

Algebraic decay and variable speeds in wavefront solutions of a scalar reaction–diffusion equation

JONATHAN A. SHERRATT AND BEN P. MARCHANT

*Nonlinear Systems Laboratory, Mathematics Institute,
University of Warwick, Coventry CV4 7AL, UK*

[Received 4 July 1995 and in revised form 19 October 1995]

Wavefront solutions of scalar reaction–diffusion equations have been intensively studied for many years. There are two basic cases, typified by quadratic and cubic kinetics. An intermediate case is considered in this paper; namely, $u_t = u_{xx} + u^2(1 - u)$. It is shown that there is a unique travelling-wave solution, with a speed $1/\sqrt{2}$, for which the decay to zero ahead of the wave is exponential with x . Moreover, numerical evidence is presented which suggests that initial conditions with such exponential decay evolve to this travelling-wave solution, independently of the half-life of the initial decay. It is then shown that for all speeds greater than $1/\sqrt{2}$ there is also a travelling-wave solution, but that these faster waves decay to zero algebraically, in proportion to $1/x$. The numerical evidence suggests that initial conditions with such a decay rate evolve to one of these faster waves; the particular speed depends in a simple way on the details of the initial condition. Finally, initial conditions decaying algebraically for a power law other than $1/x$ are considered. It is shown numerically that such initial conditions evolve either to an algebraically decaying travelling wave, or in some cases to a wavefront whose shape and speed vary as a function of time. This variation is monotonic and can be quite pronounced, and the speed is a function of u as well as of time. Using a simple linearization argument, an approximate formula is derived for the wave speed which compares extremely well with the numerical results. Finally, the extension of the results to the more general case of $u_t = u_{xx} + u^m(1 - u)$, with $m > 1$, is discussed.

1. Introduction

Wavefront solutions of reaction–diffusion equations have been studied for more than fifty years. A scalar reaction–diffusion equation in one space dimension has the basic form

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + f(u). \quad (1)$$

Equations of this form have been used in very wide range of applications, including ecological invasion (Skellam, 1951; Holmes *et al.*, 1994), wound healing (Sherratt & Murray, 1990), and intracellular calcium signalling (Lane *et al.*, 1987; Sneyd & Sherratt, 1996). In all of these applications, it is wavefront solutions that are of interest. The mathematical nature of (1) is determined by the kinetic function $f(\cdot)$. For wavefront solutions, $f(\cdot)$ must have at least two zeros, corresponding to homogeneous steady states of (1). The solution will approach one of these steady states as $x \rightarrow +\infty$, and it will approach the other as $x \rightarrow -\infty$;

the wavefront is a moving transition between these two states. The steady state left behind after the wave has passed must clearly be stable, and thus there are two basic cases to consider: firstly when the steady state ahead of the advancing wavefront is unstable, and secondly when it is stable.

The first of these cases was studied initially by Fisher (1937) and by Kolmogorov *et al.* (1937); the prototype system is the so-called Fisher equation,

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1 - u). \quad (2)$$

Here $u = 1$ is a stable steady state, while $u = 0$ is unstable. For this equation, there are wavefront solutions travelling with constant shape and speed for all wave speeds $c \geq 2$. These travelling-wave solutions have the form $u(x, t) = U(x - ct)$, and they can thus be studied using the ordinary differential equation

$$U'' + cU' + U(1 - U) = 0.$$

Moreover, a wide range of initial conditions evolve to travelling-wave solutions. In particular, if $u(x, 0)$ is a decreasing function of x , with $u(x, 0) \rightarrow 1$ as $x \rightarrow -\infty$ and $u(x, 0) = O_s(e^{-\xi x})$ as $x \rightarrow \infty$, then the solution approaches a travelling wave as $t \rightarrow \infty$; the speed of the wave is related to the initial condition as follows:

$$c = \begin{cases} 2 & \xi > 1, \\ \xi + 1/\xi & \xi < 1. \end{cases}$$

These results all generalize to a large family of equations with a qualitatively similar form to (2); in fact, this generalization was considered in the original paper by Kolomogorov *et al.* (1937). Precise statements and proofs of the various results can be found in a paper by Rothe (1978).

The second case of wavefront solutions of (1) is when the steady states behind and ahead of the wave are both stable. In this case, the prototype system is

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(u - \alpha)(1 - u), \quad (3)$$

where the constant $\alpha \in (0, 1)$. Here $u = 0$ and $u = 1$ are both stable steady states, while $u = \alpha$ is unstable. In this case, there is a travelling-wave solution with a constant shape and speed connecting $u = 0$ and $u = 1$ for exactly one value of the wave speed c . Again, this can be shown by studying the travelling-wave ordinary differential equation, which in this case is

$$U'' + cU' + U(U - \alpha)(1 - U) = 0;$$

as above, $u(x, t) = U(x - ct)$. The unique wave speed can actually be found analytically to be $(1 - 2\alpha)/\sqrt{2}$, so that direction of motion depends on the sign of $\alpha - \frac{1}{2}$. A wide range of initial conditions evolve to this travelling wave;

specifically, whenever $u(x, 0) \in [0, 1]$ for all x , with $u(x, 0) \rightarrow 0$ as $x \rightarrow -\infty$ and $u(x, 0) \rightarrow 1$ as $x \rightarrow \infty$, the solution approaches the travelling wave as $t \rightarrow \infty$. Again, these results generalize to a wide range of equations which are qualitatively similar to (3); in this case precise statements and proofs of the results have been given by Fife & McLeod (1977).

