Neural, Parallel & Scientific Computations 15 (2007) 561-570

TRAVELING FRONTS, IMPULSES AND TRAINS IN SOME TAXIS MODELS

Faina S Berezovskaya[1,*], Artem S Novozhilov[2], Georgy P Karev[2]
[1]*Howard University, 6-th Str. Washington DC 20059*
[2]*National Institutes of Health, 8600 Rockville Pike Bethesda MD 20894*

Abstract

An analysis of traveling wave solutions of certain types of chemotactic models (PDE systems with cross-diffusion) is presented. The conditions for existence of front-front, impulse-front, and front-impulse traveling waves are given for system of a "separable" type. The simplest mathematical models are presented that have an impulse-impulse solution and wave train solution. The results can be used for construction and analysis of different mathematical models describing systems with chemotaxis.

Keywords: Keller-Segel model, traveling wave solutions, cross-diffusion.

AMS (MOS) Subject Classification: 35B40, 35K20, 35K55, 92C17.

1 INTRODUCTION

In this report we study traveling wave solutions for the models in the form

$$U_t = (U_x - f(U,V)V_x)_x, \quad V_t = g(U,V), \tag{1}$$

where x is one-dimensional space variable; $f(U,V)$ and $g(U,V)$ are functions whose properties will be specified later; $U = U(x,t)$, $V = V(x,t)$.

The model (1) is known as a particular case of the models to describe chemotaxis, the movement of a population U to a chemical signal V (see, e.g., [1, 6, 8, 9, 13]). Substituting traveling wave forms $U(x,t) = U(x+ct) \equiv u(z)$, $V(x,t) = V(x+ct) \equiv v(z)$ into (1) and integrating we obtain the wave system:

$$u' = cu + f(u,s)g(u,s)/c + \alpha, \quad v' = g(u,s)/c, \tag{2}$$

where α is the constant of integration, which is considered as a new parameter in the following. Due to cross-diffusion form of (1) the dimension of system (2) is the same as the

*Corresponding author: tel.: +1 (202) 806-7125; e-mail: fsberezo@hotmail.com

1061-5369 $15.00 © Dynamic Publishers, Inc.

dimension of system (1). The problem of describing all traveling wave solutions of system (1) is reduced to the analysis of phase curves and bifurcations of solutions of the wave system (2) without a priory restrictions on boundary conditions for (1); moreover, by phase plane analysis it is possible to find the boundary conditions for (1) for which traveling wave solutions exist.

There exists a known correspondence between the traveling wave solutions of the spatial model (1) and the orbits $u(z)$, $v(z)$ of the wave system (2) (see also, e.g., [1, 15]) that we only list for the cases most important for our exposition:

Proposition 1.

i. *A wave front in U (or V) component corresponds to a heteroclinic orbit that connects singular points of (2) with different u (or v) coordinates;*

ii. *A wave impulse in U (or V) component corresponds to a heteroclinic orbit that connects singular points with identical u (or v) coordinates or to a homoclinic curve of a singular point (u, v) of (2);*

iii. *A wave train in U and V components corresponds to a limit cycle surrounding a singular point (u, v).*

Hereinafter we define the type of a traveling wave solution (U, V) of (1) by characteristics of its u-, v-profiles; e.g., a front-impulse solution means that u-profile is a front, and v-profile is an impulse (the order of the terms is important).

For system (1) several results on the existence of one-dimensional traveling waves are known; see, e.g., [1, 2, 5, 6, 7, 9, 12, 15] for references. The analysis is usually conducted using a particular model which is given in an explicit form. On the contrary, we consider a general class of models, and our task is to infer possible kinds of wave solutions under given restrictions on functions $f(U, V)$ and $g(U, V)$.

2 THE SEPARABLE MODELS

Definition 1. *We shall call model (1) the separable model if*

$$(C1) \qquad f(u,v) = f_1(u) f_2(v), \quad g(u,v) = g_1(u) g_2(v),$$

where $f_1(u)$, $g_1(u)$ are smooth functions for $a \leqslant u < \infty$; $g_2(v)$ is smooth; $f_2(v)$ is a rational function: $f_2(v) = Z(v)/R(v)$ for $b \leqslant v < \infty$; here $a, b > -\infty$ are real constant.

The class of the separable models is wide, and, in particular, includes the classical Keller-Segel model, where $f(u,v) = \delta u/v$, $g(u,v) = -ku$ with $\delta, k > 0$ [9].

