九州大学学術情報リポジトリ Kyushu University Institutional Repository

Behavior of solutions to an activator-inhibitor system with basic production terms

鈴木,香奈子 東北大学国際高等融合領域研究所

高木,泉 東北大学大学院理学研究科

 $\verb|https://hdl.handle.net/2324/13287|$

出版情報: COE Lecture Note. 14, pp.49-59, 2008-09-01. Faculty of Mathematics, Kyushu

University バージョン: 権利関係: Proceedings of the Czech-Japanese Seminar in Applied Mathematics 2008 Takachiho / University of Miyazaki, Miyazaki, Japan, September 1-7, 2008 pp. 49-59

BEHAVIOR OF SOLUTIONS TO AN ACTIVATOR-INHIBITOR SYSTEM WITH BASIC PRODUCTION TERMS

KANAKO SUZUKI¹ AND IZUMI TAKAGI²

Abstract. We consider an activator-inhibitor system proposed by A. Gierer and H. Meinhardt in 1972, which is a model of the transplantation experiment on hydra. Nontrivial spatial patterns of the activator are expected to emerge in the system, and it is postulated that a change in cells or tissues takes place in the region where the activator concentration is high. But the activator concentration may fail to form spatial patterns if the system does not have a positive basic production term for the activator. We study this phenomenon to understand a role of the basic production terms in pattern formation.

Key words. activator-inhibitor system, pattern formation

AMS subject classifications. 35K45, 35K57

1. Introduction and Statement of Results. In the celebrated paper [11], A. M. Turing found that the reaction between two chemicals with different diffusion rates may cause the destabilization of the spatially homogeneous state, thus leading to the formation of nontrivial spatial structure. Developing Turing's idea, A. Gierer and H. Meinhardt ([2]) proposed a system consisting of a slowly diffusing activator and a rapidly diffusing inhibitor. They assumed that a change in cells or tissue takes place in the region where the activator concentration is high. Suppose that the activator and the inhibitor fill a bounded domain Ω in \mathbb{R}^N with smooth boundary $\partial\Omega$ and that there is no flux through the boundary. Let A(x,t) and H(x,t) denote the respective concentrations of the activator and the inhibitor at position $x \in \overline{\Omega}$ and time $t \ge 0$. Let ν denote the unit outer normal vector to $\partial\Omega$ and $\Delta = \sum_{i=1}^{N} \partial^2/\partial x_i^2$ be the Laplace operator in \mathbb{R}^N . In this paper we consider the following activator-inhibitor system proposed by Gierer and Meinhardt:

$$\frac{\partial A}{\partial t} = \varepsilon^2 \Delta A - A + \frac{A^p}{H^q} + \sigma_a(x), \tag{1.1}$$

$$\tau \frac{\partial H}{\partial t} = D\Delta H - H + \frac{A^r}{H^s} + \sigma_h(x), \tag{1.2}$$

for $x \in \Omega$ and t > 0, subject to the boundary condition and the initial condition

$$\frac{\partial A}{\partial \nu} = \frac{\partial H}{\partial \nu} = 0 \quad \text{for } x \in \partial \Omega, \ t > 0,$$

$$A(x,0) = A_0(x), \quad H(x,0) = H_0(x) \quad \text{for } x \in \Omega.$$
(1.3)

$$A(x,0) = A_0(x), \quad H(x,0) = H_0(x) \quad \text{for } x \in \Omega.$$
 (1.4)

Here ε , D and τ are positive constants. The exponents p > 1, q > 0, r > 0, $s \ge 0$ satisfy

$$0 < \frac{p-1}{r} < \frac{q}{s+1}. (1.5)$$

¹Institute for International Advanced Interdisciplinary Research, Tohoku University, Japan.

 $^{^2{\}rm Mathematical}$ Institute, Tohoku University, Japan.

Moreover, We assume

$$\sigma_a, \ \sigma_h \in C^{\beta}(\overline{\Omega}), \quad \text{and} \quad \sigma_a(x) \ge 0, \ \sigma_h(x) \ge 0 \text{ on } \overline{\Omega}$$
 (1.6)

and concerning the initial data we assume

$$A_0, H_0 \in C^{2+\beta}(\overline{\Omega}), \quad A_0(x) > 0, H_0(x) > 0 \text{ on } \overline{\Omega} \text{ and }$$
 (1.7)

$$\frac{\partial A_0}{\partial \nu} \bigg|_{\partial \Omega} = \frac{\partial H_0}{\partial \nu} \bigg|_{\partial \Omega} = 0 \tag{1.8}$$

where $0 < \beta < 1$. The terms $\sigma_a(x)$ and $\sigma_h(x)$ are called basic production terms, which represent the amount of activator and inhibitor produced by cell in a unit time, respectively.

