Front and pulse solutions for a system of reaction-diffusion equations with degenerate source terms

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Motivated by several biological models such as the SIS model from epidemiology and the Tuckwell-Miura model describing cortical spreading depression, we investigate the types of wave solutions that can exist for reaction-diffusion systems of two equations in which the reaction terms are degenerate in the sense that they are linearly dependent. In particular, we show that there are surprising differences between the types of waves that occur in a single reaction-diffusion equation and the types of waves that occur in a degenerate system of two equations. Importantly, and in contrast to previously published results, we demonstrate that nonstationary pulse solutions can exist for a degenerate system of two equations but cannot exist for a single reaction-diffusion equation. We show that this has important consequences for the minimal model that can generate the types of waves observed in cortical spreading depression. On the other hand, stationary fronts can exist for both single reaction-diffusion equations and degenerate systems. However, for degenerate systems, such solutions cannot be accessed when perturbing a uniform rest state with a localized perturbation unless the diffusion coefficients of the two species are equal. We also give an explicit condition on the source term in a degenerate reaction-diffusion system that guarantees the existence of nonstationary and stationary pulse and front solutions. We use this approach to provide several examples of reaction terms that have analytical pulse and front solutions. We also show that the case in which one species cannot diffuse is singular in the sense that the degenerate reaction-diffusion system can admit infinite families of stationary piecewise constant solutions. We further show how such solutions can be accessed by perturbing a constant rest state with a localized continuous disturbance.

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I. INTRODUCTION

Systems of nonlinear reaction-diffusion equations have been extensively used to study a broad range of biological, chemical, and physical phenomena. In recent years, there has been an increased interest in reaction-diffusion systems in which the reaction terms are degenerate in the sense that they are linearly dependent. The simplest example of such a system is

$$u_t = u_{xx} + g(u, v), \tag{1}$$

$$v_t = Dv_{xx} - g(u, v), \tag{2}$$

where $u(x,t)$ and $v(x,t)$ are the quantities under consideration, t is the time, x is the spatial variable, and $g(u, v)$ are the reaction terms. The diffusion coefficient for u is scaled to be unity and the diffusion coefficient for v is a constant, D (i.e., the diffusion is not dependent on concentration or space). The degeneracy in the reaction terms implies that the nature of the reaction is such that it locally conserves populations; that is, a local decrease in u must be accompanied by an identical local increase in v. Such degenerate systems are extremely widespread and arise whenever the reaction term that converts a population from one state to another state obeys a local conservation law (such as mass or number of ions). A classical example in ecology is the SIS model that is used to model the propagation of nonfatal diseases for which there is no long-term immunity [1]. In this example, u and v represent the number of susceptible and infected individuals, respectively. The reaction terms are given by $g(u, v) = -ruv + bv$, where b is the rate at which infected individuals recover and become susceptible and r is the infection rate per number of susceptible individuals per infected individual. The SIS model conserves populations locally because the infection and recovery dynamics simply move individuals from the susceptible to the infected class or vice versa without births or deaths. Other examples abound in many other research areas, including biological pattern formation [2,3], biological cell dynamics [4], chemistry [5], moisture transport [6,7], and nuclear magnetic resonance imaging [8].

Another important example from neuroscience is the Tuckwell-Miura (TM) model [9] for a neurological phenomenon called cortical spreading depression (SD). SD is a wave that propagates through the brain and results in the large-scale movement of ions from the extracellular to the intracellular space and vice versa. The SD wave results in a massive depolarization of the cell membranes that suppresses the electrical activity in the part of the brain that is affected, but the cells eventually recover to their initial state and apparently no long-term damage occurs. The one-dimensional TM model involves potassium (K) and calcium (Ca) and is given by

$$\frac{\partial \mathrm{K}_o}{\partial t} = D_{\mathrm{K}}\frac{\partial^2 \mathrm{K}_o}{\partial x^2} + F(\mathrm{K}_o, \mathrm{K}_i, \mathrm{Ca}_o, \mathrm{Ca}_i), \tag{3}$$