The rational function $f_2(v) = Z(v)/R(v)$ can be presented in the form

$$f_2(v) = \frac{Z(v)}{R(v)} = \frac{\tilde{Z}(v)(v - v_1)\dots(v - v_m)}{\tilde{R}(v)(v - \breve{v}_1)\dots(v - \breve{v}_k)},$$

where $\tilde{Z}(v), \tilde{R}(v)$ do not have real roots; $m \geqslant 0, k > 0$; $v_i \neq \breve{v}_j$ for any i, j. The wave system (2) with the help of transformation of the independent variable $dy = dz/cR(v)$ becomes

$$\begin{aligned}\frac{du}{dy} &= c^2 R(v)(u + \alpha/c) + f_1(u)g_1(u)g_2(v)Z(v),\\ \frac{dv}{dy} &= g_1(u)g_2(v)R(v).\end{aligned} \tag{3}$$

The roots of functions $f_1(u), g_1(u), g_2(v), Z(v), R(v)$ do not depend on parameters c and α, hence, we will suppose that the following conditions of non-degeneracy are fulfilled:

$(B1)$ $R(v)$ and $g_2(v)$ have no common roots;

$(B2)$ $f_1(u)$ and $g_1(u)$ have no common roots;

$(B3)$ $f_1(u), g_1(u), g_2(v), R(v)$ have no multiple roots.

The topological type of the singular points of (3) can be inferred by the standard analysis. In particular, it is possible to show that under conditions $(C1)$ and $(B1)$-$(B3)$ the system (3) cannot have singular points of center or focus type.

Due to the structure of system (3) the phase plane is divided into horizontal strips, whose boundaries are given by $v = \hat{v}$, where $\hat{v}$ is a root of $R(v)$ or $g_2(v)$; all singular points of (3) are situated on these boundaries. Simple continuity arguments accounting for possible types of neighboring singular points of (3) allow us to formulate the following theorem:

Theorem 1. *The system* (1) *satisfying* $(C1)$ *and* $(B1)$-$(B3)$ *can only possess traveling wave solutions of the following kinds:* i. *front-front solutions;* ii. *front-impulse solutions;* iii. *impulse-front solutions.*

It is worth emphasizing that in most of the cases listed in Theorems 1 traveling wave solutions compose a family; that is, there are infinitely many traveling wave solutions for the fixed parameter values. The proof and extensive discussion of Theorem 1 are given in [4] together with some examples.

3 SOME GENERALIZATIONS OF THE KELLER-SEGEL MODELS

Here we consider the Keller-Segel models with more complex functions $f(u, v)$ and $g(u, v)$, which yield traveling wave solutions of the types not presented in the separable models (Theorem 1). Recall that to prove the existence of impulse-impulse solution one needs to prove the existence of a homoclinic orbit of the wave system; correspondingly, for the wave train it is necessary to have a limit cycle.

3.1 Impulse-front and impulse-impulse solution

We suppose that

$$f(u, v) = \frac{\delta u}{\beta u + v}, \quad \delta > 0, \beta \geqslant 0, \qquad g(u, v) = -ku + rv, \quad k, r \geqslant 0. \tag{4}$$

For $r = \beta = 0$ system (1), (4) is the Keller-Segel model [8]. The wave system for (1) with the functions given by (4) reads

$$u' = cu + \frac{\delta u(-ku + rv)}{c(\beta u + v)}, \qquad v' = (-ku + rv)/c, \tag{5}$$

where we put parameter α equal zero.

After the change of the independent variable $dz/(c(\beta u + v)) = dy$ system (5) takes the form

$$\frac{du}{dy} = c^2 u(\beta u + v) + \delta u(-ku + rv), \qquad \frac{dv}{dy} = (-ku + rv)(\beta u + v). \tag{6}$$

If $r = 0$ then system (6) has a line on non-isolated singular points $u = 0$; if $r \neq 0$ then $(u, v) = (0, 0)$ is an isolated non-hyperbolic singular point of (6) (i.e., it has zero eigenvalues). For $r = 0$ the model has a family of impulse-front wave solutions similar to the Keller-Segel model for values of β that belong to some interval containing $\beta = 0$ (see Fig. 1 for numerical solutions).

We did numerical simulations of system (1) for $x \in [-L, L]$, where L varied in different numerical experiments. We used no-flux boundary conditions for the spatial variable. Inasmuch as we wanted to study the behavior of the traveling wave solutions in an infinite space we chose such space interval so that to avoid the influence of boundaries.