This paper is concerned with an equation which lies 'in between' (2) and (3); namely,

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u^2(1 - u). \quad (4)$$

In this case $u = 1$ is a stable steady state, while $u = 0$ is neutrally stable to first order. This equation has certainly been considered before: for example, there is an exercise on it in the book by Murray (1989). However, to the best of our knowledge, there has not been a detailed study of wavefront solutions of (4). We will show that such solutions have a number of novel features which are not shown by either equation (2) or (3). Specifically, we will demonstrate travelling-wave solutions with algebraically decaying tails, and wavefronts moving with varying shape and speed. We do not attempt any formal proofs of the mathematical results; rather, our approach is to use a combination of numerical solution and qualitative analysis to study these new phenomena. At the end of the paper we generalize our results to the case $f(u) = u^m(1 - u)$, where m is any constant greater than unity.

2. Exponentially decaying waves

Travelling-wave solutions of (4) (that is, waves moving with constant shape and speed) can be studied using the travelling-wave ordinary differential equations

$$U' = V, \quad V' = -cV - U^2(1 - U). \quad (5)$$

Here $u(x, t) = U(z)$, with $z = x - ct$; and c is the wave speed, which we take to be positive without loss of generality. This system of two coupled ordinary differential equations can be studied using phase-plane techniques. There are two steady states, $(0, 0)$ and $(1, 0)$. Straightforward linearization shows that at $(1, 0)$ there are two real eigenvalues, one positive and one negative, given by $\frac{1}{2}[-c \pm (c^2 + 4)^{\frac{1}{2}}]$. Thus $(1, 0)$ is a saddle point, and it has exactly one trajectory originating from it and entering the fourth quadrant; we will refer to this trajectory as \mathcal{T}_c . Since any travelling-wave solution tends to unity as $z \rightarrow -\infty$, it must correspond to this unique trajectory \mathcal{T}_c . A travelling-wave solution will exist precisely for those speeds c for which this trajectory terminates at the other steady state $(0, 0)$. This steady state has one stable eigenvector $(1, -c)$, with an eigenvalue of $-c$; the other eigenvalue is zero.

It is relatively straightforward to show that the trajectory \mathcal{T}_c approaches $(0, 0)$ along the eigenvector $(1, -c)$ for exactly one value of the wave speed c ; we give a proof of this in the Appendix. For values of c smaller than this critical value, the trajectory \mathcal{T}_c leaves the fourth quadrant through the negative V -axis and terminates at infinity. In fact, Murray (1989, §11.4) lists some exact solutions of

reaction-diffusion equations which include the solution

$$u(x, t) = (1 + e^{(-t+x\sqrt{2})/2})^{-1}$$

for equation (4). For $c = 1/\sqrt{2}$, this has the form $V = cU(U - 1)$, which is exactly a trajectory originating from $(1, 0)$ in the U - V plane and approaching $(0, 0)$ along the eigenvector $(1, -c)$; thus the unique wave speed is $1/\sqrt{2}$. Figures 1(a) and (b) illustrate the U - V phase plane for $c < 1/\sqrt{2}$ and $c = 1/\sqrt{2}$, respectively.

The next issue to address is what initial conditions evolve to this travelling-wave solution. We have studied this by numerical solution of (4), using initial conditions of the form

$$u(x, 0) = \begin{cases} 1 & x < 0, \\ e^{-\xi x} & x > 0, \end{cases} \quad (6)$$

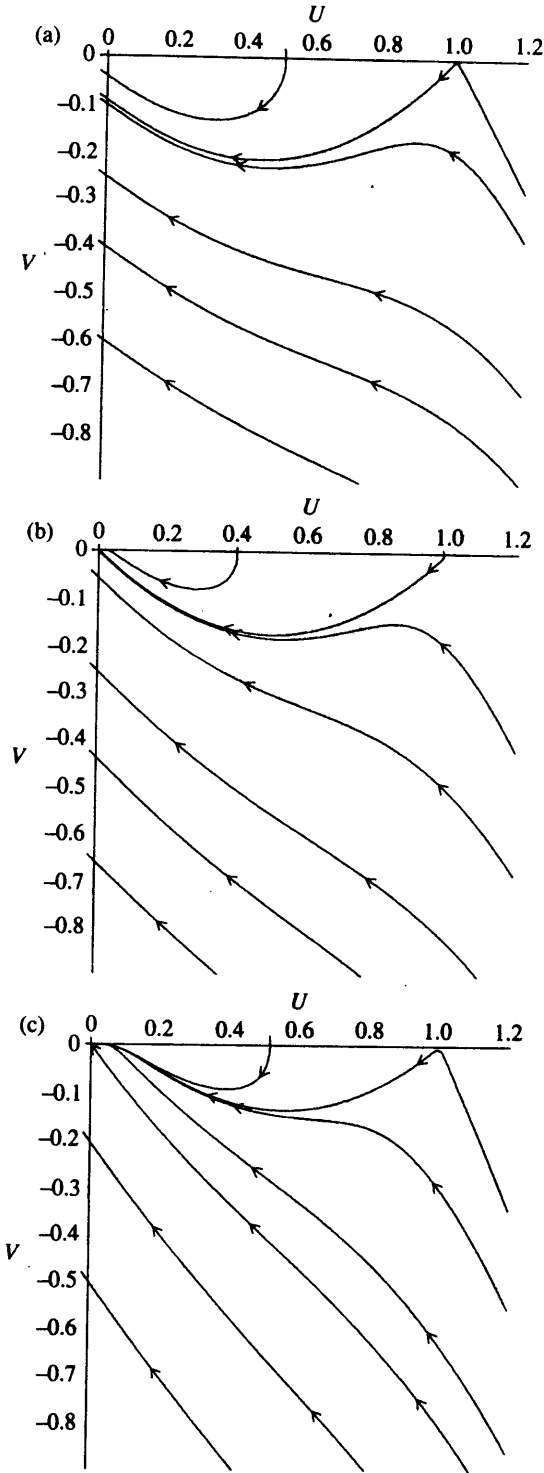
for a number of different values of ξ in the range $0.1 < \xi < 10$. In all cases we found that the solution evolved to a travelling-wave solution with a speed of $1/\sqrt{2}$, exactly in accordance with the above analysis. A typical numerical solution is illustrated in Fig. 2.

