REACTION DIFFUSION MODEL FOR THE GROWTH OF MYCELIUM

By

Walid Sharabati

An Alternate Plan Paper Submitted in Partial Fulfillment of the Requirements for

Master of Science

In Mathematics: Computer Science

Minnesota State University, Mankato

Mankato, Minnesota

December 2003

TABLE OF CONTENTS

TABLE OF FIGURES

Chapter One

Development Of The Mathematical Model

This paper presents some analysis of the growth model for mycelium in the presence and absence of diffusion based on the reaction-diffusion equation. The work and effort applied in this project is in fact a continuation of collaborative work accomplished by Dr. Ernest Boyd, Mathematics, Dr. Keith Klein, Biology, and their students. An extensive use of the computer software *Mathematica*[1] will provide significant assistance in studying the behavior of the model and the mathematical analysis of the system. This mathematical model attempts to explain the formation of regular and irregular growth patterns of mycelium. A derivation of some algebraic inequalities using the Jacobian matrix will be needed to analyze stability and instability of the system at equilibrium. These inequalities, as we shall see later, will be the conditions we are going to test as necessary conditions for irregular growth patterns. We are hoping that certain values of the parameters involved in our mathematical model will satisfy the conditions imposed by the inequalities and so providing a solution to the problem.

Suppose reaction-diffusion occurs in a two-dimensional space. Let $A(x,y,t)$ be the density of some substance at time t, then the rate of change of this substance with respect to time includes the growth term, the decay term, and the diffusion term of that substance. Namely,

---

[1] All analysis and graphs presented in this paper are generated by *Mathematica 4.1*.

$$\text{Rate of Change} = \frac{\partial A}{\partial t} = \text{growth} - \text{decay} + \text{diffusion}.$$

where, growth and decay can depend on the reaction between A and another substance. This leads to a system of two coupled partial differential equations. The biological features of the mycelium model must show two different patterns of growth. We know that mycelia grow in some environments outward in the radial direction with symmetric, regular logistic growth (Figure 1.1.)[2] In other environments the cells also produce some chemical inhibitor, which propagates radially and outwards as well causing the cells to grow irregularly when diffusion is present and a different pattern appears (Figure 1.2.)[3] This is due to the high concentration of the inhibitor and faster diffusion rate compared with the cells. We are going to use polar coordinates in our analysis. Let $U = U(r,\theta,t)$ be the density of cells of mycelium = $\left[\frac{cells}{mm^2}\right]$, $W = W(r,\theta,t)$ be the concentration of chemical inhibitor = $\left[\frac{moles}{mm^2}\right]$. In addition, suppose the cells are placed in a circular petri dish with sufficient culture media to grow. With diffusion the system of differential equations will be:

$$\frac{\partial U}{\partial t} = F(U,W) - CUW + D_1\nabla^2 U \quad (1)$$

$$\frac{\partial W}{\partial t} = AU^2 - BW + D_2\nabla^2 W \quad (2)$$

where $F(U,W)$ represents the mycelial growth rate, CUW represents the effect of the

[2] Bezzi, M., A. Ciliberto, and A.Mengoni, "Pattern Formation by Competition: A Biological Example," ***ArXiv*** , 2001, p. 8.

chemical inhibitor upon the decay of the cells, $D_1\nabla^2 U$ represents the rate at which the cells diffuse, AU^2 represents the rate of production of the chemical inhibitor, BW represents its rate of decay, and $D_2\nabla^2 W$ represents the rate at which the chemical inhibitor diffuses.

Since we are using polar coordinates, we assume $0 \le r \le r_{\max}$ and $0 \le \theta \le 2\pi$, with initial conditions $U(r,\theta,0) = \begin{cases} U_0 & if \quad r \le r_0 \\ 0 & if \quad r \ge r_0 \end{cases}$ and $W(r,\theta,0) = 0$. At the boundary, we assume there is no growth of the mycelium or production of the chemical inhibitor, i.e. $U(r_{\max},\theta,t) = 0$ and $W(r_{\max},\theta,t) = 0$. We take care of periodicity by supposing that the density of mycelium and the concentration of the chemical inhibitor do not change for all multiples of 2π; that is to say $U(r,\theta + 2\pi,t) = U(r,\theta,t)$ and $W(r,\theta + 2\pi,t) = W(r,\theta,t)$. We hypothesize that the growth rate of the mycelium is a hyperlogistic curve $F(U,W) = RU^p(1 - \frac{U}{K})$ with $p \ge 1$.[4] Here, R is the intrinsic growth rate, and K is the carrying capacity.

This system can be normalized and represented in dimensionless form as follows:

$$\frac{\partial u}{\partial \tau} = f(u,w) - uw + \nabla^2 u \tag{3}$$

$$\frac{\partial w}{\partial \tau} = au^2 - bw + d\nabla^2 w \tag{4}$$

---

[3] Bezzi, p. 8.
[4] Tsoularis, A., ***Analysis of Logistic Growth Models***, Res. Lett. Inf. Math. Sci. (2001) 2, pp. 23-46.

where $u = \frac{U}{K}$, $w = \frac{C(r_{max})^2 W}{D_1}$, $\tau = \frac{D_1 t}{(r_{max})^2}$, $a = AC\left(\frac{K(r_{max})^2}{D_1}\right)^2$, $b = \frac{B(r_{max})^2}{D_1}$, $d = \frac{D_2}{D_1}$. Here, d is the coefficient of diffusion and we assume it is greater than one. With our hypothesis $f(u,w) = ru^p(1-u)$ where $r = \frac{R(r_{max})^2 K^{p-1}}{D_1}$.[5] At equilibrium, $\frac{\partial u}{\partial \tau} = 0 = \frac{\partial w}{\partial \tau}$ and $\nabla^2 u = 0 = \nabla^2 w$. Hence, we solve (3) and (4) as $f(u^*, w^*) = u^* w^*$ and $a(u^*)^2 = bw^*$ to determine the steady-state equilibrium (u^*, w^*). Since we normalized all parameters, we restrict $0 \le u^*, w^*, r \le 1$, $a, b > 0$, and $d \ge 1$. In the later chapters, we will study $f(u,w)$ in more detail.

Experiments in Dr. Klein's laboratory show that the cells of mycelium demonstrate symmetrical growth patterns in the absence of the chemical inhibitor; however, with the presence of the inhibitor the cells form an asymmetrical spatial pattern. Therefore, in the mathematical model we need to look for a stable equilibrium without diffusion and an unstable equilibrium with diffusion. We analyze the mathematical model in (3) and (4) using standard Fourier analysis as shown in [6] leading to the following inequalities.

$$\frac{b}{d} < \frac{\partial f^*}{\partial u} - w^* < b \tag{5}$$

[5] A detailed explanation of each parameter and its representation in (1), (2), (3), and (4) can be found in [6] Qian, "Reaction Diffusion Equations for the Growth of Mycelium".

$$0 < 3a(u^*)^2 - b\frac{\partial f^*}{\partial u} - 2au^*\frac{\partial f^*}{\partial w} < d\left(\frac{d\frac{\partial f^*}{\partial u} - b - dw^*}{2d}\right)^2 \qquad (6)$$

These inequalities are necessary conditions on $f(u,w)$ in order for (u^*, w^*) to be a stable equilibrium without diffusion and an unstable equilibrium with diffusion. However, the most challenging task is to find such a growth function $f(u,w)$ that will satisfy the inequalities. We will show in the next chapter that choosing the growth function to be $f(u,w) = ru(1-u)$ contradicts the inequalities in (5) and (6). Therefore, we will modify $f(u,w)$ to be generalized logistic growth to search for possible solutions. This is what we are going to discuss in Chapter Three and setup *Mathematica* to test and analyze.

Chapter Two

Mathematical Analysis With The Logistic Growth Function

In this chapter, we will show that choosing the growth function $f(u,w)$ to be a logistic growth with $p=1$, i.e., $f(u,w)=ru(1-u)$, will lead us to a contradiction with the conditions prescribed by the inequalities in (5) and (6). Consider the Jacobian matrix

$$J-q^2D=\begin{bmatrix}\dfrac{\partial f^*}{\partial u}-w^*-q^2 & \dfrac{\partial f^*}{\partial w}-u^* \\ 2au^* & -b-q^2d\end{bmatrix} \tag{7}$$

where $D=\begin{bmatrix}1 & 0\\ 0 & d\end{bmatrix}$.[6] The characteristic eigenvalues corresponding to this matrix are of the form $\lambda=\dfrac{\mathrm{tr}(J-q^2D)\pm\sqrt{\mathrm{tr}(J-q^2D)^2-4\det(J-q^2D)}}{2}$. For instability we need $|\lambda|>0$. This holds when $\mathrm{tr}(J-q^2D)>0$ or $\det(J-q^2D)<0$, so we have two cases to probe.

