Breakdown of Pattern Formation in Activator-Inhibitor Systems and Unfolding of a Singular Equilibrium

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joint work with

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Partial Differential Equations in Mathematical Biology

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Plan of Talk

Introduction

1. Boundedness of Solutions to IBVP
2. Breakdown of Pattern Formation
3. Possible Scenario

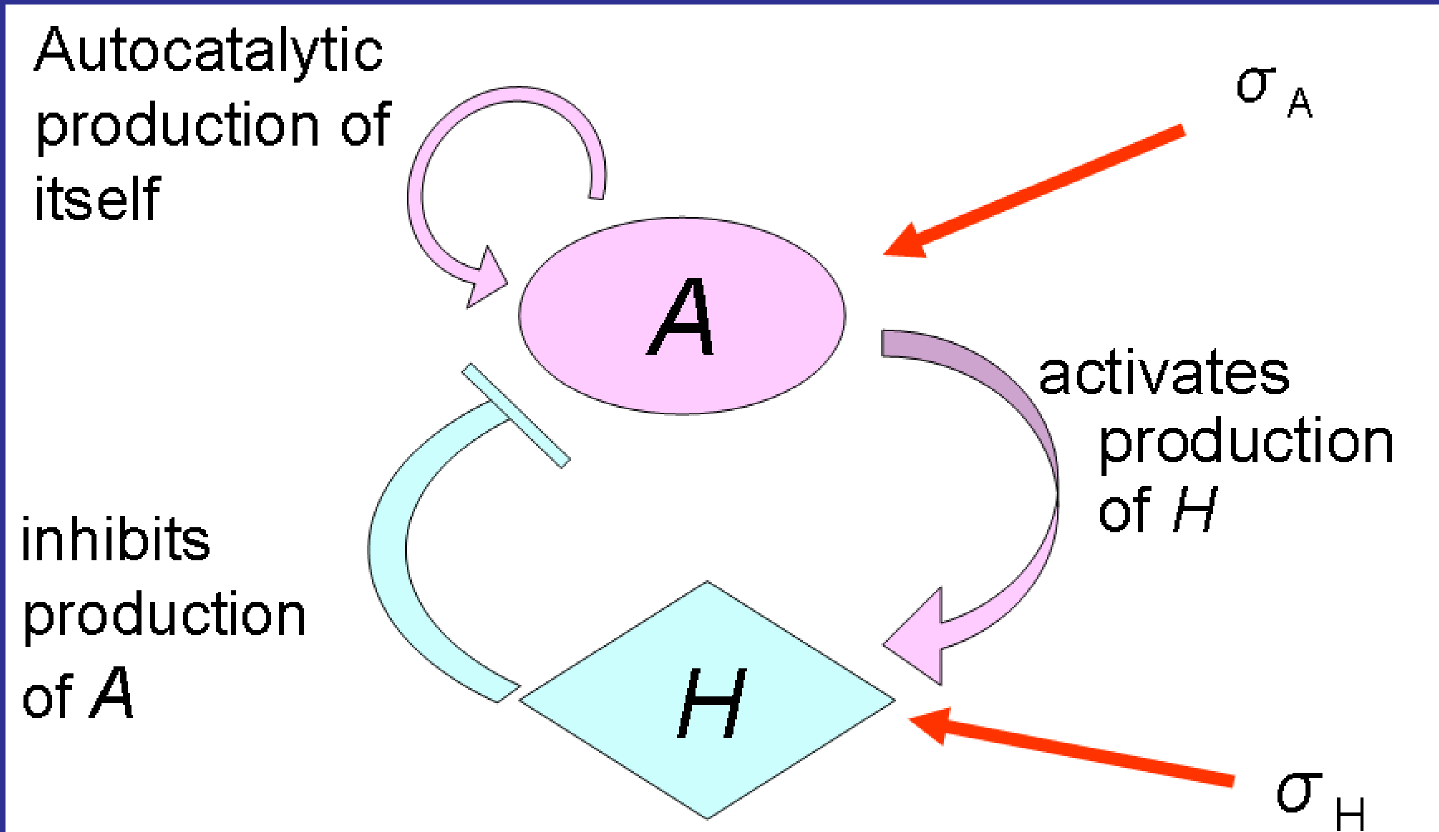
Introduction.

"Diffusion-Driven Instability" found by A. M. Turing in 1952:

> **When two chemicals with _different diffusion rates_ interact and diffuse, the spatially homogeneous state may become unstable, and as a result spatially nontrivial structure can be formed autonomously.**

Gierer and Meinhardt in 1972 developed Turing's idea and devised the following reaction-diffusion system which consists of a _slowly diffusing activator_ and a _rapidly diffusing inhibitor_ in order to simulate the transplantation experiment on _hydra_:

activator vs inhibitor



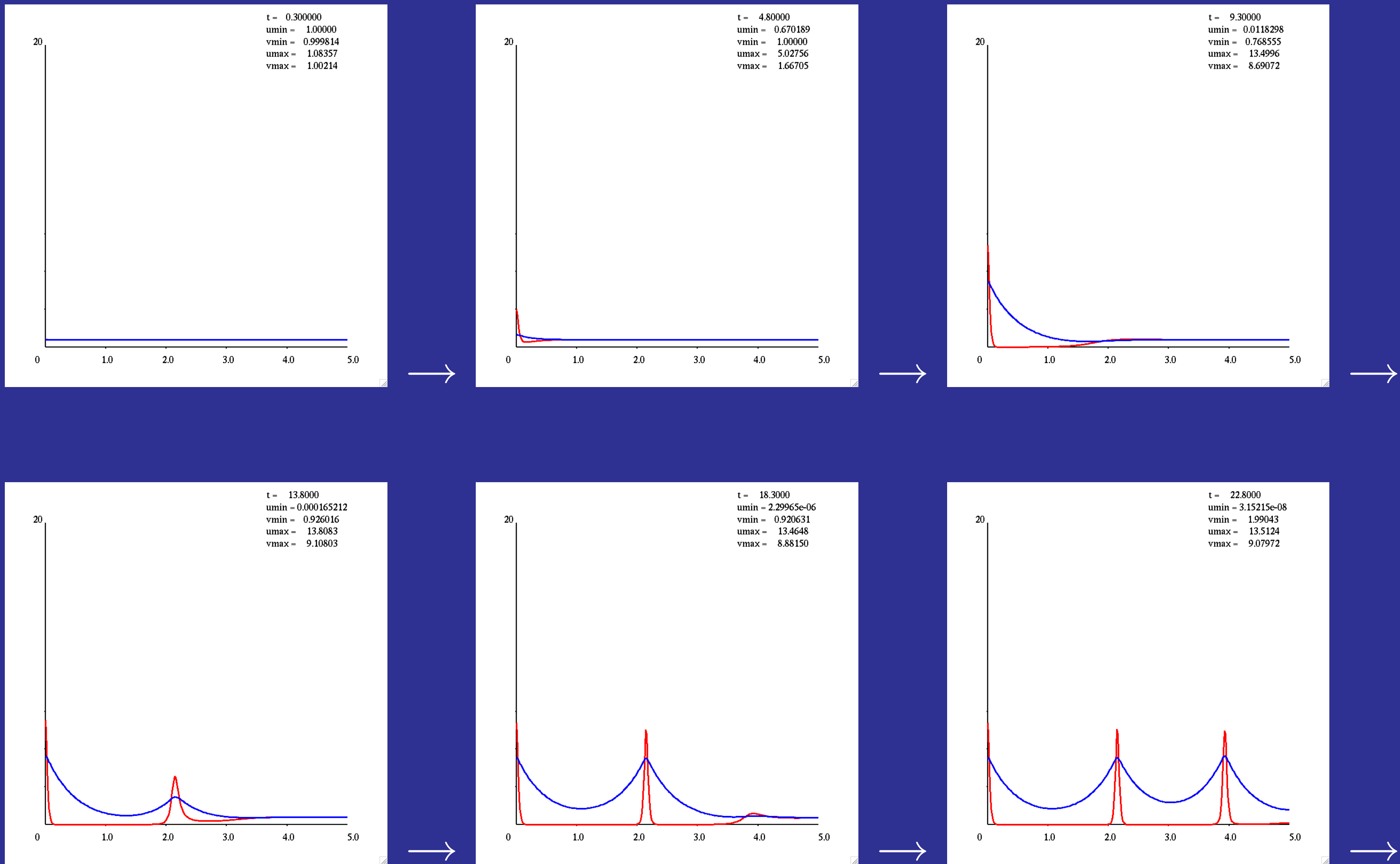
Activator-Inhibitor System with Different Sources ([GM])

$$\begin{cases} \dfrac{\partial a}{\partial t} = D_a \dfrac{\partial^2 a}{\partial x^2} - \mu a + c\rho \dfrac{a^2}{h} + \rho_0 \rho \\[2ex] \dfrac{\partial h}{\partial t} = D_h \dfrac{\partial^2 h}{\partial x^2} - \nu h + c' \rho' a^2 \end{cases}$$

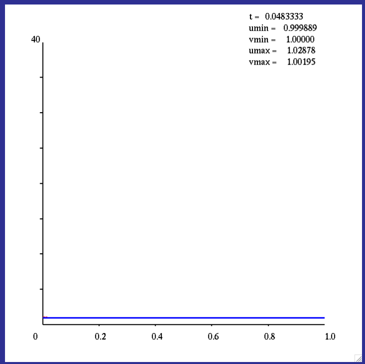
where D_a, D_h, c, c', ρ_0 are positive constants; $\mu(x)$, $\nu(x)$, $\rho(x)$, $\rho'(x)$ are positive functions. The unknowns $a = a(x,t)$ and $h = h(x,t)$ denote the concentrations at point x and time t of chemicals called an *activator* and an *inhibitor*, respectively. It is postulated that a change in cells occurs at the place where the activator concentration is high.