From a mathematical point of view, one of the fundamental questions is whether the initial-boundary value problem has a solution for all t>0 or not. There have appeared several results on this question (see, e.g., [9], [7], [12], [5], [4]). In particular, under the assumption that $\min_{x\in\overline{\Omega}}\sigma_a(x)>0$ and (p-1)/r<2/(N+2), Masuda and Takahashi [7] proved not only that the solution exists for all t>0 but also that, as $t\to +\infty$, the set $\{(A(x,t),H(x,t))\in\mathbb{R}^2\mid x\in\Omega\}$ is confined in a fixed rectangle which is independent of the initial data. On the other hand, Li, Chen and Qin [5] proved that the solution exists for all t>0 if $\min_{x\in\overline{\Omega}}\sigma_a(x)>0$ and p-1< r. We studied the initial-boundary value problem (1.1)–(1.4) in the case $\min_{x\in\overline{\Omega}}\sigma_a(x)=0$ in [10]. The following Theorems 1.1–1.3 complement the results by [7] and [5], and give us a complete understanding of the global existence and the boundedness of solutions in the case p-1< r. Jiang [4] obtained independently some results similar to ours on the global existence and boundedness of solutions.

THEOREM 1.1. Assume, in addition to (1.5), that

$$p - 1 < r \tag{1.9}$$

and, in addition to (1.6), that

$$\max_{x \in \overline{\Omega}} \sigma_a(x) > 0.$$

Then the initial-boundary value problem (1.1)–(1.4) has a unique solution for all t > 0. Moreover, there exist positive constants m_a , m_h , M_a , M_h , independent of the initial data $(A_0(x), H_0(x))$, such that

$$\begin{split} m_a & \leq \liminf_{t \to +\infty} \min_{x \in \overline{\Omega}} A(x,t) \leq \limsup_{t \to +\infty} \max_{x \in \overline{\Omega}} A(x,t) \leq M_a, \\ m_h & \leq \liminf_{t \to +\infty} \min_{x \in \overline{\Omega}} H(x,t) \leq \limsup_{t \to +\infty} \max_{x \in \overline{\Omega}} H(x,t) \leq M_h. \end{split}$$

Theorem 1.2. Assume that (1.9) is satisfied in addition to (1.5). Moreover, suppose that

$$\sigma_a(x) \equiv 0$$
 and $\max_{x \in \overline{\Omega}} \sigma_h(x) > 0$.

Then the initial-boundary value problem (1.1)–(1.4) has a unique solution for all t > 0. Moreover, there exist positive constants m_h , M_a , M_h , which are independent of the initial data $(A_0(x), H_0(x))$, such that

$$e^{-t} \min_{x \in \overline{\Omega}} A_0(x) \le A(x,t)$$
 for all $x \in \overline{\Omega}$, $t > 0$ and $\limsup_{t \to +\infty} \max_{x \in \overline{\Omega}} A(x,t) \le M_a$,
$$m_h \le \liminf_{t \to +\infty} \min_{x \in \overline{\Omega}} H(x,t) \le \limsup_{t \to +\infty} \max_{x \in \overline{\Omega}} H(x,t) \le M_h.$$

Theorem 1.3. Assume that (1.9) is satisfied in addition to (1.5). Moreover, suppose that

$$\sigma_a(x) \equiv 0$$
 and $\sigma_h(x) \equiv 0$.

Then the initial-boundary value problem (1.1)–(1.4) has a unique solution for all t > 0. Moreover, there are positive constants λ and μ which are dependent only on p, q, r, s and τ , and a positive constant C depending on initial data $(A_0(x), H_0(x))$ such that

$$e^{-t} \min_{x \in \overline{\Omega}} A_0(x) \le A(x, t) \le Ce^{\lambda t},$$

$$e^{-t/\tau} \min_{x \in \overline{\Omega}} H_0(x) \le H(x, t) \le Ce^{\mu t}$$

for all t > 0 and $x \in \overline{\Omega}$.