If $\mathrm{tr}(J-q^2D)>0$, we have $\dfrac{\partial f^*}{\partial u}-w^*-q^2-b-q^2d>0$ which implies that $\dfrac{\partial f^*}{\partial u}>w^*+b+q^2(1+d)\geq w^*+b$. Yet, in the absence of diffusion we needed $\dfrac{\partial f^*}{\partial u}<w^*+b$. This leads us to a contradiction. If $\det(J-q^2D)<0$, we have $\left(\dfrac{\partial f^*}{\partial u}-w^*-q^2\right)\left(-b-q^2d\right)-\left(\dfrac{\partial f^*}{\partial w}-u^*\right)\left(2au^*\right)<0$ which implies that

$dq^4 + \left(b + dw^* - d\frac{\partial f^*}{\partial u}\right)q^2 + b\left(w^* - \frac{\partial f^*}{\partial u}\right) - 2au^*\left(\frac{\partial f^*}{\partial w} - u^*\right) < 0$. The latter inequality is a parabola in q^2 with vertex in the forth quadrant that opens upward.

We next examine the logistic growth function $f(u,w) = ru(1-u)$. Suppose the intrinsic growth rate r is a function of w only, i.e. $r = r(w)$. Then, $\frac{\partial f^*}{\partial u} = r(1-2u^*)$ and therefore $\frac{\partial f^*}{\partial u} - w^* = r(1-2u^*) - w^*$. Note that at equilibrium we have $f(u^*, w^*) = u^* w^*$, so $w^* = r(1-u^*)$. We then substitute $\frac{\partial f^*}{\partial u}$ and w^* in (5) to obtain

$$\frac{b}{d} < \frac{\partial f^*}{\partial u} - w^* < b$$

$$\frac{b}{d} < r(1-2u^*) - r(1-u^*) < b$$

$$\frac{b}{d} < -ru^* < b$$

This is not possible because we have a negative real number trapped between two positive numbers for all $0 \le r$ and $0 \le u^*$. Hence, limiting the growth function to be $f(u,w) = ru(1-u)$ does not satisfy the inequality in (5). Dr. Boyd also tried $f(u,w) = \beta\left(1 - \frac{w}{\alpha}\right)u(1-u)$ which will give the same result.

[6] Refer to [6] Qian for more explanation.

Chapter Three

Mathematical Analysis With The Hyperlogistic Growth Function And Results

In the previous chapter, we proved by letting $p = 1$ in the modified growth function, $f(u,w) = ru^p(1-u)$, the algebraic inequality in (5) does not hold. This leads us to consider different values for *p*. Before we analyze the system of differential equations in (3) and (4) for various values of *p*, we are going to study the behavior of the model without diffusion when $p = 1$. Recall the differential equations in (3) and (4). Having no diffusion in the growth process eliminates the diffusion terms in those equations, i.e., $\nabla^2 u = 0 = \nabla^2 w$, and the system simplifies,

$$\frac{\partial u}{\partial \tau} = ru(1-u) - uw \qquad (8)$$

$$\frac{\partial w}{\partial \tau} = au^2 - bw \qquad (9)$$

Again at equilibrium, we have $\frac{\partial u}{\partial \tau} = 0 = \frac{\partial w}{\partial \tau}$. The next step is to solve (8) and (9) to determine the isoclines $w = \frac{a}{b}u^2$ and $w = r(1-u)$.

We then setup *Mathematica* to solve for the equilibrium point (u^*, w^*) to obtain

$\left(\frac{-br \pm \sqrt{br(4a+br)}}{2a}, \frac{r\left(2a+br \pm \sqrt{br(4a+br)}\right)}{2a} \right)$.[7] The Jacobian matrix corresponding to the system in (8) and (9) is,

$$\begin{bmatrix} r(1-u)-ru-w & -u \\ 2au & -b \end{bmatrix} \tag{10}$$

Now substitute (u^*, w^*) in (10) to get $\begin{bmatrix} br^2 - \sqrt{br^3(4a+br)} & \frac{br-\sqrt{br(4a+br)}}{2a} \\ -br+\sqrt{br(4a+br)} & -b \end{bmatrix}$ which has a corresponding characteristic eigenvalue of λ =

$$\frac{2ab - br^2 + \sqrt{br^3(4a+br)} \pm \sqrt{-8abr\left(4a+br-\sqrt{br(4a+br)}\right)+\left(2ab-br^2+\sqrt{br^3(4a+br)}\right)^2}}{-4a}$$

For example, let $a = 1$, $b = 0.5$, and $r = 0.9$. The isoclines are shown in Figure 3.3. Then $\lambda = -0.467 \pm 0.681i$ and so the point $(u^*, w^*) = (0.482,\ 0.465)$ is a stable equilibrium. We let *Mathematica* do the symbolic computation to determine the behavior of the vector field by calling the subroutine PlotVectorField. The path of a trajectory in time can be solved numerically with $u(0) = 0.01$, $w(0) = 0$ and plotted by calling the subroutines NDSolve and ParametricPlot; see Figure 3.4. Note that (u^*, w^*) in Figure 3.4 is a stable spiral node. The graphs of $u(\tau)$ and $w(\tau)$ as functions of τ are shown in Figures 3.5 and 3.6.

---

[7] Refer to attached Appendix One for *Mathematica* notebook.

Next, we analyze the generalized logistic growth function, $f(u,w) = ru^p(1-u)$, using the algebraic compound inequalities in (5) and (6). We are going to do three tests here. First, we test inequality (5) for given values of *b* and *d*. We are going to call it Test1. Then, we test the left side of inequality (6), and we are going to call it Test2. Finally, we take the right side of inequality (6) minus the left side, and we are going to call it Test3. The three tests in order are:

$$\frac{b}{d} < \frac{\partial f^*}{\partial u} - w^* < b$$

$$0 < 3a(u^*)^2 - b\frac{\partial f^*}{\partial u} - 2au^*\frac{\partial f^*}{\partial w}$$

$$0 < d\left(\frac{d\frac{\partial f^*}{\partial u} - b - dw^*}{2d}\right)^2 - 3a(u^*)^2 + b\frac{\partial f^*}{\partial u} + 2au^*\frac{\partial f^*}{\partial w}$$

Remember that these tests are necessary conditions for validity of the solution but not sufficient. So we may or may not obtain a solution even if these conditions are satisfied. We now proceed with the analysis as follows.

At equilibrium $f(u^*,w^*) = r\left(u^*\right)^p(1-u^*) = u^*w^*$. This gives $w^* = r\left(u^*\right)^{p-1}(1-u^*)$ and $\frac{\partial f^*}{\partial u} = rp(1-u^*)\left(u^*\right)^{p-1} - r\left(u^*\right)^p$. Substituting $\frac{\partial f^*}{\partial u}$ and w^* in (5) to get Test1,

$$\frac{b}{d} < rp\left(1-\left(u^*\right)\right)\left(u^*\right)^{p-1} - r\left(u^*\right)^p - r\left(u^*\right)^{p-1}\left(1-\left(u^*\right)\right) < b$$

$$\frac{b}{d} < r\left((p-1)\left(u^*\right)^{p-1} - p\left(u^*\right)^p\right) < b$$

$$\frac{b}{d} < r\left(u^*\right)^{p-1}\left(p\left(1-u^*\right)-1\right) < b \qquad (11)$$

Note that one u-intercept for this polynomial is $u^* = \dfrac{p-1}{p}$.

For the second test, we need to find $\dfrac{\partial f^*}{\partial w}$ and the constant a. Since, $f(u,w)$ is a function of u only, this means that $\dfrac{\partial f^*}{\partial w} = 0$. Also, since $w^* = r\left(u^*\right)^{p-1}(1-u^*)$ and $w^* = \dfrac{a}{b}\left(u^*\right)^2$ at equilibrium, then $a = rb\left(u^*\right)^{p-3}(1-u^*)$. Hence Test2 is

$$0 < 3rb\left(u^*\right)^{p-1}(1-u^*) - rbp(1-u^*)\left(u^*\right)^{p-1} + r\left(u^*\right)^p - 0$$

$$0 < rb\left(u^*\right)^{p-1}\left(3-2u^* + p(u^*-1)\right) \qquad (12)$$

Similarly, Test3 simplifies in the same manner.

$$0 < \frac{\left(b + d\left(pr\left(u^*\right)^{p-1}(u^*-1) + w^* + r\left(u^*\right)^p\right)\right)^2}{4d} - \text{Test2}$$

$$0 < \frac{\left(b + d\left(pr\left(u^*\right)^{p-1}(u^* - 1) + r\left(u^*\right)^{p-1}(1 - u^*) + r\left(u^*\right)^{p}\right)\right)^2}{4d} - \text{Test2}$$

$$0 < \frac{\left(b + rd\left(u^*\right)^{p-1}\left(p(u^* - 1) + 1\right)\right)^2}{4d} - rb\left(u^*\right)^{p-1}\left(3 - 2u + p(u - 1)\right)$$

$$0 < \left(b + rd\left(u^*\right)^{p-1}\left(p(u^* - 1) + 1\right)\right)^2 - 4rbd\left(u^*\right)^{p-1}\left(3 - 2u + p(u - 1)\right) \qquad (13)$$

At this point, we have no idea what values for *a*, *b*, *d*, *r* and *p* will satisfy the tests in (11), (12), and (13). Thus, the next phase is to search for possible values, if there are any, satisfying the necessary conditions in (11), (12), and (13). The best way to approach this is by fixing *b*, *d* and *p* and then seeking possible values for *r* and u^*. Once we find valid *r* and u^* then we retrieve *a* from $a = rb\left(u^*\right)^{p-3}(1 - u^*) = b\frac{w^*}{\left(u^*\right)^2}$ at equilibrium. Let $p = 5$, $b = 0.15$, $d = 3.5$ and assume we are looking for *r* and u^*. The solution is represented in terms of a feasible set as in Figure 3.7a; the red region implies the three tests are all satisfied. Figure 3.7b shows *a* as a function of *u* and *r*.