Let's take a look at two simulations.

movie1: covergence to a steady-state



movie2: covergence to a limit cycle (1/3)



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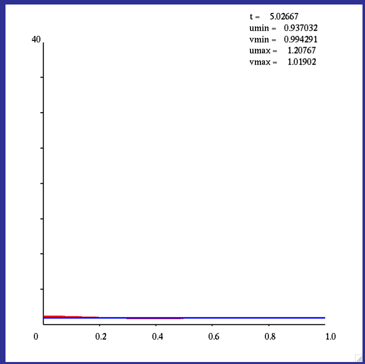

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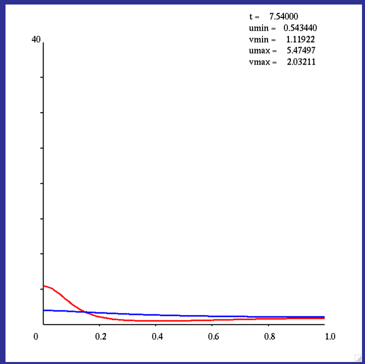

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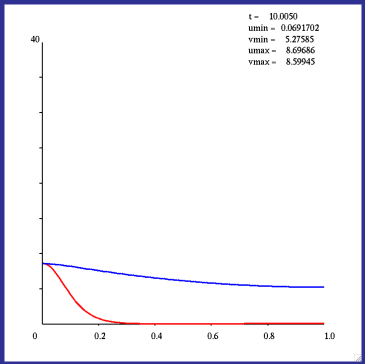

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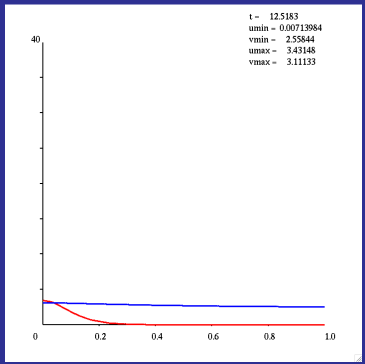

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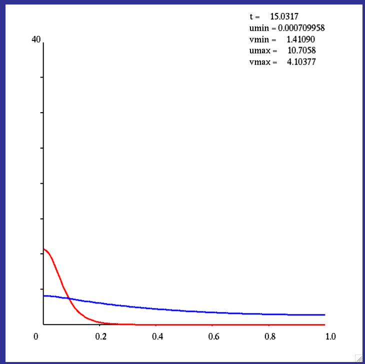

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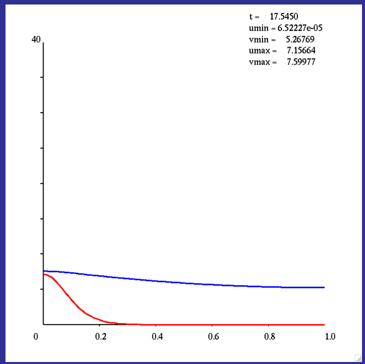

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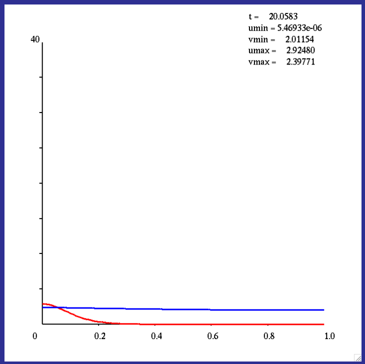

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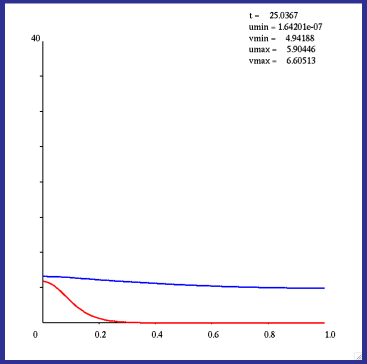
movie2: covergence to a limit cycle (2/3)



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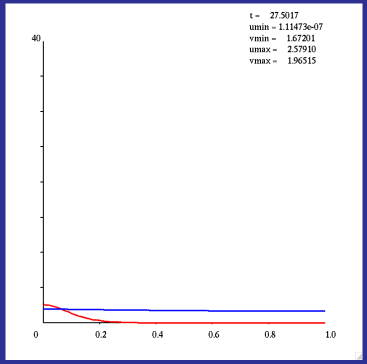

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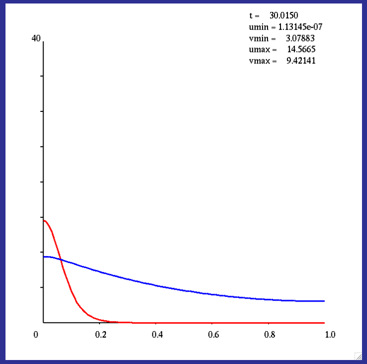

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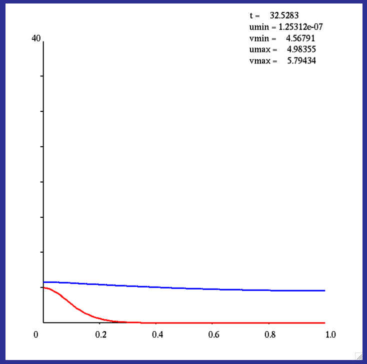

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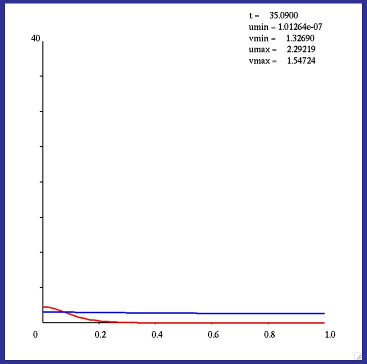

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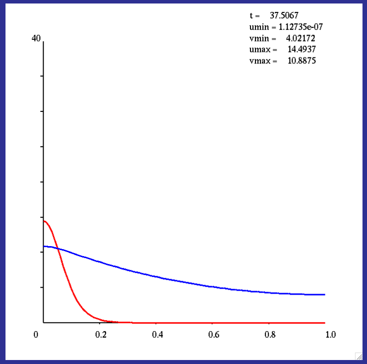

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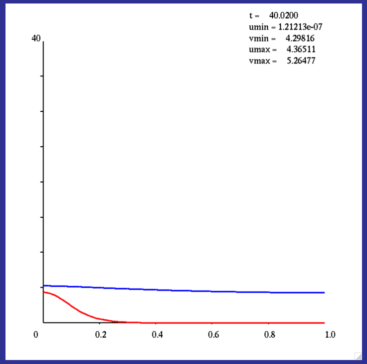

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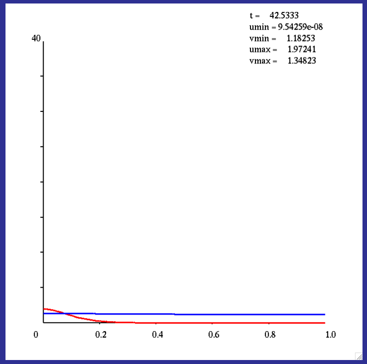

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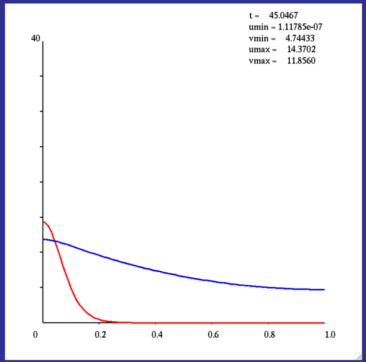
movie2: covergence to a limit cycle (3/3)



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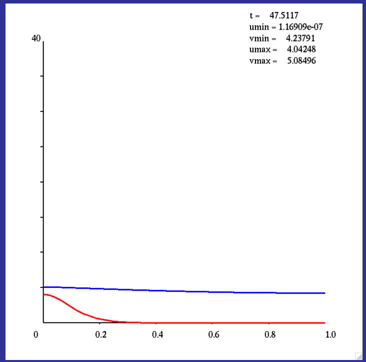