As we mentioned above, it is assumed that a change in cells or tissue takes place in the region where the activator concentration is high. Therefore, nontrivial spatial patterns of the activator are expected to emerge. But in some numerical simulations, it is observed that a solution starting from an almost uniform initial value develops localization in the activator concentration for a while, but it oscillates and eventually converges uniformly to the trivial state $u \equiv 0$. In fact, Wu and Li [12] proved that if $\sigma_a(x) \equiv 0$ and $\sigma_h(x) \equiv 0$ and if $\tau > q/(p-1)$, then there are solutions of (1.1)–(1.4) such that $(A(x,t),H(x,t)) \to (0,0)$ uniformly on $\overline{\Omega}$ as $t \to +\infty$. We call such a phenomenon the collapse of patterns. Theorem 1.1 implies patterns never collapse as long as σ_a is nontrivial, whereas for lack of uniform lower bound for the activator Theorem 1.2 suggests that patterns in the activator can collapse even though $\sigma_h > 0$. Hence, the activator concentration may fail to form spatial patterns if the system does not have a positive basic production term for the activator. In the following section, we will study this phenomenon to understand a role of the basic production terms in pattern formation.

Some remarks are in order. First, for the systematic study of global behavior of solutions of (1.1)–(1.4), it is important to know the behavior of solutions of the following kinetic system:

$$\frac{du}{dt} = -u + \frac{u^p}{v^q} + \sigma_a,\tag{1.10}$$

$$\tau \frac{dv}{dt} = -v + \frac{u^r}{v^s} + \sigma_h. \tag{1.11}$$

Here σ_a and σ_h are both nonnegative constants. When $\sigma_a = 0$ and $\sigma_h = 0$, we have obtained the complete understanding of all the behavior of solution orbits ([8]). The case $\sigma_a > 0$ is treated in an on-going project.

Second, all the three theorems assume that p-1 < r, which is important to rule out the occurrence of finite time blow-up of solutions. Indeed, it has been shown in

[5] and [8] that if p-1>r, then there exist solutions of (1.1)-(1.4) with $\sigma_a(x)\equiv$ $\sigma_h(x) \equiv 0$ which blow up in finite time.

Third, in [8] it is proved that if $p-1 \le r$ and $q \ge s+1$, then some solutions of (1.1)-(1.4) with $\sigma_a(x) \equiv \sigma_h(x) \equiv 0$ exist for all t > 0, but they are unbounded. By virtue of Theorem 1.1 all solutions are bounded if σ_a is nontrivial.

2. Collapse of Patterns. The activator concentration may fail to form spatial or spatio-temporal patterns if the system (1.1)-(1.4) does not have a positive basic production term for the activator. In order to understand the mechanism of this phenomenon, we consider the behavior of a solution of the following system as $t \rightarrow$ $+\infty$:

$$\frac{\partial A}{\partial t} = \varepsilon^2 \Delta A - A + \frac{A^p}{H^q},\tag{2.1}$$

$$\tau \frac{\partial H}{\partial t} = D\Delta H - H + \frac{A^r}{H^s} + \sigma_h(x), \qquad (2.2)$$

for $x \in \Omega$ and t > 0, subject to the boundary condition and the initial condition

$$\frac{\partial A}{\partial \nu} = \frac{\partial H}{\partial \nu} = 0 \quad \text{for } x \in \partial \Omega, \ t > 0,$$

$$A(x,0) = A_0(x), \quad H(x,0) = H_0(x) \quad \text{for } x \in \Omega.$$
(2.3)

$$A(x,0) = A_0(x), \quad H(x,0) = H_0(x) \quad \text{for } x \in \Omega.$$
 (2.4)

For the initial data, we assume (1.7) and (1.8). The exponents satisfy (1.5) and we assume

$$\sigma_h(x) \ge 0$$
 on $\overline{\Omega}$.

There exists a solution of (2.1)–(2.4) for all t > 0 by Theorem 1.2 if p - 1 < r. The main result of this paper is stated as follows:

Theorem 2.1. Let τ satisfy $\tau > q/(p-1)$ and assume that the initial data satisfies

$$\left(\min_{x\in\overline{\Omega}}H_0(x)\right)^q>\frac{p-1}{p-1-\frac{q}{\tau}}\left(\max_{x\in\overline{\Omega}}A_0(x)\right)^{p-1}.$$

Then the solution (A(x,t), H(x,t)) of (2.1)–(2.4) satisfies

$$0 < \max_{x \in \overline{\Omega}} A(x,t) \le Ce^{-t}, \quad \max_{x \in \overline{\Omega}} |H(x,t) - z(x)| \le Ce^{-t/\tau},$$

in which C is a positive constant depending on $(A_0(x), H_0(x))$, and z(x) is a solution of the problem

$$D\Delta z - z + \sigma_h(x) = 0 \quad \text{for } x \in \Omega,$$
 (2.5)

$$\frac{\partial z}{\partial u} = 0 \quad on \ \partial \Omega. \tag{2.6}$$

It is to be noted that in contrast to Theorems 1.2 and 1.3 we do not assume any further condition other than (1.5) in Theorem 2.1, yet we have a bounded solution for all t > 0 by restricting initial data.

