SOLUTIONS OF TWO SPECIES REACTION-DIFFUSION SYSTEMS

ALAN EASTON, MANMOHAN SINGH AND GURONG CUI

ABSTRACT. Reaction-diffusion equations describe interactions in a variety of systems in disciplines such as biology. An understanding of the behavior of the systems is often drawn from qualitative analyses since analytical solutions are difficult to obtain. Numerical approaches provide a key to discovering the behavior of the time dependent solutions.

We consider three two species ecological systems: a predator-prey system, a competing species system and a mutualism system. They have been solved using an operator splitting method which can be readily extended for solving multi-species non linear reaction diffusion equations.

The evolution of the biological systems and the steady state solutions in the form of travelling waves are accurately presented for each model. These solutions include phenomena such as waves of pursuit and evasion, competitive exclusion and cooperation for mutual advantage.

1. Introduction. The one dimensional reaction-diffusion equation for a single species has been solved by a number of authors including Puckett [3], Tang and Weber [5] and Wait and Mitchell [7]. Murray [2] discusses one and two species equations and their application to ecological and biological phenomena such as the study of predator-prey interactions, the spread of diseases and the generation of patterns. The splitting method developed by Yanenko [8] and applied by a number of authors including Grandal and Majda [1] is used here to solve reaction-diffusion systems for two species for which usually only qualitative results are discussed by Murray [2] and Smoller [4].

2. The equations. The one dimensional reaction-diffusion equations for two species are given by Smoller [4]

\[
\frac{\partial u}{\partial t} = D_1 \frac{\partial^2 u}{\partial x^2} + f_1(u, v), \quad x \in \Omega, \ t > 0,
\]

Received by the editors on September 3, 1996, and in revised form on June 19, 1997.

Key words and phrases. Reaction-diffusion, splitting method, predator-prey, competition, mutualism.

Copyright ©1997 Rocky Mountain Mathematics Consortium
\[
\frac{\partial v}{\partial t} = D_2 \frac{\partial^2 v}{\partial x^2} + f_2(u, v), \quad x \in \Omega, \quad t > 0,
\]

where \( u \) and \( v \) are the population densities of the two species, \( D_1 \) and \( D_2 \) are the constant diffusion coefficients, and \( f_1(u, v) \) and \( f_2(u, v) \) are the nonlinear reaction terms. We further define

\[
f_1(u, v) = uG_1(u, v)
\]

and

\[
f_2(u, v) = vG_2(u, v),
\]

where \( G_1 \) and \( G_2 \) are the growth rates. The type of biological system being modelled is specified by the choice of these growth rate functions.

For predator-prey investigations, species \( u \) is the prey and species \( v \) is the predator. Since the prey growth rate decreases as the predator population increases, and the predator growth rate increases with the prey population, the growth rate functions \( G_1 \) and \( G_2 \) satisfy

\[
\frac{\partial G_1(u, v)}{\partial v} < 0, \quad \frac{\partial G_2(u, v)}{\partial u} > 0.
\]

As a specific model, we take the growth rate functions given by Smoller [4]

\[
G_1(u, v) = (u - d)(1 - u) - ev,
\]

(3)

\[
G_2(u, v) = -\mu - D_1 v + eu,
\]

(4)

where \( 0 < d < 1 \), and \( e \) and \( \mu \) are positive constants with \( d < \mu/e < 1 \). Parameter \( d \) is the minimum survival density of species \( u \), parameter \( \mu \) is the linear death rate of species \( v \), and parameter \( e \) is the coefficient of interaction between the species.

For competing species, the growth rate functions \( G_1 \) and \( G_2 \) satisfy

\[
\frac{\partial G_1(u, v)}{\partial v} < 0, \quad \frac{\partial G_2(u, v)}{\partial u} < 0.
\]

Murray [2] discusses a simple two-species Lotka-Volterra competition model where \( u \) and \( v \) have logistic growth in the absence of the other.
We use a modified two-species Lotka-Volterra competition model in which the diffusion coefficients play an important role. The growth rate functions \( G_1 \) and \( G_2 \) are taken in the form

\[
(5) \quad G_1(u, v) = 1 - D_2u - \alpha_2v,
(6) \quad G_2(u, v) = \rho(1 - D_1v - \alpha_1u),
\]

where \( \rho \) is the constant birth ratio

\[
\rho = \frac{\text{the linear birth rate of } v}{\text{the linear birth rate of } u},
\]

\( D_1 \) and \( D_2 \) are the diffusion coefficients of the two species, and \( \alpha_1 \) and \( \alpha_2 \) represent the interactions of the species.