3. Algebraically decaying waves

We have not yet considered the behaviour of the trajectory \mathcal{T}_c in the case $c > 1/\sqrt{2}$. In fact, \mathcal{T}_c terminates at $(0, 0)$ for all $c \geq 1/\sqrt{2}$; but for $c > 1/\sqrt{2}$ the approach is not along the eigenvector $(1, -c)$, but rather it is along the centre manifold, corresponding to the zero eigenvalue. Again we leave proof of this to the Appendix. Figure 1(c) illustrates the U - V phase plane for a value of c greater than $1/\sqrt{2}$. Initially we were perplexed that none of the initial conditions given by (6) evolve to waves travelling with these faster speeds. However, the resolution of this became clear when we considered the form of the centre manifold. Standard theory, which is described in the Appendix, shows that the equation of the centre manifold is $V = -U^2/c$, which implies that $U(z) \sim c/z$ as $z \rightarrow \infty$.

Thus travelling waves with speeds greater than $1/\sqrt{2}$ all decay *algebraically* towards zero. This is in marked contrast to the case $c = 1/\sqrt{2}$ and to all the travelling-wave solutions of equations (2) and (3). Indeed we are only aware of one previous example of travelling waves with algebraically decaying tails, which is mentioned briefly in a paper by Billingham & Needham (1991) on a reaction-diffusion model for autocatalytic chemical reactions. Although their equations are quite different from (4), these authors also found wave solutions with decays proportional to z^{-1} as $z \rightarrow \infty$; however, they did not consider

FIG. 1. Plots of the U - V phase plane for the travelling-waves for the ordinary differential equations of (5) with: (a) $c = 0.5$, (b) $c \approx 1/\sqrt{2}$, and (c) $c = 1$. The qualitative form of the phase plane is the same for all $c \in (0, 1/\sqrt{2})$ and for all $c > 1/\sqrt{2}$. Note, in particular, that in all the cases a unique trajectory leaves $(1, 0)$ and enters the fourth quadrant, and that in (a) this trajectory leaves the fourth quadrant across the negative V -axis, while in (b) the trajectory terminates at $(0, 0)$ with an approach along the eigenvector $(1, -c)$, and in (c) the trajectory terminates at $(0, 0)$ with an approach along the centre manifold, corresponding to the zero eigenvalue. The equations were integrated numerically using a Runge-Kutta-Merson method.



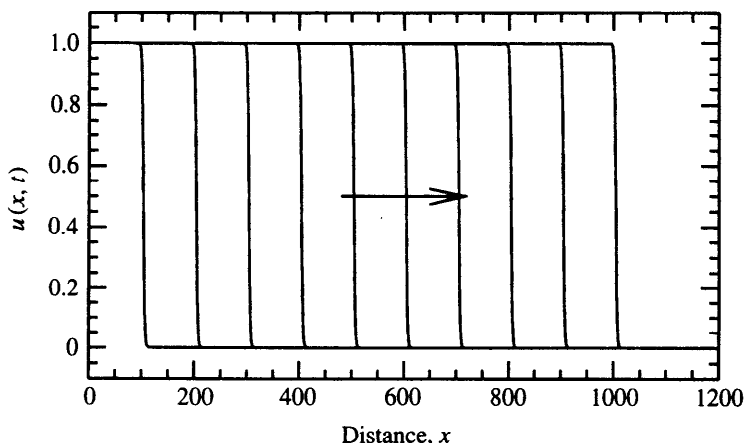


FIG. 2. A typical numerical solution of the reaction-diffusion system given in (4) with exponentially decaying initial conditions of the form given by (6). The solution is plotted as a function of the distance x at equally spaced times; it rapidly evolves to a travelling wavefront with a constant shape and with a speed of $1/\sqrt{2}$. The spatial domain used in the numerical solution was considerably larger than the portion illustrated. The equations were solved numerically using the method of lines and Gear's method.

evolution from initial data even numerically, and there is certainly no mention of variable wave speeds.

In view of this algebraic decay, we consider the solution of (4) with algebraically decaying initial conditions, specifically with

$$u(x, 0) = \begin{cases} 1 & x < A, \\ A/x & x > A, \end{cases} \quad (7)$$

where A is a positive constant. We consider only numerical solution of this initial-value problem; evolution from algebraically decaying initial data has recently been studied analytically by Grundy & Peletier (1990) in a very different type of reaction-diffusion equation, which does not support wave solutions. For $A > 1/\sqrt{2}$, our numerical simulations suggest that these initial conditions evolve to a wave of speed A ; this is exactly the wave whose behaviour as $x \rightarrow \infty$ matches that of the initial condition. A typical numerical solution is illustrated in Fig. 3. It is instructive to compare Figs. 2 and 3; there is clearly a much slower decay to zero in Fig. 3. We must point out that, because algebraic decay is very slow, very large spatial domains are required for numerical solution; to compensate for this we used a variable mesh spacing; the details are given in the caption to Fig. 3.

