Biological phenomena : description, modelling and mathematical approach

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Lecture 2

Parabolic equations in biology

Outline of lecture 2

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Parabolic equation in biology

Let us denote $n(t,x)$ the density of cells at time t, position $x \in \mathbb{R}^d$. We assume that cells

- move randomly according to Brownian motions,
- are subjected to an external force field $U(t,x) \in \mathbb{R}^d$,
- growth and die ; we denote by $B(t,x)$ and $D(t,x)$ respectively the birth and death term.

The system governing the dynamics of the population n reads

$$\partial_t n \underbrace{-D\ \Delta n}_{\text{active motion}} + \underbrace{\mathrm{div}(U(t,x)n)}_{\text{oriented drift}} = \underbrace{B(t,x) - D(t,x)}_{\text{growth and death}}.$$

The quantity $D > 0$ is the diffusion coefficient.

Such system enters into the class of parabolic equations.

Laplacian operator

The notation Δ is for the Laplacian operator :

$$\Delta n := \mathrm{div}(\nabla n) = \sum_{i=1}^{d} \frac{\partial^2 n}{\partial x_i^2}.$$

Laplacian operator

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$$\Delta n := \operatorname{div}(\nabla n) = \sum_{i=1}^{d} \frac{\partial^2 n}{\partial x_i^2}.$$

In the following, Ω will always denote a bounded domain of $\mathbb{R}^d$, whose frontier is denoted $\partial\Omega$ and ν is the unit outward normal at the boundary.
We use also the following notation :

- $L^2(\Omega)$ the space of measurable functions with square integrable. The associated norm is denoted

$$\|f\|_{L^2(\Omega)}^2 = \int_\Omega |f(x)|^2 \, dx.$$

- $H^1(\Omega) = \{ f \in L^2(\Omega) \text{ s.t. } \forall\, i = 1, \dots, d,\ \partial_{x_i} f \in L^2(\Omega) \}$. The associated norm is

$$\|f\|_{H^1(\Omega)}^2 = \int_\Omega \Big(|f(x)|^2 + \sum_{i=1}^{d} |\partial_{x_i} f(x)|^2 \Big) \, dx.$$

Laplacian operator

In the same spirit, we may define

- $H^2(\Omega) = \{f \in H^1(\Omega) \text{ s.t. } \forall\, i = 1,\dots,d,\ \partial_{x_i} f \in H^1(\Omega)\}$. The associated norm is

$$\|f\|^2_{H^2(\Omega)} = \int_\Omega \Big(|f(x)|^2 + \sum_{i=1}^{d} |\partial_{x_i} f(x)|^2 + \sum_{i,j=1}^{d} |\partial^2_{x_i x_j} f(x)|^2 \Big)\, dx.$$

When $f \in H^2(\Omega)$, then $\Delta f \in L^2(\Omega)$. Moreover, we have the important formula

Green formula (integration by parts)

$$\forall\, f, g \in H^2(\Omega), \qquad -\int_\Omega \Delta f\, g\, dx = \int_\Omega \nabla f \cdot \nabla g\, dx - \int_{\partial\Omega} \partial_\nu f\, g\, d\sigma.$$

(Recall the notation $\partial_\nu f = \nabla f \cdot \nu$ where ν is the unit outward normal at the boundary).

Laplacian operator : boundary conditions

- When Ω is not bounded, $\Omega = \mathbb{R}^d$, we will always assume that we are considering integrable functions which vanish at infinity. Then, boundary terms will always vanish.
- When Ω is bounded, we usually consider two kinds of boundary data
  - Dirichlet boundary conditions. In this case the function is prescribe at the boundary : $\boxed{f = \alpha \text{ on } \partial\Omega.}$

    It corresponds to situation where we know the quantity entering into the domain.
  - Neumann boundary conditions. In this case the normal derivative is prescribe at the boundary : $\boxed{\partial_\nu f = \alpha \text{ on } \partial\Omega.}$

    It corresponds to situation where we knwo the flux entering into the domain. In the case of homogeneous Neumann boundary conditions $\partial_\nu f = 0$, we say that the system is insolated.

Poincaré inequality

For the case of homogeneous Dirichlet boundary conditions : $f = 0$, we introduce the functional space

$$H_0^1(\Omega) = \{f \in H^1(\Omega) \text{ s.t. } f_{|\partial\Omega} = 0\}.$$

Then we have

Poincaré inequality

$$\exists\, \lambda > 0, \quad \forall\, u \in H_0^1(\Omega), \quad \lambda \|u\|_{L^2(\Omega)} \leq \|\nabla u\|_{L^2(\Omega)}.$$

We say that λ is the *best constant in the Poincaré inequality* if $\lambda = \sup_{u \neq 0} \frac{\|\nabla u\|_{L^2(\Omega)}}{\|u\|_{L^2(\Omega)}}$.

Asymptotic behaviour

In population dynamics, assuming Dirichlet boundary conditions boils down to consider that individuals reaching the boundary of the domain are killed. As a consequence, if the diffusion is stronger than the reaction, then all solutions to reaction diffusion system will converge to 0.
Indeed, let us consider a reaction-diffusion system of I populations

$$\partial_t u_i - D_i \Delta u_i = F_i(t, x, u_1, \dots, u_I), \qquad i = 1, \dots, I, \quad x \in \Omega,$$
$$u_i(t, x) = 0, \qquad \text{on } \partial\Omega,$$
$$u_i(t = 0, x) = u_i^0(x) \in L^2(\Omega).$$

Assume $F_i(t, x, 0) = 0$ such that 0 is a steady state. Is it stable and attractive ?

Lemma

Assume that there is a constant $L > 0$ such that $\|\mathbf{F}(t, x, \mathbf{u})\| \le L|\mathbf{u}\|$.
Assume moreover that $\min_i D_i = d > 0$ and L is small enough such that $\delta = d\lambda^2 - L > 0$, where λ is the best constant in the Poincaré inequality. Then,

$$\int_\Omega \|\mathbf{u}\|^2 \, dx := \sum_{i=1}^{I} \int_\Omega |u_i(t, x)|^2 \, dx \le e^{-2\delta t} \sum_{i=1}^{I} \int_\Omega |u_i^0(x)|^2 \, dx.$$

Asymptotic behaviour

Proof. Multiply the equation by u_i and integrate, we get (thanks to the Green formula)

$$\frac{1}{2}\frac{d}{dt}\int_\Omega |u_i|^2\,dx + D_i\int_\Omega |\nabla u_i|^2 dx = \int_\Omega u_i F_i(\mathbf{u})\,dx.$$

Applying the Poincaré inequality in the second term and summing over i, we get

$$\begin{aligned}\frac{1}{2}\sum_{i=1}^{I}\frac{d}{dt}\int_\Omega |u_i|^2\,dx + d\lambda^2\sum_{i=1}^{I}\int_\Omega |u_i|^2 dx &\le \sum_{i=1}^{I}\int_\Omega u_i F_i(\mathbf{u})\,dx \\ &\le \int_\Omega \|\mathbf{u}\|\,\|\mathbf{F}(\mathbf{u})\|\,dx \le L\int_\Omega \|\mathbf{u}\|^2\,dx,\end{aligned}$$

where we use the Cauchy-Schwarz inequality $\Big(\sum_i |x_i y_i| \le \|\mathbf{x}\|\,\|\mathbf{y}\|$ with $\|\mathbf{x}\| = (\sum_i |x_i|^2)^{\frac{1}{2}}\Big)$. Hence,

$$\frac{d}{dt}\int_\Omega \|\mathbf{u}\|^2\,dx \le -2\delta\int_\Omega \|\mathbf{u}\|^2\,dx.$$

The conclusion follows after an integration in time. □

Asymptotic behaviour

In the case of homogeneous Neumann boundary conditions, we make use of the

Poincaré-Wirtinger inequality

$$\exists\, \mu > 0, \quad \forall\, v \in H^1(\Omega), \quad \mu \int_\Omega |v - \langle v\rangle|^2\, dx \le \int_\Omega |\nabla v|^2\, dx,$$

with the notation $\langle v\rangle = \frac{1}{|\Omega|}\int_\Omega v(x)\, dx$.