In a mutualism system the growth rate functions \( G_1 \) and \( G_2 \) satisfy

\[
\frac{\partial G_1(u, v)}{\partial v} > 0, \quad \frac{\partial G_2(u, v)}{\partial u} > 0.
\]

We consider two representations for \( G_1 \) and \( G_2 \), namely the modified Lotka-Volterra model

\[
(7) \quad G_1(u, v) = 1 - D_2u + \alpha_2v,
(8) \quad G_2(u, v) = \rho(1 - D_1v + \alpha_1u),
\]

and the modified Smoller model

\[
(9) \quad G_1(u, v) = (u - d)(1 - u) + ev,
(10) \quad G_2(u, v) = -\mu - D_1v + eu.
\]

3. Numerical schemes. In this paper, the reaction-diffusion equations (1) and (2) are solved numerically using the operator splitting method. The equations are split into two systems of subequations, the nonlinear reaction equations

\[
(11) \quad \frac{1}{2} \frac{\partial u}{\partial t} = f_1(u, v),
(12) \quad \frac{1}{2} \frac{\partial v}{\partial t} = f_2(u, v),
\]
which are used for the first half of the time step, and the linear diffusion equations

\begin{align}
(13) \quad \frac{1}{2} \frac{\partial u}{\partial t} &= D_1 \frac{\partial^2 u}{\partial x^2}, \\
(14) \quad \frac{1}{2} \frac{\partial v}{\partial t} &= D_2 \frac{\partial^2 v}{\partial x^2},
\end{align}

which are used for the second half of the time step.

All of the computations are carried out over an interval \([a, b]\) including \(\Omega\) which is sufficiently large that the end points \(a\) and \(b\) are far removed from the disturbance. The boundary conditions are applied for this larger interval as

\[ u(a, t) = u(b, t) = 0, \]

and

\[ v(a, t) = v(b, t) = 0, \]

for all \(t \in [0, T]\).

The interval \([a, b]\) is sub-divided into a mesh with \(J\) equal subintervals of length \(h = \Delta x = (b - a)/J\) so that the coordinates of the nodes are given by

\[ x_j = a + jh, \quad j = 0, 1, \ldots, J. \]

The numerical solutions at \(x = x_j\) and \(t = t_n\) are denoted \(u_j^n\) and \(v_j^n\), i.e., \(u_j^n = u(x_j, t_n)\) and \(v_j^n = v(x_j, t_n)\), where \(t_n = nk = n\Delta t\) and \(n = 0, 1, 2, \ldots, N\) is the number of time steps with length \(k = \Delta t\). Let \(\bar{u}_{j+1/2}^n\) and \(\bar{v}_{j+1/2}^n\) be the solutions of equations (11) and (12), i.e., after the first half time step, and let \(u_j^{n+1}\) and \(v_j^{n+1}\) be the solutions of (13) and (14), i.e., after the second half time step.

The numerical method used for the reaction equations (11) and (12) is usually the forward Euler scheme

\begin{align}
(15) \quad \bar{u}_{j+1/2}^n &= u_j^n + k f_1(u_j^n, v_j^n), \\
(16) \quad \bar{v}_{j+1/2}^n &= v_j^n + k f_2(u_j^n, v_j^n),
\end{align}
with initial values $u^n_j$ and $v^n_j$. This applies for the predator-prey system with growth rate functions (3) and (4), the competition system with growth rate functions (5) and (6) and the mutualism system with growth rate functions (7) and (8). However, the numerical method used for the reaction equations (11) and (12) is the backward Euler scheme

$$
\tilde{u}_{j}^{n+1/2} = u^n_j + k f_1(\tilde{u}_{j}^{n+1/2}, \tilde{v}_{j}^{n+1/2}), \tag{17}
$$

$$
\tilde{v}_{j}^{n+1/2} = v^n_j + k f_2(\tilde{u}_{j}^{n+1/2}, \tilde{v}_{j}^{n+1/2}). \tag{18}
$$

when the growth rate functions (9) and (10) are used for the mutualism system. We solve these equations using the iterative forms

$$
\tilde{u}_{j}^{n+1/2,(k+1)} = u^n_j + k f_1(\tilde{u}_{j}^{n+1/2,(k+1)}, \tilde{v}_{j}^{n+1/2,(k+1)}),
$$

$$
\tilde{v}_{j}^{n+1/2,(k+1)} = v^n_j + k f_2(\tilde{u}_{j}^{n+1/2,(k+1)}, \tilde{v}_{j}^{n+1/2,(k+1)}),
$$

where $\kappa$ is the iteration number. The values for the initial guess are those from the previous time step, i.e., $u^n_j$ and $v^n_j$.