We used an explicit difference scheme. The approximation of the taxis term is an "upwind" explicit scheme [11] which is frequently used for cross-diffusion systems (e.g., [14]). More precisely,

$$u_i^{t+1} = u_i^t + \frac{\Delta t}{(\Delta x)^2}(u_{i+1}^t - 2u_i^t + u_{i-1}^t) - \frac{\Delta t}{(\Delta x)^2}(A(v_{i+1}^t - v_i^t) - B(v_i^t - v_{i-1}^t)),$$
$$v_i^{t+1} = v_i^t + (\Delta t) g(u_i^t, v_i^t), \quad i = 2, ..., N-1,$$

where for the positive taxis (pursuit) (i.e., $f(u, v) < 0$),

$$\begin{aligned} A &= f(u_i^t, v_i^t) \quad \text{if } v_{i+1} \geqslant v_i, \\ A &= f(u_{i+1}^t, v_{i+1}^t) \quad \text{if } v_{i+1} < v_i, \\ B &= f(u_{i-1}^t, v_{i-1}^t) \quad \text{if } v_i \geqslant v_{i-1}, \\ B &= f(u_i^t, v_i^t) \quad \text{if } v_i < v_{i-1}. \end{aligned}$$

For the negative taxis (invasion):

$$\begin{aligned} A &= f(u_i^t, v_i^t) \quad \text{if } v_{i+1} < v_i, \\ A &= f(u_{i+1}^t, v_{i+1}^t) \quad \text{if } v_{i+1} \geqslant v_i, \\ B &= f(u_{i-1}^t, v_{i-1}^t) \quad \text{if } v_i < v_{i-1}, \\ B &= f(u_i^t, v_i^t) \quad \text{if } v_i \geqslant v_{i-1}. \end{aligned}$$

We used $\Delta t = 0.001$, $\Delta x = 0.1$. For the boundary conditions:

$$u_1^{t+1} = u_2^t, \quad u_N^{t+1} = u_{N-1}^t,$$
$$v_1^{t+1} = v_2^t, \quad v_N^{t+1} = v_{N-1}^t.$$

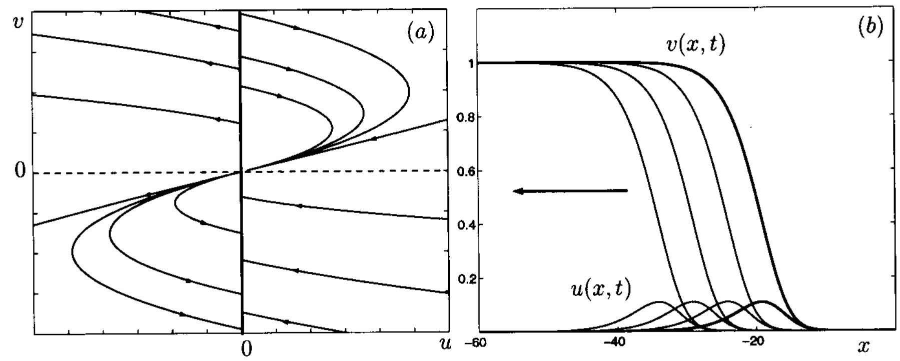

Figure 1: (a) The phase plane of system (5); the parameters are $r = 0, \beta = 0, \alpha = 0, k = 1, \delta = 4, c = 0.5$. (b) Numerical solutions of the Keller-Segel system with the parameters given in (a). The solutions are shown for the time moments $t_0 = 0$ (bold curves) $< t_1 < t_2 < t_3 = 30$ in equal time intervals

For the initial conditions we used numerical solutions of the corresponding wave systems.

For $r \neq 0$ the singular point (0, 0) of (6) possesses two elliptic sectors in its neighborhood (see [3, 4] and Fig. 2a). Asymptotics of homoclinics composing the elliptic sector are $u = 0$ (trivial) and $v = K^+u$, where K^+ is the biggest root of the equation

$$K^2(c^2 + r(\delta - 1)) + K(\beta c^2 - k(\delta - 1) - \beta r) + \beta k = 0.$$

The family of homoclinics in the phase plane (u, v) corresponds to the family of wave impulses for the system (1). In Fig. 2bb numerical solution of corresponding chemotaxis system is presented.