Then, solution to reaction-diffusion system with Neumann boundary conditions tends to become homogeneous :

Lemma

Let us consider the same reaction-diffusion system with Neumann boundary conditions (instead of Dirichlet). Assume that there exists $L > 0$ such that, for all $\mathbf{u}$, $\mathbf{v}$, $(\mathbf{F}(\mathbf{u}) - \mathbf{F}(\mathbf{v}))\cdot(\mathbf{u}-\mathbf{v}) \le L|\mathbf{u}-\mathbf{v}|^2$. Assume $\min_i D_i = d > 0$ and L is small enough such that $\delta = d\mu - L$ (where μ is the best constant in the Poincaré-Wirtinger inequality). Then,

$$\int_\Omega \|\mathbf{u} - \langle \mathbf{u}\rangle\|^2\, dx \le e^{-2\delta t}\int_\Omega \|\mathbf{u}^0 - \langle \mathbf{u}^0\rangle\|^2\, dx.$$

Asymptotic behaviour

Proof. We follow the same analysis as above. First, by integrating the equation, using the Green formula with Neumann boundary conditions, we get

$$\frac{d}{dt}\langle u_i\rangle = \langle F_i(\mathbf{u})\rangle.$$

Therefore,

$$\frac{d}{dt}(u_i - \langle u_i\rangle) - D_i\Delta(u_i - \langle u_i\rangle) = F_i(\mathbf{u}) - \langle F_i(\mathbf{u})\rangle.$$

Then, multiplying by $u_i - \langle u_i\rangle$, summing over i, and integrating, we get

$$\begin{aligned}
&\frac{1}{2}\frac{d}{dt}\int_\Omega \|\mathbf{u} - \langle \mathbf{u}\rangle\|^2\,dx + d\int_\Omega \|\nabla(\mathbf{u} - \langle \mathbf{u}\rangle)\|^2\,dx \\
&\leq \sum_{i=1}^{I}\int_\Omega (F_i(\mathbf{u}) - \langle F_i(\mathbf{u})\rangle)(u_i - \langle u_i\rangle)\,dx = \sum_{i=1}^{I}\int_\Omega F_i(\mathbf{u})(u_i - \langle u_i\rangle)\,dx \\
&\quad = \sum_{i=1}^{I}\int_\Omega (F_i(\mathbf{u}) - F_i(\langle \mathbf{u}\rangle))(u_i - \langle u_i\rangle)\,dx \leq L\int_\Omega \|\mathbf{u} - \langle \mathbf{u}\rangle\|^2\,dx.
\end{aligned}$$

We conclude using the Poincaré-Wirtinger inequality, by the same token as above.

Outline of lecture 2

Introduction

An interesting phenomena modelled by reaction-diffusion equation in full space is propagation phenomenon, mathematically described thanks to traveling waves.
In biology, traveling waves have been used in many situations to explain invasiveness of a species, spread of a genetic trait, propagation of epidemy, ...

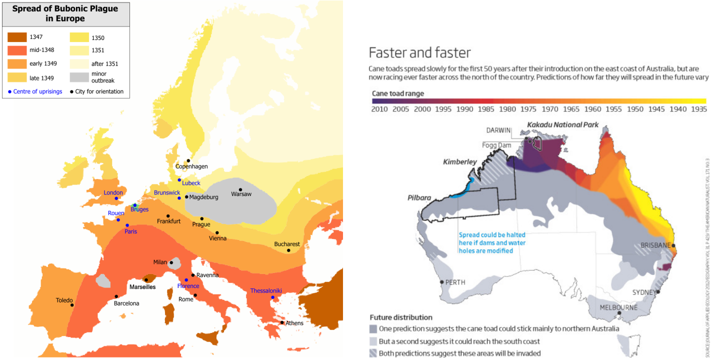


FIGURE – Two examples of invasion phenomena : Left : bubonic plague in Europe during the middle age ; Right : cane toads in Australia nowadays.

Setting of the problem

To simplify, we work in one space dimension and consider one species whose dynamics is governed by the reaction-diffusion equation :

$$\partial_t u - \partial_{xx} u = f(u), \quad t > 0, x \in \mathbb{R}.$$

Definition

A traveling wave solution is a solution of the form $u(t,x) = v(x - ct)$ with $c \in \mathbb{R}$ a constant called traveling speed.

We usually consider the case where the function f admits two stationary states $f(0) = f(1) = 0$:

- Fisher/KPP (monostable) equation : $f(u) = u(1 - u)$.
- Allen-Cahn (bistable) equation : $f(u) = u(1 - u)(u - \theta)$.

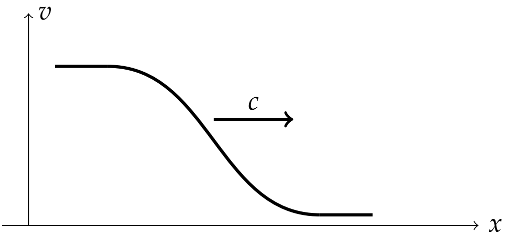
We complete the definition by the conditions $v(-\infty) = 1$, and $v(+\infty) = 0$.
When $c > 0$, this expresses the fact that the state $v = 1$ invades the state $v = 0$.
When $c < 0$, the state $v = 0$ invades the state $v = 1$.
Injecting the expression $u(t,x) = v(x - ct)$ into the equation, we arrive at the system :

Setting of the problem

Problem

We look for a real-valued function v and a real c such that

$$v'' + cv' + f(v) = 0, \quad \text{on } \mathbb{R},$$
$$v(-\infty) = 1, \quad v(+\infty) = 0.$$



When $c = 0$, we say that we have a stationary state or a standing wave.

Setting of the problem

Observations :

- The problem is invariant by translation :
  If $v(x)$ is a solution, then $v(x+a)$ is a solution for any $a \in \mathbb{R}$. Then, we normalize by setting for instance $v(0) = \frac{1}{2}$.
- Multiplying by v', we get

$$\frac{1}{2}((v')^2)' + c(v')^2 + (F(v))' = 0, \quad \text{where } F(v) = \int_0^v f(s)\,ds.$$

Integrating (using the fact that $v'(\pm\infty) = 0$), we find

$$c\int_{\mathbb{R}} (v'(x))^2\,dx = F(1) = \int_0^1 f(s)\,ds.$$

An important consequence is that

c has the same sign as $\int_0^1 f(s)\,ds$.

For instance, in the Fisher/KPP case, $f(u) = u(1-u) \geq 0$ for $u \in [0,1]$, thus $F(1) > 0$, it means that $v = 1$ is invading.

Outline of lecture 2

The monostable equation with ignition temperature

For $\theta \in (0,1)$, $\mu > 0$, we take $f(u) = \begin{cases} 0 & \text{for } 0 \le u < \theta, \\ \mu(1-u) & \text{for } \theta < u \le 1. \end{cases}$

Lemma

For f as above, there is a unique traveling wave solution (c^*, v) with v decreasing and normalized with $v(0) = \theta$.