Now, recall the Jacobian matrix in (7). We already have shown that $\frac{\partial f^*}{\partial w} = 0$ and $\frac{\partial f^*}{\partial u} = r\left(u^*\right)^{p-1}\left(p(1 - u^*) - u^*\right)$. Moreover, $w^* = r\left(u^*\right)^{p-1}(1 - u^*)$, $a = rb\left(u^*\right)^{p-3}(1 - u^*)$. Hence, we can write (7) as,

$$J - q^2 D = \begin{bmatrix} r(u^*)^{p-1}\left(p(1-u^*) - u^*\right) - q^2 & -u^* \\ 2au^* & -b - q^2 d \end{bmatrix}$$

At equilibrium, $\frac{\partial u}{\partial \tau} = 0 = \frac{\partial w}{\partial \tau}$, and $\nabla^2 u = 0 = \nabla^2 w$. In general, the isoclines are functions w in terms of u, i.e. $w = \frac{a}{b}u^2$ and $w = ru^{p-1}(1-u)$. For example when $p = 5$, one isocline is, $w = 0.9u^4(1-u)$ while the other is $w = 0.133u^2$; see Figure 3.8.

Note that we have two equilibra other than $(0,\ 0)$. It is obvious that $(0,\ 0)$ is a stable equilibrium. One equilibrium point is $(0.630,\ 0.051)$ which has eigenvalues $\lambda_1 = -0.071$ and $\lambda_2 = 0.038$. Consequently, $(0.630,\ 0.051)$ is a saddle point. The second equilibrium is $(0.709,\ 0.065)$ which has eigenvalues $\lambda = -0.025 \pm 0.059i$. So, we conclude that $(0.709,\ 0.065)$ is a stable equilibrium. The graphs of the vector field and the path of a trajectory in time with $u(0) = 0.55$, $w(0) = 0$ are shown in Figures 3.9. The graphs of $u(\tau)$, $\mathrm{w}(\tau)$ are shown in Figures 3.10 and 3.11. The mycelial cells will grow until they reach their maximum, which is the carrying capacity.

The next example presents another interesting result. Suppose $p = 3$, $a = 0.053$, $b = 0.095$, $d = 2.1$, $r = 0.99$ and $q^2 = 0.0001$. The isoclines $w = 0.558u^2$ and $w = 0.99u^2(1-u)$ are shown in Figure 3.12. Then the equilibrium point is $(0.437,\ 0.106)$ which has corresponding eigenvalues of the form $\lambda = 0.017 \pm 0.087i$. Figure 3.13 shows the behavior of the vector field and the path of a trajectory in time with initial conditions

$u(0)=0.2$, $w(0)=0$. Figures 3.14 and 3.15 show the trajectory $u(\tau)$ and $w(\tau)$ as functions of time τ. Note that in this case we are experiencing a limit cycle, which is not biologically possible.

The next example is more biologically realistic. Suppose $p=3$, $a=0.05$, $b=0.09$, $d=1.01$, $r=0.99$ and $q^2=0.01$. Here, the isoclines $w=0.556u^2$ and $w=0.99u^2(1-u)$ are shown in Figure 3.16. Then the equilibrium point is $(0.444,\ 0.098)$ which has corresponding eigenvalues of the form $\lambda=0.015\pm 0.08i$. Figure 3.17 shows the behavior of the vector field, and the path of the trajectory in time with initial conditions $u(0)=0.2$, $w(0)=0$. In this case, the cells of mycelium die completely after they reach their maximum growth. The graphs of $u(\tau)$ and $w(\tau)$ are shown in Figures 3.18 and 3.19.

Appendix Two is a *Mathematica* code to search for possible values for *r*, *u* and *a* given fixed values for *b*, *d* and *p*. We claim that there exists a solution inside the feasible region where the three tests are fulfilled. We have found some good results. For instance, Figure 3.20a shows the feasible region for $p=3$, $b=0.1$, $d=5.5$. Figure 3.21a shows the feasible region for $p=3$, $b=0.1$, $d=8$. Figure 3.22a shows the feasible region for $p=3$, $b=0.13$, $d=9$. Figure 3.23a shows the feasible region for $p=3$, $b=0.05$, $d=5.5$. Figure 3.24a shows the feasible region for $p=3$, $b=0.01$, $d=5.5$. Figure 3.25a shows the feasible region for $p=4$, $b=0.1$, $d=3$. Figure 3.26a shows the feasible region for $p=4$, $b=0.1$, $d=7$. Figure 3.27a shows the feasible region for

$p = 4$, $b = 0.05$, $d = 12.5$. Figure 3.28a shows the feasible region for $p = 4$, $b = 0.25$, $d = 12$. Figure 3.29a shows the feasible region for $p = 5$, $b = 0.1$, $d = 2.5$. Figure 3.30a shows the feasible region for $p = 5$, $b = 0.1$, $d = 7.5$. Figure 3.31a shows the feasible region for $p = 5$, $b = 0.09$, $d = 7$. Figure 3.32a shows the feasible region for $p = 5$, $b = 0.05$, $d = 17.5$. Figure 3.33a shows the feasible region for $p = 7$, $b = 0.07$, $d = 10$. On the other hand, Figures 3.20b through 3.33b show *a* as a function of *u* and *r* according to the values of the parameters given in Figures 3.20a through 3.33a.

In conclusion, we have found some promising numerical values satisfying the necessary conditions introduced by the inequalities. A value for the parameter *a* will be determined from the experiments by Dr. Klein. The surface for *a* as a function of *u* and *r* will be drawn to determine the level curve for that value of *a*. The value of *r* will be chosen and then the point on the level curve for that value of *r* will determine the equilibrium level *u* that is contained in the feasible region. Next we need to compare these values with numerical simulations of the model. This project is the ground foundation for further work solving the model numerically using either a finite difference method or a finite element method. Finally, the numerical values described in this paper must be examined by biologists to determine if they are biologically meaningful.

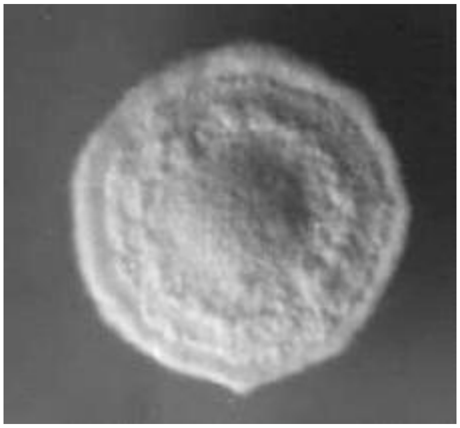

Figure 1.1. Pattern formed without diffusion. (Courtesy of M. Bezzi.)

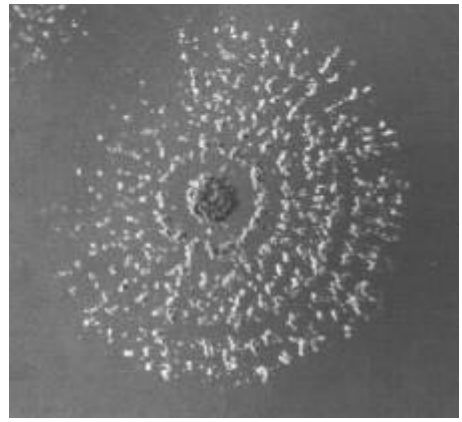

Figure 1.2. Pattern formed with diffusion. (Courtesy of M. Bezzi.)

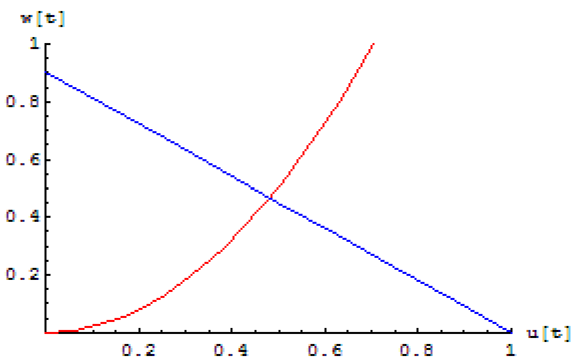

Figure 3.3. Isoclines for $p = 1$, $a = 1$, $b = 0.5$, $r = 0.9$.

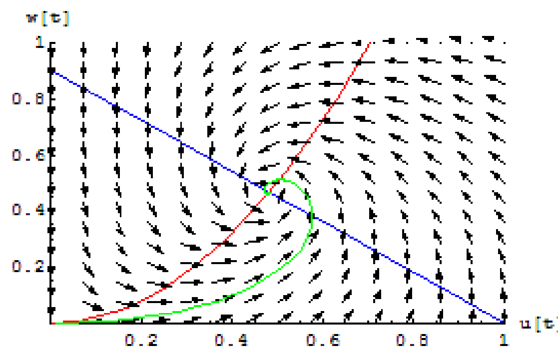

Figure 3.4. Phase diagram for $p = 1$, $a = 1$, $b = 0.5$, $r = 0.9$.