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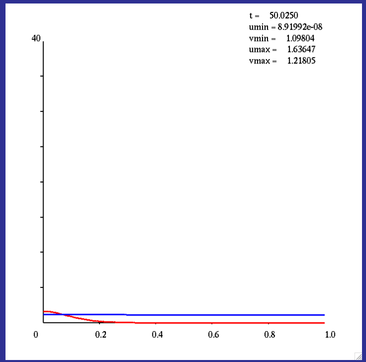

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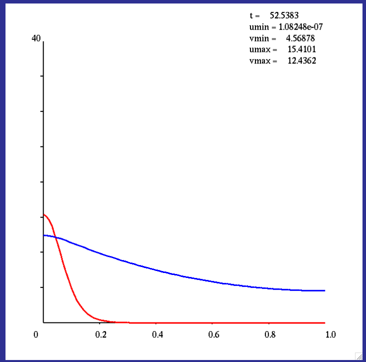

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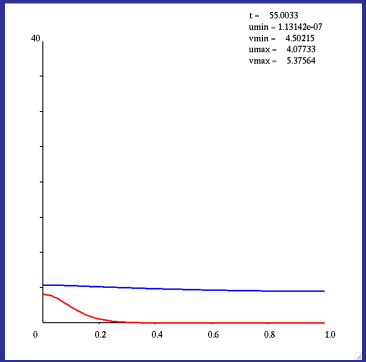

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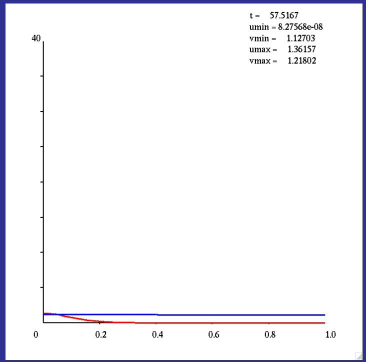

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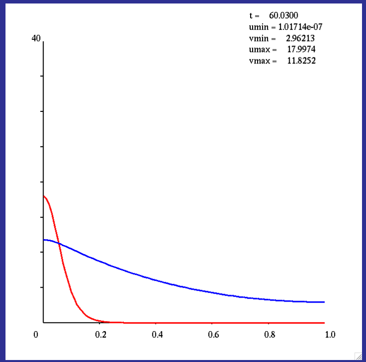

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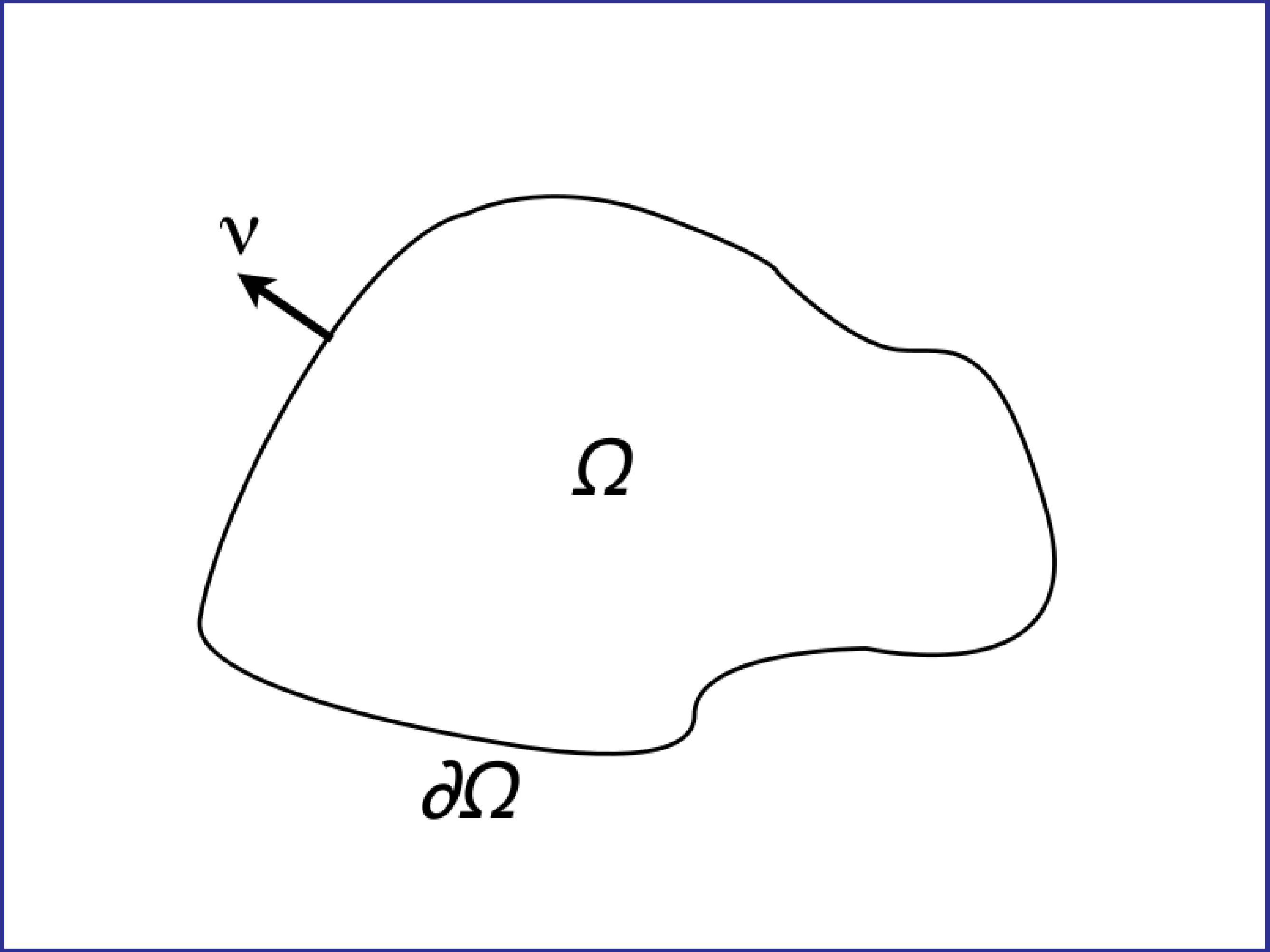


⋆ Ω is a bounded domain in $\mathbb{R}^n$ with smooth boundary $\partial\Omega$; $\nu = (\nu_1, \ldots, \nu_n)$ is the unit outer normal to $\partial\Omega$.

(GM)

$$\begin{cases} \dfrac{\partial A}{\partial t} = \varepsilon^2 \boldsymbol{\Lambda}_a A - \mu_a A + \rho_a \dfrac{A^p}{H^q(1+\kappa A^p)} + \sigma_a \quad \text{in } \Omega, \\ \tau \dfrac{\partial H}{\partial t} = D\boldsymbol{\Lambda}_h H - \mu_h H + \rho_h \dfrac{A^r}{H^s} + \sigma_h \qquad \text{in } \Omega, \\ \boldsymbol{B}_a A = \boldsymbol{B}_h H = 0, \qquad \text{on } \partial\Omega \\ A(x,0) = A_0(x), \quad H(x,0) = H_0(x) \qquad \text{in } \Omega. \end{cases}$$

$$\boldsymbol{\Lambda}_a = \sum_{i,j=1}^n \frac{\partial}{\partial x_i}\left(d_{ij}^{(a)} \frac{\partial}{\partial x_j}\right), \quad \boldsymbol{\Lambda}_h = \sum_{i,j=1}^n \frac{\partial}{\partial x_i}\left(d_{ij}^{(h)} \frac{\partial}{\partial x_j}\right),$$

$$\boldsymbol{B}_a = \sum_{i,j=1}^n \nu_i d_{ij}^{(a)} \frac{\partial}{\partial x_j}, \quad \boldsymbol{B}_h = \sum_{i,j=1}^n \nu_j d_{ij}^{(h)} \frac{\partial}{\partial x_j}.$$

⋆ Here, $\boldsymbol{\Lambda}_a$ and $\boldsymbol{\Lambda}_h$ are uniformly strongly elliptic operators in Ω.