Proof. We have seen above that $c > 0$. Thanks to the normalization $v(0) = \theta$ and the fact that v is decreasing, we look for a solution with $v > \theta$ for $x < 0$. Then $f(v) = \mu(1 - v)$ for $x < 0$,

$$cv' + v'' + \mu(1 - v) = 0.$$

The solution is given by $v = 1 - (1 - \theta)e^{\lambda_+ x}$, $x \le 0$ with $\lambda_+ = \frac{1}{2}(-c + \sqrt{c^2 + 4\mu}) > 0$.
For $x > 0$, we look for $v < \theta$, then $f(v) = 0$. The solution reads $v(x) = \theta e^{-cx}$ for $x \ge 0$.
It remains to check that v is differentiable at $x = 0$, that is

$$-c\theta = -(1 - \theta)\lambda_+.$$

This equation admits an unique solution $c^* > 0$ (since $c \mapsto \lambda_+$ is decreasing). □

Bistable equation

We can extend the argument above to the bistable case. We take for $\theta \in (0,1), \mu > 0, \nu > 0$, $f(u) = \begin{cases} -\nu u & \text{for } 0 \leq u < \theta, \\ \mu(1-u) & \text{for } \theta < u \leq 1. \end{cases}$

Lemma

For f as above, there is a unique solution (c^*, v) with v decreasing and normalized with $v(0) = \theta$.

Proof. For $x < 0$, the equation reads $v'' + cv' + \mu(1-v) = 0$. Then, $v(x) = 1 - (1-\theta)e^{\lambda_1 x}$, $\lambda_1 = \frac{1}{2}(-c + \sqrt{c^2 + 4\mu})$.
For $x > 0$, the equation reads $v'' + cv' - \nu v = 0$. Then, $v(x) = \theta e^{-\lambda_2 x}$, $\lambda_2 = \frac{1}{2}(c + \sqrt{c^2 + 4\nu})$.
To match the derivatives at $x = 0$, we have to impose $\lambda_2 \theta = (1-\theta)\lambda_1$. The function $c \mapsto \lambda_1$ is decreasing, whereas $c \mapsto \lambda_2$ is increasing, and the limits at $\pm\infty$ are opposite infinity. Thus this latter equation admits a unique solution c^*. □

Outline of lecture 2

Analytical example

We take for $\theta \in (0,1), \mu > 0$, $f(u) = \begin{cases} \mu(1-\theta)u & \text{for } 0 \le u < \theta, \\ \mu\theta(1-u) & \text{for } \theta < u \le 1. \end{cases}$

Lemma

For f given as above. There exists a minimal speed $c^* = 2\sqrt{(1-\theta)\mu}$ and for all $c \ge c^*$ a unique solution (c, v) with v decaying and normalized by $v(0) = \theta$.

Proof. For $x < 0$, we want $v > \theta$, then the equation reads

$$v'' + cv' + \mu\theta(1-v) = 0.$$

The unique solution that tends to 1 at $-\infty$ is

$$v(x) = 1 - (1-\theta)e^{\lambda_+ x}, \quad x \le 0, \qquad \lambda_+ = \frac{1}{2}(-c + \sqrt{c^2 + 4\mu\theta})$$

For $x > 0$, we look for $v < \theta$, then $v'' + cv' + \mu(1-\theta)v = 0$. The characteristic polynomial for this ODE is $\lambda^2 + c\lambda + \mu(1-\theta)$. If $c < c^*$, then the roots of this polynomial are complex conjugate, then there no solutions decaying and nonnegative to the ODE. For $c \ge c^*$, both roots of the polynomial are negative and are given by $\mu_\pm = \frac{1}{2}(-c \pm \sqrt{c^2 - 4\mu(1-\theta)})$.

Analytical example

Then, for $x \geq 0$,

$$v(x) = \theta e^{\mu_- x} + a(e^{\mu_+ x} - e^{\mu_- x}), \qquad \mu_\pm = \frac{1}{2}(-c \pm \sqrt{c^2 - 4\mu(1-\theta)}).$$

This function is positive iff $a \geq 0$. It remains to check that the derivatives match at $x = 0$, that is $-(1-\theta)\lambda_+ = \theta a \mu_- + a(\mu_+ - \mu_-)$. It reads

$$c - (1-\theta)\sqrt{c^2 + 4\mu\theta} + \theta\sqrt{c^2 - 4\mu(1-\theta)} = 2a\sqrt{c^2 - 4\mu(1-\theta)}.$$

For $c > c^*$, the left hand side is positive. Therefore we can compute a unique $a > 0$ satisfying this equality for any $c \geq c^*$. This allows to contruct a positive and decaying function v. □

The monostable equation with ignition temperature

θ=*ignition temperature* : minimal temperature required to burn a gas and start the reaction.

$$\partial_t u - \partial_{xx} u = f_\theta(u), \qquad f_\theta(u) = \begin{cases} 0 & 0 \le u \le \theta \\ > 0 & \theta < u < 1 \\ 0 & u = 1 \end{cases}$$

Traveling wave problem

Find c and v such that

$$-v'' - cv' = f_\theta(v), \quad x \in \mathbb{R},$$
$$v(-\infty) = 1, \qquad v(+\infty) = 0.$$

Theorem

There is a unique decreasing traveling wave solution (c^*, v) normalized with $v(0) = \frac{1}{2}$ and it holds that $c^* > 0$.

The monostable equation with ignition temperature

Proof. Such result is known since decades. There are several techniques of proof. We provide here a simple proof based on a phase space method for ODE [1]. The proof is divided into three steps :

1. reduction to a simple ODE ;
2. monotonicity in c ;
3. existence by a continuity argument.

- 1st step : Reduction to a simple ODE

We set $w = -v'$ (so that $w > 0$ since we look for v decreasing). The equation becomes

$$v' = -w \qquad w' = -cw + f(v)$$
$$v(-\infty) = 1,\ w(-\infty) = 0, \quad v(+\infty) = 0,\ w(+\infty) = 0.$$

1. H. Berestycki, B. Nikolaenko, and B. Scheurer, Travelling waves solutions to combustion models and their singular limits, SIAM J. Math. Anal., 16 (1985)

The monostable equation with ignition temperature

By monotonicity of v, we can invert $v(x)$ as a function $X(v)$, $0 \le v \le 1$. We set $\tilde{w}(v) = w(X(v))$. The system becomes

$$\frac{d\tilde{w}}{dv} = \frac{dw}{dx}\Big(\frac{dv}{dx}\Big)^{-1} = c - \frac{f(v)}{\tilde{w}(v)}, \qquad 0 \le v \le 1,$$
$$\tilde{w}(0) = \tilde{w}(1) = 0, \quad \tilde{w} \ge 0.$$

Problem

Finally, we arrive at the question to know if the solution to the Cauchy problem

$$\frac{d\tilde{w}}{dv} = c - \frac{f(v)}{\tilde{w}(v)}, \qquad 0 \le v \le 1, \tag{1}$$
$$\tilde{w}(0) = 0,$$

can also achieve for a special value of c the conditions $\tilde{w}_c(1) = 0$, $\tilde{w}_c \ge 0$.

Notice that there is a priori a singularity at $v = 0$. But for $0 \le v \le \theta$, $f(v) = 0$ and the solution is simply $\tilde{w}_c(v) = cv$, $0 \le v \le \theta$.