To prove Theorem 2.1 we follow the approach due to [12].

2.1. Boundedness of solutions.

2.1.1. Lower bounds. First, we estimate A(x,t) and H(x,t) from blow. Let $\underline{\mathbf{u}}(x,t)$ be a solution of the initial-boundary value problem:

$$\frac{\partial \underline{\mathbf{u}}}{\partial t} = \varepsilon^2 \Delta \underline{\mathbf{u}} - \underline{\mathbf{u}},\tag{2.7}$$

$$\underline{\mathbf{u}}(x,0) = A_0(x), \tag{2.8}$$

$$\frac{\partial \underline{\mathbf{u}}}{\partial \nu}\Big|_{\partial \Omega} = 0, \tag{2.9}$$

and v(t) be a solution of

$$\tau \frac{d\underline{\mathbf{v}}}{dt} = -\underline{\mathbf{v}} + \min_{x \in \overline{\Omega}} \sigma_h(x), \qquad (2.10)$$
$$\underline{\mathbf{v}}(0) = \min_{x \in \overline{\Omega}} H_0(x). \qquad (2.11)$$

$$\underline{\mathbf{v}}(0) = \min_{x \in \overline{\Omega}} H_0(x). \tag{2.11}$$

The following lemma is obtained:

LEMMA 2.2. The solution (A(x,t), H(x,t)) of (2.1)–(2.4) satisfies

$$A(x,t) \ge \underline{\mathbf{u}}(x,t), \quad H(x,t) \ge \underline{\mathbf{v}}(t)$$

for all t > 0, $x \in \Omega$.

This lemma can be proved easily by using the maximum principle. Moreover, we see that the solution (2.7)–(2.9) satisfies

$$e^{-t} \min_{x \in \overline{\Omega}} A_0(x) \le \underline{\mathbf{u}}(x,t) \le e^{-t} \max_{x \in \overline{\Omega}} A_0(x)$$

for all $x \in \overline{\Omega}$, t > 0 and the solution (2.10)–(2.11) is given by

$$\underline{\mathbf{v}}(t) = e^{-t/\tau} \min_{x \in \overline{\Omega}} H_0(x) + \min_{x \in \overline{\Omega}} \sigma_h(x) (1 - e^{-t/\tau}).$$

2.1.2. Upper bounds. In order to derive an estimate of A(x,t) from above, we need the following lemma. For simplicity, we put $\psi = \min_{x \in \overline{\Omega}} H_0(x)$.

LEMMA 2.3. Let τ satisfy $\tau > q/(p-1)$ and m_0 be a positive number satisfying

$$m_0^{p-1} < \left(1 - \frac{q}{(p-1)\tau}\right)\psi^q.$$

Then the problem

$$\frac{dm}{dt} = -m + \frac{m^p}{\underline{\mathbf{v}}^q},\tag{2.12}$$

$$m(0) = m_0 (2.13)$$

has a unique solution for all t > 0 and there exists a positive constant C such that $m(t) \le Ce^{-t}$.

Proof. Put $M(t) = 1/m(t)^{p-1}$. Differentiating M(t) in t, we have

$$\begin{split} \frac{dM}{dt} &= -(p-1)\frac{1}{m(t)^p}\frac{dm}{dt} \\ &= -(p-1)\frac{1}{m(t)^p}\left(-m + \frac{m^p}{\underline{\mathbf{v}}^q}\right) \\ &= (p-1)M - (p-1)\frac{1}{\underline{\mathbf{v}}^q}. \end{split}$$

Since $M(0) = 1/m_0^{p-1}$, we obtain that

$$M(t) = \frac{1}{m_0^{p-1}} e^{(p-1)t} - (p-1) \int_0^t \frac{e^{(p-1)(t-\xi)}}{\underline{\mathbf{v}}(\xi)^q} d\xi.$$

It follows from (2.10) that $\underline{\mathbf{v}}(t) \geq e^{-t/\tau}\underline{\mathbf{v}}(0)$. Thus

$$\begin{split} M(t) &\geq \frac{1}{m_0^{p-1}} e^{(p-1)t} - \frac{p-1}{\underline{v}(0)^q} \int_0^t e^{(p-1)(t-\xi) + \frac{q}{\tau}\xi} \, d\xi \\ &= \left\{ \frac{1}{m_0^{p-1}} + \frac{p-1}{\underline{v}(0)^q} \cdot \frac{1 - e^{\left[\frac{q}{\tau} - (p-1)\right]t}}{\frac{q}{\tau} - (p-1)} \right\} e^{(p-1)t}. \end{split}$$

