots with negative real parts for any off-diagonal choice of the delays, i.e., $\tau_{ij} \geq 0$, $1 \leq i \neq j \leq n$, and $\tau_{ii} = 0$, $1 \leq i \leq n$.

Note that this definition implies that A itself is stable.

Definition 4. Let \tilde{A} be the matrix obtained from A by replacing a_{ij} by $|a_{ij}|$ for all $i \neq j$. Then A is called *weakly diagonally dominant* if all principal minors of $-\tilde{A}$ are non-negative or $-\tilde{A}$ is a P_0 -matrix.

In the case of A having only negative entries on the diagonal, $-\tilde{A} = \mathcal{M}(A)$.

The following theorem characterizes strongly stable matrices with respect to delay and was proved in [11].

Theorem 1. The zero solution of system (5) is asymptotically stable for all choices of off-diagonal delays if and only if $a_{ii} < 0$ for all i , $\det A \neq 0$ and A is weakly diagonally dominant.

We extend Proposition 4 from [13] to the n -dimensional case when the delays are off-diagonal.

Proposition 4. Let A be an $n \times n$ -matrix where $a_{ii} < 0$ for all i . The following statements are equivalent

- (i) A is strongly stable with respect to delay,
- (ii) A is stable and weakly diagonally dominant.

Proof. (i) \Rightarrow (ii). The definition of strong stability with respect to delay includes the case $\tau_{ij} = 0$ for all i, j , hence A is stable. By Theorem 1, A is weakly diagonally dominant.

(ii) \Rightarrow (i). If A is stable, then $\det A \neq 0$. Since A is weakly diagonally dominant and $a_{ii} < 0$, again by Theorem 1, A is strongly stable with respect to delay. \square

5. Reaction-diffusion systems with delays

If reaction, diffusion and delay interact, various different models of delayed reaction-diffusion systems are possible. If we assume that the delay and diffusion act independently from each other, the general reaction-diffusion system with delays is

$$\frac{\partial u_i}{\partial t}(x, t) = f_i(u_1(t - \tau_{i1}), \dots, u_n(t - \tau_{in})) + d_i \Delta u_i, \quad i = 1, 2, \dots, n. \quad (7)$$

The corresponding linearized model is

$$\frac{\partial u_i}{\partial t}(x, t) = \sum_{j=1}^n a_{ij} u_j(t - \tau_{ij}) + d_i \Delta u_i$$

with characteristic polynomial (in λ)

$$\det \begin{bmatrix} a_{11} - d_1 - \lambda & a_{12}e^{-\lambda\tau_{12}} & \dots \\ a_{21}e^{-\lambda\tau_{21}} & a_{22} - d_2 - \lambda & \dots \\ \dots & \dots & \dots \end{bmatrix} = 0. \quad (8)$$

Next we restate [13, Proposition 7] for completeness.

Proposition 5. If the delayed reaction-diffusion system (7) exhibits a Turing instability for some set of diffusion rates and delays, then the non-delayed system (2) also exhibits Turing instability for the same set of diffusion rates.

Proposition 5 shows that Turing instability arising from zero eigenvalue occurs regardless of the presence of delay. Before proving the main theorem we need the following result.

Proposition 6. Let A be strongly stable with respect to delay and assume that $\det(\mathcal{M}(A)) \neq 0$. Then $\det(A - D) \neq 0$ for any diffusion matrix $D \geq 0$.