The monostable equation with ignition temperature

Then the solution can be continued smoothly as a simple ODE until $\tilde{w}_c$ vanishes and the problem is not defined any longer. There are two possibilities :

- either $\tilde{w}_c(v) > 0$ for $0 \leq v \leq 1$, we call this solution *Type 1* and we set $v_c = 1$.
- or there exists $v_c < 1$ such that $\tilde{w}_c(v_c) = 0$, we call this solution *Type 2*.

We are interested in the limiting case.

The monostable equation with ignition temperature

Then the solution can be continued smoothly as a simple ODE until $\tilde{w}_c$ vanishes and the problem is not defined any longer. There are two possibilities :

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We are interested in the limiting case.

- 2nd step : Monotonicity in c.

Lemma

The mapping $c \mapsto \tilde{w}_c(v)$ is increasing for those v where it is defined, i.e. for $0 < v < v_c$.

Proof. We set $z_c(v) = \frac{d\tilde{w}(v)}{dc}$. From (1), it satisfies

$$\frac{dz_c(v)}{dv} = 1 + \frac{f(v)}{(\tilde{w}_c(v))^2} z_c(v), \quad z_c(0) = 0.$$

We deduce that z_c cannot vanish for $v > 0$ and thus $z_c(v) \geq v$ as long as it is defined, i.e. for $v < v_c$. □

The monostable equation with ignition temperature

Consequently $\tilde{w}_c(1)$ is an increasing function of c. Therefore there can be at most one value of c satisfying the condition $\tilde{w}_c(1) = 0$.

- 3rd step : Existence.

Let us define

$$\underline{c}^2 = \int_0^1 \frac{f(v)}{v}\,dv, \qquad \overline{c}^2 = 4 \max_{0\le v\le 1} \frac{f(v)}{v}.$$

Clearly $\underline{c} < \overline{c}$. Moreover, we have

Lemma

For $c > \overline{c}$, the solution is of *Type 1*. For $c < \underline{c}$, the solution is of *Type 2*.

Once this lemma is proved, the existence of a c such that $\tilde{w}_c(1) = 0$ follows by a continuity argument. The uniqueness is a consequence of the monotonicity.

The monostable equation with ignition temperature

Proof of the Lemma.

• *For $c > \overline{c}$ the solution is Type 1 :*

We consider the largest interval $[0, v_0] \subset [0, 1]$ on which $\tilde{w}_c(v) \geq \frac{c}{2} v$. Since $\tilde{w}_c(v) = cv$ on $[0, \theta]$, clearly $v_0 > \theta$. If $v_0 < 1$, then $\tilde{w}'_c(v_0) \leq \frac{c}{2}$ and we would have

$$\frac{c}{2} \geq \frac{d\tilde{w}_c(v_0)}{dv} = c - 2\frac{f(v_0)}{cv_0} \geq c - \frac{\overline{c}^2}{2c}.$$

This is a contradiction with the fact that $c > \overline{c}$.

• *For $c < \underline{c}$ the solution is Type 2 :*

Since $\frac{f(v)}{\tilde{w}(v)} \geq 0$, we have from (1) $\tilde{w}_c(v) \leq cv$ as long as it is defined. Thus,

$$\frac{d\tilde{w}_c(v)}{dv} = c - \frac{f(v)}{\tilde{w}_c(v)} \leq c - \frac{f(v)}{cv}.$$

It implies that, if the solution did not vanish before $v = 1$, we could integrate on $(0, 1)$ and get

$$0 \leq \tilde{w}_c(1) < c - \int_0^1 \frac{f(s)}{cs}\, ds = c - \frac{\underline{c}^2}{c}.$$

Contradiction with the fact that $c < \underline{c}$. □

The Fisher/KPP equation

The situation is quite different than the case with ignition temperature. A famous result is

Theorem

For any $c \geq c^* = 2$, there is a unique traveling wave solution v with $0 \leq v \leq 1$ and v monotically decreasing.

- The quantity c^* is called the minimal propagation speed.
- This result can be extended to general equation

$$\partial_t u - \nu \partial_{xx} u = f(u), \text{ with } f(0) = f(1) = 0, \ f(u) > 0 \text{ for } 0 < u < 1.$$

In this case, the minimal propagation speed is $c^* = 2\sqrt{f'(0)\nu}$.

Outline of lecture 2

Allen-Cahn (bistable) equation

We consider the *bistable* case, i.e. 0 and 1 are both stable steady state.

Traveling wave solution

We look for $c \in \mathbb{R}$ and a real-valued function v such that

$$v'' + cv' + f(v) = 0$$
$$v(-\infty) = 1, \quad v(+\infty) = 0, \quad v(0) = \frac{1}{2}.$$

We will make use of the notation $F(u) = \int_0^u f(v)\, dv$. We assume that

$$f(0) = 0, \quad f'(0) < 0, \quad f(\alpha) = 0, \quad f(1) = 0, \quad f'(1) < 0,$$
$$f(u) < 0 \text{ on } (0, \alpha), \qquad f(u) > 0 \text{ on } (\alpha, 1).$$

Adapting the phase space method, we may prove :

Theorem

Under these assumptions, there exists a unique traveling wave solution (c^*, v) with v decreasing.
We have $c^* > 0$ for $F(1) > 0$, $c^* = 0$ for $F(1) = 0$, $c^* < 0$ for $F(1) < 0$.

Allen-Cahn (bistable) equation

A simple choice of bistable function satisfying the assumptions is

$$f(u) = u(1-u)(u-\alpha).$$

In this case, we have the explicit expression of the traveling wave solution

$$v(x) = \frac{e^{-x/\sqrt{2}}}{1+e^{-x/\sqrt{2}}}, \qquad c^* = \sqrt{2}(\frac{1}{2}-\alpha).$$

Indeed, we may compute with this expression,

$$v' = \frac{1}{\sqrt{2}}v(v-1), \qquad v'' = \frac{v'}{\sqrt{2}}(2v+1) = v(v-1)(v+\frac{1}{2}).$$

Thus, $-c^*v' - v'' = v(1-v)(v + \frac{c^*}{\sqrt{2}} + \frac{1}{2}) = f(v)$.

Outline of lecture 2

Eigenelements of the Laplace operator

Let Ω be a regular bounded domain in $\mathbb{R}^d$.
We consider the Laplace operator on Ω with either Dirichlet or Neumann boundary conditions

$$\begin{cases} -\Delta u = f, & \text{in } \Omega, \\ u = 0, & \text{on } \partial\Omega. \end{cases} \quad \text{(D)} \qquad \begin{cases} -\Delta u = f, & \text{in } \Omega, \\ \partial_\nu u = 0, & \text{on } \partial\Omega. \end{cases} \quad \text{(N)}$$

Eigenelements are defined by (λ, w), $\lambda \in \mathbb{R}$ such that

$$\begin{cases} -\Delta w = \lambda w, & \text{in } \Omega, \\ u = 0, & \text{on } \partial\Omega. \end{cases} \qquad \begin{cases} -\Delta w = \lambda w, & \text{in } \Omega, \\ \partial_\nu u = 0, & \text{on } \partial\Omega. \end{cases}$$

Since this problem is linear, w is defined up to a constant. Then, we fix this constant by setting $\int_\Omega w^2 = 1$.

