TRAVELLING WAVES FOR THE FISHER-KOLMOGOROV-PETROVSKII-PISKUNOV EQUATION WITH EXAMPLES[1]

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Abstract: *In this paper we consider the famous Fisher–Kolmogorov–Petrovskii–Piskunov partial differential equation, closely following (Kolmogorov, A. et. al., 1937). The subject is introduced as a biological problem of diffusing an advantageous gene. After the equation is formulated, the travelling-wave type solution is extensively studied. The first result discussed here concerns the existence of heteroclinic solutions for the corresponding ODE system depending on the travelling-wave rate which is not known in advance. The phase plane analysis is employed. The second result cited in this paper is about the intermediate asymptotic invariance of the solutions (as the time tends to infinity) for the initial value problem with respect to the initial data satisfying some boundary conditions. Finally, numerical experiments are presented and the paper concludes with some notes about the scientific vitality of the considered problem.*

Keywords: *Fisher-Kolmogorov-Petrovskii-Piskunov equation, advantageous gene, travelling wave, heteroclinic solution, intermediate asymptotic state.*

INTRODUCTION

The Fisher-Kolmogorov-Petrovskii-Piskunov (FKPP) equation plays a fundamental role in science since it was developed in 1937. It has not gained much popularity in biology, but has been applied in many areas of mathematical physics and been used as a ground for more sophisticated models. Firstly, R. Fisher published an article (Fisher, R., 1937) about the gene-advance-waves problem in biology. In the same year, A. Kolmogorov and his collaborators, based on the article and the Fisher's book about the genetical theory, published earlier, developed a solid mathematical theory for the first time about a method for solution to the problem of the so called "intermediate asymptotics" in a non-linear problem in (Kolmogorov, A. et. al., 1937). They applied the concept to this particular problem. We will follow the latter, and illustrate the theorems with a couple of examples.

Let us consider a population, uniformly distributed in a linear habitat (e. g. a shore line). At some locus a mutation might occur, which leads to origination of a new gene. We will study the case the gene is advantageous to survival. This means we can expect the individuals with this mutant gene, in the stuggle to existence, to increase their density at the expense of the individuals not having the gene, occupying the same place. Of course, this process firstly exhibits in the neighbourhood of the occurrence of the mutation, and later, the advantageous gene is diffused into the surrounding environment. If the considered domain is relatively long compared with the

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distance the offsprings travel from their parents, a wave of increase in the gene density occurs (Fisher, R., 1937).

More rigorously, let at some time t the dominant gene A is distributed over the area with density $v(x,t)$. Furthermore, the species with the gene A (belonging to the genotypes AA and Aa) have an advantage in survival over the species not possessing this gene (belonging to the genotype aa). To put it in a more precise way, the ratio of the probability that an individual with the gene A survives to the corresponding probability for an individual without the gene is

$$1+\alpha : 1,$$

where $0 < \alpha \ll 1$.

Let us now consider the case when some area has already been populated by species with the gene A with concentration v close to 1. If v changes smoothly (in the sense v is a smooth function w. r. t. x and t), it is natural to assume that there exists an intermediate concentration region along the boundary of the area, where the concentration is between 0 and 1. In view of positive selection, the area occupied by the gene A expands, i. e. its boundary moves towards places that have not been yet occupied by the gene A, and the intermediate concentration region always remains. Our first problem is to find the *rate of advance of the gene A*, in other words, the rate of which the boundary of the area occupied by A moves alongs the normal to this boundary. This rate is denoted by λ. The next problem is to find a functional dependence of the gene propagation and its density for every spatial point x and every time t.

FORMULATION OF THE PROBLEM

Let v be the density of the mutant gene A, and $w = 1 - v$ that of its only alternative allelomorph. Let α be the intensity of selection in favour of the mutant gene, supposed independent of v. If we suppose that the rate of duffusion per generation across any boundary may be expressed as

$$-k\frac{\partial v}{\partial x}$$

at that boundary, then v satisfies the partial differential equation

$$\frac{\partial v}{\partial t} = k\frac{\partial^2 v}{\partial x^2} + \alpha v(1-v), \tag{1}$$

where t stands for time in generations (Fisher, R., 1937).

The coefficient $k > 0$ is the coefficient of diffusion analogous to that used in physics. The use of this analogy is justified when the distances of dispersion in a single generation are small compared with the length of the wave. We will consider the simple case when k is constant.