For $A \leq 1/\sqrt{2}$, there are no travelling waves whose decay rate is the same as the initial condition. Our numerical simulations suggest that such initial conditions evolve to a travelling wave with a speed approximately equal to $1/\sqrt{2}$. It must be stressed that there is a definite difference in wave character between the cases $c = 1/\sqrt{2}$ and $c = (1/\sqrt{2})^+$: in the former case the decay towards zero is exponential; in the latter case it is algebraic. Thus careful investigation is required when numerical simulations predict a speed of $1/\sqrt{2}$. In the case of initial condition (7) with $A \leq 1/\sqrt{2}$, such careful investigation shows that the decay to

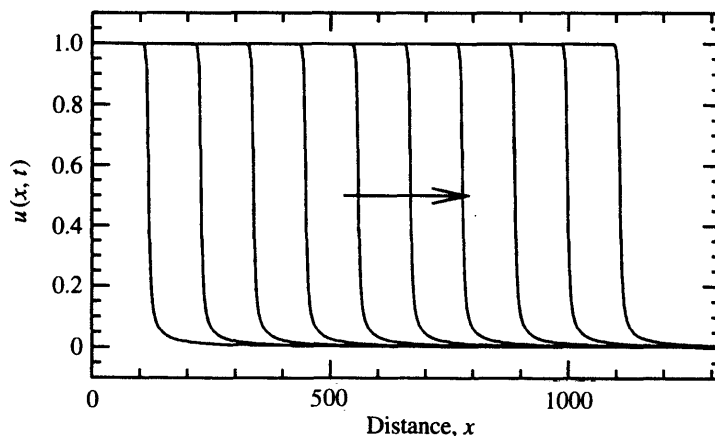


FIG. 3. The numerical solution of the reaction-diffusion system given in (11) for initial conditions given by (7) with $A = 1$, so that $u(x, 0) \sim 1/x$ as $x \rightarrow \infty$. The solution is plotted as a function of distance x at equally spaced times; it rapidly evolves to a travelling wavefront with a constant shape and with a speed of 1. A comparison with Fig. 2 clearly shows that the decay to zero ahead of the wavefront is very much slower in the case shown here; this is a reflection of the decay being algebraic rather than exponential. This algebraic decay means that a very large spatial domain is required in order that the boundary condition at the right of the domain does not significantly influence the solution. Such a boundary condition is of course required in a numerical solution, and we use the Dirichlet condition $u = 0$. For this reason, in all our numerical solutions we have used a spatial mesh with variable spacing. The spacing is even in a region $0 \leq x \leq x_0$, and it increases geometrically for $x > x_0$, with each mesh spacing being 1% larger than the previous spacing. The integration is stopped when $u(x_0, t)$ exceeds a small value, taken as 0.1. We used a total of 3000 mesh points; in the case illustrated here x_0 was equal to 1100, and the value of x at the right-hand boundary was 145 000.

zero ahead of the wave is in fact algebraic; there is no contradiction between this and the measured wave speed being equal to $1/\sqrt{2}$ since, formally, the travelling wave is only a limiting solution form as $t \rightarrow \infty$ in all cases. In contrast, for initial condition (6), the decay is exponential, exactly as one would expect intuitively.

4. Variable wave speeds

Another natural case to consider is initial conditions which decay algebraically, but with a power law different to x^{-1} . To study these conditions, we solved (4) numerically with the initial conditions

$$u(x, 0) = \begin{cases} 1 & x < A^{1/\alpha}, \\ A/x^\alpha & x > A^{1/\alpha}. \end{cases} \quad (8)$$

We were expecting evolution to one of the algebraically decaying travelling waves; however, the numerical solutions showed quite different and extremely surprising results. We begin by discussing the case when $\alpha < 1$. In this case, initial conditions given by (8) do evolve to a wavefront, but the front does not have a constant shape or speed. Rather, the speed increases with time, while the