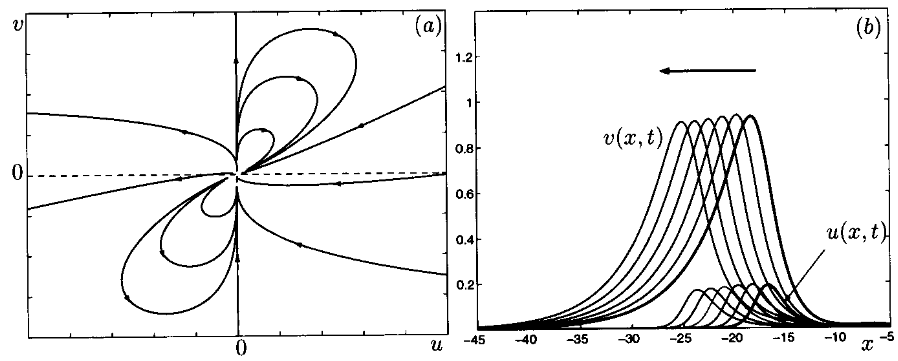

Figure 2: (a) The phase plane of system (5); the parameters are $k = 1, \beta = 1, \delta = 2, c = 0.43, r = 0.1$. (b) Numerical solutions of system (1) with the functions given by (4) and the parameter values as in (a). The solutions are shown for the time moments $t_0 = 0$ (bold curves) $< t_1 < t_2 < t_3 < t_4 < t_5 = 20$ in equal time intervals

3.2 Wave train solution

The simplest example of a mathematical model that possesses wave train solution can be given by the system (1) with

$$f(u,v) = \delta u,\ \delta > 0, \quad g(u,v) = -u + v.$$

Invoking the Poincare-Andronov-Hopf bifurcation theorem it is straightforward to prove that the corresponding wave system has a stable limit cycle.

More realistic model of the Keller-Segel type is given by

$$f(u,v) = \frac{-\delta u}{v}, \quad \delta > 0, \qquad g(u,v) = (-\beta + ku + v)v, \quad k, \beta \geqslant 0. \tag{7}$$

The wave system for (1) with the functions given by (7) reads

$$u' = cu - \delta u(-\beta + ku + v)/c + \alpha, \qquad v' = (-\beta + ku + v)v/c. \tag{8}$$

System (8) can have up to three singular points. First, there is always $A = (-\alpha/c,\ (c\beta + \alpha k)c)$, two other singular points are $B_{1,2} = (\hat{u}_{1,2}, 0)$, where $\hat{u}_{1,2}$ are the solutions (if they exist) of $cu - \delta u(-\beta + ku + v)/c + \alpha = 0$.

Inasmuch as our models are motivated by biological systems, in the following we consider the case $\alpha < 0$, $c\beta + \alpha k > 0$ to guarantee that point A belongs to $\mathbb{R}^+_2$. The standard linear analysis shows that the Jacobian of (8) evaluated at A has the following trace and determinant:

$$\operatorname{tr} J = \frac{c\beta + c^3 + \alpha(1+\delta)k}{c}, \qquad \det J = \frac{c\beta + \alpha k}{c}.$$

Due to the requirement $c\beta + \alpha k > 0$ we obtain that A always has complex conjugate eigenvalues (unless $\det J \neq 0$) which can be written in the form $\lambda_{1,2} = \mu \pm i\omega$, $\omega > 0$. That is, A is a stable or unstable focus depending on the sign of $\operatorname{tr} J$. Moreover, when $\operatorname{tr} J = 0$ a bifurcation occurs in the system (8). If we chose α as a bifurcation parameter then the condition $\operatorname{tr} J = 0$ is equivalent to $\alpha_c = -(c^2 + \beta)c/(k(\delta+1))$. It is straightforward to check that $\frac{d\mu(\alpha)}{d\alpha}|_{\alpha=\alpha_c} \neq 0$ and that the first Lyapunov value $l(\alpha_c) < 0$. Therefore all the conditions of Poincare-Andronov-Hopf bifurcation are satisfied [10], the bifurcation is supercritical, and the stable limit cycle appears in a small neighborhood of A when parameter α crosses the critical value a_c.

Two other singular points, if they exist, satisfy $\hat{u}_{1,2} > 0$. Their eigenvalues are real and have opposite signs, i.e., they are saddles for any parameter values.