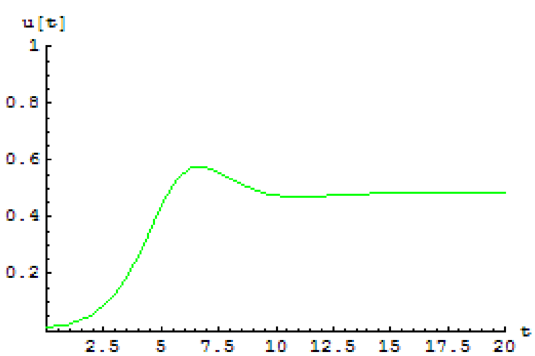

Figure 3.5. $u(\tau)$ as a function of τ.

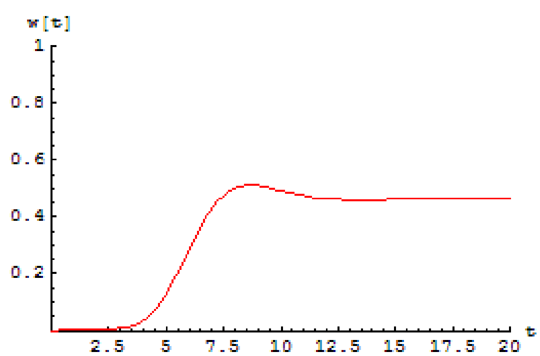

Figure 3.6. $w(\tau)$ as a function of τ.

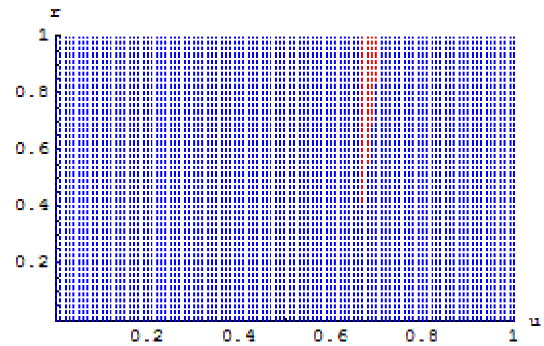

Figure 3.7a. Feasible region in red for $p = 5$, $b = 0.15$, $d = 3.5$.

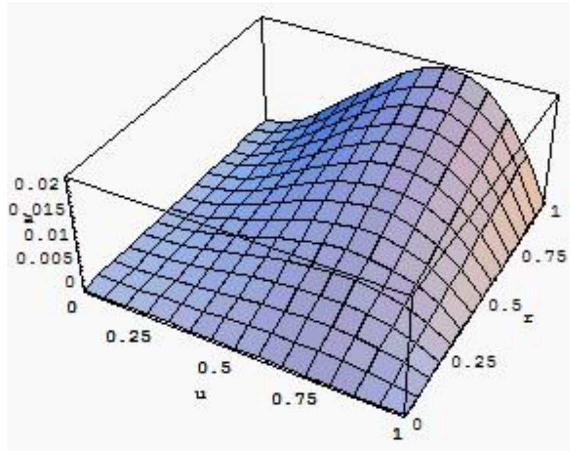

Figure 3.7b. a as a function of u and r.

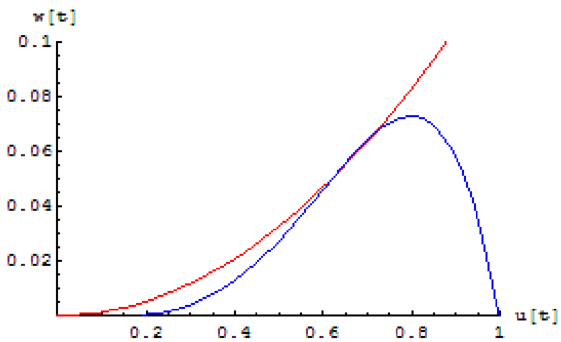

Figure 3.8. Isoclines for $p = 5$, $a = 0.02$, $b = 0.15$, $r = 0.9$.

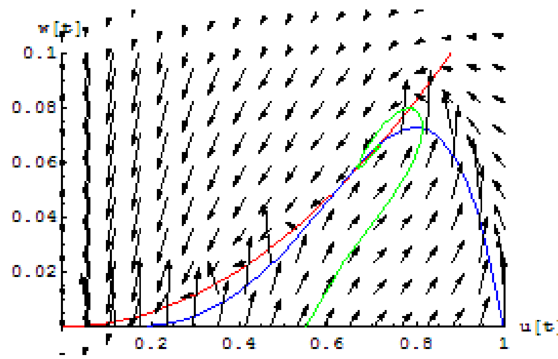

Figure 3.9. Phase diagram for $q^2 = 0.001$, $p = 5$, $a = 0.02$, $b = 0.15$, $r = 0.9$, $d = 3.5$.

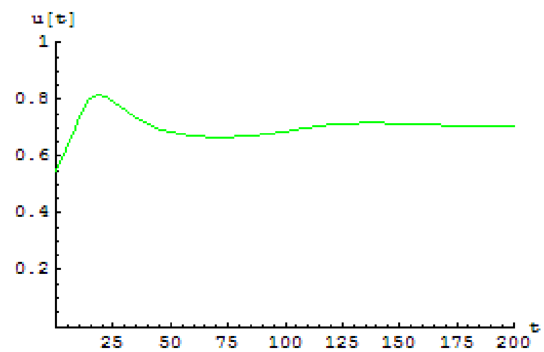

Figure 3.10. $u(\tau)$ as a function of τ.

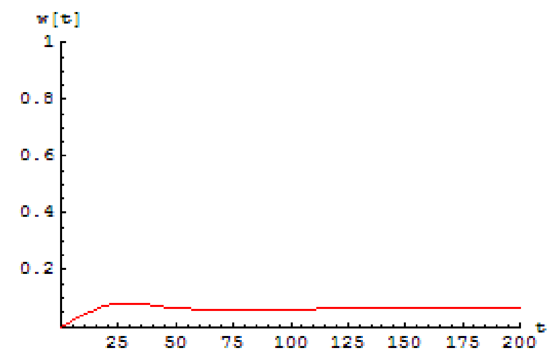

Figure 3.11. $w(\tau)$ as a function of τ.

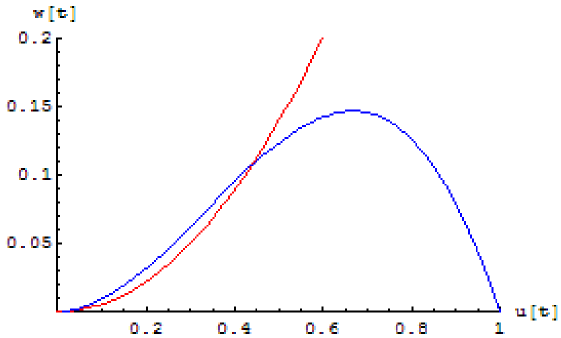

Figure 3.12. Isoclines for $p = 3$, $a = 0.053$, $b = 0.095$, $r = 0.99$.

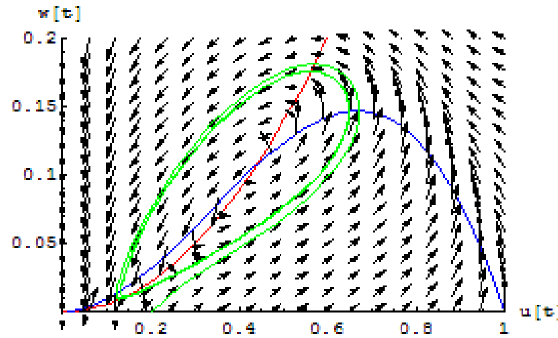

Figure 3.13. Phase diagram for $q^2 = 0.0001$, $p = 3$, $a = 0.053$, $b = 0.095$, $r = 0.99$, $d = 2.1$.

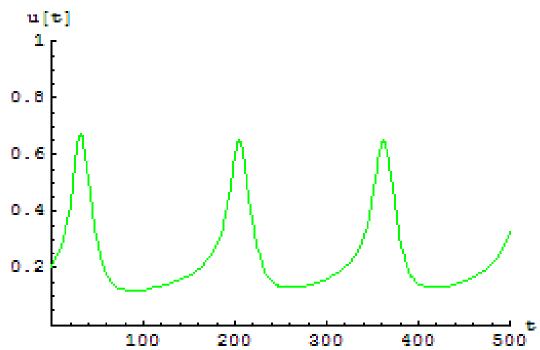

Figure 3.14. $u(\tau)$ as a function of τ.

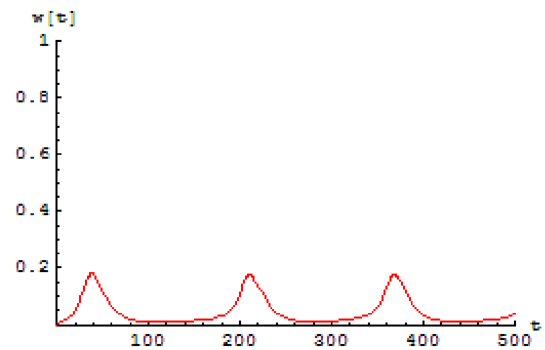

Figure 3.15. $w(\tau)$ as a function of τ.