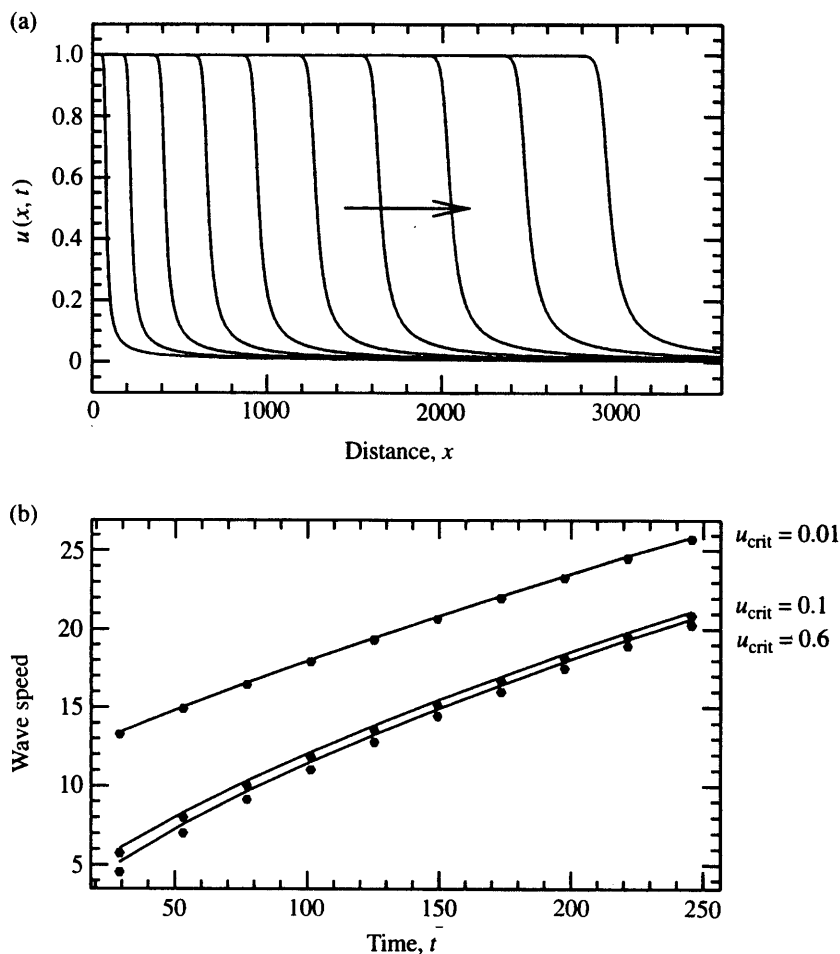


FIG. 4. The numerical solution of the reaction-diffusion system given by (4) for initial conditions given by (8), with $A = 0.5$ and $\alpha = 0.6$, so that $u(x, 0) \sim 1/(2x^{0.6})$ as $x \rightarrow \infty$. (a) The solution is plotted as a function of distance x at equally spaced times. It evolves to wavefronts whose speed increases with time; the shape of the wave also varies. (b) The speed of the wavefront as a function of time for three different values of u_{crit} . The points indicate numerically calculated wave speeds; the method of calculation is described in the main text. The curves show the corresponding predictions of formula (10) for the three values of u_{crit} . The numerical method is described in the caption to Fig. 3, and variable mesh spacing with 3000 space points was again used; in this case x_0 was equal to 3000 and the value of x at the right-hand boundary was 397 000. When α is just less than 1 (but typically greater than 0.9) and A is small, there is a transient period, which can be quite long, before the solution acquires the form of accelerating waves whose speed is given by (10); during this transient period, the solution has the form of waves with a speed approximately equal to $1/\sqrt{2}$.

wavefront itself becomes shallower; a typical solution is illustrated in Fig. 4(a). Note that this change in shape means that the wave speed must depend on the value of u as well as on time. To investigate this more closely, we performed a careful measurement of the wave speed in the numerical solutions. The wave speed s at a given time t was measured by calculating the values x^\pm at which $u = u_{\text{crit}}$ in the numerical solution at times $t \pm \Delta t$, for some suitably small Δt ; the

values of x^\pm were determined by linearly interpolating between the space-mesh points. The speed s was then calculated using

$$s(t; u_{\text{crit}}) = \frac{x^+ - x^-}{2\Delta t}.$$

Figure 4(b) illustrates the wave speed, calculated in this way, for the solution shown in Fig. 4(a), for three different values of u_{crit} . The speed increases with time, and it decreases with u_{crit} ; this latter dependence explains the flattening of the wavefront with time. We should emphasize that we have performed very-long-term solutions (up to a maximum time $t = 12\,000$) for a few cases and the speed continues to increase, and it does not settle down to a constant value.

The key to understanding this variable speed came from a careful study of the way in which the variable-speed wavefront approaches zero as $x \rightarrow \infty$; at all times, we found that the approach was in proportion to $x^{-\alpha}$, as in the initial conditions. For such algebraic decay, the diffusion term $\partial^2 u / \partial x^2$ will have a lower order of magnitude than the time derivative $\partial u / \partial t$. Thus, to leading order ahead of the wave, the reaction-diffusion equation of (4) has a form for which

$$\frac{\partial u}{\partial t} = u^2 \Rightarrow u(x, t) = [G(x) - t]^{-1},$$

where $G(\cdot)$ is an arbitrary function of x . For the decay rate to be the same as the initial condition, $G(x) = x^\alpha / A$ to leading order. Thus the leading-order solution is

$$u(x, t) = \frac{A}{x^\alpha - At}. \quad (9)$$

Suppose now that $u(x + \delta x, t + \delta t) = u(x, t) = u_{\text{crit}}$, where δx and δt are small increments. Substituting this into (9) and expanding in a Taylor series shows that, to leading order, $\delta x / \delta t = (A/\alpha)x^{1-\alpha}$. On substitution for x in terms of t and u_{crit} , using (9), this gives

$$\frac{\delta x}{\delta t} = \frac{A^{1/\alpha}}{\alpha} \left(t + \frac{1}{u_{\text{crit}}} \right)^{(1-\alpha)/\alpha} \quad (10)$$

This is an analytical approximation for the wave speed, as a function of t and u_{crit} . The curves in Fig. 4(b) illustrate this approximation, superimposed on the numerical predictions of wave speed. The approximation is extremely good when u_{crit} is small, and it is reasonable even when u_{crit} is as large as 0.6, which is rather more than could reasonably be expected for an approximation based on linearization about $u = 0$. The comparison is equally good for a wide range of values of A and u_{crit} . Note that formula (10) implies that at large values of t the speed will be independent of u_{crit} to leading order, so that the wave shape will be approximately constant, while the speed continues to increase. Again, this is consistent with the numerical results.