- ⋆ The coefficients ε, τ, D are positive constants, whereas κ is a nonnegative constant.
- ⋆ The basic production terms $\sigma_a = \sigma_a(x)$, $\sigma_h = \sigma_h(x)$ are non-negative, and the cross-reaction rates $\rho_a = \rho_a(x, A, H)$, $\rho_h = \rho_h(x, A, H)$ are sufficiently smooth positive functions:

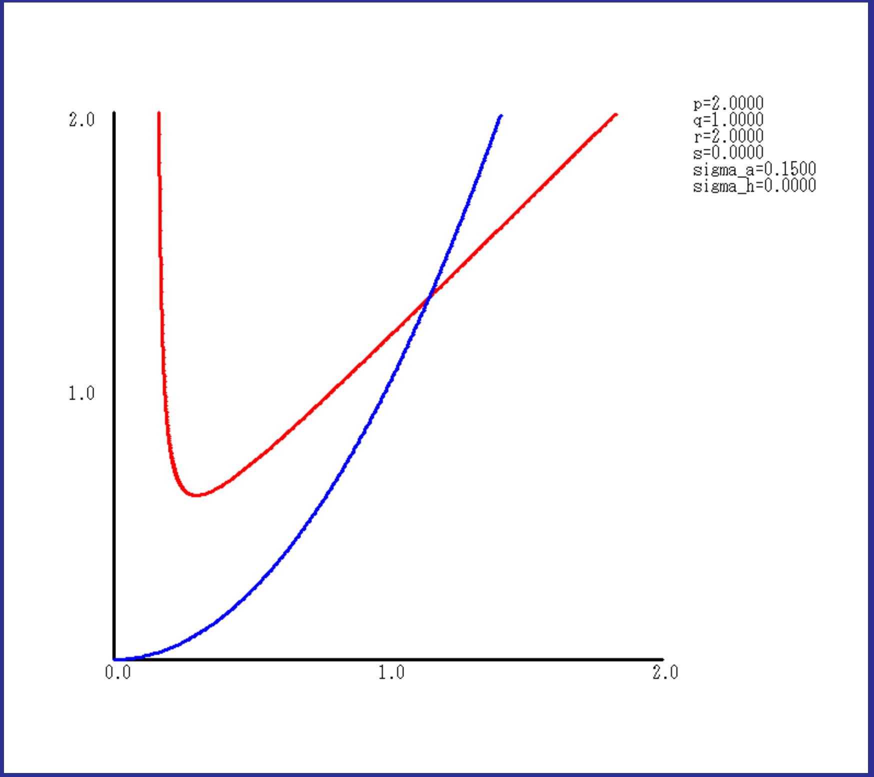
$$0 < \rho_a \leqslant C_a, \quad 0 < c_h \leqslant \rho_h \leqslant C_h \quad \text{for } x \in \overline{\Omega},\ A \in \mathbb{R},\ H \in \mathbb{R}.$$

- ⋆ The decomposition rates $\mu_a = \mu_a(x)$, $\mu_h = \mu_h(x)$ are positive functions: $0 < k_1^{(a)} \leqslant \mu_a(x) \leqslant k_2^{(a)}$, $0 < k_1^{(h)} \leqslant \mu_h(x) \leqslant k_2^{(h)}$.
- ⋆ The initial data $u_0(x)$, $v_0(x)$ are positive on $\overline{\Omega}$.

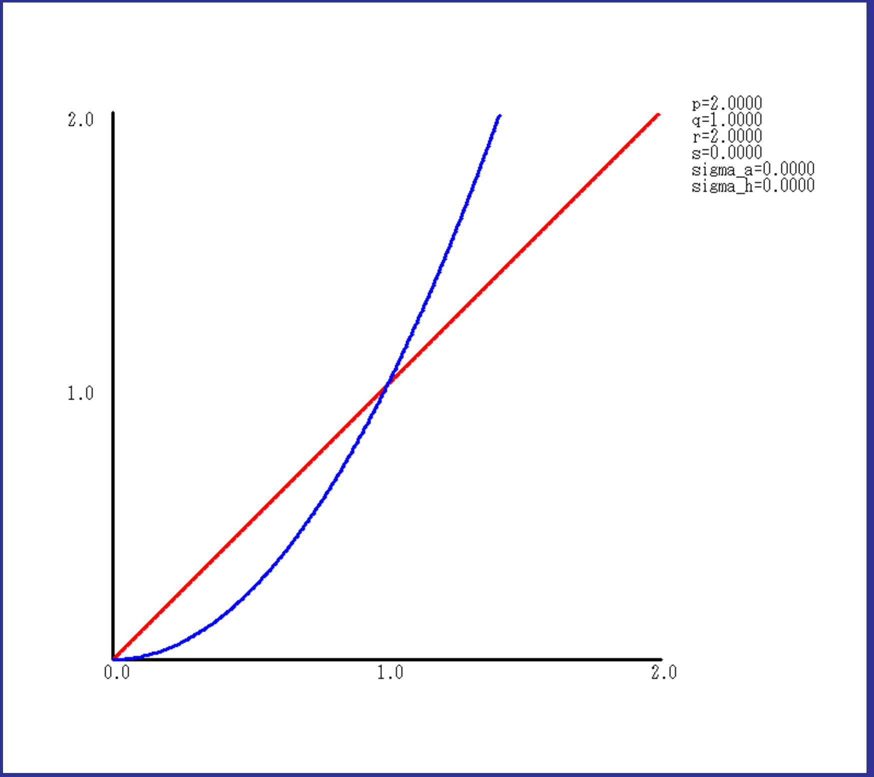
The exponents p, q, r, s are assumed to satisfy

$$(A)\quad p > 1,\ q > 0,\ r > 0,\ s \geqslant 0, \qquad \frac{p-1}{q} < \frac{r}{s+1}.$$

Nullclines in the Case of Homogeneous Media

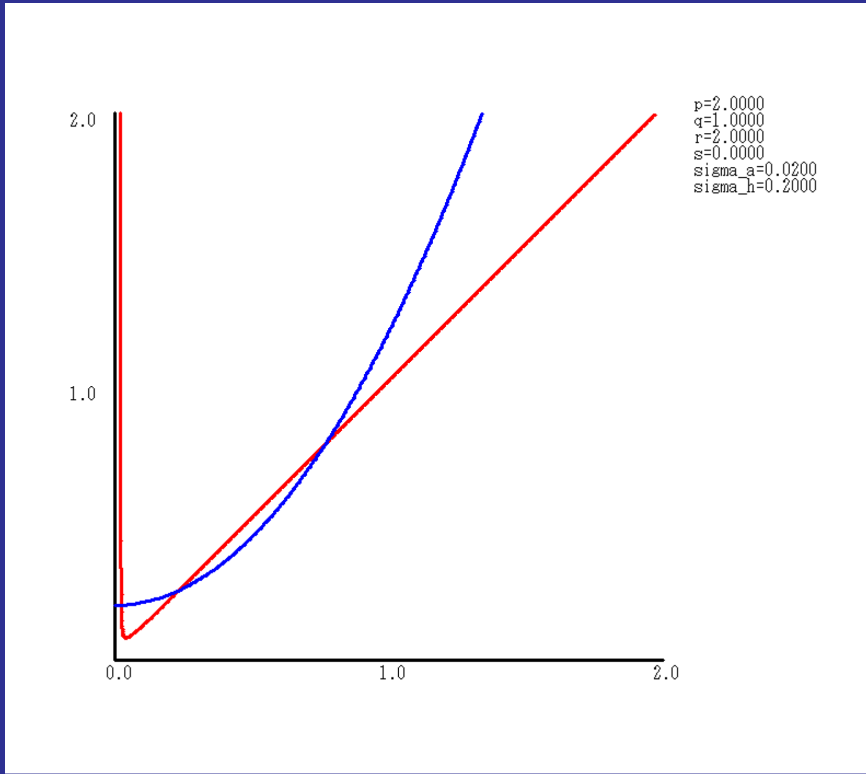


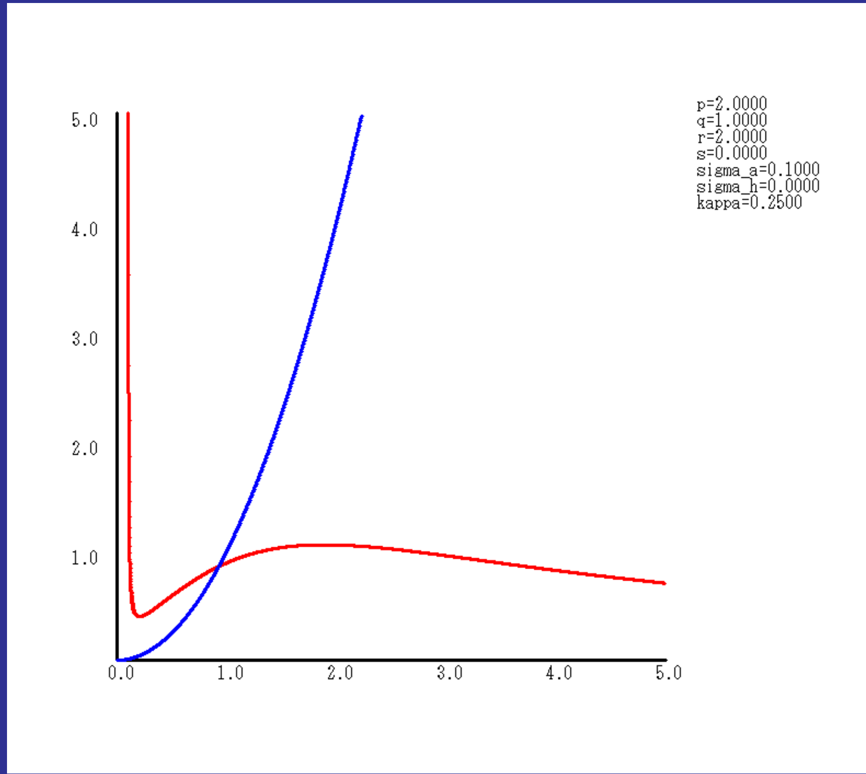
$\sigma_a > 0,\ \sigma_h = 0$



$\sigma_a = \sigma_h = 0$

$$f(A,H) = -A + \frac{A^p}{H^q} + \sigma_a = 0,\ \ g(A,H) = -H + \frac{A^r}{H^s} + \sigma_h = 0$$