If

$$\frac{1}{m_0^{p-1}} > \frac{p-1}{\underline{v}(0)^q} \cdot \frac{1}{p-1 - \frac{q}{\tau}},$$

then we see that M(t) > 0 for all t > 0. Therefore m(t) exists for all t > 0 and there is a positive constant C such that $m(t) \le Ce^{-t}$. \square

From Lemma 2.3, if $\tau > q/(p-1)$ and

$$\left(\max_{x\in\overline{\Omega}}A_0(x)\right)^{p-1} < \left(1 - \frac{q}{(p-1)\tau}\right) \left(\min_{x\in\overline{\Omega}}H_0(x)\right)^q,\tag{2.14}$$

then the following problem

$$\frac{d\bar{\mathbf{u}}}{dt} = -\bar{\mathbf{u}} + \frac{\bar{\mathbf{u}}^p}{\underline{\mathbf{v}}^q},\tag{2.15}$$

$$\bar{\mathbf{u}}(0) = \max_{x \in \overline{\Omega}} A_0(x) \tag{2.16}$$

has a solution $\bar{\mathbf{u}}(t)$ for all t>0 and $\bar{\mathbf{u}}(t)\leq Ce^{-t}$ for some C>0. Applying the maximum principle, we see that $A(x,t)\leq \bar{\mathbf{u}}(t)$ for all $x\in\Omega,\,t>0$, that is

$$A(x,t) < Ce^{-t}. (2.17)$$

Next, we consider the initial value problem

$$\tau \frac{d\bar{\mathbf{v}}}{dt} = -\bar{\mathbf{v}} + \frac{\bar{\mathbf{u}}^r}{\bar{\mathbf{v}}^s} + \sigma_1, \tag{2.18}$$

$$\bar{\mathbf{v}}(0) = \max_{x \in \bar{\Omega}} H_0(x), \tag{2.19}$$

where we put $\sigma_1 = \max_{x \in \overline{\Omega}} \sigma_h(x)$. Because of (2.17), the right-hand side of (2.18) is estimated as follows:

$$\tau \frac{d\bar{\mathbf{v}}}{dt} \le -\bar{\mathbf{v}} + \frac{Ce^{-rt}}{\bar{\mathbf{v}}^s} + \sigma_1. \tag{2.20}$$

Multiplying the both sides of (2.20) by $\bar{\mathbf{v}}^s$ and putting $\bar{\mathbf{v}}^{s+1} = W$, we have that

$$\frac{dW}{dt} \le -\frac{s+1}{\tau}W + \frac{\sigma_1(s+1)}{\tau}W^{s/(s+1)} + \frac{C(s+1)}{\tau}e^{-rt}.$$
 (2.21)

Using Lemma 2.5 below due to Masuda and Takahashi [7], we obtain easily the following lemma:

Lemma 2.4. Suppose that $\tau > q/(p-1)$ and (2.14) is satisfied. Then the initial value problem (2.18)–(2.19) has a unique solution $\bar{\mathbf{v}}(t)$ for all t>0. Moreover, it satisfies that

$$\limsup_{t \to +\infty} \bar{\mathbf{v}}(t) \le \sigma_1.$$

To state Lemma 2.5, some preparations are needed. Let $L^+(0,T)$ be the set of all integrable functions $f(t) \geq 0$ on (0,T) such that the quantity

$$K[f] = \sup_{0 < t < T} \int_0^t e^{-\mu(t-\xi)} f(\xi) \, d\xi \tag{2.22}$$

is finite for $\mu > 0$. If $T = +\infty$, we further set

$$K_{\infty}[f] = \limsup_{t \to +\infty} \int_0^t e^{-\mu(t-\xi)} f(\xi) d\xi \tag{2.23}$$

for $f \in L^+(0, +\infty)$.

LEMMA 2.5 ([7]). Let $0 \le \theta_j < 1$ and $\gamma_j \in L^+(0,T)$ for $j = 1,\ldots,J$. Let w = w(t) be a positive function on [0,T) satisfying the differential inequality

$$\frac{dw}{dt} \le -\mu w(t) + \sum_{j=1}^{J} \gamma_j(t) w(t)^{\theta_j} \qquad \text{for } 0 \le t < T.$$
 (2.24)

Then

$$w(t) < \kappa$$

for $0 \le t < T$. Moreover, if $T = +\infty$, then

$$\limsup_{t \to +\infty} w(t) \le \kappa_{\infty}.$$

Here κ , κ_{∞} are the maximal roots of the algebraic equations

$$x - \sum_{i=1}^{J} K[\gamma_i] x^{\theta_j} = w(0), \tag{2.25}$$

$$x - \sum_{i=1}^{J} K_{\infty}[\gamma_i] x^{\theta_i} = 0, \qquad (2.26)$$

respectively.