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$$\frac{\partial \mathrm{K}_i}{\partial t} = -\alpha F(\mathrm{K}_o, \mathrm{K}_i, \mathrm{Ca}_o, \mathrm{Ca}_i), \quad (4)$$

$$\frac{\partial \mathrm{Ca}_o}{\partial t} = D_{\mathrm{Ca}} \frac{\partial^2 \mathrm{Ca}_o}{\partial x^2} + G(\mathrm{K}_o, \mathrm{K}_i, \mathrm{Ca}_o, \mathrm{Ca}_i), \quad (5)$$

$$\frac{\partial \mathrm{Ca}_i}{\partial t} = -\alpha G(\mathrm{K}_o, \mathrm{K}_i, \mathrm{Ca}_o, \mathrm{Ca}_i), \quad (6)$$

where $\mathrm{K}_o, \mathrm{K}_i, \mathrm{Ca}_o, \mathrm{Ca}_i$ are the extracellular and intracellular concentrations of potassium and calcium, respectively. The functions F and G are nonlinear source terms that represent currents of ions across the membrane arising from ion leakage through channels, and ion transport due to metabolic pumps that move ions against their electrochemical gradients. Here D_{K} and D_{Ca} are the diffusion coefficients for potassium and calcium in the aqueous solution in the extracellular space, respectively, and α accounts for the difference between the intracellular and extracellular volumes. The degeneracy in the source terms in the TM model arises because the ion currents simply transport ions from the extracellular space to the intracellular space and vice versa, and hence locally conserve the total numbers of each ion species. We note that ions that are in the intracellular space cannot diffuse over the length scales considered in the TM model and therefore the diffusion coefficients in Eqs. (4) and (6) for K_i and Ca_i are identically zero. In their review article, Miura *et al.* [10] presented an intuitive argument that suggested that the TM model was probably the minimal model that could generate a nonstationary pulse in which the ionic concentrations returned to their initial values after the pulse had passed. Hence, according to this argument, the TM model should be the minimal model that could reproduce the SD-like phenomenon in which the brain eventually recovers to its normal state. That is, it was believed that the minimal model that could generate a nonstationary pulse in a reaction-diffusion system with degenerate source terms required two ionic species (four equations) and that such a pulse solution could not exist for a degenerate system with a single ionic species (two equations) of the form (1)–(2). However, in this paper, we show that the system (1)–(2) can exhibit nonstationary pulses. Moreover, we determine sufficient conditions on the source terms for nonstationary pulses to exist and and give examples of source terms for which explicit nonstationary pulse solutions can be found.

In order to understand the effect of zero diffusion in one of the variables (as occurs in the TM model), we set $D = 0$ in (1)–(2) and show that there are a number of peculiarities that occur only for $D = 0$ and are absent for finite D no matter how small; that is, $D = 0$ represents a singular limit. In particular, for $D = 0$ stationary waves (both pulses and fronts) can exist with arbitrarily large numbers of discontinuities. We determine conditions for such discontinuous solutions to exist, show how to construct such solutions and explain how discontinuous stationary waves can arise from continuous initial conditions. On the other hand, we show that the case of $D = 0$ does not represent a singular limit in the case of nonstationary pulses and fronts.

Given the physical importance of reaction-diffusion systems with degenerate reactions terms, it is extremely surprising that there has been relatively little previous work. Much of the pioneering work has focused on systems with relatively simple reaction terms that are proportional to $u^a v^b$ where $a > 0$ and $b > 0$ are constants. In the context of pattern formation in bacteria growth, this model was proposed by Kawasaki *et al.* [2], and extensive mathematical properties have been established by Satnoianu *et al.* [11]. In the study of autocatalytic chemical reactions for the case $D = 1$, Billingham and Needham [12], Merkin and Needham [13], and Merkin *et al.* [14] have proved a very broad range of results. More complicated reaction terms have been considered by Mori *et al.* [4,15] who considered a system with positive feedback to its own activation and were able to shed significant light on the phenomenon of wave pinning. Huang *et al.* [6,7] considered problems of moisture transport in porous media and developed numerical methods to determine the dynamics of propagating moisture fronts. The reaction terms in all of these papers allow only for traveling fronts that replace an unstable rest state in front of the wave by a stable rest state behind the wave. Diffusive spreading in a system with barriers for the case of linear reaction terms was considered by Huang *et al.* [8], but this system does not admit traveling waves. Wylie and Miura [16,17] considered a very general form of reaction terms and derived conditions that are required to trigger traveling fronts that replace one stable rest state with another stable rest state when a stable uniform steady-state solution is perturbed by a highly localized disturbance. However, their analysis was restricted to the case of fronts, and the techniques they used cannot be applied to pulses.