The equation (1) can be interpreted in the following way. If we neglect the diffusion term, this means there are no movement of the offspring from their parents, we arrive at a logistic equation or Verhulst model:

$$\frac{\partial v}{\partial t} = \alpha v(1-v).$$

The above equation models the change of a population having a growth rate α, which is also called the Malthusian parameter. When a diffusion term is added, it means that a bump somewhere in the quantity v will propagate in space x.

Let us now consider the more general case of the diffusion equation, where the diffusion term is accompanied by increase in the amount of substance at a rate which depends on the density at given point and time. We then obtain the equation

$$\frac{\partial v}{\partial t} = k\frac{\partial^2 v}{\partial x^2} + F(v). \tag{2}$$

We are only interested in the values of $F(v)$ for $v \geq 0$. Assume that $F(v)$ is a continuous and differentiable function, satisfying

$$F(0) = F(1) = 0,$$
$$F(v) > 0 \text{ for } 0 < v < 1, \tag{3}$$
$$F'(0) = \alpha > 0, F'(v) < \alpha \text{ for } 0 < v \le 1.$$

We thus assume for very small v the rate $F(v)$ of increase in v is proportional to v (linear with proportionality factor α), and as v approaches 1, it is reached a state of saturation when v no longer increases. Accordingly we will consider only solutions to (2) satisfying the condition

$$0 \le v \le 1.$$

Let us recall that v is the density of the gene A in point x and time t. As we already mentioned, it is natural to seek the solution to (2) in the form of a *travelling wave*:

$$v(x,t) = v(x + \lambda t),$$

where λ is the speed of the wave (fig. 1).

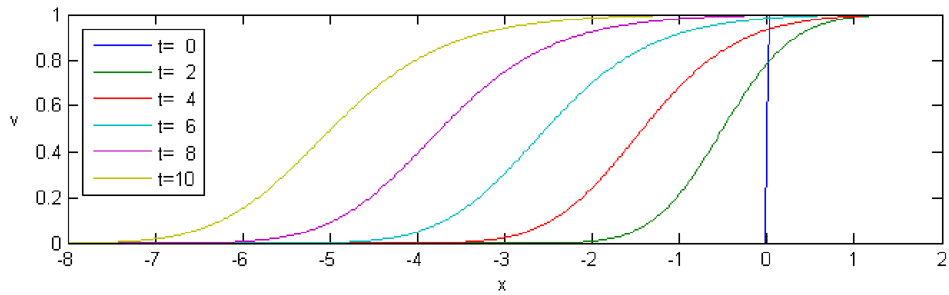

Fig. 1. Example of a travelling wave

Then equation (2) becomes a second order ordinary differential equation

$$\lambda \frac{dv}{dx} = k \frac{d^2 v}{dx^2} + F(v). \tag{4}$$

We are going to establish a relation between λ, k and $\alpha = F'(0)$ for which (4) has a solution $v(x)$ such that

$$0 \le v(x) \le 1, \qquad v(-\infty) = 0, \qquad v(+\infty) = 1.$$

Such solution $v(x)$ to (4) is called a *heteroclinic solution*.

EXPOSITION AND SOLUTION

The following theorem could be proven.

Theorem 1. Equation (4) has a unique (to within a translation $x' = x + c$) heteroclinic solution $v(x)$, s. t. $0 \le v(x) \le 1, v(-\infty) = 0, v(+\infty) = 1, v'(\pm\infty) = 0$ for $\forall \lambda \ge \lambda_0$, where $\lambda_0 = 2\sqrt{k\alpha}$.

Proof. Let $\frac{dv}{dx} =: p$. Then substituting in (4) yields

$$\frac{dp}{dv} = \frac{\lambda p - F(v)}{kp}. \tag{5}$$

We are interested in those integral curves of (5) that pass between the straight vertical lines $v = 0$ and $v = 1$ in the phase plane Ovp. Generally, these curves can be of the following types:

1. Integral curves that are separated from the lines $v = 0$ and $v = 1$ by at least a distance $\epsilon > 0$;
2. Integral curves that go infinitely far away from the axis v and asymptotically approach one of the lines $v = 0$ or $v = 1$;
3. Integral curves that intersect one of the lines $v = 0$ or $v = 1$ at a finite point lying below or above the v-axis;

4. Integral curves that approach the points $v = 0, p = 0$ and $v = 1, p = 0$ and do not belong to any of the former types.