Proof. Since A is strongly stable with respect to delays, it follows $\det(A) \neq 0$. We want to show that $\det(A - D) \neq 0$. By Lemma 4 from [11], it follows that $A_{ii} < 0$ for all i . Thus in this case $-A = \mathcal{M}(A)$. Let D be a diagonal matrix with non-negative entries and we define $r(s) = \det(A - sD)$ for $s \geq 0$. By the linearity of the determinant we have

$$\begin{aligned} \frac{d}{ds}r(s) = & - \sum_{i=1}^n d_i \det(A[\{i\}^c]) + 2s \sum_{i,j=1, i \neq j}^n d_i d_j \det(A[\{i, j\}^c]) \\ & - 3s^2 \sum_{i,j,k=1, i \neq j \neq k \neq i}^n d_i d_j d_k \det(A[\{i, j, k\}^c]) + \dots + ns^{n-1}(-1)^n \prod_{i=1}^n d_i. \end{aligned} \quad (9)$$

By assumption $\mathcal{M}(A)$ has non-negative principal minors and no eigenvalue zero. Thus the spectrum of $\mathcal{M}(A)$ lies in the positive half plane, and so $\mathcal{M}(A)$ is an M -matrix. This implies that $-A$ is an H -matrix. By [20, GENERATING METHOD 4.11], it follows that $-A$ is a P -matrix, that is, all its principal minors are positive. The sign of a complementary minor of $-(-A)(I)$ is $(-1)^{n-|I|}$. Since all $d_i \geq 0$, all expressions in equation (9) have the same sign, and the function r is monotone increasing if n is even and monotone decreasing if n is odd (and this is strict unless all d_i are zero). Since $r(0) = \det A$ has the sign $(-1)^n$, the function r has no zero. \square

We wish to remark that a singular matrix in the image of the operator \mathcal{M} can be the image of both singular and non-singular matrices [24]. The assumption that $\det \mathcal{M}(A) \neq 0$ can therefore not be omitted. We now state the main theorem on delay stability for reaction-diffusion system with delays.

Theorem 2. Let A be strongly stable with respect to delay and assume that $\det(\mathcal{M}(A)) \neq 0$. Then $A - D$ is strongly stable with respect to delay for any diagonal matrix $D \geq 0$. In other words, if (4) is strongly stable with respect to delays, then so is (7).

Proof. We use again [11, Theorem 1]. First we consider the case that A is irreducible. Since A is strongly stable, by Proposition 4, it is weakly diagonally dominant. By [25, Theorem 5.8], there exists a vector $c > 0$ such that $\tilde{A}c \leq 0$. We have

$$a_{ii}c_i + \sum_{j \neq i} |a_{ij}|c_j \leq 0 \quad i = 1, 2, \dots, n.$$

It follows that

$$(a_{ii} - d_i)c_i + \sum_{j \neq i} |a_{ij}|c_j \leq 0 \quad i = 1, 2, \dots, n$$

is also satisfied for any $d_i \geq 0$ and the same $c > 0$. By Theorem 5.4 and Definition 5.2. in [25] it follows that $-(\widetilde{A - D}) = -\tilde{A} + D$ has non-negative principal minors of all orders. Therefore $A - D$ is weakly diagonally dominant.

The case of a reducible matrix follows as in the second part of the proof of Lemma 1 in [11] applied to the matrix $A - D$. By relabeling the indices a reducible matrix $A - D$ can be represented as an upper block triangular matrix with irreducible blocks (or possibly null 1×1 -blocks) along the diagonal [26]. Index relabeling is done by multiplying $A - D$ with permutation matrices, which does not change the principal minors of $A - D$. Therefore each irreducible block is weakly diagonally dominant and the result follows using the argument above.

By Proposition 6 it follows that $\det(A - D) \neq 0$ for any $D \geq 0$. □

Corollary 1. If A is strongly stable with respect to delay and $\det(\mathcal{M}(A)) \neq 0$, then A is strongly stable with respect to diffusion.

Proof. For any diagonal matrix $D \geq 0$, $A - D$ is strongly stable with respect to delay. Hence by Proposition 4, $A - D$ is stable. Thus A is strongly stable with respect to diffusion. □

Next we consider the case that A is strongly stable with respect to diffusion.

Theorem 3. If A is strongly stable with respect to diffusion, then $A - D$ is strongly stable with respect to delay if $d_i > 0$, $i = 1, 2, \dots, n$ are sufficiently large.