We will study traveling waves with coordinate $z = x - ct$, where c is the constant wave speed, and make some general conclusions about the types of solutions that may exist for reaction-diffusion systems with degenerate reaction terms. The terminology that we will use in this paper is that a *front* is a solution to (1)–(2) for which the state far ahead of the wave $(u_+, v_+) = \lim_{z\to\infty}(u(z), v(z))$ is different from the state far behind the wave $(u_-, v_-) = \lim_{z\to-\infty}(u(z), v(z))$; see Fig. 1(b). On the other hand, a *pulse* is a solution for which the states far ahead and far behind the waves are the same, that is, $(u_-, v_-) = (u_+, v_+)$; see Fig. 1(a). We will also refer to waves (pulses or fronts) as *stationary* if they have $c = 0$ and *nonstationary* if $c \neq 0$.

In this paper, we will derive conditions regarding the existence of traveling waves (both fronts and pulses) for (1)–(2). We will compare these results with those for a single reaction-diffusion equation that we derive in Sec. II. When considering traveling waves, we will show in Sec. III B that in the case of equal diffusivities $D = 1$, the system (1)–(2) can be reduced to a single reaction-diffusion equation. In particular, we will show that no nonstationary pulses can exist for the single reaction-diffusion equation and hence for (1)–(2) with $D = 1$. However, in Sec. III A, for (1)–(2) with $D \neq 1$, we will show that nonstationary pulses can exist and show how to explicitly obtain infinite families of reaction terms that admit nonstationary pulse solutions. Moreover, we will give examples in which simple explicit solutions can be obtained. As mentioned above, this explicitly demonstrates that the TM model is not the minimal degenerate reaction-diffusion model that admits pulse solutions. Then in Sec. III C, we will consider the physically relevant case of $D = 0$ and show that discontinuous stationary solutions with an arbitrary number of discontinuities can exist. This is in direct contrast with $D \neq 0$

or for nonstationary waves with $D = 0$ for which no such discontinuous solutions can exist. We also show how such solutions can develop from smooth initial conditions.

II. FRONT AND PULSE SOLUTIONS FOR A SINGLE REACTION-DIFFUSION EQUATION

One of the main aims of this paper is to show that the degenerate coupled system (1)–(2) has waves whose properties differ significantly from the properties of waves that occur in a single reaction-diffusion equation. In order to highlight the differences, we briefly investigate the possible types of wave solutions for a single reaction-diffusion equation and will contrast these results with those found in later sections for the coupled system. The generic single reaction-diffusion equation is given by

$$u_t = u_{xx} + f(u). \tag{7}$$

Transforming Eq. (7) to the traveling wave coordinate $z = x - ct$, we obtain

$$u_{zz} + cu_z + f(u) = 0, \tag{8}$$

where the boundary conditions are

$$u \to u_\pm \quad \text{and} \quad u_z \to 0 \quad \text{as} \quad z \to \pm\infty.$$

By first multiplying by u_z, Eq. (8) can be directly integrated to obtain

$$-c\int_{-\infty}^{\infty}(u_z)^2\,dz = \left[\frac{1}{2}(u_z)^2 + F(u)\right]_{z=-\infty}^{z=\infty} = F(u_+) - F(u_-), \tag{9}$$

where

$$F(u) = \int_0^u f(u')\,du',$$

and where we have used the fact that for nonstationary front and pulse solutions, $u_z \to 0$ as $z \to \pm\infty$.

For nonstationary and stationary fronts, we require that the initial and final states of the system are different, so that $u_+ \neq u_-$ and, in general, $F(u_+) \neq F(u_-)$. From Eq. (9), we see that in general, front-type solutions will have a nonzero wave speed, i.e., they will be nonstationary fronts. Stationary fronts can only exist in the case where $F(u_+) = F(u_-)$. This is summarized in Table II below.

For a pulse solution, we require that both the solution and its derivative decay to some background level in the far field and $u_+ = u_-$. Using this property and the definition of $F(u)$, we see that in the case of a pulse solution, the right-hand side of (9) is zero. Since the integral on the left-hand side is strictly positive, the wave speed must be zero, $c = 0$. As a result, we conclude that all pulse solutions must be stationary, and nonstationary pulse solutions cannot exist.

Despite this seemingly straightforward result, a number of examples in the literature claim to have obtained analytic nonstationary pulse solutions. However, these solutions are in fact erroneous. One example appears in Ref. [18]. This paper presents a new technique which facilitates the generation of a wide variety of exact solutions to reaction-diffusion equations. A pulse solution to a generalized Fisher equation is presented, and, in that particular example, the reaction term contains $cu^{1/2}$, where c is the wave speed. The pulse solution that is presented only satisfies the reaction-diffusion equation if the negative square root is taken when $z < 0$, and the positive square root is taken when $z > 0$. As a result, the reaction term is not a function of u only, unless the wave speed is taken to be identically zero. So the solution is valid only in the stationary case.