$\sigma_a > 0.\ \sigma_h > 0$

$$f(A,H) = -A + \frac{A^p}{H^q(1+\kappa A^p)} + \sigma_a$$

1. Existence of Solutions of the Initial-Boundary Value Problem

To begin with, let us summarize the known results on the existence of solutions of the initial-boundary value problem (GM), to which many people contributed:

- F. Rothe [Rf], K. Masuda and K. Takahashi [MT] in 1980's
- M. Lin, S. Chen and Y. Qin [LCQ] in 1990's
- W.-M. Ni, K. Suzuki and I.T. [NST], H. Jiang [J], K. Suzuki and I.T. [ST] in 2000's

  In the following Theorems A–C, we assume

$$p - 1 < r \tag{1.1}$$

in addition to (A).

Theorem A. ([MT]+[LCQ]) *If* $\sigma_a(x) \not\equiv 0$*, then the initial-boundary value problem* (GM) *has a unique solution for all* $t > 0$ *and there exist positive constants* r_a*,* R_a*,* r_h*,* R_h *(*$r_a < R_a$*,* $r_h < R_h$*) independent of the initial value* $(A_0(x), H_0(x))$ *such that*

$$r_a \leqslant \liminf_{t\to+\infty} \min_{x\in\overline{\Omega}} A(x,t) \leqslant \limsup_{t\to+\infty} \max_{x\in\overline{\Omega}} A(x,t) \leqslant R_a,$$

$$r_h \leqslant \liminf_{t\to+\infty} \min_{x\in\overline{\Omega}} H(x,t) \leqslant \limsup_{t\to+\infty} \max_{x\in\overline{\Omega}} H(x,t) \leqslant R_h.$$

Theorem B. ([J], [ST]) *If* $\sigma_a(x) \equiv 0$ *and* $\sigma_h(x) \not\equiv 0$, *then there exist positive constants* R_a, r_h, R_h *independent of the initial value such that*

$$e^{-k_2^{(a)} t} \min_{x \in \overline{\Omega}} A_0(x) \leqslant \min_{x \in \overline{\Omega}} A(x,t) \text{ for all } t \geqslant 0,$$

$$\text{and} \quad \limsup_{t \to +\infty} \max_{x \in \overline{\Omega}} A(x,t) \leqslant R_a,$$

$$r_h \leqslant \liminf_{t \to +\infty} \min_{x \in \overline{\Omega}} H(x,t) \leqslant \limsup_{t \to +\infty} \max_{x \in \overline{\Omega}} H(x,t) \leqslant R_h.$$

Theorem C. ([J], [ST]) *If* $\sigma_a(x) \equiv 0$ *and* $\sigma_h(x) \equiv 0$, *then there exist positive constants* λ, μ *depending only on* p, q, r, s, τ *and a positive constant* C *depending on the initial value such that*

$$e^{-k_2^{(a)} t} \min_{x \in \overline{\Omega}} A_0(x) \leqslant A(x,t) \leqslant Ce^{\lambda t},$$

$$e^{-k_2^{(h)} t/\tau} \min_{x \in \overline{\Omega}} H_0(x) \leqslant H(x,t) \leqslant Ce^{\mu t}$$

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

Results on the existence of global solutions appeared more than twenty years ago; see, e.g., [Rf], [MT]. In particular, [MT] proved the assertion of Theorem A under the condition $(p-1)/r < N/(N+2)$. It was [LCQ] that proved Theorem A, while Theorems B and C were obtained recently by [J], [S], [ST].

On the other hand, in the case of $p-1>r$ we have the following result.

Proposition D. ([LCQ], [NST]) *Assume that μ_a, μ_h, ρ_a, ρ_h are all positive constants and $\sigma_a(x) \equiv \sigma_h(x) \equiv 0$. If*

$$p-1>r \tag{1.2}$$

then (GM) *has solutions which blow up in finite time.*

The case $p-1<r$

Basic production terms	Solutions
$\sigma_a(x) \not\equiv 0$	are ultimately uniformly bounded.
$\sigma_a(x) \equiv 0$, $\sigma_h(x) \not\equiv 0$	are ultimately uniformly bounded.
$\sigma_a(x) \equiv 0$, $\sigma_h(x) \equiv 0$	may become unbounded.

The case $p-1>r$

Some **solutions blow up in finite time.**

- **$p-1$ is the self-activation index of the activator, whereas**
- **r is the cross-activation index of the activator.**

Obviously, for the systematic study of global behavior of solutions of (GM), it is important to know the behavior of solutions of the following kinetic system:

$$(\mathrm{K}) \qquad \begin{cases} \dfrac{du}{dt} = -u + \dfrac{u^p}{v^q} + \sigma_a, \\ \tau \dfrac{dv}{dt} = -v + \dfrac{u^r}{v^s} + \sigma_h. \end{cases}$$

Here we assume that σ_a, σ_h are both nonnegative constants. In this aspect, [NST] classified all the behavior of solution orbits in the case of $\sigma_a = 0$ and $\sigma_h = 0$ The case $\sigma_a > 0$ is treated in an on-going project [NS].

2. Breakdown of Pattern Formation

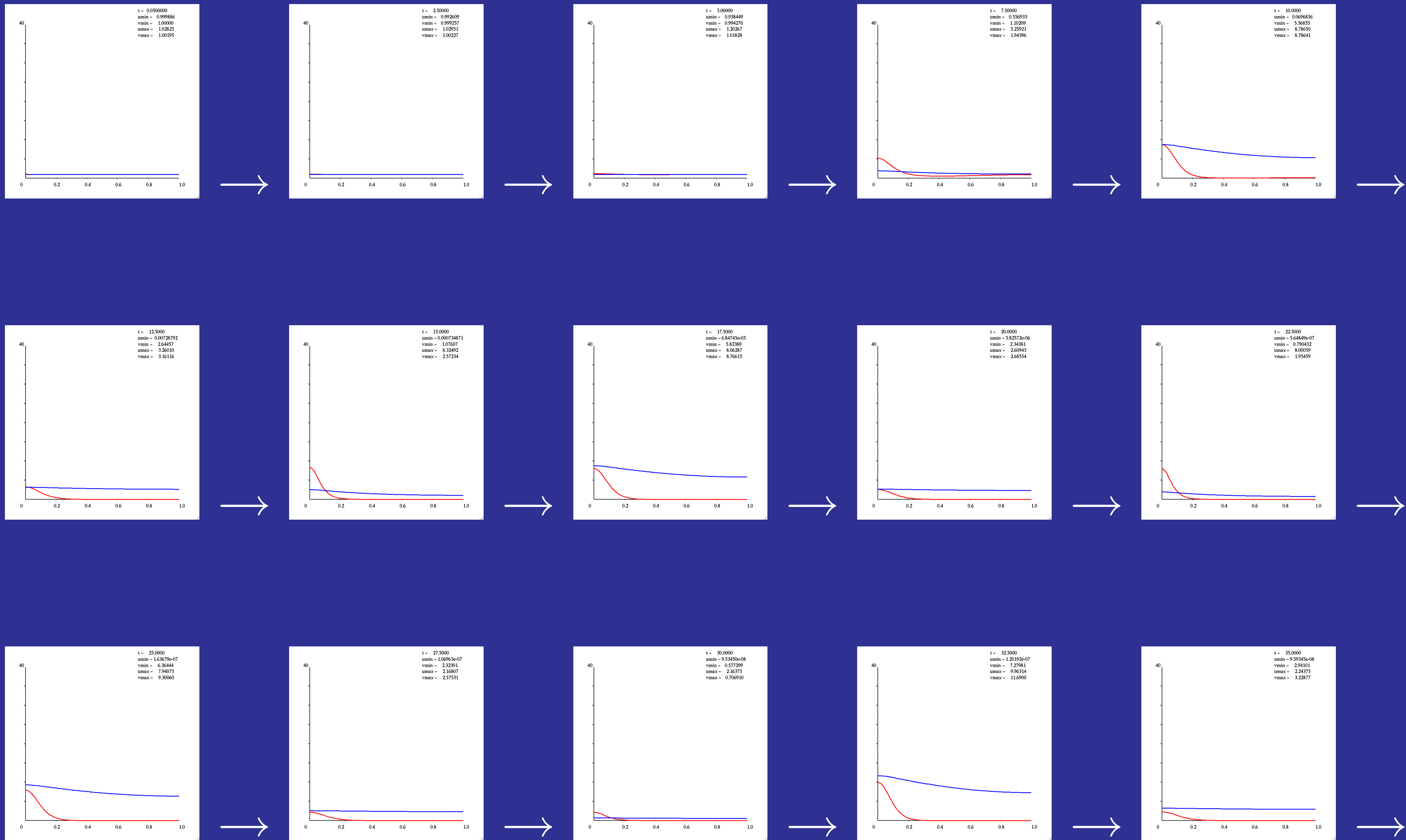
In some numerical simulations, it is observed that a solution starting from an almost uniform initial value develops localization in the activator concentration for a while, but it begins to oscillate and eventually converges uniformly to the trivial state $u \equiv 0$. We call this kind of phenomenon the *collapse of patterns*. In this section we would like to understand the mechanism behind the collapse of patterns and to know when it occurs. This section is based on the paper [ST4].