Now we are ready to obtain upper bounds on H(x,t). From the maximum principle, it is easy to see that

$$H(x,t) \le \bar{v}(t)$$
 for $x \in \Omega$, $t > 0$.

Moreover, it follows from Lemma 2.4 that

$$\limsup_{t\to\infty} \max_{x\in\overline{\Omega}} H(x,t) \le \sigma_1.$$

Putting the discussions above together, we obtain

LEMMA 2.6. Let (A(x,t), H(x,t)) be a solution of (2.1). If $\tau > q/(p-1)$ and

$$\left(\max_{x\in\overline{\Omega}}A_0(x)\right)^{p-1} \le \left(1 - \frac{q}{(p-1)\tau}\right) \left(\min_{x\in\overline{\Omega}}H_0(x)\right)^q,$$

then there exists a C > 0 such that

$$e^{-t} \min_{x \in \overline{\Omega}} A_0(x) \le A(x, t) \le Ce^{-t} \quad \text{for all } x \in \overline{\Omega}, \ t > 0,$$
 (2.27)

$$\min_{x \in \overline{\Omega}} \sigma_h(x) \le \liminf_{t \to +\infty} \min_{x \in \overline{\Omega}} H(x, t) \le \limsup_{t \to +\infty} \max_{x \in \overline{\Omega}} H(x, t) \le \max_{x \in \overline{\Omega}} \sigma_h(x).$$
(2.28)

2.2. Proof of Theorem 2.1. It is easy to see from (2.27) that $A(x,t) \to 0$ uniformly on $\overline{\Omega}$ as $t \to +\infty$. We consider the behavior of H(x,t) as $t \to +\infty$.

Let z(x) be the unique solution of (2.5) and (2.6). Put W(x,t) = H(x,t) - z(x). Then it is a solution of the following problem:

$$\begin{split} \tau \frac{\partial W}{\partial t} &= D\Delta W - W + \frac{A^r}{H^s} \quad \text{for } x \in \Omega, \ t > 0, \\ \frac{\partial W}{\partial \nu} &= 0 \quad \text{for } x \in \partial \Omega, \ t > 0, \\ W(x,0) &= H_0(x) - z(x) \quad \text{for } x \in \Omega. \end{split}$$

Let G(t, x, y) be the Green function of

$$\frac{\partial V}{\partial t} = \frac{D}{\tau} \Delta V - \frac{1}{\tau} V$$

under the Neumann boundary condition. Since

$$\int_{\Omega} G(t, x, y) \, dy \le e^{-t/\tau} \quad \text{for all } x \in \overline{\Omega}, \ t > 0,$$

we have that

$$\begin{split} |W(x,t)| &= \left| \int_{\Omega} G(t,x,y) (H_0(y) - z(y)) \, dy + C_1 \int_0^t d\xi \int_{\Omega} G(t-\xi,x,y) \frac{A^r(y,\xi)}{H^s(y,\xi)} \, dy \right| \\ &\leq \max_{x \in \overline{\Omega}} |H_0(x) - z(x)| \int_{\Omega} G(t,x,y) \, dy + \int_0^t d\xi \int_{\Omega} G(t-\xi,x,y) \frac{Ce^{-r\xi}}{(\min_{x \in \overline{\Omega}} H_0(x))^s e^{-s\xi/\tau}} \, dy \\ &\leq \left(\max_{x \in \overline{\Omega}} |H_0(x) - z(x)| + C \int_0^t e^{-(r-\frac{s+1}{\tau})\xi} \, d\xi \right) e^{-t/\tau} \\ &\leq \left(\max_{x \in \overline{\Omega}} |H_0(x) - z(x)| + \frac{C}{r - \frac{s+1}{\tau}} \left(1 - e^{-(r-\frac{s+1}{\tau})t} \right) \right) e^{-t/\tau}. \end{split}$$

Here we have used the estimates $H(x,t) \ge e^{-t/\tau} \min_{x \in \overline{\Omega}} H_0(x)$ and (2.27). It follows from the assumption (1.5) and $\tau > q/(p-1)$ that

$$r - \frac{s+1}{\tau} > r - \frac{(p-1)(s+1)}{q} > 0.$$

Therefore,

$$\max_{x \in \overline{\Omega}} |H(x,t) - z(x)| \le Ce^{-t/\tau},$$

where C depends on A_0 and H_0 .