Proof. The proof follows again from Theorem 1 above. First we have that $a_{ii} - d_i < 0$ if $d_i > 0$ are sufficiently large. Since A is strongly stable with respect to diffusion, it follows that $\det(A - D) \neq 0$. It remains to be shown that all principal minors of $-\tilde{A} + D$ are non-negative. This follows similarly as above by showing that

$$-a_{ii} + d_i > \sum_{j \neq i} |a_{ij}|, \quad i = 1, 2, \dots, n \quad (10)$$

for sufficiently large $d_i > 0$. That is, $-\tilde{A} + D$ is strictly diagonally dominant. Thus by Theorem 5.1. in [22] with a choice of the vector $c = (1, 1, \dots, 1)$ it follows that all principal minors of $-\tilde{A} + D$ are positive. \square

In the next proposition we show that off-diagonal delays can destabilize a diffusion stable system.

Proposition 7. Let A be strongly stable with respect to diffusion and $a_{ii} < 0$ for all i . Suppose that $\det(-\tilde{A} + D) < 0$ for some D . Then there exist off-diagonal delays such that the characteristic polynomial (8) has a root with a positive real part.

Proof. The proof follows the proof of Lemma 2 in [11]. We let

$$F_\epsilon(z) = \det \begin{bmatrix} a_{11} - d_1 - z\epsilon & a_{12}e^{-z\eta_{12}} & \dots \\ a_{21}e^{-z\eta_{21}} & a_{22} - d_2 - z\epsilon & \dots \\ \dots & \dots & \dots \end{bmatrix}.$$

where $\eta_{ij} = 1/2$ for $a_{ij} < 0$ and $\eta_{ij} = 1$ for $a_{ij} \geq 0$ and $\epsilon > 0$ is small. We let $z = x + 2\pi i$ and

$$F_0(x) = \det \begin{bmatrix} a_{11} - d_1 & |a_{12}|e^{-x\eta_{12}} & \dots \\ |a_{21}|e^{-x\eta_{21}} & a_{22} - d_2 & \dots \\ \dots & \dots & \dots \end{bmatrix}.$$

By assumption $\det(-\tilde{A} + D) = (-1)^n F_0(0) < 0$ and

$$\lim_{x \rightarrow \infty} (-1)^n F_0(x) = (-1)^n (a_{11} - d_1) \dots (a_{nn} - d_n) > 0.$$

By the Intermediate Value Theorem, there exists $\bar{x} > 0$ such that $F_0(\bar{x}) = 0$. Thus $\bar{z} = \bar{x} + 2\pi i$ is a zero of $F_0(z)$. By Rouché's Theorem $F_\epsilon(z)$ has a root $\bar{z}(\epsilon)$ since $F_0(z)$ has a root \bar{z} . It follows that $\lambda = \bar{z}(\epsilon)\epsilon$ where $\Re(\lambda) > 0$ and $\tau_{ij} = \frac{\eta_{ij}}{\epsilon}$ satisfy (8). \square

6. Example

We consider as an example a simplification of a reaction-diffusion system investigated in Satnoianu *et al.* [5] for Turing instability. We add delays to the three-dimensional reaction-diffusion system and consider the system

$$\begin{aligned}\frac{\partial u_1}{\partial t} &= \frac{1}{u_2^a(t - \tau_{12})} - u_1 + d_1 \Delta u_1, \\ \frac{\partial u_2}{\partial t} &= u_3(t - \tau_{23}) - u_2 + d_2 \Delta u_2, \\ \frac{\partial u_3}{\partial t} &= u_1(t - \tau_{31}) - u_3 + d_3 \Delta u_3.\end{aligned}\tag{11}$$

where $a > 0$. We can think of this model as of a chain of “activations” $u_1 \nearrow u_3 \nearrow u_2$ and an “inhibition” $u_2 \searrow u_1$, provided that $a > 0$. Here an arrow “ \nearrow ” indicates a positive feedback (activation) and an arrow “ \searrow ” indicates a negative feedback (inhibition). The system has a constant equilibrium $u^* = (1, 1, 1)$.