The numerical method for the diffusion equations (13) and (14) is the backward time and central space difference scheme with initial data $\tilde{u}_{j}^{n+1/2}$ and $\tilde{v}_{j}^{n+1/2}$ obtained from (15) and (16) or from (17) and (18). The discrete forms are given by

$$
u^n_j + 1 = \tilde{u}_{j}^{n+1/2} + D_1 s(u^n_{j+1} - 2u^n_j + u^n_{j-1}), \tag{19}
$$

$$
u^n_j + 1 = \tilde{v}_{j}^{n+1/2} + D_2 s(v^n_{j+1} - 2v^n_j + v^n_{j-1}), \tag{20}
$$

where $s = k/h^2$. The solutions of equations (19) and (20) are the solutions after the complete time step, i.e., at $t = (n + 1)k$, $n = 0, 1, \ldots, N$.

The operator splitting scheme described here produces stable solutions with accuracy $O(k, h^2)$.

4. Numerical results. The initial conditions for the species $u$ and $v$ are taken as

$$
u(x, 0) = \begin{cases}
e^{10(x+1)} & x \leq -1, \\
1 & -1 \leq x \leq 1, \\
e^{-10(x-1)} & x \geq 1,
\end{cases} \tag{21}
$$

$$
v(x, 0) = \text{sech}^2(10x), \tag{22}
$$
where the population of $u$ is much greater than the population of $v$, or as

$$u(x, 0) = \text{sech}^2(10x),$$

$$v(x, 0) = \begin{cases} 
e^{10(x+1)} & x \leq -1, \\ 1 & -1 \leq x \leq 1, \\ e^{-10(x-1)} & x \geq 1, \end{cases}$$

where the population of $v$ is much greater than the population of $u$. These are standard continuous functions which have been used, for example, for one species by Tang, Qin and Weber [6] to show that the shape of the final steady state is independent of the initial conditions. For two species problems the relative size of the initial populations is important.

4.1 Predator-prey. The predator-prey equations have been solved with time step $k = \Delta t = 0.05$ and space step $h = \Delta x = 0.05$. Results for three sets of parameters are used to illustrate the basic features of the systems.

(i) The parameter values are taken as $d = 0.4$, $\mu = 0.3$, $e = 0.4$, $D_1 = 0.2$, and $D_2 = 0.1$ and the initial conditions are (21) and (22).

(ii) The parameter values are taken as $d = 0.1$, $\mu = 0.6$, $e = 0.8$, $D_1 = 0.2$, and $D_2 = 0.1$ and the initial conditions are (21) and (22).

(iii) The parameter values are taken as $d = 0.1$, $\mu = 0.6$, $e = 0.8$, $D_1 = 0.2$, and $D_2 = 0.1$ and the initial conditions are (23) and (24). These values are the same as in case (ii) except that the initial conditions are changed.

Figure 1 displays the results for case (i) at $t = 0, 2, 4, \ldots$. Both species suffer diffusion with decrease in the maximum values and spread of the populations. However, the populations of both species continue to decrease and they die out. We note that both the survival density $d$ and the relative value $\mu/e$ have significant values.

Figures 2 and 3 display the results for case (ii) using the same diffusion parameters $D_1$ and $D_2$ as in case (i) while the other parameters take the new values $d = 0.1$, $\mu = 0.6$ and $e = 0.8$. Figure 2 contains the results at $t = 0, 2, 4, \ldots, 10$. The population of the prey decreases from $t = 0$ until $t = 2$. Between $t = 2$ and $t = 4$, the maximum
FIGURE 1. Predator-prey populations at $t = 0, 2, 4, \ldots$ with $d = 0.4$, $\mu = 0.3$, $e = 0.4$, $D_1 = 0.2$ and $D_2 = 0.1$.