To illustrate the analysis we fix parameter values at $\beta = 2$, $\delta = 1$, $k = 1$, $c = 0.5$. In this case the bifurcation value of α is $\alpha_c \approx -0.56$. The phase portraits of (8) with the given parameter values are shown in Fig. 3. Our calculations reveal three structurally stable phase portraits of (8). The portrait in Fig. 3a shows a traveling wave corresponding to the separatrix connecting saddle B_2 and focus A. The portrait in Fig. 3b possesses three types of traveling waves: first, it is an orbit from A to the limit cycle, second, the separatrix from

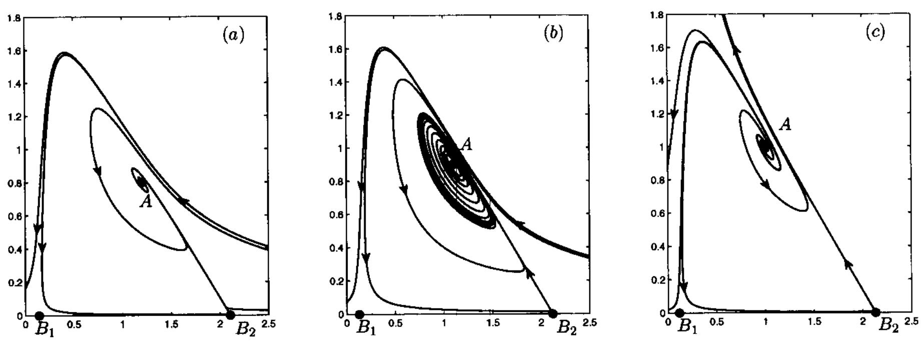

Figure 3: The Poincare-Andronov-Hopf bifurcation in system (8). Parameters are $\beta = 2$, $\delta = 1$, $k = 1$, $c = 0.5$ (a) $\alpha = -0.6$, singular point A is a stable focus. When $\alpha \approx 0.56$ the bifurcation occurs; (b) $\alpha = -0.55$, there is a stable limit cycle in a small neighborhood of A; (c) $\alpha = -0.5$, singular point A is an unstable focus and the limit cycle disappeared

B_2 to the limit cycle, and, third, the limit cycle itself. The portrait in Fig. 3c has only one bounded orbit that corresponds to a traveling wave solution of (1), namely, the separatrix connecting unstable focus A and saddle B_1. Numerical solutions of (1), (7) are presented in Fig. 4 (here we used periodic in time boundary conditions).

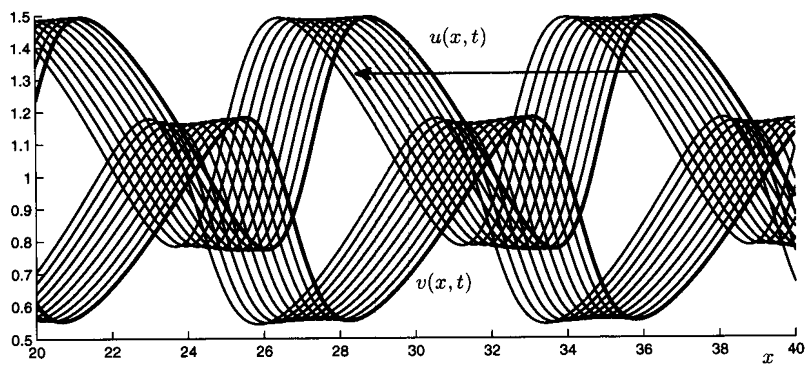

Figure 4: Numerical solutions of (1) with the functions (7). The parameter values are the same as in Fig. 3b

The particular form of $g(u, v)$ can be changed such that $g(u, v) = (-\beta + ku + v - \epsilon v^2)v$, $k, \beta, \epsilon \geqslant 0$, for small ϵ the qualitative picture remains the same.

It is worth noting that, as in the case of the separable models, there exists a family of traveling wave solutions if the wave system has a limit cycle.

Definition 2. *We shall call traveling wave solution* $(u(z), v(z))$ *of* (1) *asymptotic train if* $u(z)$, $v(z)$ *tend to periodic functions having the same period when* $z \to \infty$ *or* $z \to -\infty$.

Proposition 2. *If system* (1) *with a rational function* $f(u, v)$ *and a polynomial function* $g(u, v)$ *has a traveling wave train then it has a family of asymptotic trains.*

Proof of this proposition immediately follows from Proposition 1 and the well-known properties of two-dimensional ODE systems applied to the wave system (2). Every orbit starting within the limit cycle belongs to the family of asymptotic fronts (see Fig. 3b).