It can be seen, however, that integral curves of the first type cannot satisfy the boundary conditions $v(-\infty) = 0, v(+\infty) = 1$.

Integral curves of second type are not solutions to (4) since for large $|p|$ the derivative $\left|\frac{dp}{dv}\right|$ should also be arbitrary large. However, from (5) we have that $\frac{dp}{dv} = \frac{\lambda p - F(v)}{kp} \approx \frac{\lambda}{k}$ for large $|p|$ in view of the boundedness of $F(v)$ in (0,1).

Integral curves from the third type do not necessarily remain between 0 and 1. Then it remains to consider integral curves of the fourth type. Each of the points $v = 0, p = 0$ and $v = 1, p = 0$ is a singular point of the differential equation (5). An integral curve of the fourth type should approach each of these points without intersecting the lines $v = 0$ and $v = 1$ and therefore it does not twist. Thus, in order such curves to exist, the characteristic equation for each of these points should have real roots. We write (5) in the equivalent autonomous form

$$\left|\begin{aligned} \frac{dp}{dt} &= \lambda p - F(v) \\ \frac{dv}{dt} &= kp \end{aligned}\right. .$$

The linearized system around $v = 0, p = 0$ is

$$\left|\begin{aligned} \frac{dp}{dt} &= \lambda p - \alpha v \\ \frac{dv}{dt} &= kp \end{aligned}\right.$$

with characteristic equation

$$\begin{vmatrix} \lambda - \rho & -\alpha \\ k & -\rho \end{vmatrix} = 0$$

or $\rho^2 - \lambda\rho + k\alpha = 0$. The equation has real roots when

$$\boldsymbol{\lambda^2 \geq 4k\alpha}$$

and they are $\rho_{1,2} = \frac{(\lambda \pm \sqrt{\lambda^2 - 4k\alpha})}{2}$, respectively. Obviously $\rho_{1,2} > 0$ and the singular point $v = 0, p = 0$ is unstable node for the linearized system and for (5).

Considering $v = 1, p = 0$, we make a change of variables, putting $v = 1 - u$. This yields

$$\frac{dp}{du} = \frac{-\lambda p + F(1-u)}{kp}.$$

The corresponding autonomous system is

$$\left|\begin{aligned} \frac{dp}{dt} &= -\lambda p + F(1-u) \\ \frac{du}{dt} &= kp \end{aligned}\right.$$

and the linearized counterpart is

$$\left|\begin{aligned} \frac{dp}{dt} &= -\lambda p - F'(1-u)|_{u\equiv 0} u \\ \frac{du}{dt} &= kp \end{aligned}\right. .$$

The characteristic equation is

$$\begin{vmatrix} -\lambda - \rho & -F'(1) \\ k & -\rho \end{vmatrix} = 0$$

or $\rho^2 + \lambda\rho - \mathrm{A}k = 0$, where $\mathrm{A} = -F'(1) > 0$. This equation always has real roots since $\lambda^2 > -4\mathrm{A}k$ and they are $\rho_{1,2} = \frac{(-\lambda \pm \sqrt{\lambda^2 + 4\mathrm{A}k})}{2}$. Clearly, $\mathrm{sgn}\rho_1 \neq \mathrm{sgn}\rho_2$ so the point $v = 1, p = 0$ is a saddle. Since the saddle is a hyperbolic stationary point, from the Stable Manifold Theorem

(Perko, L., 1991, p. 104) follows that there exist only two integral curves I and II through $v = 1, p = 0$ (fig. 2) s. t. one of them is stable manifold of the nonlinear system, whis is tangent to the stable subspace of the linearized system, and the other is unstable manifold, which is tangent to the unstable subspace in the point $v = 1, p = 0$.

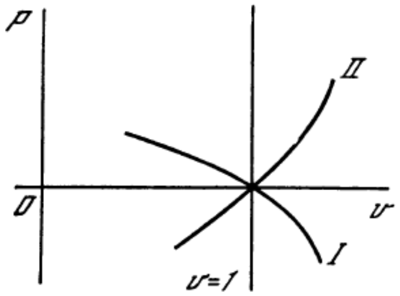

Fig. 2. Approximate configuration of curves I and II

The curve II intersects p-axis below the origin since (5) implies

$$\frac{dp}{dv} = \frac{\lambda p - F(v)}{kp} = \frac{\lambda}{k} - \frac{F(v)}{kp} > 0$$

in the part of the strip between $v = 0$ and $v = 1$ that lies below the v-axis. Therefore the curve II can be excluded from further considerations and it remains to study curve I.