Examples in 1D

In one dimension, $\Omega = (0,1)$, $-w'' = \lambda w$,

- Dirichlet : $w(0) = w(1) = 0$. Then, necessarily $\lambda > 0$ (otherwise the only solution would be $w = 0$),

$$w(x) = A\cos(\sqrt{\lambda}x) + B\sin(\sqrt{\lambda}x).$$

With the condition $w(0) = 0$, it implies $A = 0$. The condition $w(1) = 0$ implies $B\sin(\sqrt{\lambda}) = 0$. Since we look for non-zero solutions, it implies $\lambda_k = (k\pi)^2$, for $k \in \mathbb{N}^*$, and the condition $\int_0^1 w^2(x)dx = 1$ implies $B = 1$.

$$w_k(x) = \sin(k\pi x), \quad k \in \mathbb{N}^*.$$

- Neumann : $w'(0) = w'(1) = 0$. By the same token as above, we find $\lambda_k = ((k-1)\pi)^2$, $k \in \mathbb{N}^*$, and

$$w_k(x) = \cos((k-1)\pi x), \quad k \in \mathbb{N}^*.$$

Examples in 2D

In two dimensions, $\Omega = (0, L_1) \times (0, L_2)$, $-\partial_{xx} w - \partial_{yy} w = \lambda w$.
We look for a solution under the form $w(x, y) = f(x)g(y)$. Then we get $-\frac{f''}{f}(x) - \frac{g''}{g}(y) = \lambda$. Therefore, we have

$$-f''(x) = \mu f(x), \qquad -g''(y) = \nu g(y),$$

with μ independent of x and ν independent of y.

- Dirichlet : We get

$$f(x) = A \sin(\sqrt{\mu_k} x), \quad \mu_k = (\frac{k}{L_1}\pi)^2,$$
$$g(y) = B \sin(\sqrt{\nu_\ell} y), \quad \nu_\ell = (\frac{\ell}{L_2}\pi)^2.$$

Thus the eigenelements for the Dirichlet problem are given by

$$w_{k\ell} = a_{k\ell} \sin\left(k\pi \frac{x}{L_1}\right) \sin\left(\ell\pi \frac{y}{L_2}\right), \qquad \lambda_{k\ell} = \Big((\frac{k}{L_1})^2 + (\frac{\ell}{L_2})^2 \Big) \pi^2.$$

The constant $a_{k\ell}$ is computed thanks to the normalisation condition.

Examples in 1D

- Neumann : By the same token, we find

$$w_{k\ell} = b_{k\ell} \cos\big((k-1)\pi \frac{x}{L_1}\big) \cos\big((\ell-1)\pi \frac{y}{L_2}\big),$$
$$\lambda_{k\ell} = \Big(\big(\frac{k-1}{L_1}\big)^2 + \big(\frac{\ell-1}{L_2}\big)^2\Big)\pi^2, \qquad k,\ell \in \mathbb{N}^*.$$

We notice that 0 is an eigenvalue for Neumann problem. Eigenvalues may be multiple, except the first one.

Outline of lecture 2

Main results

Theorem (Dirichlet case)

Let Ω be a bounded connected open and regular set of $\mathbb{R}^d$. Then there exists a spectral basis for (D) i.e. (λ_k, w_k) which satisfy

1. $0 < \lambda_1 < \lambda_2 \leq \lambda_3 \leq \ldots \leq \lambda_k \ldots,\ \lambda_k \underset{k\to+\infty}{\longrightarrow} +\infty$.
2. $-\Delta w_k = \lambda_k w_k$, in Ω, with $w_k = 0$, on $\partial\Omega$.
3. $(w_k)_{k\geq 1}$ is an orthonormal basis of $L^2(\Omega)$.
4. We have $w_1(x) > 0$ in Ω and the first eigenvalue λ_1 is simple.

Main results

Theorem (Neumann case)

Let Ω be a bounded connected open and regular set of $\mathbb{R}^d$. Then there exists a spectral basis for (N) i.e. (λ_k, w_k) which satisfy

1. $0 = \lambda_1 < \lambda_2 \leq \lambda_3 \leq \ldots \leq \lambda_k \ldots,\ \lambda_k \underset{k\to+\infty}{\to} +\infty$.
2. $-\Delta w_k = \lambda_k w_k$, in Ω, with $\partial_\nu w_k = 0$, on $\partial\Omega$.
3. $(w_k)_{k\geq 1}$ is an orthonormal basis of $L^2(\Omega)$.
4. We have $w_1(x) = \frac{1}{\sqrt{|\Omega|}} > 0$.

Main results

Some remarks :

- In the Dirichlet case, we have

$$\lambda_1 = \inf_{\int_\Omega |u|^2=1} \left\{ \int_\Omega |\nabla u|^2\,dx, \quad u \in H_0^1(\Omega) \right\}.$$

  Then, λ_1^{-1} is the best constant in the Poincaré inequality :

$$\forall\, u \in H_0^1(\Omega), \quad \int_\Omega u^2\,dx \le \frac{1}{\lambda_1}\int_\Omega |\nabla u|^2\,dx,$$

  this inequality being an equality for $u = \alpha w_1$.

- Defining $E_k =$ Span$\{w_1,\dots,w_k\}$, other eigenvalues are given by,

$$\lambda_{k+1} = \min_{u\in E_k^\perp \cap H_0^1(\Omega), \int_\Omega u^2=1} \left\{ \int_\Omega |\nabla u|^2\,dx \right\}.$$

- In the Neumann case, we have $\forall\, v \in H^1(\Omega)$,

$$\lambda_2 \int_\Omega |v(x) - \langle v\rangle|^2\,dx \le \int_\Omega |\nabla v|^2\,dx, \text{ with } \langle v\rangle = \frac{1}{|\Omega|}\int_\Omega v(x)\,dx.$$

Outline of lecture 2

Main result

An amazingly counter-intuitive observation is the instability mechanism proposed by Allen Turing.
Consider the ODE system

$$\frac{d}{dt}u = au + bv \qquad \frac{d}{dt}v = cu + dv,$$

with $a, b, c, d \in \mathbb{R}$ such that

$$T = a + d < 0, \qquad D = ad - bc > 0. \tag{2}$$

Then the matrix $A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$ has two eigenvalues with negative reals part : $r_\pm = \frac{1}{2}(T \pm \sqrt{T^2 - 4D})$. We deduce that the equilibrium $(0, 0)$ is stable (and attractive).

Main result

Adding diffusion (and restricting to bounded domain), we consider now :

$$\partial_t u - \sigma_u \Delta u = au + bv, \qquad \partial_t v - \sigma_v \Delta v = cu + dv, \quad \text{on } \Omega.$$

We complement by Dirichlet or Neumann boundary conditions on $\partial\Omega$.
Clearly $(0,0)$ is still a steady state for this equation. In principle, we expect that adding diffusion would help for stability, but surprisingly, we have

Theorem

Under the above assumptions (2) with moreover $a > 0$ and $d < 0$. Then for σ_u small enough, the steady state $(u,v) = (0,0)$ is linearly unstable. Moreover, only a finite number of eigenmodes are unstable.

Proof of the main result

Proof. We consider the eigenfunctions $(w_k)_{k\geq 1}$ for the Laplace operator with Dirichlet or Neumann boundary conditions (according to the one considered here). Then we decompose

$$u(t,x) = \sum_{k=1}^{\infty} \alpha_k(t) w_k(x), \qquad v(t,x) = \sum_{k=1}^{\infty} \beta_k(t) w_k(x).$$

This leads to, for $k \geq 1$,

$$\begin{aligned} \frac{d}{dt}\alpha_k(t) + \sigma_u \lambda_k \alpha_k &= a\alpha_k + b\beta_k \\ \frac{d}{dt}\beta_k(t) + \sigma_v \lambda_k \beta_k &= c\alpha_k + d\beta_k \end{aligned}$$

We look for a solution with exponential growth in time : $\alpha_k(t) = e^{\lambda t}\overline{\alpha}_k$, $\beta_k(t) = e^{\lambda t}\overline{\beta}_k$, with $\lambda > 0$.