It is convenient to classify the basic production terms into four cases:

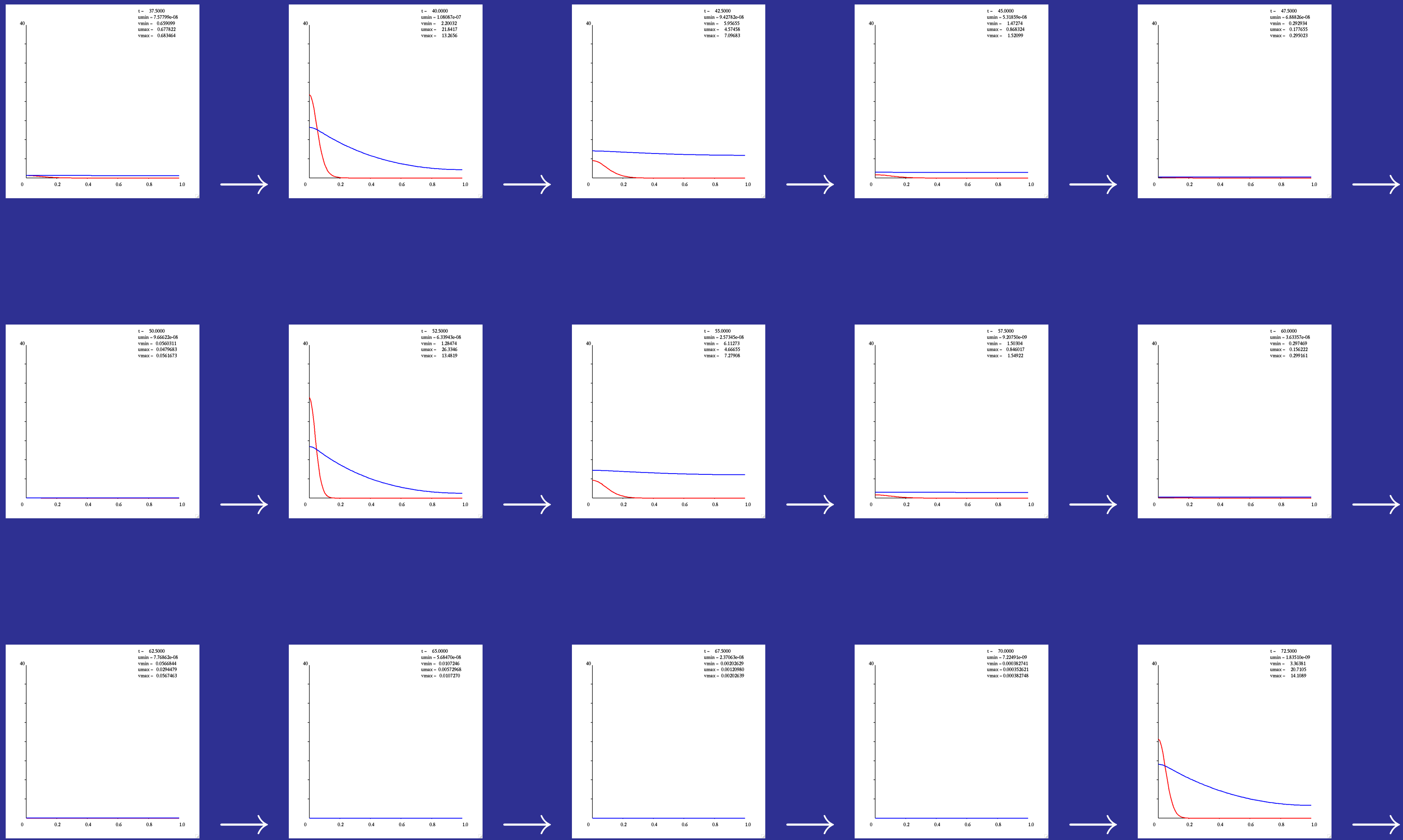
Case I: $\sigma_a \equiv \sigma_h \equiv 0$; Case II: $\sigma_a \equiv 0$ and $\sigma_h \not\equiv 0$;

Case III: $\sigma_a \not\equiv 0$ and $\sigma_h \not\equiv 0$; Case IV: $\sigma_a \not\equiv 0$ and $\sigma_h \equiv 0$.

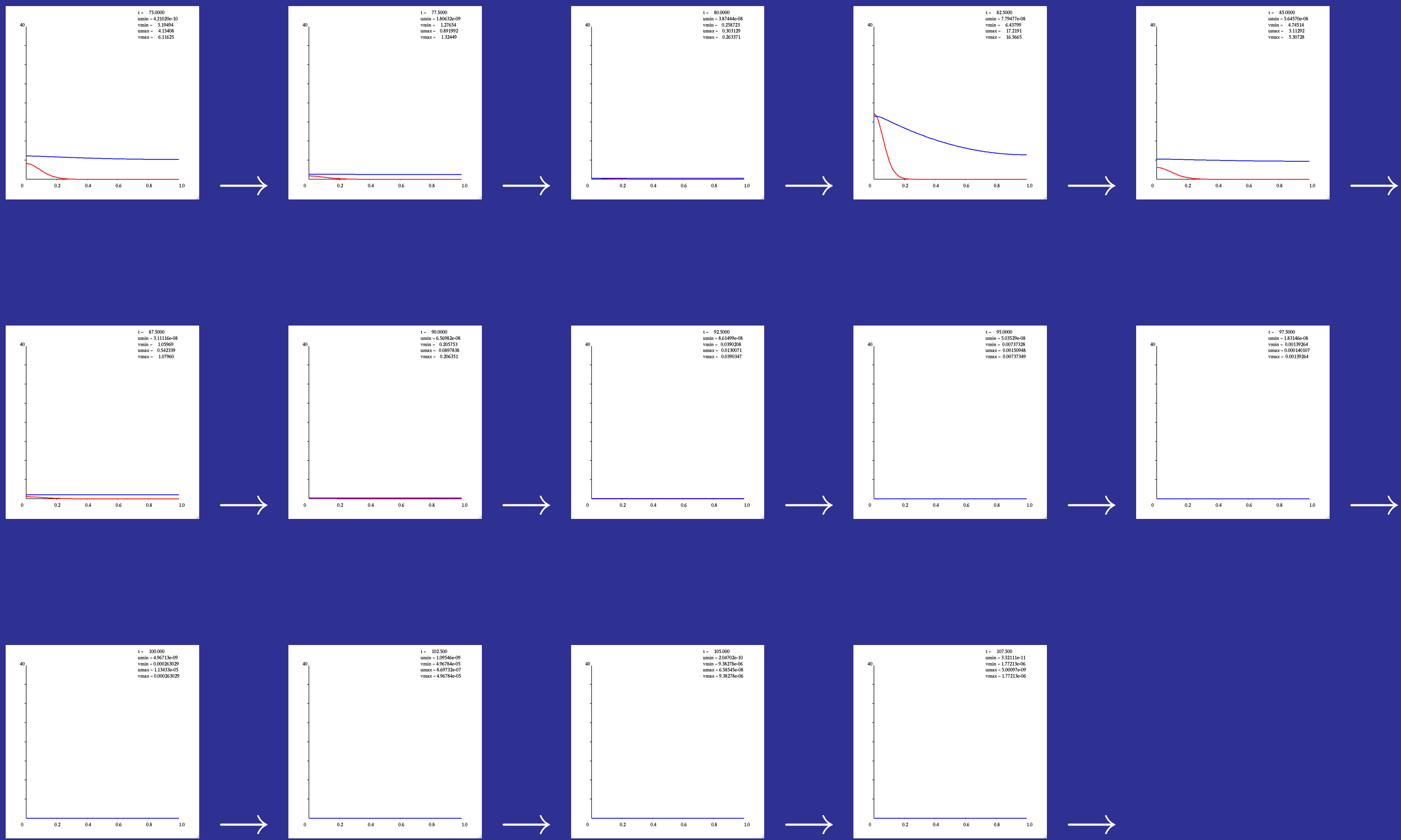
movie3: collapse of patterns (1/3)



movie3: collapse of patterns (2/3)



movie3: collapse of patterns (3/3)