4 CONCLUSIONS

In this work we have shown that simple taxis models of the Keller-Segel type with cross-diffusion terms can possess all main types of traveling wave solutions: front-front, front-impulse, impulse-front, impulse-impulse and wave trains. The existence of traveling wave solutions of different types was proved by the well-known method of reducing of the initial PDE system to the wave system of ODEs.

Analyzing bifurcation portraits of the wave system we can trace rearrangements of the wave solutions with changing of the model parameters such as the wave propagation velocity.

In this report we paid especial attention to the wave train solutions, which correspond to oscillations in the wave system. To the best of our knowledge such kind of traveling wave solutions were not analyzed in taxis cross-diffusion models. We presented a simple model with a wave train within the considered class. Additionally, we have shown that the Keller-Segel type model also possesses wave train solution (and asymptotic wave trains). Within the frameworks of the models considered we observed appearance and disappearance of the wave trains with the change of the wave propagation velocity. It is worth noting that the wave trains appear with parameter changes as an intermediate stage between the front-front solutions of "opposite profiles" (see Fig. 4) together with a family of non-monotonous traveling fronts.

We did not discuss the issue of stability of the traveling wave solutions found, but we note that in all numerical simulations we conducted it is possible to observe traveling waves, albeit in some cases (e.g., for the wave train) the found solutions annihilate with time indicating probable instability. The important question of stability of the solutions found can be a subject of future research.

Acknowledgments. The work of FSB has been supported in part by NSF Grant #634156 to Howard University.

References

[1] F.S. Berezovskaya, G.P. Karev, "Bifurcations of traveling waves in population taxis models", Uspekhi Fizicheskikh Nauk, vol. 169(9), pp. 1011-1024, 1999.

[2] F.S. Berezovskaya, G.P. Karev, Traveling waves in cross-diffusion models of the dynamics of populations, Biofizika 45(4) (2000) 751-756.

[3] F.S. Berezovskaya, A.S. Novozhilov, G.P. Karev, "Population models with singular equilibrium", Mathematical Biosciences, 208 (2007) 270-299.

[4] F.S. Berezovskaya, A.S. Novozhilov, G.P. Karev, "Families of traveling impulses and fronts in some models with cross-diffusion", Nonlinear Analysis: Real World Applications, *in press.*

[5] S. Gueron, N. Liron, A Model of Herd Grazing as a Traveling Wave, Chemotaxis and Stability, Journal of Mathematical Biology 27(5) (1989) 595-608.

[6] D. Horstmann, A. Stevens, "A constructive approach to traveling waves in chemotaxis", Journal of Nonlinear Science, vol. 14(1), pp. 1-25, 2004.

[7] D.L. Feltham, M.A.J. Chaplain, Travelling waves in a model of species migration, Applied Mathematics Letters 13(7)(2000) 67-73.

[8] E.F. Keller, L.A. Segel, "Model for chemotaxis", Journal of Theoretical Biology, vol. 30(2), pp. 225-234, 1971.

[9] E.F. Keller, L.A. Segel, "Traveling Bands of Chemotactic Bacteria - Theoretical Analysis", Journal of Theoretical Biology vol. 30(2), pp. 235-248, 1971.

[10] Y.A. Kuznetsov, Elements of Applied Bifurcation Theory Springer, 2004.

[11] K. W. Morton, D. F. Mayers, Numerical solutions of partial differential equations, Cambrige University Press, 1989.

[12] T. Nagai, T. Ikeda, Traveling Waves in a Chemotactic Model, Journal of Mathematical Biology 30(2) (1991) 169-184.

[13] M.A. Tsyganov, V.N.Biktashev, J. Brindley, A.V. Holden, G.R. Ivanitsky, Waves in systems with cross-diffusion as a new class of nonlinear waves, Uspekhi Fizicheskikh Nauk 177(3) (2007) 275-300.

[14] M. A. Tsyganov, J. Brindley, A. V. Holden, V. N. Biktashev, Soliton-like phenomena in one-dimensional cross-diffusion systems: a predator-prey pursuit and evasion example, Physica D: Nonlinear Phenomena, 197(1-2) (2004) 18-33.

[15] A.I. Volpert, V.A. Volpert, V.A. Volpert, Traveling Wave Solutions of Parabolic Systems, AMS, 1994.