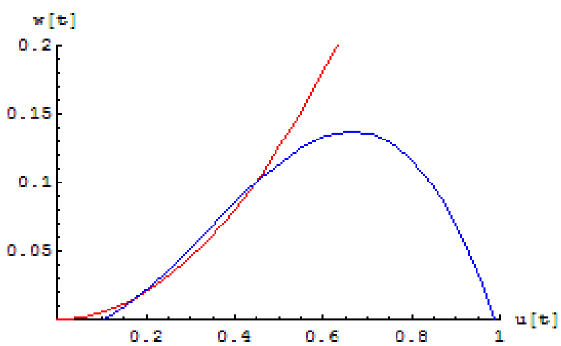

Figure 3.16. Isoclines for $p = 3$, $a = 0.05$, $b = 0.09$, $r = 0.99$.

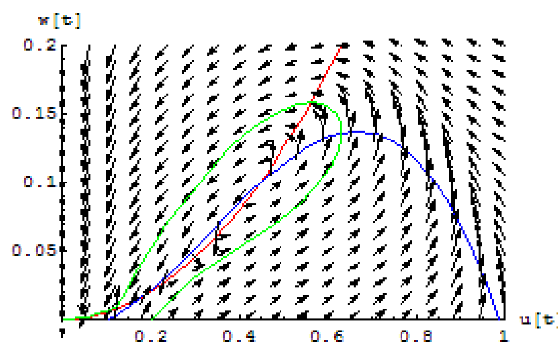

Figure 3.17. Phase diagram for $q^2 = 0.01$, $p = 3$, $a = 0.05$, $b = 0.09$, $r = 0.99$, $d = 1.01$.

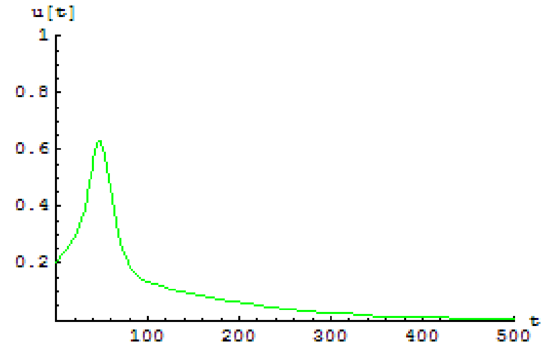

Figure 3.18. $u(\tau)$ as a function of τ.

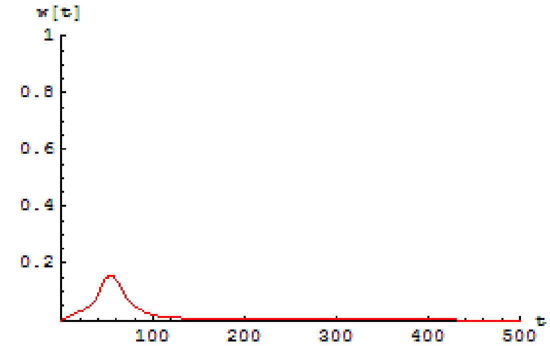

Figure 3.19. $w(\tau)$ as a function of τ.

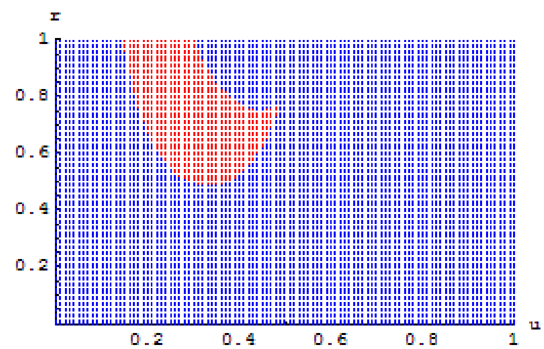

Figure 3.20a. Feasible region in red for $p = 3$, $b = 0.1$, $d = 5.5$.

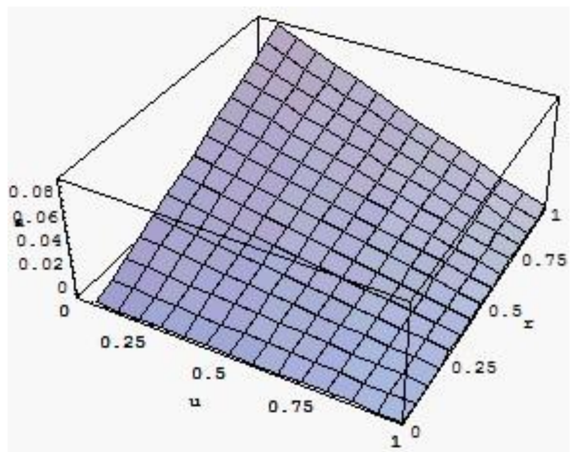

Figure 3.20b. *a* as a function of *u* and *r*.

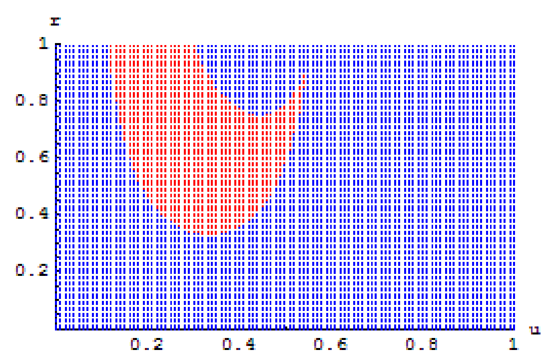

Figure 3.21a. Feasible region in red for $p = 3$, $b = 0.1$, $d = 8$.

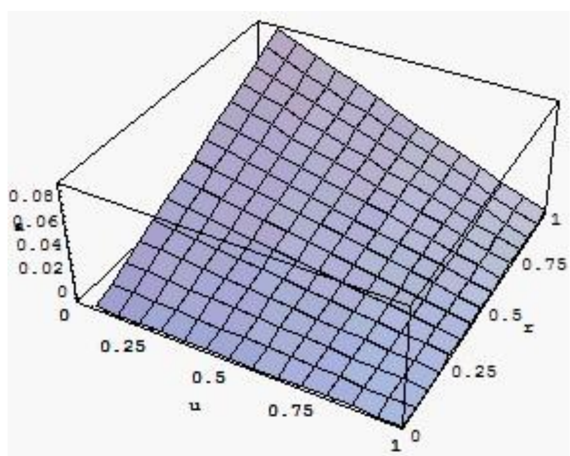

Figure 3.21b. *a* as a function of *u* and *r*.

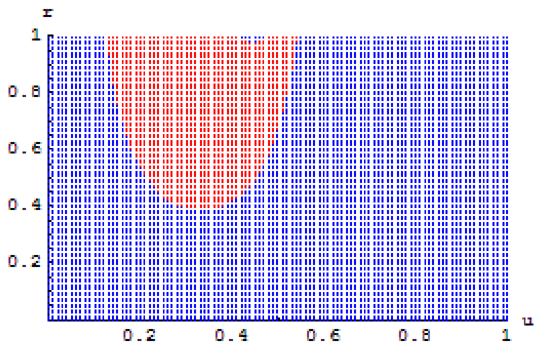

Figure 3.22a. Feasible region in red for $p = 3$, $b = 0.13$, $d = 9$.

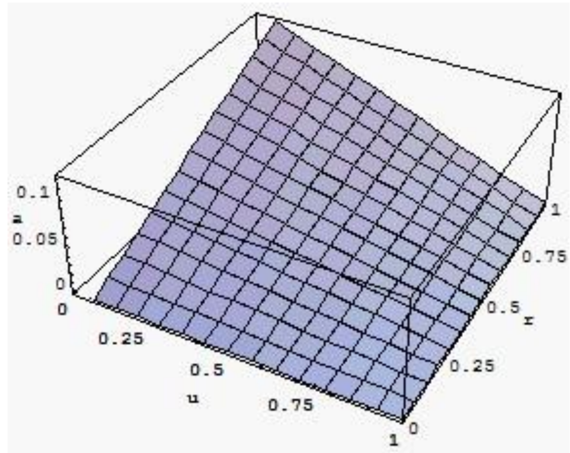

Figure 3.22b. *a* as a function of *u* and *r*.

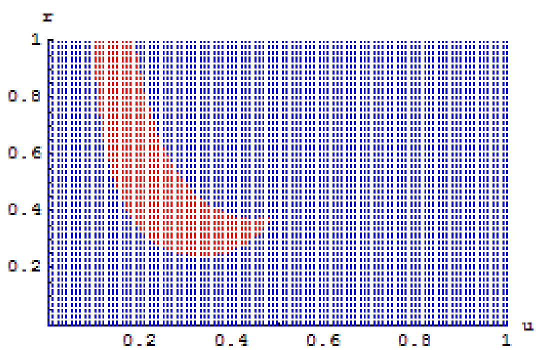

Figure 3.23a. Feasible region in red for $p = 3$, $b = 0.05$, $d = 5.5$.