3. Collapse of patterns in a more general case. The assertion in Theorem 2.1 holds in a more general case, that is, we consider the following system which generalizes (1.1)–(1.4) slightly:

$$\frac{\partial u}{\partial t} = \varepsilon^2 \Delta u - u + f(x, u, v) + \sigma_a(x), \tag{3.1}$$

$$\tau \frac{\partial v}{\partial t} = D\Delta v - v + g(x, u, v) + \sigma_h(x), \tag{3.2}$$

$$\frac{\partial u}{\partial \nu}\Big|_{\partial \Omega} = \frac{\partial v}{\partial \nu}\Big|_{\partial \Omega} = 0, \tag{3.3}$$

$$u(x,0) = u_0(x), \quad v(x,0) = v_0(x). \tag{3.4}$$

$$u(x,0) = u_0(x), \quad v(x,0) = v_0(x).$$
 (3.4)

Here, f(x,u,v) and g(x,u,v) are continuous functions in $x \in \overline{\Omega}$, $0 \le u < +\infty$, $0 < v < +\infty$, and locally Lipschitz continuous with respect to u and v (uniformly in x); moreover, they satisfy the inequalities

$$0 \le f(x, u, v) \le C_1 \frac{u^p}{v^q}, \quad 0 \le g(x, u, v) \le C_2 \frac{u^r}{v^s} \quad (x \in \overline{\Omega}, \ u \ge 0, \ v > 0), \quad (3.5)$$

where C_1 and C_2 are positive constants independent of (x, u, v). As examples of fand g, we give (a) the Gierer-Meinhardt system with saturation:

$$f(x, u, v) = \frac{u^p}{v^q(1 + \kappa u^p)}, \quad g(x, u, v) = \frac{u^r}{v^s},$$

where $\kappa > 0$, and (b) the activator-inhibitor system proposed by MacWilliams [6]:

$$f(x,u,v) = \frac{u^p}{u^p + v^q}, \quad g(x,u,v) = \frac{\alpha u^r}{u^r + \beta}.$$

Here α and β are positive constants. MacWilliams used this model to simulate the head-regeneration experiment on hydra.

Let $\sigma_a \equiv 0$ in (3.1). If we assume $\max_{x \in \overline{\Omega}} \sigma_h(x) > 0$, we see that for any $\eta > 0$ satisfying $0 < \eta < 1$ there exists a positive number δ such that

$$v(x,t) \ge \eta(\min_{x \in \overline{\Omega}} v_0(x) + \delta)$$

for $x \in \overline{\Omega}$, t > 0. Let U(t) be a solution of the initial value problem

$$\frac{dU}{dt} = -U + C_1 \gamma U^p, \quad U(0) = \max_{x \in \overline{\Omega}} u_0(x),$$

where we put $\gamma = [\eta(\min_{x \in \overline{\Omega}} v_0(x) + \delta)]^{-q}$. We obtain that if $C_1 \gamma U(0)^{p-1} < 1$, then U(t) is monotone decreasing and satisfies

$$U(t) \le Ce^{-t}$$

for all t > 0. Here, C is a positive constant depending on C_1 , γ , U(0). Hence it follows that

$$\max_{x \in \overline{\Omega}} |v(x, t) - z(x)| \le Ce^{-t/\tau}$$

for all t > 0. We note that the condition $C_1 \gamma U(0)^{p-1} < 1$ is equivalent to

$$\left(\max_{x\in\overline{\Omega}}u_0(x)\right)^{p-1} < \frac{\eta^q}{C_1}\left(\min_{x\in\overline{\Omega}}v_0(x) + \delta\right)^q,\tag{3.6}$$

which does not contain τ unlike the case $\sigma_h(x) \equiv 0$.

The following proposition explains why the collapse can occur for any τ in this case.

PROPOSITION 3.1. Let f(x, u, v), g(x, u, v) satisfy (3.5) and be differentiable with respect to (u, v) in $0 \le u < +\infty$, $0 < v < +\infty$, and $\partial f/\partial u$, $\partial f/\partial v$, $\partial g/\partial u$, $\partial g/\partial v$ are continuous in (x, u, v). (Hence, the case 0 < r < 1 is excluded for the Gierer-Meinhardt system.) Assume that $\sigma_a \equiv 0$ and $\max_{x \in \overline{\Omega}} \sigma_h(x) > 0$. Then the stationary solution (u(x), v(x)) = (0, z(x)) is asymptotically stable. Here the initial values $u_0(x)$ and $v_0(x)$ are assumed to be positive.