Proof of the main result

The system reduces to

$$\lambda\overline{\alpha}_k + \sigma_u\lambda_k\overline{\alpha}_k = a\overline{\alpha}_k + b\overline{\beta}_k,$$
$$\lambda\overline{\alpha}_k + \sigma_v\lambda_k\overline{\beta}_k = c\overline{\alpha}_k + d\overline{b}eta_k.$$

This linear system admits a non-zero solution $(\overline{\alpha}_k, \overline{\beta}_k)$ iff
$\det\begin{pmatrix}\lambda + \sigma_u\lambda_k - a & -b \\ -c & \lambda + \sigma_v\lambda_k - d\end{pmatrix} = 0.$
Thus this system has a solution with exponential growth for those eigenvalues λ_k for which there exists a root $\lambda > 0$ to the *dispersion relation*

$$\lambda^2 + \lambda(\underbrace{(\sigma_u + \sigma_v)\lambda_k - T}_{>0 \text{ since } T<0}) + \sigma_u\sigma_v\lambda_k^2 - \lambda_k(d\sigma_u + a\sigma_v) + D = 0$$

This polynomial admits a positive root iff $\sigma_u\sigma_v\lambda_k^2 - \lambda_k(d\sigma_u + a\sigma_v) + D < 0$, which is equivalent to

$$\lambda_k^2 - \lambda_k(\frac{d}{\sigma_v} + \frac{a}{\sigma_u}) + \frac{D}{\sigma_u\sigma_v} < 0. \qquad (3)$$

Proof of the main result

Finally, the question boils down to know if there exist eigenvalues λ_k which satisfy the latter inequality. The roots of this second order polynomial in λ_k are given by

$$\Lambda_\pm = \frac{1}{2\sigma_v\theta}\left(d\theta + a \pm \sqrt{(d\theta+a)^2 - 4D\theta}\right), \qquad \theta = \frac{\sigma_u}{\sigma_v}.$$

Thus the λ_k satisfying (3) are the ones such that $\lambda_k \in [\Lambda_-, \Lambda_+]$, for $a > 0$, $d < 0$, $D > 0$.
Assuming $\sigma_u \ll \sigma_v$, we consider the case $\theta \ll 1$ Then, we make an expansion

$$\Lambda_\pm = \frac{d\theta + a}{2\sigma_v\theta}\left(1 \pm \sqrt{1 - \frac{4D\theta}{(d\theta+a)^2}}\right) \sim \frac{a}{2\sigma_v\theta}\left(1 \pm (1 - \frac{2D\theta}{(d\theta+a)^2})\right).$$

Thus, $\Lambda_- \sim \frac{D}{\sigma_v a}$ and $\Lambda_+ \sim \frac{a}{\sigma_v\theta} \gg 1$.
Finally in the regime $\sigma_u \ll 1$ for $\sigma_v \sim 1$, we deduce that the interval $[\Lambda_-, \Lambda_+]$ becomes very large. Hence we know that some eigenvalues λ_k will belong to this interval. Notice, however, that since $\lambda_k \to +\infty$ as $k \to +\infty$, there are only a finite number of unstable modes k. □

Remark

Since $a > 0$ and $d < 0$, the quantity u is called activator, v is called inhibitor. The previous result state that $\sigma_u \ll 1$ induces Turing instability. We usually summarize this observation as

- Turing instability $\Leftrightarrow$ short range activator, long range inhibitor.
- Traveling waves $\Leftrightarrow$ long range activator, short range inhibitor.

Application

Application : *a possible explanation on spots on body and stripes on tail.*
For many species of animal, we observe that the skin (or the fur) has spots on the body and stripes on the tail, i.e. in a long and narrow domain (a tail) typical eigenfunctions are *bands* and with better shaped domain the eigenfunctions are *spots* or *chessboards*.

Application

Consider Neumann boundary conditions and a rectangle $[0, L_1] \times [0, L_2]$. The eigenelements of the Laplace operator are given by : for $k, \ell \in \mathbb{N}$,

$$\lambda_{k\ell} = \left(\frac{\pi k}{L_1}\right)^2 + \left(\frac{\pi \ell}{L_2}\right)^2, \qquad w_{k\ell}(x,y) = \cos\left(\frac{k\pi x}{L_1}\right)\cos\left(\frac{\ell\pi y}{L_2}\right).$$

These modes create instability if $\lambda_{k\ell} \in [\Lambda_-, \Lambda_+]$.

- If the domain is narrow : $L_2 \sim 0$ and $L_1 \gg 1$, then the condition $\lambda_{k\ell} \in [\Lambda_-, \Lambda_+]$ imposes that $\ell = 0$, otherwise $\lambda_{k\ell}$ will be very large. Then the corresponding eigenelement w_{k0} are bands parallel to y axis.
- When $L_2 \sim L_1$ then the condition $\lambda_{k\ell} \in [\Lambda_-, \Lambda_+]$ generically imposes $\ell \sim k$.

See also J. D. Murray, *Mathematical Biology, Vols 1 and 2*, 2nd edition, Springer, New York, 2002.

Outline of lecture 2

Non-local Fisher/KPP equation

One of the simplest model to explain what is a Turing instability is the nonlocal Fisher/KPP equation :

$$\partial_t u - \nu \partial_{xx} u = ru(1 - K * u), \qquad t \geq 0, \quad x \in \mathbb{R}.$$

In this model we have $r > 0$, $\nu > 0$ and the convolution kernel K is a smooth probability density function

$$K \geq 0, \quad \int_{\mathbb{R}} K(x)\, dx = 1, \quad K \in L^\infty(\mathbb{R}).$$

As a consequence $u = 1$ is a steady state.

Compared to Fisher/KPP, it takes into account that competition for resources can be of long range. For example in ecology, the roots of trees in semi-arid region can cover 10 times the external size to look for water (in temperated region the ratio is roughly one to one). This leads to the so-called *tiger bush* landscape. Due to convolution term, the maximum principle is lost.

Non-local Fisher/KPP equation

FIGURE – Examples of tiger bush landscapes.

Definition

Definition

The steady state $u = 1$ is called linearly unstable if there are perturbations such that the linearized system has exponential growth in time.
A steady state u_0 is said nonlinearly Turing unstable if

- it is between two unstable states (no blow-up, no extinction) ;
- it is linearly unstable ;
- the corresponding growth modes are unbounded (no high frequency oscillations).

When Turing instability occurs, solutions exhibit strange behaviour (Turing patterns) : they remain bounded, cannot converge to the steay state u_0 and cannot oscillate rapidly.

Result

In practice :

- in bounded domain we can use eigenfunctions of the Laplace operator
- on the full line, we may use Fourier modes (kind of generalized eigenfunctions).

We recall the definition of the Fourier transform

$$\widehat{u}(\xi) = \int_{\mathbb{R}} u(x) e^{-ix\xi}\, dx.$$

Theorem

Assume $\exists\, \xi_0$ such that $\widehat{K}(\xi_0) < 0$ and $\frac{\nu}{r}$ small enough (depending on ξ_0 and $K(\xi_0)$). Then the nonlocal Fisher/KPP equation is nonlinearly Turing unstable.

Proof

Proof.