In another example [19], the author presents a wide variety of new exact solutions, including a new nonstationary pulse solution for the Fisher equation. However, there is a typographical error in the final solution. Using the values of the constants as given, the solution derived in Ref. [19] has $u_+ \neq u_-$, so that the solution is a nonstationary front, not a pulse.

III. FRONT AND PULSE SOLUTIONS FOR A SYSTEM OF REACTION-DIFFUSION EQUATIONS

We now turn our attention to traveling waves of the system (1)–(2). On transforming to the coordinate, $z = x - ct$, Eqs. (1)–(2) become

$$u'' + cu' + g(u, v) = 0, \tag{10}$$

$$Dv'' + cv' - g(u, v) = 0, \tag{11}$$

where primes refer to differentiation with respect to z. Without loss of generality, we assume that $(u_-, v_-) = (0, 0)$ is a rest state so that $g(0, 0) = 0$. The boundary conditions for a traveling wave solution are then

$$(u, v) \to (0, 0) \ \text{and}\ (u', v') \to (0, 0) \quad \text{as}\ z \to -\infty,$$
$$(u, v) \to (u_+, v_+) \ \text{and}\ (u', v') \to (0, 0) \quad \text{as}\ z \to +\infty.$$

As described in Sec. I, a front solution satisfies $(u_+, v_+) \neq (0, 0)$, and pulse solution satisfies $(u_+, v_+) = (0, 0)$.

Singular points and nonstationary front solutions to this system of equations were examined in Ref. [16]. Here we reexamine the possibility of stationary and nonstationary front solutions and investigate the stationary and nonstationary pulse solutions.

A. The generic case, $D \neq 0, 1$

The special cases when the diffusivities are equal, $D = 1$, or when one of the species does not diffuse, $D = 0$, are simpler and exhibit different dynamics to the general case. These two cases are considered in later sections. In this subsection we will consider the generic case in which the diffusivities of both species are distinct and nonzero, $D \neq 0, 1$. We examine the behavior of stationary and nonstationary pulses and fronts separately.

1. *Stationary pulses, $c = 0$*

For stationary pulses (and fronts), $c = 0$, and the traveling wave equations (10)–(11) take the form

$$u'' + g(u, v) = 0, \tag{12}$$

$$Dv'' - g(u, v) = 0. \tag{13}$$

By adding the above equations and integrating twice using the boundary conditions for a pulse solution, we obtain

$$u = -Dv. \tag{14}$$

Substituting this into (13) we find

$$Dv'' - g(-Dv, v) = 0, \tag{15}$$

and multiplying through by v_z, we can integrate to obtain

$$v'^2 = G_1(v) \quad \text{where} \quad G_1(v) = \tfrac{2}{D}\int_0^v g(-Dv', v')\,dv'.$$

Pulse solutions require the existence of a homoclinic orbit and hence a saddle point at the origin in phase space $(v, v_z) = (0, 0)$. By taking a Taylor series expansion of G_1, we can write

$$v'^2 = \frac{1}{2}\frac{d^2G_1}{dv^2}\bigg|_{v=0} v^2 + \cdots$$

since $G_1(0) = 0$ by definition and $dG_1/dv|_{v=0} = 0$ because $g(0, 0) = 0$. For a saddle point in the phase plane, we must have $d^2G_1/dv^2|_{v=0} > 0$ so that we require

$$\frac{d}{dv}g(-Dv, v)\bigg|_{v=0} = -Dg_u(0, 0) + g_v(0, 0) > 0,$$

which is the same as the stability constraint for the solution $(u, v) = (0, 0)$ in the full reaction-diffusion system in the case when $D > 1$ [16]. If this condition is not satisfied, then a stationary pulse solution cannot exist. Satisfaction of this constraint and consequent existence of a saddle point does not guarantee the existence of a stationary pulse solution, rather, it is a minimum requirement.

A simple example that has an explicit solution is the function $g(u, v) = -u(2 - 6v)$. This gives $g(-Dv, v) = Dv(2 - 6v)$, which upon integrating (15) gives $v'^2 = 4(v^2 - v^3 + C)$ where C is a constant. Choosing $C = 0$, we obtain a homoclinic orbit that connects the stationary points $v = 0$ back to itself. This can then be further integrated to obtain the explicit form of the solution $v = \text{sech}^2(\pm z + B)$ where B is an arbitrary constant. Using (14) we obtain the corresponding solution $u = -D\text{sech}^2(\pm z + B)$.