We will first prove that curve I does not intersect Op below the origin. For that purpose we consider the isoclines of (5). The isoclines are curves, on which the different solutions to (5) attain the same slope, i. e.

$$\frac{dp}{dv} = \frac{\lambda p - F(v)}{kp} \equiv \text{const} = C.$$

Thus all isoclines of (5) are given by

$$p = \frac{F(v)}{\lambda - Ck}. \tag{6}$$

This means that all the isoclines coincide with the graph of $F(v)$, multiplied by the respective constant (fig. 3).

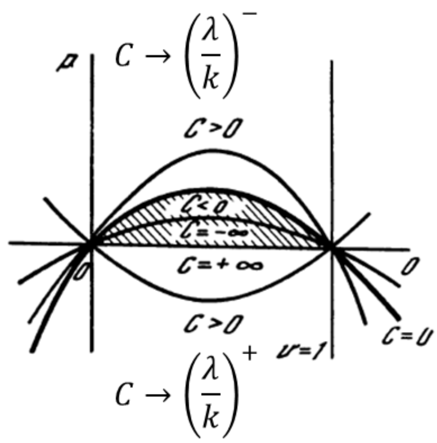

Fig. 3. Isoclines of (5)

Now it is easily seen that the integral curve I cannot intersect the axis Op below the origin. Indeed, in this case the curve I should grow from the point below the origin until it crosses the axis Ov between 0 and 1 with vertical tangent $\left(\frac{\partial p}{\partial v} \to +\infty \text{ below } Ov\right)$ and after that it should go back $\left(\frac{\partial p}{\partial v} \to +\infty \text{ above } Ov\right)$, never reaching the point $(v = 1, p = 0)$.

We will now prove that the integral curve I cannot intersect the p-axis above the origin. To this end it suffices to prove that there exists a ray passing through the origin and lying in the first quadrant that does not intersect any integral curve intersecting the positive semi-axis p. From (6) we have

$$\left(\frac{dp}{dv}\right)_{v=0} = \frac{\alpha}{\lambda - Ck}.$$

We now find C for which $\left(\frac{dp}{dv}\right)_{v=0} = C$. This C defines an isocline which slope at the origin is C and the slope of all integral curves of (5) on it is also C. Equating yields $kC^2 - C\lambda + \alpha = 0$ and eventually

$$C_{1,2} = \frac{\lambda \pm \sqrt{\lambda^2 - 4\alpha k}}{2k}.$$

Having assumed that $\lambda^2 \geq 4\alpha k$, both $C_{1,2}$ are real and positive. Let one of them is denoted by C_0. Consider the line $p = C_0 v$. For all the points from the strip between $v = 0$ and $v = 1$ that lie above the line, and even on the line itself (except for the origin), we have $\frac{dp}{dv} > C_0$. Therefore none of the integral curves passing through a point on the p-axis above the origin can cross part of the line located above the v-axis. Thus each integral curve of type I passes through the origin.

Now we will prove that there exists only one integral curve of type I. (This is valid for A $>$ 0; if A$:= -F'(1) = 0$, uniqueness cannot be stated.) Indeed, we have proven that all curves of type I pass through the origin. On the other hand, it follows from (5) that for $p > 0$ and fixed v the derivative $\frac{dp}{dv}$ increases with p. It follows that two integral curves issuing from the origin cannot pass through the point $v = 1, p = 0$.

Finally it can be shown that the curve I corresponds to the solution to (4) and satisfies the conditions (3).

Next, we will state the following theorem, omitting the proof.

Theorem 2. For every initial function $v(x,0) = v_0(x)$ such that $v(x,0) \equiv 0$ for $x \leq a$ and $v(x,0) \equiv 1$ for $x \geq b$ $(a < b)$ and $v(x,0)$ taking arbitrary values between 0 and 1 for $a < x < b$ the initial value problem for the equation (2) with F satisfying conditions (3) possesses unique solution $v(x,t)$. As $t \to \infty$ the solution $v(x,t)$ tends to a solution $v(x + \lambda_0 t + c)$ for the equation (4) with $\lambda_0 = 2\sqrt{k\alpha}$ and unique value of c.