- $u = 0$ and $u = \infty$ are formally unstable.
- We linearize around $u = 1$ by setting $u = 1 + \tilde{u}$. Keeping only the first order terms, we get
$$\partial_t \tilde{u} - \nu \partial_{xx} \tilde{u} = -rK * \tilde{u}.$$
We look for solutions of the form $\tilde{u}(t,x) = e^{\lambda t} v(x)$ with $\lambda > 0$:
$$\lambda v - \nu \partial_{xx} v = -rK * v.$$
We look for possible Fourier mode $v(x) = e^{ix\xi_1}$ for which we have existence of such $\lambda > 0$:
$$\lambda + \nu \xi_1^2 = -r\widehat{K}(\xi_1).$$
It is possible to find such $\lambda > 0$ by taking e.g. $\xi_1 = \xi_0$ and $\frac{r}{\nu}$ small enough.
- The possible unstable modes ξ_0 are bounded because $\widehat{K}$ is bounded $|\widehat{K}| \leq 1$ since K is a probability measure.

Notice however that the mode ξ_1 we observe in practice is that with the highest growth rate λ.

Outline of lecture 2

A cell polarity model

We consider the following reaction-diffusion system with two species and conservation of mass

$$\begin{cases} \partial_t u - \sigma_1 \Delta u = -f(u) + v, \qquad t \geq 0, \ x \in \Omega, \\ \partial_t v - \sigma_2 \Delta v = f(u) - v \\ u(t,x) = v(t,x) = 0 \qquad \text{on } \partial\Omega. \end{cases}$$

We assume that $f \in C^2(\mathbb{R}^+, \mathbb{R}^+)$ such that $f(0) = 0$, $f'(u) > 0$ on $[0, u_c)$, $1 < f'(u) < 0$, for $u > u_c$, $f(+\infty) = 0$.
For this system, we can prove $u > 0$, $v > 0$, $\frac{d}{dt} \int_\Omega (u + v)\, dx = 0$. These properties give the non-extinction and non blow-up condition.

A cell polarity model

Let us first conider the corresponding dynamical system

$$\frac{d}{dt}U = -f(U) + V \qquad \frac{d}{dt}V = f(U) - V,$$

complemented with initial data $U(0) > 0$, $V(0) > 0$. We have $U + V = U(0) + V(0) = M_0$. Thus we can simplify it into

$$\frac{d}{dt}U = -f(U) + M_0 - U = G(U).$$

It preserves the positive cone $U > 0, V > 0$. Indeed at the first time t_0 where $U(t_0) = 0$, we get $\frac{d}{dt}U(t_0) = M_0 > 0$ which cannot be (same argument for V).
The function G defined by $G(x) = M_0 - x - f(x)$ is decreasing ($G'(x) = -1 - f'(x)$), $G(0) > 0$, $G(+\infty) = -\infty$, thus there exists a unique $\overline{u}$ such that $G(\overline{u}) = 0$.
Therefore there exists a unique non zero steady state $(\overline{u}, \overline{v})$ with $\overline{u} + \overline{v} = M_0$ and $\overline{v} = f(\overline{u})$.

A cell polarity model

The differential matrix of the right hand side at $(\overline{u}, \overline{v})$ is given by

$$\begin{pmatrix} -f'(\overline{u}) & 1 \\ f'(\overline{u}) & -1 \end{pmatrix} \qquad T = -f'(\overline{u}) - 1 < 0, \quad D = 0.$$

Then $(\overline{u}, \overline{v})$ is stable.

A cell polarity model

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Then $(\overline{u},\overline{v})$ is stable.

Turing instability.
The only possibility is that u is the activator (from the scripture of the system).
From the first Theorem, to have instability that is to have u activator we should have $f'(\overline{u}) < 0 \Leftrightarrow \overline{u} > u_c$.
Then the unstable modes $e^{\lambda t}(\alpha w_k, \beta w_k)$ exist if there is a positive root to the polynomial

$$\lambda^2 + \lambda(\lambda_k(\sigma_1+\sigma_2) + f'(\overline{u}) + 1) + (\sigma_1\lambda_k + f'(\overline{u}))(\sigma_2\lambda_k + 1) - f'(\overline{u}) = 0.$$

That is

$$(\sigma_1\lambda_k + f'(\overline{u}))(\sigma_2\lambda_k + 1) - f'(\overline{u}) < 0.$$

This is equivalent to $\lambda_k + \dfrac{1}{\sigma_2} \leq \dfrac{|f'(\overline{u})|}{\sigma_1}$. This is clearly satisfied for some eigenvalues λ_k when σ_1 is small enough.

The CIMA reaction

The chlorite-iodide-malonic acid (CIMA) reaction is well-known as it is the first experimental evidence of Turing instability.

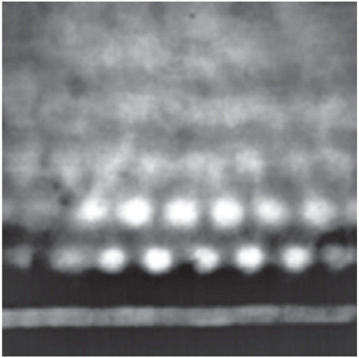

FIGURE – Historical observation of Turing patterns in the CIMA reaction. Picture from the original December 1989 experiments.

Example of a numerical simulation.

The CIMA reaction

The system reads

$$\partial_t u - \sigma_u \Delta u = a - u - \frac{4uv}{1+u^2}$$
$$\partial_t v - \sigma_v \Delta v = bcu - \frac{cuv}{1+u^2}$$
$$\partial_\nu u = \partial_\nu v = 0.$$

Here u (the activator) denotes the iodide (I^-) concentration, v (the inhibitor) denotes the chlorite (ClO_2^-) concentration. We have $a > 0$, $b < 0$, $c > 0$.

The CIMA reaction

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$$\partial_t v - \sigma_v \Delta v = bcu - \frac{cuv}{1+u^2}$$
$$\partial_\nu u = \partial_\nu v = 0.$$

Here u (the activator) denotes the iodide (I^-) concentration, v (the inhibitor) denotes the chlorite (ClO_2^-) concentration. We have $a > 0$, $b < 0$, $c > 0$.

Steady state.
There is a single homogeneous steady state (non zero) :

$$\overline{u} = \frac{a}{4b+1} \quad ; \qquad \overline{v} = b(1+\overline{u}^2).$$

By maximum principle we get $0 \leq \overline{u} \leq a$ and $b \leq v \leq b(1+a^2)$.

The CIMA reaction

Turing instability.
From these bounds, the solution cannot get extinct nor blow-up. Then to study the Turing instability, it remains to study the linearized operator around $(\overline{u}, \overline{v})$. The differential matrix at $(\overline{u}, \overline{v})$ is given by

$$\begin{pmatrix} -1 - 4\overline{v}\frac{(1-\overline{u}^2)}{(1+\overline{u}^2)^2} & -\frac{4\overline{u}}{1+\overline{u}^2} \\ bc - c\overline{v}\frac{1-\overline{u}^2}{(1+\overline{u}^2)^2} & -\frac{c\overline{u}^2}{1+\overline{u}^2} \end{pmatrix} = \begin{pmatrix} -1 - 4\frac{b^2(1-\overline{u}^2)}{\overline{v}} & -\frac{4b\overline{u}}{\overline{v}} \\ bc - \frac{cb^2(1-\overline{u}^2)}{\overline{v}} & -\frac{cb\overline{u}}{\overline{v}} \end{pmatrix}$$

From the first Theorem, we have to check the conditions

$$-1 - 4\frac{b^2(1-\overline{u}^2)}{\overline{v}} > 0, \quad T = -1 - 4\frac{b^2(1-\overline{u}^2)}{\overline{v}} - \frac{cb\overline{u}}{\overline{v}} < 0,$$

$$D = (1 + 4\frac{b^2(1-\overline{u}^2)}{\overline{v}})\frac{cb\overline{u}}{\overline{v}} + \frac{4b\overline{u}}{\overline{v}}\left(bc - \frac{cb^2(1-\overline{u}^2)}{\overline{v}}\right) = \frac{cb\overline{u}(1+4b)}{\overline{v}} > 0.$$

The condition $D > 0$ is always satisfied.