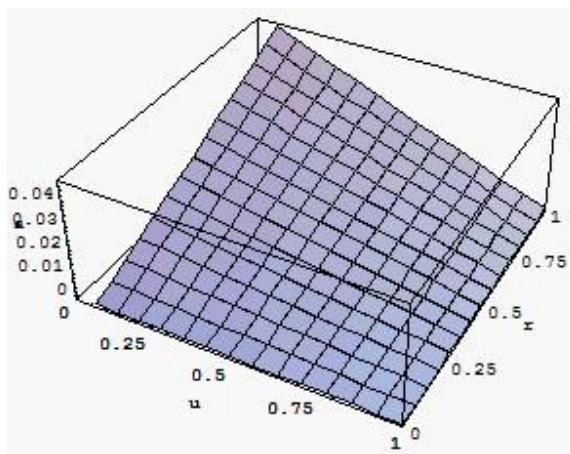

Figure 3.23b. *a* as a function of *u* and *r*.

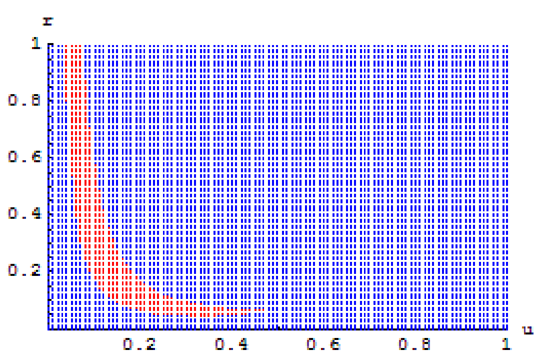

Figure 3.24a. Feasible region in red for $p = 3$, $b = 0.01$, $d = 5.5$.

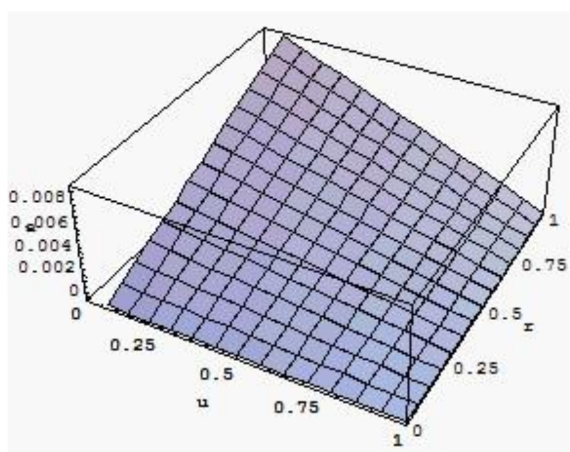

Figure 3.24b. *a* as a function of *u* and *r*.

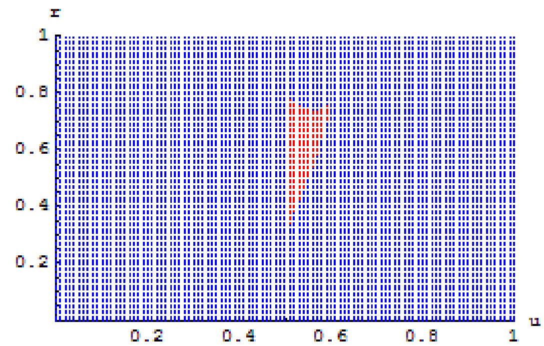

Figure 3.25a. Feasible region in red for $p = 4$, $b = 0.1$, $d = 3$.

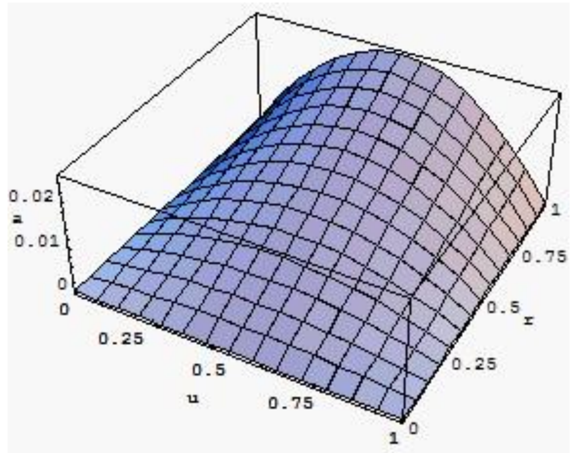

Figure 3.25b. *a* as a function of *u* and *r*.

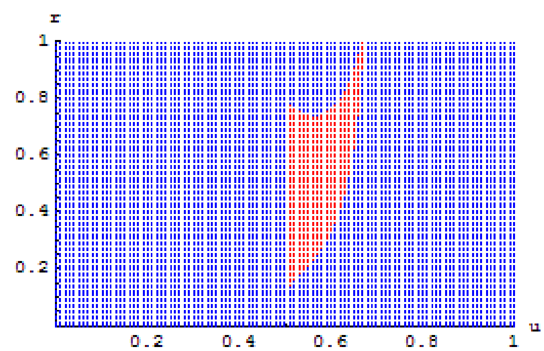

Figure 3.26a. Feasible region in red for $p = 4$, $b = 0.1$, $d = 7$.

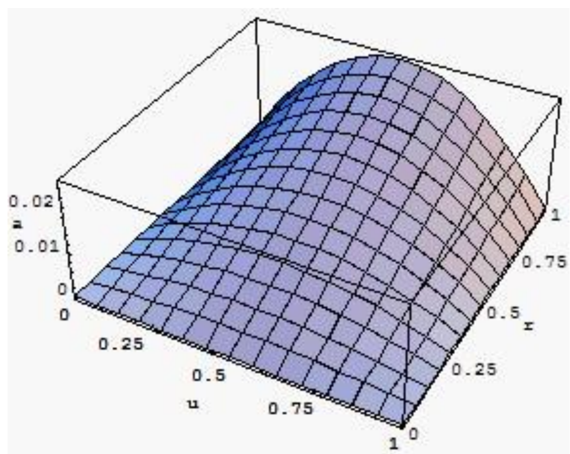

Figure 3.26b. *a* as a function of *u* and *r*.

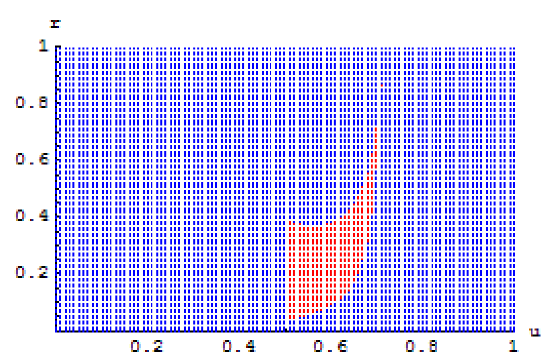

Figure 3.27a. Feasible region in red for $p = 4$, $b = 0.05$, $d = 12.5$.

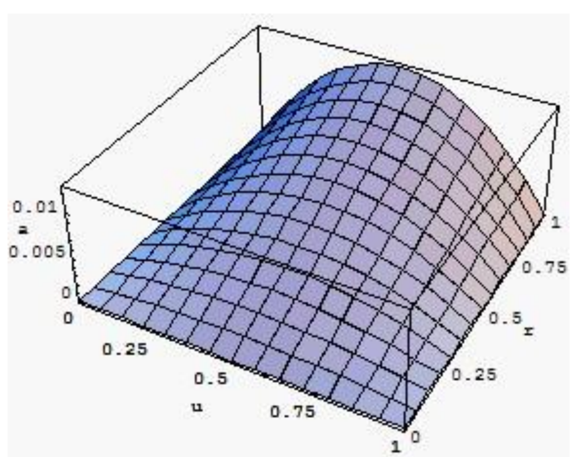

Figure 3.27b. *a* as a function of *u* and *r*.

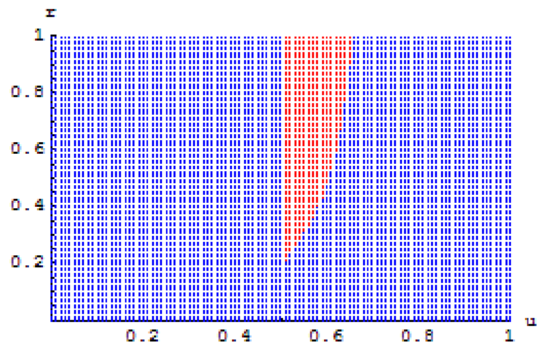

Figure 3.28a. Feasible region in red for $p = 4$, $b = 0.25$, $d = 12$.

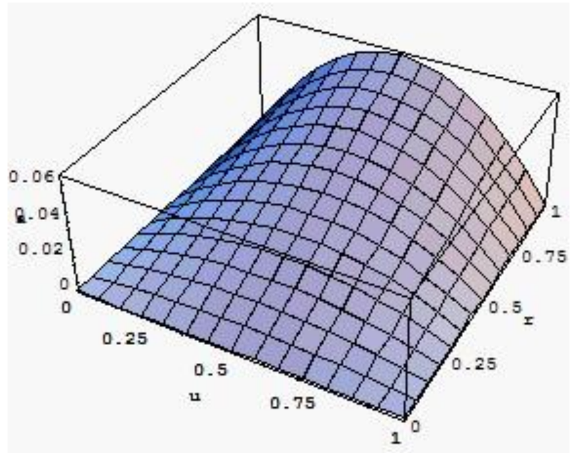

Figure 3.28b. *a* as a function of *u* and *r*.