Theorem 2.1. (Cases I and II) *Assume that* $\sigma_a(x) \equiv 0$. *If*

$$(2.1)\ \tau > \frac{k_2^{(h)}\, q}{k_1^{(a)}\,(p-1)},$$ and

$$(2.2)\quad \left(\min_{x\in\overline{\Omega}} H_0(x)\right)^q > \frac{C_a(p-1)}{k_1^{(a)}\,(p-1) - \frac{k_2^{(h)}\, q}{\tau}} \left(\max_{x\in\overline{\Omega}} A_0(x)\right)^{p-1},$$

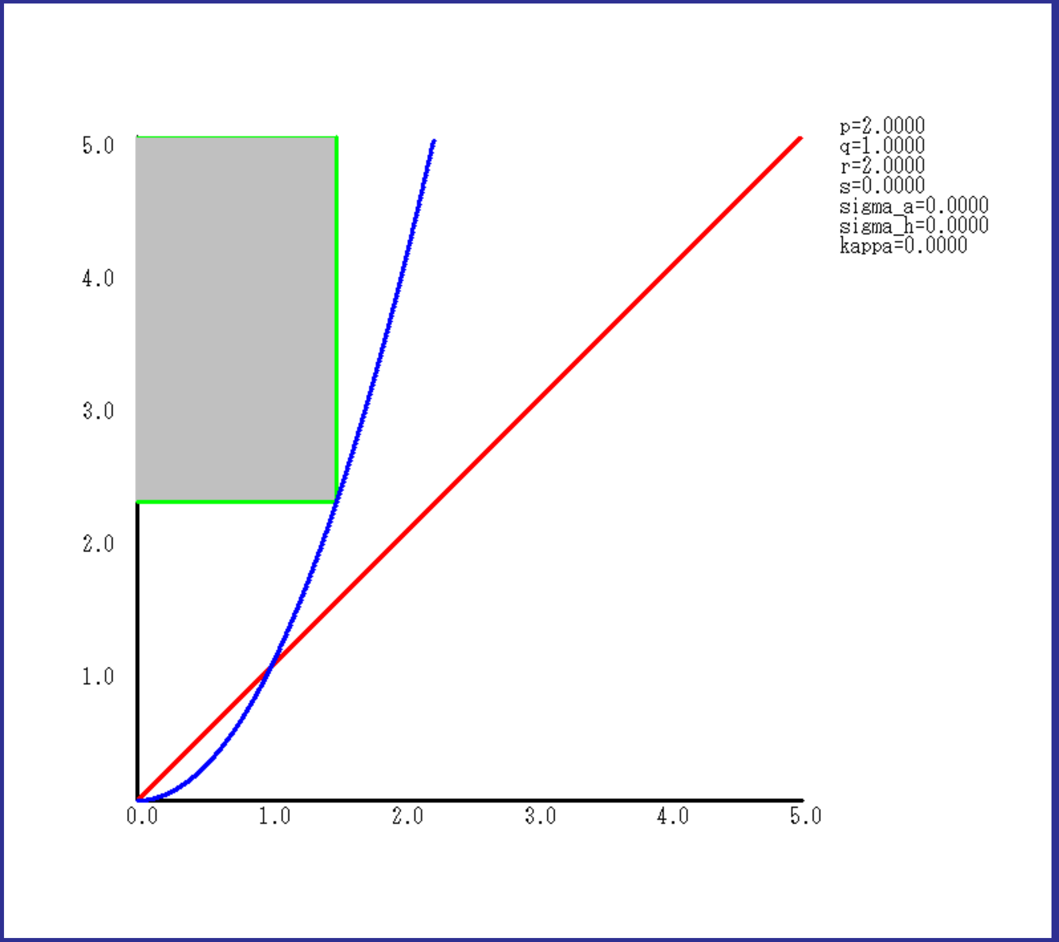
then the solution $(A(x,t), H(x,t))$ *of* (GM) *satisfies*

$$0 < \max_{x\in\overline{\Omega}} A(x,t) \leqslant Ce^{-\mu_1^{(a)}\, t},\ \max_{x\in\overline{\Omega}} |H(x,t) - \Sigma_{h,D}(x)| \leqslant Ce^{-\mu_1^{(h)}\, t/\tau},$$

in which C *is a positive constant depending on* $(A_0(x), H_0(x))$, *and* $u = \Sigma_{h,D}(x)$ *is the solution of the boundary value problem*

$$(2.3)\quad D\boldsymbol{\Lambda}_h u - \mu_h u + \sigma_h(x) = 0 \quad (x\in\Omega), \quad \boldsymbol{B}_h u = 0\ (x\in\partial\Omega).$$

Collapse of Patterns / Theorem 2.1



$$\tau > \frac{k_2^{(h)}\, q}{k_1^{(a)}\,(p-1)}$$

Collapse occurs for initial data contained in the gray region.

Theorem 2.2. (Case II) *Assume that* $\sigma_a \equiv 0$ *and* $\sigma_h \not\equiv 0$. *Let* $\delta_h = \min_{x\in\overline{\Omega}} \Sigma_{h,D}(x)$, $\quad \Gamma_h = \max_{x\in\overline{\Omega}} \Sigma_{h,D}(x)$. *If the initial data* $(A_0(x), H_0(x))$ *satisfies*

$$\min\left\{\left((\delta_h/\Gamma_h)^{k_2^{(h)}/k_1^{(h)}} \min_{x\in\overline{\Omega}} H_0(x)\right)^q, \left(\delta_h k_1^{(h)}/k_2^{(h)}\right)^q\right\} > \frac{C_a}{k_1^{(a)}}\left(\max_{x\in\overline{\Omega}} A_0(x)\right)^{p-1},$$

then $(A(x,t), H(x,t))$ *converges exponentially to* $(0, \Sigma_{h,D}(x))$ *uniformly on* $\overline{\Omega}$ *as* $t \to +\infty$.

Theorem 2.3. (Almost decoupled stationary patterns) *Assume that* $\sigma_a(x) \not\equiv 0$, $\sigma_h(x) \not\equiv 0$. *Let* $\min_{x\in\overline{\Omega}} \sigma_a(x) > \gamma_a \left(\max_{x\in\overline{\Omega}} \sigma_a(x)\right)^p$ *for some positive constant* γ_a *if* $0 < r < 1$. *If* $\max_{x\in\overline{\Omega}} \sigma_a(x)$ *is sufficiently small, then there exists a stationary solution* $(A_*(x), H_*(x))$ *of (GM) which satisfies*

$$\|A_* - \Sigma_{a,\varepsilon}\|_\infty \leqslant C\|\sigma_a\|_\infty{}^p, \quad \|H_* - \Sigma_{h,D}\|_\infty \leqslant C\|\sigma_a\|_\infty{}^r,$$

where C *is a positive constant and* $\Sigma_{a,\varepsilon}$, $\Sigma_{h,D}$ *are solutions of*

$$\varepsilon^2 \boldsymbol{\Lambda}_a \Sigma_{a,\varepsilon} - \mu_a \Sigma_{a,\varepsilon} + \sigma_a = 0, \text{ and } D\boldsymbol{\Lambda}_h \Sigma_{h,D} - \mu_h \Sigma_{h,D} + \sigma_h = 0$$

subject to the boundary conditions $\boldsymbol{B}_a \Sigma_{a,\varepsilon} = 0$, $\boldsymbol{B}_h \Sigma_{h,D} = 0$, *respectively. Furthermore, this stationary solution is asymptotically stable.*

To treat the case $\sigma_a \neq 0$ and $\sigma_h \neq 0$, we need an algebraic observation: Consider the equation

$$-k_1^{(a)}\xi + \frac{C_a}{(\min_{x\in\overline{\Omega}} \Sigma_{h,D}(x))^q}\xi^p + \|\sigma_a\|_\infty = 0.$$

If $\|\sigma_a\|_\infty > 0$ is sufficiently small (depending on $\min \Sigma_{h,D}$), then this equation has exactly two positive roots $0 < \kappa_* < K_*$ and they satisfy

$$\kappa_* = \frac{\|\sigma_a\|_\infty}{k_1^{(a)}} + O(\|\sigma_a\|_\infty^p),$$

$$K_* = \left\{ \frac{k_1^{(a)}(\min_{x\in\overline{\Omega}} \Sigma_{h,D}(x))^q}{C_a} \right\}^{1/(p-1)} - \frac{\|\sigma_a\|_\infty(1+o(1))}{(p-1)k_1^{(a)}}$$

as $\|\sigma_a\|_\infty \to 0$.