The CIMA reaction

The first condition is equivalent to (replacing $\overline{v}$ by its value)

$$4b^2\overline{u}^2 - 4b^2 - b(1+\overline{u}^2) > 0 \Leftrightarrow \overline{u}^2 > \frac{4b+1}{4b-1}.$$

The condition on the trace $(4b-1)\overline{u}^2 - c\overline{u} - (4b+1) < 0$ implies

$$\frac{c-\sqrt{c^2-4(16b^2-1)}}{2(4b-1)} < \overline{u} < \frac{c+\sqrt{c^2+4(16b^2-1)}}{2(4b-1)}.$$

Thus under these conditions, for $\sigma_u \ll \sigma_v$, we have from the first Theorem that Turing instability occurs.

The Gray-Scott system

Another well-known system giving rise to instability is the Gray-Scott system :

$$
\begin{aligned}
\partial_t u - d_u \Delta u &= u^2 v - Au \\
\partial_t v - d_v \Delta v &= -u^2 v + B(1-v) \\
\partial_\nu u = \partial_\nu v &= 0.
\end{aligned}
$$

We consider the case $B > 4A^2$.

Here u denotes the concentration of a component that reacts with v (and consumes it).

Example of a numerical simulation.

The Gray-Scott system

Steady states.
We solve

$$\overline{U}^2\overline{V} - A\overline{U} = 0$$
$$-\overline{U}^2\overline{V} + B(1-\overline{V}) = 0.$$

There are three steady states :

- $U_0 = 0$, $V_0 = 1$;
- $U_- = \dfrac{B - \sqrt{B^2 - 4A^2B}}{2A}$, $V_- = \dfrac{B + \sqrt{B^2 - 4A^2B}}{2B}$;
- $U_+ = \dfrac{B + \sqrt{B^2 - 4A^2B}}{2A}$, $V_+ = \dfrac{B - \sqrt{B^2 - 4A^2B}}{2B}$.

The Gray-Scott system

Turing instability.
Let us denote $u = \overline{U} + \tilde{u}$, $v = \overline{V} + \tilde{v}$, the linearized system satisfied by $(\tilde{u}, \tilde{v})$ is given by

$$\partial_t \tilde{u} - d_u \Delta \tilde{u} = (2\overline{U}\,\overline{V} - A)\tilde{u} + \overline{U}^2 \tilde{v},$$
$$\partial_t \tilde{v} - d_v \Delta \tilde{v} = -2\overline{U}\,\overline{V}\tilde{u} - (\overline{U}^2 \overline{V}\tilde{u} - (\overline{U}^2 + B)\tilde{v}.$$

- For $(U_0, V_0) = (0, 1)$, we have $D = AB > 0$, $T = -A - B < 0$, then the corresponding ODE is lnearly attractive and because $-A < 0$ and $-D < 0$ there is no activator.
- For $(U_\pm, V_\pm)$, we have $D_\pm = A(U_\pm^2 - B)$, and $T_\pm = A - B - U_\pm^2$. We have $D_+ > 0$ and $D_- < 0$. Hence,
  - the steady state (U_-, V_-) is linearly unstable for the corresponding ODE ;
  - for (U_+, V_+) the trace condition reads $T = A - \frac{B^2}{2A^2} - \frac{B}{2A^2}\sqrt{B^2 - 4A^2 B} < 0$. It is an additional condition to be checked. Notice that $2U_+ V_+ - A = A > 0$, then u is the activator.

The Gray-Scott system

We consider the particular case where $d_u = d_v$, $A = B$. Then, by choosing $v = 1 - u$ the system of two equations reduce to the single equation

$$\partial_t u - d_u \Delta u = u^2(1-u) - Au.$$

This corresponds to the situation of the Allen-Cahn (bistable) equation where, for A small enough, we have three steady states U_0 is stable, U_- is unstable, $U_+ > u_-$ is stable. We have already seen that this equation exhibits a traveling wave solution on the real line $\mathbb{R}$.

The Brusselator

Another simple system exhibiting Turing pattern is the so-called Brusselator [2] [3].

Let $A > 0$ and $B > 0$, we consider, on a bounded domain Ω, the system

$$\partial_t u - d_u \Delta u = A - (B+1)u + u^2 v$$
$$\partial_t v - d_v \Delta v = Bu - u^2 v,$$

complemented with Neumann boundary conditions .

2. G. Nicolis, I. Prigogine, *Self-organization in Non-equilibrium Systems*. Wiley Interscience, New-York (1977).
3. I. Prigogine, R. Lefever, *Symmetry breaking instabilities in dissipative systems, II.* J. Chem. Phys. 48, 1695–1700 (1968).

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$$\partial_t v - d_v \Delta v = Bu - u^2 v,$$

complemented with Neumann boundary conditions .

Steady state.
The only homogeneous steady state is given by $U = A$, $V = \frac{B}{A}$. Indeed, it is obtained by solving

$$BU = U^2 V, \qquad A = (B+1)U - U^2 V.$$

2. G. Nicolis, I. Prigogine, *Self-organization in Non-equilibrium Systems*. Wiley Interscience, New-York (1977).
3. I. Prigogine, R. Lefever, *Symmetry breaking instabilities in dissipative systems, II.* J. Chem. Phys. 48, 1695–1700 (1968).

The Brusselator

Turing instability.
The linearized system is obtained by setting $u = U + \tilde{u}$, $v = V + \tilde{v}$:

$$\partial_t \tilde{u} - d_u \Delta \tilde{u} = (B-1)\tilde{u} + A^2 \tilde{v}$$
$$\partial_t \tilde{v} - d_v \Delta \tilde{v} = -B\tilde{u} - A^2 \tilde{v}.$$

For $\tilde{u}$ to be the activator, we need $B > 1$. The trace of the corresponding matrix is given by $T = B - 1 - A^2$, the determinant is $D = A^2 > 0$. Then the trace condition leads to $B < 1 + A^2$. As a consequence, under this assumption on the parameters, the steady state is attractive for the corresponding ODE.

Let (λ_i, w_i) be an eigenpair of the Laplace equation with Neumann boundary conditions. As in the general theory, the condition that should be satisfied is

$$d_u d_v \lambda_i^2 + \lambda_i (A^2 d_u - (B-1) d_v) + A^2 < 0.$$

The Brusselator

To have two positive roots, we need a negative slope at the origin, that is $B > 1 + \frac{d_u}{d_v}A^2$ and also

$$(B-1)d_v - A^2 d_u > 2A\sqrt{d_u d_v} \iff B > 1 + 2\sqrt{\frac{d_u}{d_v}}A + \sqrt{\frac{d_u}{d_v}}A^2.$$

This is compatible with the condition $B < 1 + A^2$ iff $d_u < d_v$.
Let us denote $\theta = \frac{d_u}{d_v}$, we have

$$\Lambda_\pm = \frac{1}{2d_v\theta}\left(B - 1 - A^2\theta \pm \sqrt{(B-1-A^2\theta)^2 - 4A^2\theta}\right).$$

Making a Taylor expansion for $\theta \ll 1$, we get

$$\Lambda_- \sim \frac{A^2}{d_v} \qquad \Lambda_+ \sim \frac{B-1}{d_v\theta}.$$

For d_v fixed and θ small enough, this interval contain eigenvalues λ_i.