FIGURE 2. Predator-prey populations at $t = 0, 2, 4, \ldots, 10$ with $d = 0.1$, $\mu = 0.6$, $e = 0.8$, $D_1 = 0.2$ and $D_2 = 0.1$. 
value remains approximately constant while the spread continues and is accompanied by growth. The prey then experience a period of strong growth and spread outward in a wave like form. The population of the predator decreases until \( t = 4 \). It then experiences a period of consolidation during which the maximum value changes only marginally but the population of the predator begins to spread outward. The sequence continues in Figure 3 for \( t = 12, 14, \ldots, 50 \). After reaching its maximum value, the prey population continues to spread outward. The growth of the predator population toward its maximum value causes a decrease in the population of the prey to its long term steady state value in the region occupied by both species. The prey population continues to increase to its maximum value \( u = 0.97 \) at its edges and moves outward with a uniform shape at a speed 0.24. The overall solutions are the waves of pursuit and evasion characteristic of predator-prey systems. The pursuit by the predators causes the prey density to approach a limiting stable state, a travelling wave with two high density peaks surrounding a region of lower density values. In the area occupied by both species the population densities are constant \( (u = 0.79 \text{ and } v = 0.18) \). The travelling wave of prey has a saddle-like form while the travelling wave of the predator population has a bell-like form.
For case (iii) the parameters are the same as for case (ii) except that the initial conditions are (23) and (24) rather than (21) and (22). Since the initial population density of predator is greater than for the prey the population of prey quickly approaches zero and both species become extinct.

4.2 Competition. For the competition model we use the computational scheme given by (15), (16), (19) and (20) with $k = \Delta t = 0.05$ and $h = \Delta x = 0.1$. Two different situations are considered and in each case the initial conditions (21) and (22) are used so that the species $u$ initially has advantage over the species $v$.

(i) The parameters are taken as $\rho = 0.4$, $\alpha_1 = 1.6$, $\alpha_2 = 1.2$, $D_1 = 0.1$ and $D_2 = 0.5$. These satisfy the properties that $\rho < 1$, $\alpha_1 > 1$, $\alpha_2 > 1$, $\alpha_1 > \alpha_2$, $D_1 < D_2$, and imply that the reaction effect of species $u$ on $v$ is larger than of species $v$ on $u$, but species $v$ has stronger ability of aggressive spread than species $u$.

(ii) The parameters are taken as $\rho = 0.4$, $\alpha_1 = 1.2$, $\alpha_2 = 1.6$, $D_1 = 0.5$ and $D_2 = 0.1$. The reaction effect of species $u$ on $v$ is lower than that of species $v$ on $u$, but species $u$ has stronger ability of aggressive spread than species $v$.

The solutions for case (i) are illustrated in the series of diagrams in Figures 4 to 6 and present the typical evolution of competition behavior. Figure 4 shows the development of both species for $t = 0, 4, \ldots, 40$. The species $u$ increases and quickly achieves its stable travelling wave state with maximum value $u = 2$ and propagates outward. Initially, species $v$ decreases to very small levels. However, since it propagates outward faster than species $u$, it is able to form two colonies at the wavefronts of species $u$. At $t = 40$ these have increased to a value of approximately 1 and the spread of species $u$ is beginning to slow. In the next time sequence shown in Figure 5 for $t = 44, 48, \ldots, 80$, the dominant features are the growth of species $v$ to its maximum value $v = 10$, its movement outward to claim the new territory and its movement inward to occupy the territory of species $u$. Meanwhile, species $u$ is forced to retreat so that the propagating speeds of species $u$ have changed from outward to inward. The time sequence continues for $t = 84, 88, \ldots, 120$ in Figure 6. Species $u$ continues to lose its territory due to the plundering of species $v$. Finally, at about $t = 120$, species $u$ dies out and species $v$ is the winner. Its final state is a travelling wave.
FIGURE 4. Competition system at $t = 0.4, \ldots, 40$ with $\rho = 0.4$, $\alpha_1 = 1.6$, $\alpha_2 = 1.2$, $D_1 = 0.1$ and $D_2 = 0.5$.

FIGURE 5. Competition system at $t = 44, 48, \ldots, 80$ with $\rho = 0.4$, $\alpha_1 = 1.6$, $\alpha_2 = 1.2$, $D_1 = 0.1$ and $D_2 = 0.5$. 
FIGURE 6. Competition system at $t = 84, 88, \ldots, 120$ with $\rho = 0.4$, $\alpha_1 = 1.6$, $\alpha_2 = 1.2$, $D_1 = 0.1$ and $D_2 = 0.5$.

FIGURE 7. Competition system at $t = 0, 4, \ldots, 40$ with $\rho = 0.4$, $\alpha_1 = 1.2$, $\alpha_2 = 1.6$, $D_1 = 0.5$ and $D_2 = 0.1$. 

solution with a bell-like shape propagating outward. This illustrates the exclusion principle for a typical segregation-aggregation process.