Theorem 2.4. (Case III) *Under the same assumptions as in Theorem 2.3, if the initial data* $(A_0(x), H_0(x))$ *satisfies*

$$\max_{x\in\overline{\Omega}} A_0(x) < K_* \quad \text{and} \quad H_0(x) \geqslant \max_{x\in\overline{\Omega}} \Sigma_{h,D}(x),$$

then

$$\max_{x\in\overline{\Omega}}(|A(x,t) - A_*(x)| + |H(x,t) - H_*(x)|) \leqslant Ce^{-\gamma t}$$

for all $t \geqslant 0$*. Here,* $(A_*(x), H_*(x))$ *is the almost decoupled stationary pattern given by Theorem 2.3;* C *and* γ *are positive constants depending also on* $(A_0(x), H_0(x))$*.*

Remarks.

(i) **A precise definition of the almost decoupled pattern:** A stationary solution $(A(x), H(x))$ is called an *almost decoupled pattern* if

$$\left.\begin{aligned} &-\mu_a(x)+\rho_a(A(x),H(x),x)\frac{A(x)^{p-1}}{H(x)^q}<0,\\ &-\mu_h(x)+\rho_h(A(x),H(x),x)\frac{A(x)^r}{H(x)^{s+1}}<0 \end{aligned}\right\} \quad \text{for all } x\in\overline{\Omega}.$$

(ii) If $\sigma_a \not\equiv 0$ and $\sigma_h \equiv 0$, then there is no almost decoupled pattern. Hence, patterns never collapse in Case IV.

(iii) In the case where $\sigma_h(x) \not\equiv 0$, the condition on the initial data does not contain τ. On the other hand, we have

Lemma. Let $\sigma_a(x) \equiv \sigma_h(x) \equiv 0$. If a solution $(A(x,t), H(x,t))$ of (GM) converges to $(0,0)$ as $t \to +\infty$ uniformly on $\overline{\Omega}$ and satisfies

$$-\mu_a A(x,t) + \rho_a \frac{A^p}{H^q} \leqslant 0 \qquad \text{for all} \quad x \in \overline{\Omega},\ t > 0,$$

then $\tau \geqslant [k_1^{(h)} q]/[k_1^{(a)}(p-1)]$.

(iv) It was Professor Niro Yanagihara who, more than thirty years ago, found a solution of (GM) such that $u(x,t) \to 0$, $v(x,t) \to 0$ as $t \to +\infty$ in the case where both of ρ_a, ρ_h are constants, $\sigma_a(x) \equiv 0$, $\sigma_h(x) \equiv 0$, $\kappa = 0$, and $(p,q,r,s) = (2,1,2,0)$.

From a view point of the possibility of collapse, the results may be summarized as in the table below:

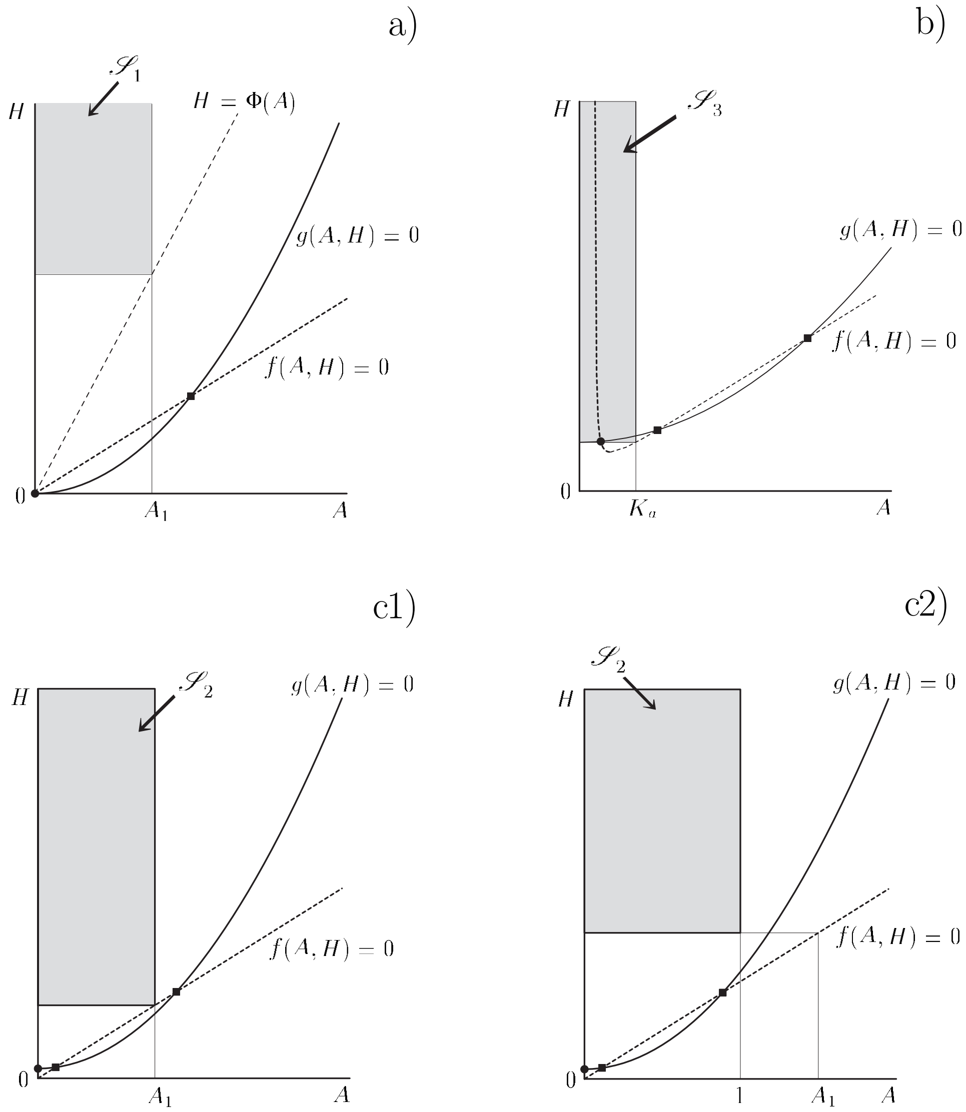
Cases	Basic production terms	Collapse
Case I	$\sigma_a(x) \equiv 0$, $\sigma_h(x) \equiv 0$	occurs for $\tau > q/(p-1)$.
Case II	$\sigma_a(x) \equiv 0$, $\sigma_h(x) \not\equiv 0$	occurs (for any $\tau > 0$).
Case III	$\sigma_a(x) \not\equiv 0$, $\sigma_h(x) \not\equiv 0$	occurs (if σ_a is small) for any $\tau > 0$.
Case IV	$\sigma_a(x) \not\equiv 0$, $\sigma_h(x) \equiv 0$	never occurs.

Activator-Inhibitor System with Different Sources

$$\begin{cases} \dfrac{\partial A}{\partial t} = \varepsilon^2 \Delta A - A + \dfrac{A^2}{H} + \sigma_a \\ \tau \dfrac{\partial H}{\partial t} = D \Delta H - H + A^2 + \sigma_h \\ \dfrac{\partial A}{\partial \nu} = \dfrac{\partial H}{\partial \nu} = 0 \qquad \text{on } \partial\Omega \\ A(x,0) = A_0(x), \quad H(x,0) = H_0(x) \end{cases}$$

$$f(A,H) = -A + \frac{A^2}{H} + \sigma_a, \quad g(A,H) = -H + A^2 + \sigma_h.$$

Inhibitor-Dominant Strips: a) Case I, b) Case III, c) Case II



3. Possible Scenario.

Summing up, the breakdown of pattern formation seems to contain the following three ingredients:

- Destabilization of the constant stationary solution by diffusion-induced instability (Turing instability) — local property
- Existence of an unstable periodic solution (or a "spiral-out mechanism") that amplifies disturbances — global property
- Existence of an (almost) decoupled stationary pattern

Or, more precisely, it is an orbit connecting the unstable constant stationary solution with the almsot decoupled stationary pattern (in the case $\sigma_h \not\equiv 0$).

4. Idea of Proof. To prove the theorems we follow the approach due to Wu and Li [WL] and make use of the following two lemmas:

Lemma 4.1. *If* $H_0(x) \geqslant \Sigma_{h,D}(x)$, *then*

$$H(x,t) \geqslant \max\{\min_{x\in\overline{\Omega}} H_0(x)e^{-k_2^{(h)}\,t/\tau},\ \Sigma_{h,D}(x)\}.$$

Lemma 4.2. *Let* $w(t) = \min_{x\in\overline{\Omega}} H_0(x)e^{-k_2^{(h)}\,t/\tau}$, *and let* $U(t)$ *be the solution of the initial value problem*

$$\frac{dU}{dt} = -k_1^{(a)}\,U + C_a\frac{U^p}{w(t)^q} + \|\sigma_a\|_\infty\ (t>0), \quad U(0) = \max_{x\in\overline{\Omega}} A_0(x).$$

Then $A(x,t) \leqslant U(t)$ *for all* $x \in \overline{\Omega}$ *and* $t \geqslant 0$ *in the maximal existence interval of* $U(t)$.

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