Proof. Since $f_u(x,0,z) = 0$, $f_v(x,0,z) = 0$ and $g_v(x,0,z) = 0$, the linearized operator around the stationary solution (0,z(x)) becomes

$$\mathcal{L} = \left(\begin{array}{cc} \varepsilon^2 \Delta - 1 & 0 \\ g_u(x, 0, z(x)) / \tau & (D\Delta - 1) / \tau \end{array} \right).$$

The assertion is verified by showing that all the eigenvalues of $\mathcal L$ have negative real part. \square

4. Concluding Remarks. Let us consider the system (2.1)–(2.4) with $\sigma_h(x) \ge$ on $\overline{\Omega}$. The definition of the *collapse of patterns* is that the activator concentration converges uniformly to the trivial state $A \equiv 0$. Theorem 2.1 shows that the collapse of patterns occur if $\tau > q/(p-1)$ and the initial data is restricted. Moreover, if we assume that $\max_{x \in \overline{\Omega}} \sigma_h(x) > 0$, then collapse of patterns can occurs for any τ , which has been mentioned in Section 3. Therefore, the results may be summarized as follows:

Basic production terms	Collapse
$\sigma_a(x) \not\equiv 0$	never occurs.
$\sigma_a(x) \equiv 0, \sigma_h(x) \not\equiv 0$	occurs.
$\sigma_a(x) \equiv 0, \sigma_h(x) \equiv 0$	occurs for $\tau > q/(p-1)$.

Therefore, the case $\sigma_a(x) \equiv \sigma_h(x) \equiv 0$ may be regarded as a "regular perturbation" from the case $\sigma_a(x) \equiv 0$ and $\sigma_h(x) \not\equiv 0$, but it is a "singular limit" as $\max_{x \in \overline{\Omega}} \sigma_a(x) \downarrow 0$ of the case $\sigma_a(x) \not\equiv 0$ and $\sigma_h(x) \equiv 0$.

Behavior of solutions to an activator-inhibitor system

Acknowledgment. The first author is supported in part by Grant-in-Aid for Young Scientists (B) 20740087. The second author is supported in part by the Grant-in-Aid for Scientific Research (A) 18204010, Japan Society for the Promotion of Science.

REFERENCES

- [1] A. Friedman, Partial Differential Equations of Parabolic Type, Prentice-Hall, Inc., Englewood Cliffs, N.J. 1964.
- [2] A. Gierer and H. Meinhardt, A theory of biological pattern formation, Kybernetik (Berlin) 12 (1972), 30-39.
- [3] D. Henry, Geometric Theory of Semilinear Parabolic Equations, Lecture Notes in Math. 840, Springer-Verlag, Berlin-New York, 1981.
- [4] H. Jiang, Global existence of solutions of an activator-inhibitor system, Discrete Contin. Dyn. Syst., 14 (2006), 737–751.
- [5] M. Li, S. Chen and Y. Qin, Boundedness and blow up for the general activator-inhibitor model, Acta Math. Appl. Sinica 11 (1995), 59-68.
- [6] H. K. MacWilliams, Numerical simulations of Hydra head regeneration using a proportional-regulating version of the Gierer-Meinhardt model, J. Theor. Biol. 99 (1982), 681-703.
- [7] K. Masuda and K. Takahashi, Reaction-diffusion systems in the Gierer-Meinhardt theory of biological pattern formation, Japan J. Appl. Math. 4 (1987), 47-58.
- [8] W.-M. Ni, K. Suzuki and I. Takagi, The dynamics of a kinetic activator-inhibitor system, J. Differential Equations 299 (2006), 426-465.
- [9] F. Rothe, Global Solutions of Reaction-Diffusion Systems, Lecture Notes in Math. 1072, Springer, 1984.
- [10] K. Suzuki and I. Takagi, On the role of the source terms in an activator-inhibitor system proposed by Gierer and Meinhardt, Adv. Stud. Pure Math. 47-2, Math. Soc. Japan, Tokyo, 2007.
- [11] A. M. Turing, The chemical basis of morphogenesis, Philos. Trans. Roy. Soc. London, Ser. B 237 (1952), 37-72.
- [12] J. Wu and Y. Li, Classical global solutions for the activator-inhibitor model, Acta Math. Appl. Sinica 13 (1990), 501-505.