The Jacobian A_a of the kinetic system at the equilibrium $(1, 1, 1)$ is

$$A_a = \begin{bmatrix} -1 & -a & 0 \\ 0 & -1 & 1 \\ 1 & 0 & -1 \end{bmatrix}.$$

This matrix is nonsingular and weakly diagonally dominant for $a \in (0, 1]$. Thus A_a is strongly stable with respect to delay. If $a \neq 1$, then $\det(\mathcal{M}(A)) \neq 0$. By Theorem 2, it follows that then $A_a - D$ is also strongly stable with respect to delay for any $D \geq 0$, $a \neq 1$. By Corollary 1, A_a is also strongly stable with respect to diffusion for $a \in (0, 1)$. If we begin with the pure delay system, i.e. $d_i = 0$, $i = 1, 2, 3$ in (11), the equilibrium $(1, 1, 1)$ is asymptotically stable for any values of the delays by Theorem 1. If at least one positive diffusion term is added, the equilibrium $(1, 1, 1)$ remains stable for any values of the delays by Theorem 2.

It can be verified that the negative Jacobian $-A_a$ at the equilibrium $(1, 1, 1)$ is a P -matrix for $a > 0$. Also, A_a is a stable matrix as long as $a < 8$. It follows by [6, Theorem 3.2], that the matrix A_a is strongly stable with respect to diffusion if $0 < a < 8$. Thus no Turing instability can exist for any diffusion matrix $D \geq 0$ if $0 < a < 8$. On the other hand, $\det(-\tilde{A}_a) = 1 - a$ and A_a is not strongly stable with respect to delay if $a > 1$. By Theorem 3, $A_a - D$ where $1 < a < 8$ will be strongly stable with respect to delay if the diffusion rates $d_i > 0$ are sufficiently large. In particular the diffusion rates d_i , $i = 1, 2, 3$ have to satisfy the inequality (10), or, $d_1 > 7$ and $d_2 > 0$, $d_3 > 0$. In this case initially all delays in (11) are set to zero

and we start with a reaction-diffusion system with asymptotically stable equilibrium $(1, 1, 1)$ if $0 < a < 8$. If the delays are included in the model and $1 < a < 8$, the equilibrium remains stable (with respect to the delays) only if the diffusion rates are sufficiently large.

7. Conclusion

In this paper we have investigated the interplay between space diffusion and time delays and the effects on the stability of equilibrium solutions of a reaction-diffusion system with delays. We have extended the results of [13] on stability of reaction-diffusion systems with delays from two-dimensional to n -dimensional systems. All stability results, shown for two-dimensional systems remain true in the general case, although the requirements for stability on the Jacobian matrix appear to be slightly different. However, in [13] the Jacobian matrix is required to satisfy certain inequalities for strong stability with respect to delay that make it in effect weakly diagonally dominant.

The example (and the theory used) show that an asymptotically stable equilibrium of a delay system maintains its stability if diffusion is added to the model (Theorem 2). Therefore diffusion cannot destabilize a delay stable equilibrium. On the other hand, an equilibrium that is stable as a solution of a reaction-diffusion system, may not be stable as a solution of the reaction-diffusion system with added delays. Such a stable equilibrium of a reaction-diffusion system remains stable if delays are added to the system, only if the diffusion rates are large enough (Theorem 3). For the n -dimensional system it is not possible to compute explicitly the delays that can bring instability as for the two-dimensional system, in contrast to [13, Proposition 9].

Acknowledgments

We are grateful for financial support from the Simons Foundation grant “Collaboration on Mathematical Biology” (awarded to PH) during a work visit of MM to the University of Wisconsin - Milwaukee. MM thanks the Bulgarian Academy of Sciences in Sofia, Bulgaria for its hospitality during her sabbatical year. We appreciate the valuable comments of two unknown readers.

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