The solutions for case (ii) at $t = 0, 4, \ldots, 40$ are shown in Figure 7. The reaction effect of species $u$ on $v$ is lower than species $v$ on $u$, but since species $u$ has stronger ability of aggressive spread than species $v$ to occupy the others' territory, species $u$ wins and species $v$ dies out. Only the initial distribution of $v$ is visible in this figure. The steady state solution for $u$ is a travelling wave with a bell-like shape travelling outward.

4.3 Mutualism. We solve two mutualism systems.

(i) The first system is a modified Lotka-Volterra model with growth rate functions (7) and (8) with parameter values $\rho = 0.4$, $\alpha_1 = 0.1$, $\alpha_2 = 0.4$, $D_1 = 0.1$ and $D_2 = 0.5$, and initial conditions given by (21) and (22).

(ii) The second system is a modified Smoller model with the nonlinear growth rate functions (9) and (10) with parameters $\delta = 0.1$, $\mu = 0.6$, $e = 0.8$, $D_1 = 0.1$ and $D_2 = 0.2$, and initial conditions given by (21) and (22).

For case (i), the numerical method consists of the forward Euler scheme (15) and (16) and the backward time and central space scheme (19) and (20) with time step $k = \Delta t = 0.05$ and space step $h = \Delta x = 0.1$. The results are shown in Figure 8 for times $t = 0, 4, \ldots, 40$. Initially both species spread and grow until the populations of both species reach their steady state values (50 for species $u$ and 60 for species $v$). The two species settle down to their uniform state, two travelling waves with the same speeds propagating to the right and to the left. The steady state has mutual benefit to both species.

For case (ii), we initially used the same numerical procedure as for case (i), i.e., the forward Euler scheme (15) and (16) for the reaction part and the backward time and central space scheme (19) and (20) for the diffusion part with the time step $k = \Delta t = 0.05$ and the space step $h = \Delta x = 0.1$. However, when the growth rate increased, oscillations were observed in the solutions. Hence, we tried a second method. This consisted of the implicit backward time Euler scheme (17) and (18) for the reaction part and the backward time and central space (19) and (20) for the diffusion part. Initially, this also proved unsatisfactory since,
FIGURE 8. Mutualism system at $t = 0, 4, \ldots, 40$ with $\rho = 0.5$, $\alpha_1 = 0.1$, $\alpha = 0.4$, $D_1 = 0.1$ and $D_2 = 0.5$.

FIGURE 9. Mutualism system at $t = 0, 4, \ldots, 40$ with $d = 0.1$, $\mu = 0.6$, $e = 0.8$, $D_1 = 0.1$ and $D_2 = 0.2$. 
with time step \( k = \Delta t = 0.05 \) and the space step \( h = \Delta x = 0.1 \), the solutions became unbounded at about \( t = 28 \). The results presented in Figure 9 for \( t = 0, 4, \ldots, 40 \) were obtained using these schemes with the same conditions and parameters except that the time step was reduced to \( k = \Delta t = 0.01 \). After initial growth the two species reach their steady state values \( u = 6.8 \) and \( v = 48.2 \) and settle down to their uniform steady state, two travelling waves with the same speeds propagating to the right and to the left.

5. Conclusions. The operator splitting method has been successfully applied to solve the two species reaction-diffusion equations. In general the forward Euler scheme has been used for the nonlinear reaction equations and a backward time difference scheme has been used for the diffusion terms. However, for one of the mutualism cases it was necessary to use a backward Euler scheme for the nonlinear reaction equations to avoid chaotic oscillations. The solutions exhibit the known properties of two species predator-prey systems, competition systems and mutualism systems described by Murray [2].

The characteristics of predator-prey systems depend on the values of the parameters. One set of conditions (high death rate of the prey) results in the decay from the initial values leading to extinction of both predator and prey. Another shows the initial diffusion of predator and prey followed by growth to the steady state solutions of coexistence and the travelling waves of evasion and pursuit. The speed of spread of the species as a wave into new territory depends on the rate of diffusion. These are the known observed characteristic features of two species predator-prey systems.

For the competition system the usual exclusion principle of one species completely replacing the other has been demonstrated. We have also observed that a species may initially be driven from its territory until it has generated enough strength to stop the further spread of the other species and cause the initially stronger species to retreat until it becomes extinct. Again, the steady state solution is a travelling wave with a bell-like shape travelling outward.

Greater care was needed to obtain a stable numerical solution of the mutualism system. After initial growth the two species reach their steady state values and settle down to their uniform state, two travelling
waves with the same speeds propagating outward to the right and to the left.

REFERENCES