For $\alpha > 1$, formula (10) predicts a wave speed that decreases with time and that tends to zero as $t \rightarrow \infty$. However, numerical simulations show a rather different

behaviour. The initial conditions of (8) do evolve at first to a wavefront that has a varying shape and decreasing speed, but eventually the solution settles down to an algebraically decaying travelling wave with a speed of $1/\sqrt{2}$; an example is given in Fig. 5. Thus, whatever the values of α and A , the solution never evolves

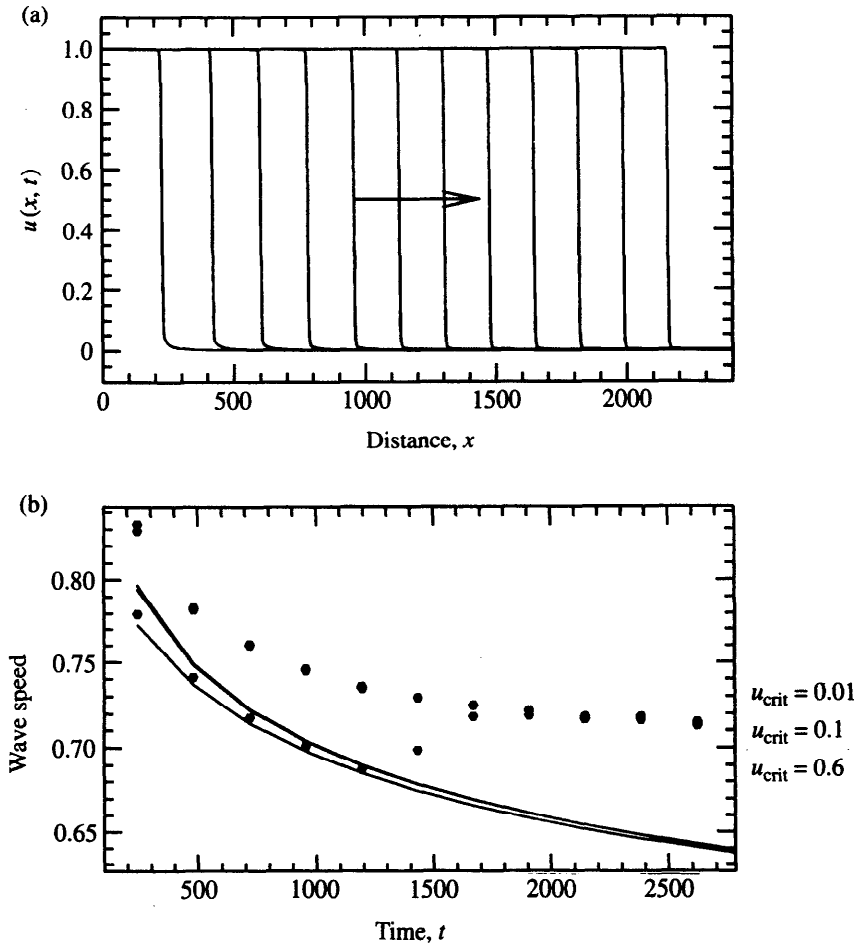


FIG. 5. The numerical solution of the reaction-diffusion system given by (11) for initial conditions given by (8), with $A = 1.5$ and $\alpha = 1.1$, so that $u(x, 0) \sim 3/2x^{1.1}$ as $x \rightarrow \infty$. (a) The solution is plotted as a function of distance x at equally spaced times. Initially it has the form of wavefronts with decreasing speed, but at longer times the speed settles to a constant value of $1/\sqrt{2}$, so that the solution is a travelling wave. Careful investigation shows that this travelling wave decays to zero algebraically rather than exponentially. (b) The speed of the wavefront as a function of time for three different values of u_{crit} . The points indicate numerically calculated wave speeds; the method of calculation is described in the main text. For large times the calculated speeds are almost identical for $u_{\text{crit}} = 0.1$ and $u_{\text{crit}} = 0.6$, and they cannot be distinguished in the figure. The curves show the corresponding predictions of formula (10) for the three values of u_{crit} . The initial decrease in the wave speed compares well with the analytical approximation; however, the formula does not reflect the change to a constant wave speed. The method of numerical solution was as described in the caption to Fig. 3, and variable mesh spacing with 3000 space points was again used; in this case x_0 was equal to 2000 and the value of x at the right-hand boundary was 265 000.

to wavefronts moving with a speed, either variable or constant, that is less than $1/\sqrt{2}$. The initial decrease in speed does in fact match formula (10) quite closely (see Fig. 5(b)); the duration of this initial phase decreases as α and A increases.

5. Extension to $u^m(1-u)$

All of the above results can be generalized to the equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u^m(1-u) \quad (11)$$

for any $m > 1$. Again, there is an exponentially decaying travelling wave for a unique wave speed c_{crit} , and for each speed c greater than c_{crit} there is an algebraically decaying wave; the decay has the form $U \sim \{c/[(m-1)z]\}^{1/(m-1)}$ as $z \rightarrow \infty$. However, for general m , we have been unable to determine a formula for the critical wave speed c_{crit} ; numerical results suggest that it decreases monotonically with m , as expected intuitively (Fig. 6). Again, numerical simulations suggest that initial conditions decaying exponentially to zero as $x \rightarrow \infty$ evolve to the exponentially decaying wave, while initial conditions that are $O_s(x^{1/(1-m)})$ as $x \rightarrow \infty$ evolve to an algebraically decaying wave; however, there is a long transient period before the travelling waveform is acquired for large values of m .