An example illustrating this phenomenon is included in the following section.

NUMERICAL EXAMPLE

Let us consider (1) again. In (Polyanin, A. & Zaitsev, V., 2004) the authors have found analytical travelling wave solution to (1) as

$$v(x,t) = \frac{1}{\left(-1 + C\exp\left(\frac{-5\alpha}{6}t - \sqrt{\frac{\alpha}{6k}}x\right)\right)^2} = v\left(x + 5\frac{\sqrt{\alpha k}}{\sqrt{6}}t\right).$$

Note that the travelling wave solution $v(z)$ satisfies the boundary conditions $v(-\infty) = 0, v(+\infty) = 1$. Note also that the speed of the wave is $\lambda = \frac{5}{\sqrt{6}}\sqrt{\alpha k} > 2\sqrt{\alpha k}$.

Now we are going to illustrate numerically Theorem 2. We consider the initial value problem for the equation (1) subjected to two different initial data. As expected, the limiting curves of the solutions as $t \to \infty$ coinside (to within the translation $x' = x + c$).

For the numerical solutions we have to truncate the spatial domain from $(-\infty, +\infty)$ to $[-L, L]$, where $L > 0$ is a large number. What is more, we impose the boundary conditions of Dirichlet type, considering the asymptotical behaviour at infinity:

$$v(-L,t) = 0, \qquad v(L,t) = 1.$$

For the numerical experiments we take the following parameters: $L = 10, k = 0.1, \alpha = 1, T = 10$, there T is the final time. The first example (fig. 4) is conducted with the "classical" initial condition

$$v(x,0) = v_0(x) = \begin{cases} 0, x \in [-10,0], \\ 1, x \in (0,10]. \end{cases}$$

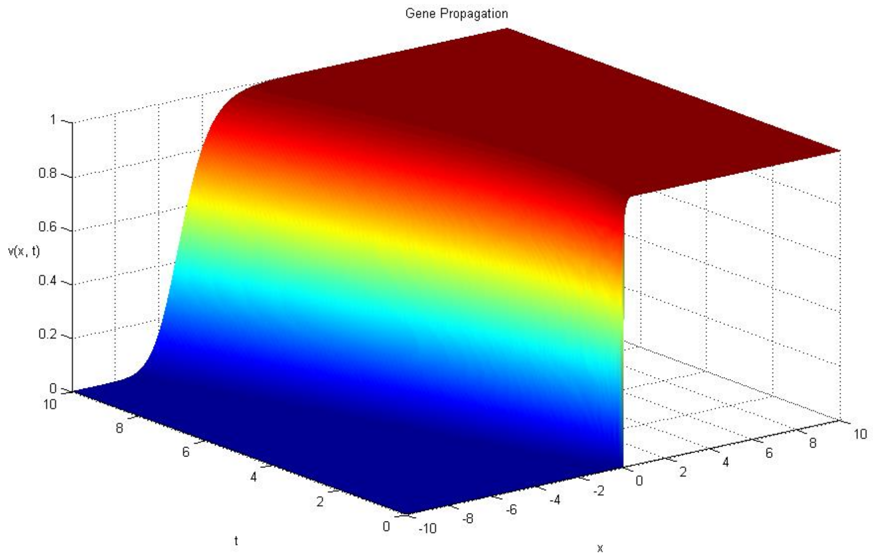

Fig. 4. Solution to (1)

As expected, the discontinuity in the initial data is smoothed, an intermediate region with $v \in (0,1)$ is formed and the wave is travelling in the negative direction.