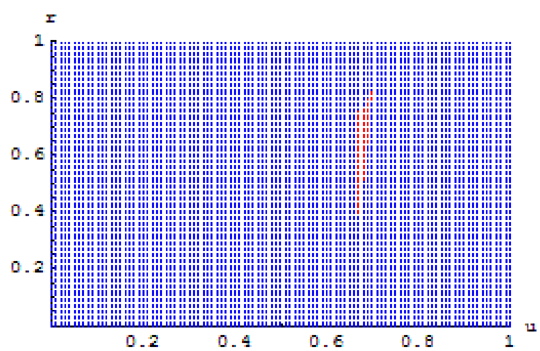

Figure 3.29a. Feasible region in red for $p = 5$, $b = 0.1$, $d = 2.5$.

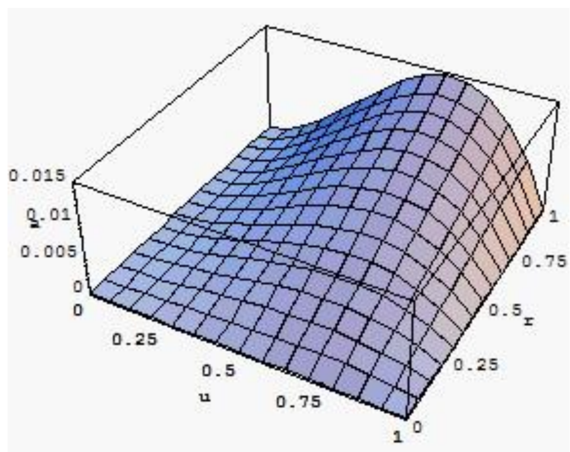

Figure 3.29b. *a* as a function of *u* and *r*.

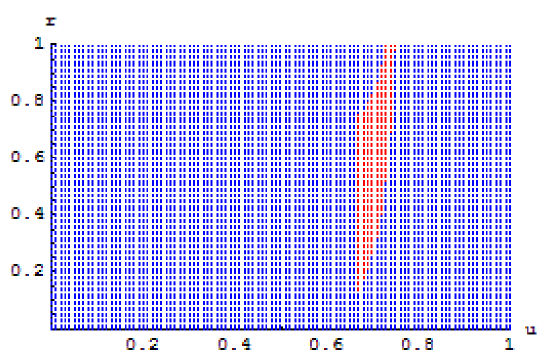

Figure 3.30a. Feasible region in red for $p = 5$, $b = 0.1$, $d = 7.5$.

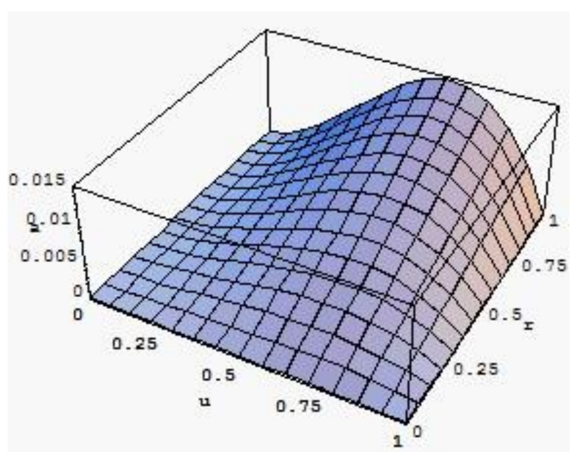

Figure 3.30b. *a* as a function of *u* and *r*.

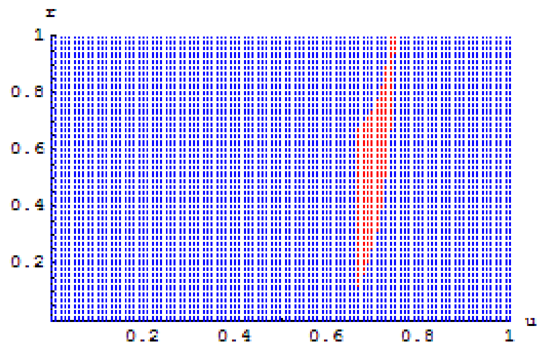

Figure 3.31a. Feasible region in red for $p = 5,\ b = 0.09,\ d = 7$.

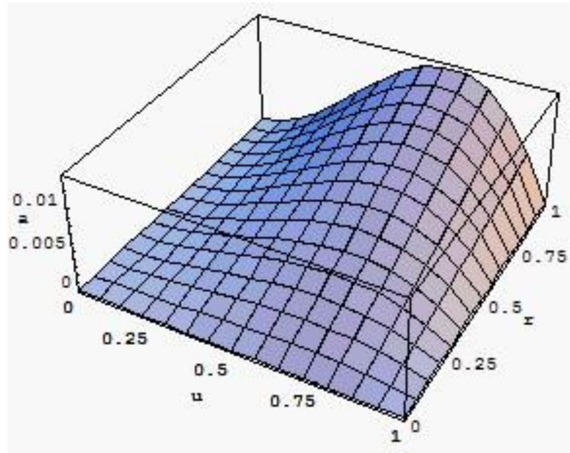

Figure 3.31b. *a* as a function of *u* and *r*.

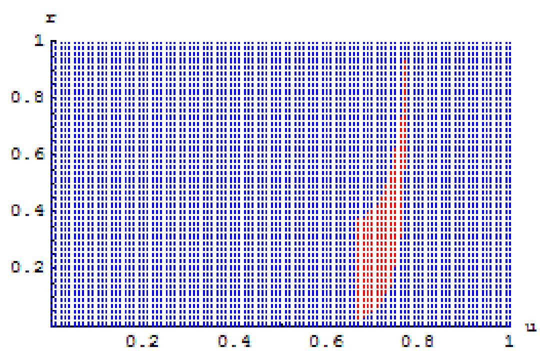

Figure 3.32a. Feasible region in red for $p = 5,\ b = 0.05,\ d = 17.5$.

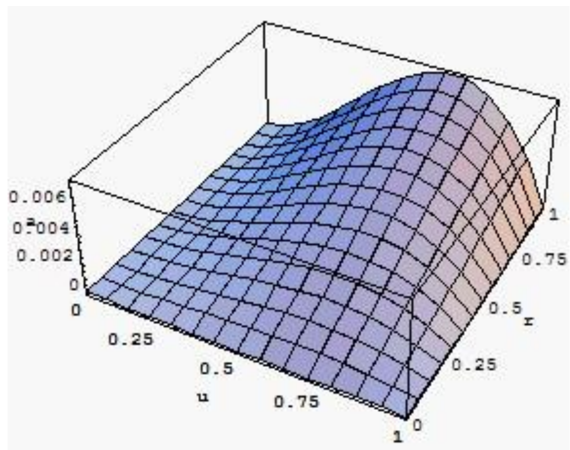

Figure 3.32b. *a* as a function of *u* and *r*.

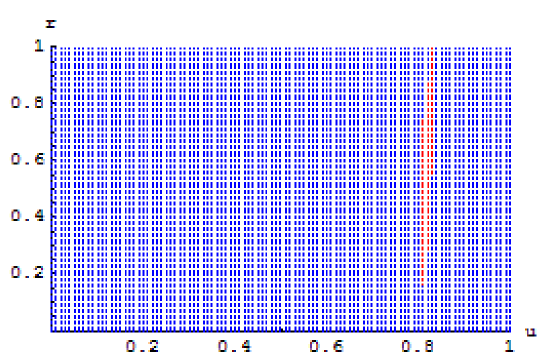

Figure 3.33a. Feasible region in red for $p = 7,\ b = 0.07,\ d = 10$.

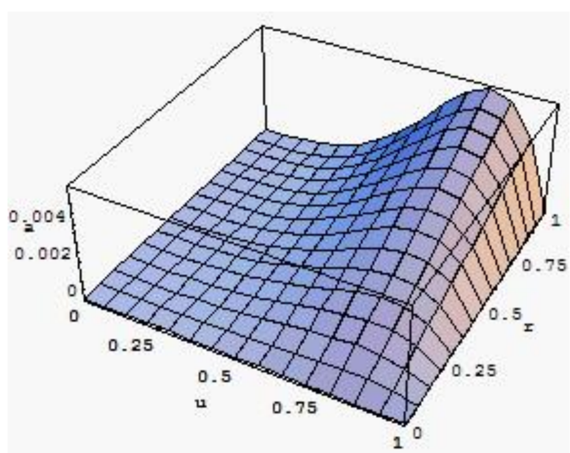

Figure 3.33b. *a* as a function of *u* and *r*.