The generalization of the variable-wave-speed formula (10) is

$$\frac{\delta x}{\delta t} = \frac{A^{1/\alpha}}{\alpha} \left(\frac{1}{u_{\text{crit}}^{m-1}} + (m-1)t \right)^{[1-(m-1)\alpha]/(m-1)\alpha} \quad (12)$$

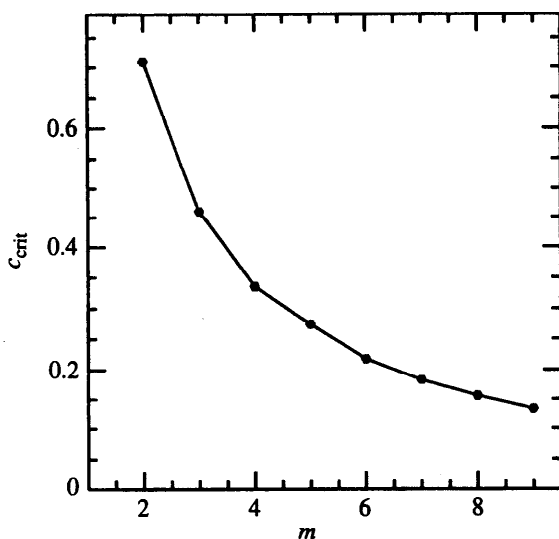


FIG. 6. The variation with m of the speed c_{crit} of the exponentially decaying travelling wave. As expected intuitively, the speed decreases monotonically with m . To calculate c_{crit} , system (11) was integrated numerically for a suitably long time period, with exponentially decaying initial conditions of the form (6), and then the wave speed was calculated as described in the main text. Again, the numerical solutions used the method of lines and Gear's method.

Again, numerical simulations suggest that initial data in the form of (8) evolve to variable-speed wavefronts corresponding to (12) if $\alpha < 1/(m-1)$, while if $\alpha > 1/(m-1)$ the long-term behaviour is algebraically decaying travelling waves with a speed of c_{crit} .

Appendix

In this Appendix we prove results referred to in the main text concerning the phase plane of the ordinary differential equations governing travelling-wave solutions of our reaction-diffusion equation. Since there is no real increase in difficulty, we will consider the more general equation, equation (11), for which the travelling-wave ordinary differential equations are

$$U' = V, \quad V' = -cV - U^m(1 - U). \quad (13)$$

This system has two equilibrium points: $(0, 0)$ and $(1, 0)$. Straightforward linearization shows that $(1, 0)$ is a saddle point with eigenvalues $\lambda^\pm = \frac{1}{2}[-c \pm (c^2 + 4)^{\frac{1}{2}}]$ and corresponding eigenvectors $(1, \lambda^\pm)$. Here λ^+ is positive while λ^- is negative, so that $(1, 0)$ is a saddle point. Thus there is a unique trajectory \mathcal{T}_c originating from $(1, 0)$ and entering the fourth quadrant, and there is a travelling-wave solution of (11) if and only if this trajectory terminates at $(0, 0)$.

Linearization shows that at the equilibrium point $(0, 0)$ there is one negative eigenvalue $-c$ corresponding to the eigenvector $(1, -c)$; the other eigenvalue is 0, and it corresponds to the eigenvector $(1, 0)$. We will show that the qualitative behaviour of \mathcal{T}_c depends on the relation between the value of c and the critical wave speed c_{crit} as follows:

- (i) $c < c_{\text{crit}} \Rightarrow \mathcal{T}_c$ terminates at infinity;
- (ii) $c = c_{\text{crit}} \Rightarrow \mathcal{T}_c$ terminate at $(0, 0)$ and the approach is along $(1, -c)$;
- (iii) $c > c_{\text{crit}} \Rightarrow \mathcal{T}_c$ terminates at $(0, 0)$ and the approach is along the centre manifold, corresponding to the zero eigenvalue.

The proof of this involves only simple phase-plane arguments, which are quite similar to those used to prove the uniqueness of the travelling-wave speed in (3); a simple account of this proof is given in the book by Grindrod (1991).

To begin the proof, we let P_c be the point on either the negative V -axis or the positive U -axis at which the trajectory \mathcal{T}_c first leaves the fourth quadrant; we will show in due course that such a point always exists for $c \geq 0$. For $c = 0$, system (13) can be solved exactly, and the solution which passes through $(1, 0)$ is given by

$$\frac{1}{2}V^2 = \frac{U^{m+1}}{m+2} \left(U - \frac{m+2}{m+1} \right) + \frac{1}{(m+1)(m+2)}.$$

This is the trajectory \mathcal{T}_0 . The full qualitative form of this solution depends on m , but crucially, for all $m > 1$, both U and V decrease monotonically from $(1, 0)$ until the trajectory crosses the negative V -axis at a point P_0 . Suppose now that $c > 0$. Since dV/dU decreases as c increases, for fixed U and V , the trajectory \mathcal{T}_c moves up above its previous position in the U - V plane as c increases. It is for this reason that \mathcal{T}_c must always leave the fourth quadrant when $c \geq 0$.