Of course, the initial condition $v_0(x)$ could be every function satisfying $0 \leq v \leq 1$. The next example (fig. 5) has the initial condition

$$v(x,0) = v_0(x) = \begin{cases} 0, x \in [-10,-2], \\ \frac{1}{4}, x \in (-2,0], \\ 0, x \in (0,6], \\ 1, x \in (6,10]. \end{cases}$$

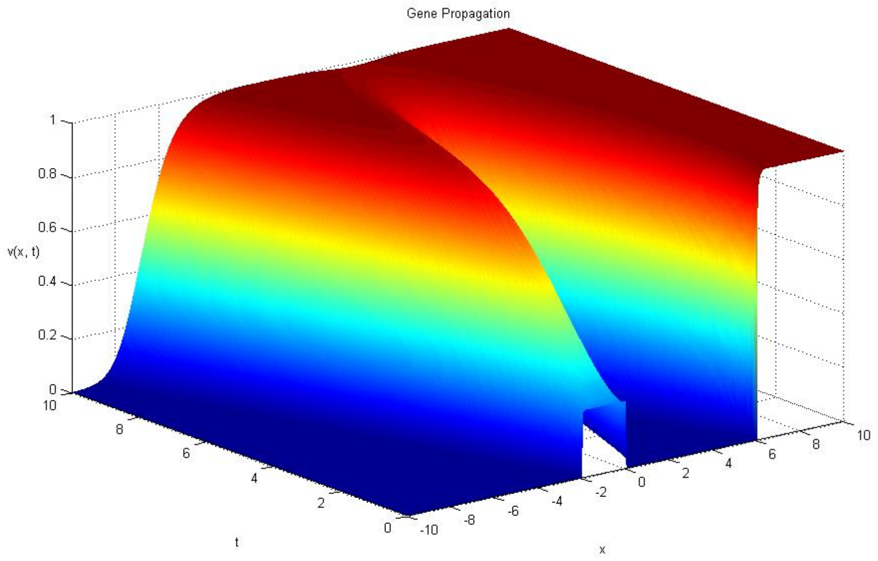

Fig. 5. Solution to (1)

Analogously to the previous case, the area with low density of the dominant gene is wiped out and absorbed by the waves, which can travel in both negative and positive directions.

What is more, the limiting curves of the travelling waves from the different initial conditions $v_0(x)$ practically coincide within the translation $x' = x + 1.7$: the maximum norm $\|v_4(\cdot,T) - v_5(\cdot,T)\|_\infty < 10^{-3}$ due to numerical roundoff (fig. 6).

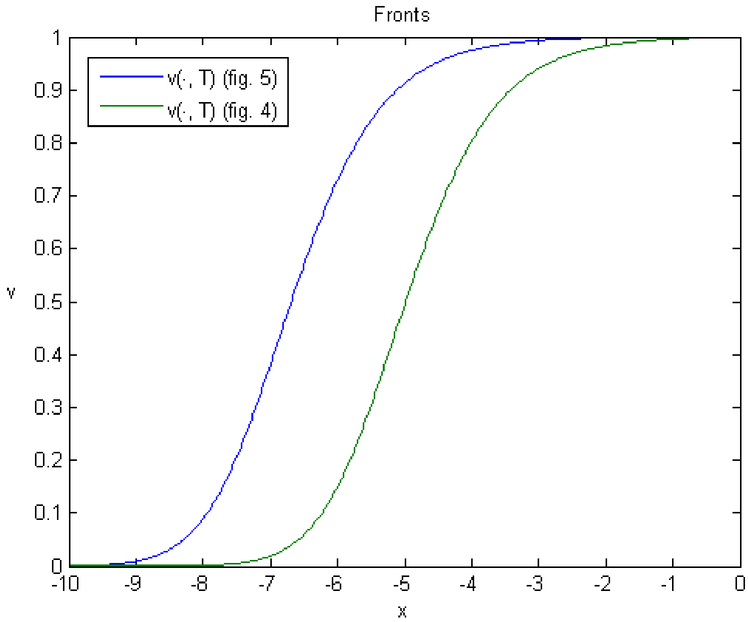

Fig. 6. Travelling wave fronts with both the initial conditions $v_0(x)$.

CONCLUSION

In this paper the Fisher–Kolmogorov–Petrovskii–Piskunov equation is studied, which is essentially a diffusion equation with a special nonlinear right-hand side. It is shown that the equation has invariant solutions of travelling-wave type. The described process is notable in the sense that as it continues at an "intermediate asymptotic" state, it becomes independent from the initial condition, but the system is far from its equilibrium state.

Although it has not attracted much attention in biology, it turned out to be very useful in the theory of burning and flame propagation. What is more, it has influenced the theory development for a lot of problems, including the well-known problem for the electrochemical model of excitating pulse propagation along a nerve, plasma front propagation through different types of fields and problems in other areas of physics and science.

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