APPENDIX ONE

This *Mathematica* notebook plots the phase plane diagram.

```
ClearAll[a, b, d, r, q2, u, w];

Solution1 = {a = 0.05; r = 0.99; b = 0.09; d = 1.01; q2 = 0.01; p = 3; };

Solution2 = {a = 0.04; r = 0.81; b = 0.08; d = 1.01; q2 = 0.01; p = 3; };

Solution3 = {p = 5; a = 0.015; b = 0.112; d = 3.5; r = 0.9; q2 = 0.0004; };

Solution4 = {p = 5; a = 0.015; b = 0.111; d = 3.5; r = 0.9; q2 = 0.001; };

Solution5 = {p = 5; a = 0.015; b = 0.11; d = 3.5; r = 0.9; q2 = 0.0016; };

f[u_, w_] := {r*u^p*(1 - u) - u*w - q2*u, a*u^2 - b*w - d*q2*w};

equilibrium = N[Solve[{f[u, w] == 0}, {u, w}]];

{SuperStar[u] = u /. equilibrium[[p + 1]],  SuperStar[w] = w /. equilibrium[[p + 1]]}

J[u_, w_] = {D[f[u, w], u], D[f[u, w], w]};

MatrixForm[Transpose[J[u, w]]];

JacobianMatrix = Simplify[J[SuperStar[u], SuperStar[w]]];

\[Lambda] = Eigenvalues[JacobianMatrix]

Needs["Graphics`PlotField`"]

isoclines = Plot[{(a/(b + d*q2))*u^2, r*u^(p - 1)*(1 - u) - q2}, {u, 0, 1}, PlotRange ->
{{0, 1},                    {0, 0.09}}, PlotStyle ->  {{RGBColor[1, 0, 0]}, {RGBColor[0, 0,
1]}}, AxesLabel -> {u[t], w[t]}, DisplayFunction -> Identity]

directionField = PlotVectorField[f[u, w], {u, 0, 1}, {w, 0, 0.2},   ScaleFunction -> (1 & ),
ScaleFactor -> 0.025, PlotPoints -> 0.2,  Axes -> True, DisplayFunction -> Identity]

Show[isoclines, directionField, DisplayFunction -> $DisplayFunction]

ClearAll[u, w]

tmax = 500;
```

```
sol1 = NDSolve[{Derivative[1][u][t] == r*u[t]^p*(1 - u[t]) - u[t]*w[t] - q2*u[t],
Derivative[1][w][t] == a*u[t]^2 - b*w[t] - d*q2*w[t], u[0] == 0.47, w[0] == 0}, {u[t],
w[t]}, {t, 0, tmax}];

traj1 = ParametricPlot[Evaluate[{u[t], w[t]} /. sol1], {t, 0, tmax},  PlotRange -> {{0, 1},
{0, 0.2}}, PlotStyle -> RGBColor[0, 1, 0],  DisplayFunction -> Identity]

Show[isoclines, directionField, traj1, DisplayFunction -> $DisplayFunction]

ClearAll[u, w]

sol2 = NDSolve[{Derivative[1][u][t] == r*u[t]^p*(1 - u[t]) - u[t]*w[t] - q2*u[t],
Derivative[1][w][t] == a*u[t]^2 - b*w[t] - d*q2*w[t], u[0] == 0.47, w[0] == 0}, {u[t],
w[t]}, {t, 0, tmax}];

traj2 = ParametricPlot[Evaluate[{t, u[t]} /. sol2], {t, 0, tmax}, PlotRange -> {{0, tmax},
{0, 1}}, PlotStyle -> RGBColor[0, 1, 0],  AxesLabel -> {t, u[t]}, DisplayFunction ->
Identity]

Show[traj2, DisplayFunction -> $DisplayFunction]

sol3 = NDSolve[{Derivative[1][u][t] == r*u[t]^p*(1 - u[t]) - u[t]*w[t] - q2*u[t],
Derivative[1][w][t] == a*u[t]^2 - b*w[t] - d*q2*w[t], u[0] == 0.47, w[0] == 0}, {u[t],
w[t]}, {t, 0, tmax}];

traj3 = ParametricPlot[Evaluate[{t, w[t]} /. sol3], {t, 0, tmax}, PlotRange -> {{0, tmax},
{0, 1}}, PlotStyle -> RGBColor[1, 0, 0], AxesLabel -> {t, w[t]}, DisplayFunction ->
Identity]

Show[traj3, DisplayFunction -> $DisplayFunction]

p = 5; r = 0.9; d = 3.5;

HyperLogistic[u] = r*u^p*(1 - u);

f[u_, w_] := {HyperLogistic[u] - u*w - q2*u, a*u^2 - b*w - d*q2*w};

Equilibrium = N[Solve[{f[u, w] == 0}, {u, w}]];

For[b = 0.1, b <= 0.2, b += 0.001,
  For[a = 0.015, a <= 0.025, a += 0.001,
    For[q2 = 0.0001, q2 <= 0.01, q2 += 0.0001,
      For[j = 1, j <= p + 1, j++,
             If[VectorQ[{u, w} /. Equilibrium[[j]], Head[#1] === Real && 0 <= #1 <= 1 & ],

              {SuperStar[u] = u /. Equilibrium[[j]], SuperStar[w] =   w /. Equilibrium[[j]]};
```

```
J[u_, w_] = {D[f[u, w], u], D[f[u, w], w]};

 MatrixForm[Transpose[J[u, w]]];

 JacobianMatrix =   Simplify[J[SuperStar[u], SuperStar[w]]];

 \[Lambda] = Eigenvalues[JacobianMatrix];

If[Negative[Re[\[Lambda][[1]]]] && Negative[Re[\[Lambda][[2]]]], Null,
If[Positive[Re[\[Lambda][[1]]]] && Positive[Re[\[Lambda][[2]]]],
Print["{u,w}=", {u, w} /. Equilibrium[[j]], " \[Lambda]=", \[Lambda], " Instable
Equilibrium, q^2=",  q2, ", a=", a, ", b=", b], Null]], Null]]]]]
```

APPENDIX TWO

This *Mathematica* notebook plots the feasible region and the surface for *a*(*u*, *r*).

```
ClearAll[a, b, d, f, r, p, u, w]

f[u_, w_] = r*u^p*(1 - u);

equil = Solve[f[u, w] == u*w, w];

SuperStar[w][u_] = Simplify[w /. equil[[1]]];

a = (b*SuperStar[w][u])/u^2;

Test1[u_] = Simplify[D[f[u, w], u] - SuperStar[w][u]];

Test2[u_] = Simplify[3*a*u^2 - b*D[f[u, w], u] - 2*a*u*D[f[u, w], w]];

Test3[u_] = Simplify[(d*Test1[u] - b)^2/(4*d)];

Clear[r, u]

b = 0.15; d = 3.5; p = 5;

feasibleSet = {{0, 0}};

nonfeasibleSet = {};

usteps = 100;

rsteps = 100;

Do[If[Test2[u] > 0 && Test3[u] > Test2[u] && b/d < Test1[u] < b,
AppendTo[feasibleSet, {u, r}], AppendTo[nonfeasibleSet, {u, r}]], {u, 0, 1, 1/usteps}, {r,
0, 1, 1/rsteps}]

feasiblePlot = ListPlot[feasibleSet, PlotRange -> {{0, 1}, {0, 1}}, PlotStyle ->
RGBColor[1, 0, 0], DisplayFunction -> Identity]

nonfeasiblePlot = ListPlot[nonfeasibleSet, PlotRange -> {{0, 1}, {0, 1}}, PlotStyle ->
RGBColor[0, 0, 1], DisplayFunction -> Identity]

Show[feasiblePlot, nonfeasiblePlot, Prolog -> PointSize[0.005], AxesLabel -> {"u", "r"},
DisplayFunction -> $DisplayFunction]

Plot3D[a, {u, 0, 1}, {r, 0, 1}, AxesLabel -> {"u", "r", "a"}]
```

```
Needs["Graphics`ImplicitPlot`"]

ImplicitPlot[a == 0.005, {u, 0.001, 1}, {r, 0.001, 1}]
```

BIBLIOGRAPHY

1. Bezzi, M., A. Ciliberto and A. Mengoni, "Pattern Formation by Competition: a Biological Example," ***ArXiv***, 2001.
2. Bogomolova, E.V., A. Bulianitsa, E. Bystrova, V. Kurochkin, L. Panina, "Spatial periodicity in mycelial fungi growth with respect to their life strategies," ***http://www.interjournal.org***, Abstract 348, and ***http://www.geocities.com/ppp5029***.
3. Croan, Suki C., "Lyophilization of Hypha-Forming Tropical wood-inhabiting Basidiomycotina," ***Mycological Society of America***, 92(4), 2000, pp. 810-817.
4. Murray, J. D., ***Mathematical Biology: An Introduction***, Third Edition, Springer-Verlag, New York, 2001.
5. Murray, J. D., ***Mathematical Biology: Spatial Models and Biomedical Applications***, Third Edition, Springer-Verlag, New York, 2001.
6. Qian, Ningfang, ***Reaction Diffusion Equations for the Growth of Mycelium***, M.S. Alternate Plan Paper, Mankato State University, 1994.
7. Tsoularis, A., ***Analysis of Logistic Growth Models***, Res. Lett. Inf. Math. Sci. (2001) 2, pp. 23-46.
8. Zhang, Feng, ***A Mathematical Model for the Growth of Mycelium in Two Dimensions with Circular Symmetry***, M.S. Alternate Plan Paper, Mankato State University, 1992.