The next key step in the proof is to observe that the nature of the steady state

$(0, 0)$ means that there is only one trajectory \mathcal{T}_c^* , say, approaching $(0, 0)$ along the eigenvector $(1, -c)$ from the fourth quadrant. This is most easily seen from the fact that near the origin and away from the U -axis $dV/dU = -c$ to leading order; that is, it is independent of U and V . Moreover, the fact that dV/dU decreases as c increases, for fixed U and V , means that \mathcal{T}_c^* must move down below its previous position in the U - V plane as c increases. This behaviour is the opposite of that of \mathcal{T}_c simply because of the way in which the slopes of the relevant eigenvectors at $(0, 0)$ and $(1, 0)$ vary with c . Therefore, as c increases from 0, there will be a unique value at which the trajectories \mathcal{T}_c and \mathcal{T}_c^* coincide; this is c_{crit} .

It remains to show that \mathcal{T}_c terminates at the origin for $c > c_{\text{crit}}$; if this is so then it must approach along the centre manifold corresponding to the zero eigenvalue, since we have already ruled out the other possibility, the eigenvector $(1, -c)$. This part of the proof is straightforward. If \mathcal{T}_c does not terminate at $(0, 0)$ then it must cross the portion $0 < U < 1$ of the U -axis. At the crossing point, V' and $U^m(1 - U)$ will both be positive, while $V = 0$; this is a clear contradiction of the governing equations, equations (13).

Having completed this proof, we discuss briefly the calculation of the form of the centre manifold corresponding to the zero eigenvalue at $(0, 0)$; this is crucial to the paper since it is this that implies the algebraic decay of the travelling waves with greater than minimum speed. The calculation is a very standard centre-manifold determination; a full account of the method, with several worked examples, is given in the book by Carr (1981). Rewriting system (13) using the variables $p = cu + v$ and $q = v$ gives

$$p' = -\left(\frac{p-q}{c}\right)^m \left(1 - \frac{p-q}{c}\right), \quad q' = -cq - \left(\frac{p-q}{c}\right)^m \left(1 - \frac{p-q}{c}\right). \quad (14)$$

For equations of this form, the centre manifold will have the form $q = h(p)$. Standard theory implies that if a function $H(p)$ satisfies $M(H(p)) = O(|p|^k)$ as $p \rightarrow 0$ for a given k then $H(\cdot)$ is related to the centre manifold $h(\cdot)$ in that $|h(p) - H(p)| = O(|p|^k)$ as $p \rightarrow 0$. Here $M(\cdot)$ is defined by

$$M(H(p)) = [1 - H'(p)] \left(\frac{p - H(p)}{c}\right)^m \left(1 - \frac{p - H(p)}{c}\right) H'(p).$$

Taking $H(p) = -p^m/c^{m+1}$ gives $M(H(p)) = O(p^{m+1})$, so that to leading order $q = -p^m/c^{m+1}$, which corresponds to $V = -U^m/c$, to leading order, in the original coordinates. Simple substitution of $q = -p^m/c^{m+1}$ into (14) shows that this centre manifold is in fact a stable manifold.

REFERENCES

- BILLINGHAM, J., & NEEDHAM, D., 1991. The development of travelling waves in quadratic and cubic autocatalysis of unequal diffusion rates. I. Permanent form travelling waves. *Phil. Trans. R. Soc. Lond. A* **334**, 1-24.
- CARR, J., 1981. *Applications of Centre Manifold Theory*. Berlin: Springer.
- FIFE, P. C., & MCLEOD, J. B., 1977. The approach of solutions of nonlinear diffusion equations to travelling wave solutions. *Archiv. Rat. Mech. Anal.* **65**, 335-61.

- FISHER, R. A., 1937. The wave of advance of advantageous genes. *Ann. Eugenics* **7**, 353–69.
- GRINDROD, P., 1991. *Patterns and Waves*. Oxford: Clarendon Press.
- GRUNDY, R. E., & PELETIER, L. A., 1990. The initial interface development for a reaction diffusion equation with power law initial data. *Quart. J. Mech. Appl. Math.* **43**, 535–59.
- HOLMES, E. E., LEWIS, M. A., BANKS, J. E., & VEIT, R. R., 1994. Partial differential equations in ecology: Spatial interactions and population dynamics. *Ecology* **75**, 17–29.
- KOLMOGOROV, A., PETROVSKY, I., & PISCOUNOV, N., 1937. Etude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique. *Moscow Univ. Bull. Math.* **1**, 1–25.
- LANE, D. C., MURRAY, J. D., & MANORANJAN, V. S., 1987. Analysis of wave phenomena in a morphogenetic mechanochemical model and an application to post-fertilisation waves on eggs. *IMA J. Math. Appl. Med. Biol.* **4**, 309–31.
- MURRAY, J. D., 1989. *Mathematical Biology*. Berlin: Springer.
- ROTHE, F., 1978. Convergence to travelling fronts in semilinear parabolic equations. *Proc. R. Soc. Edin. A* **80**, 213–34.
- SHERRATT, J. A., & MURRAY, J. D., 1990. Models of epidermal wound healing. *Proc. R. Soc. Lond. B* **241**, 29–36.
- SKELLAM, J. G., 1951. Random dispersal in theoretical populations. *Biometrika* **38**, 196–218.
- SNEYD, J., & SHERRATT, J. A., 1996. On the propagation of calcium waves in an inhomogeneous medium. *SIAM J. Appl. Math.* in press.