2. Stationary fronts, $c = 0$

Stationary fronts can exist whenever (15) has a heteroclinic orbit. This can clearly occur for an appropriately chosen function $g(u, v)$. A simple example of such a function is $g(u, v) = 2u(1 - v^2)$. This gives $g(-Dv, v) = 2Dv(v^2 - 1)$, which upon integrating (15) gives $v'^2 = (v^4 - 2v^2 + C)$ where C is a constant. Choosing $C = 1$, we obtain a heteroclinic orbit that connects the stationary points $v = -1$ and $v = 1$ and vice versa. This can then be further integrated to obtain the explicit form of the solution $v = \tanh(\pm z + B)$ where B is an arbitrary constant. Using (14) we obtain the corresponding solution $u = -D\tanh(\pm z + B)$.

However, despite the fact that such solutions exist, it is interesting to note that such solutions are not accessible from generic initial conditions. We will illustrate this point by considering the case of a uniform rest state that is perturbed by a localized disturbance. Without loss of generality we will assume that the initial rest state is given by $(u, v) = (0, 0)$. In this case, one can add (1) and (2), integrate over space and apply the boundary conditions at infinity to obtain

$$\frac{\partial}{\partial t}\left[\int_{-\infty}^{\infty}(u + v)\,dx\right] = 0.$$

Then, given that the initial localized disturbance has a finite mass, we can integrate the above equation with respect to time and apply the initial condition to obtain

$$\int_{-\infty}^{\infty}(u + v)\,dx = C, \tag{16}$$

where C is the constant that represents the initial mass of $(u + v)$ in the localized disturbance. On the other hand, adding Eqs. (12) and (13), integrating, and using the boundary conditions on u_z and v_z, we obtain $(u + Dv)_z = 0$. Integrating again, and rearranging, we find $(u + v) + (D - 1)v =$ constant. In order for the integral in (16) to remain finite, we require that $u + v \to 0$ as $z \to \pm\infty$. This implies that $(D - 1)v =$ constant as $z \to \pm\infty$. If $D \neq 1$, we obtain $v(\infty) = v(-\infty)$. Moreover, using $u + v \to 0$ as $z \to \pm\infty$, we immediately see that $u(\infty) = u(-\infty)$. Since this solution takes the same values far ahead and far behind the wave, it cannot represent a stationary front. We therefore conclude that stationary fronts can exist, but that the global conservation law (16) implies that such solutions cannot be accessed if one perturbs a uniform rest state with a localized disturbance.

3. Nonstationary pulses, $c \neq 0$

We now turn our attention to nonstationary pulse solutions of (1)–(2). As we noted in Sec. II, the single reaction-diffusion equation cannot give rise to nonstationary pulse solutions. In contrast, we will show that traveling pulse solutions can exist for a large family of degenerate systems, and we will give examples of source terms for which explicit solutions can be obtained.

Adding Eqs. (10) and (11), integrating once with respect to z and using the boundary conditions, we find

$$u' + Dv' + c(u + v) = 0. \tag{17}$$

Defining

$$p \equiv u + Dv \tag{18}$$

we can rewrite (17) as

$$Dp' + cp = c(1 - D)u. \tag{19}$$

By rearranging for u and substituting into (10), we obtain the following third-order equation for p:

$$\begin{aligned} &Dp''' + c(1 + D)p'' + c^2p' \\ &+ c(1 - D)g\left(\frac{Dp' + cp}{c(1 - D)}, -\frac{p' + cp}{c(1 - D)}\right) = 0. \end{aligned} \tag{20}$$

Whether pulse solutions exist or not depends on whether values of the wave speed c can be found such that (20) has a homoclinic orbit. We now show that a large family of functions $g(u, v)$ can indeed give rise to such homoclinic orbits.

Theorem. Suppose that the function $g(u, v)$ can be expressed in the form

$$g(u, v) = \frac{(D+1)}{(D-1)}Q + \frac{D[k^2(u+v) - DQ]}{k^2(D-1)^2}\frac{\partial Q}{\partial u} + \frac{D[-k^2(u+v) + Q]}{k^2(D-1)^2}\frac{\partial Q}{\partial v} - \frac{k^2(u+v)}{(D-1)}, \tag{21}$$

where $k \neq 0$ is a constant and $Q(u, v)$ is a once-differentiable function of u and v. If the system

$$p'' = Q\left(\frac{-Dp' - kp}{k(D-1)}, \frac{p' + kp}{k(D-1)}\right)$$

has a bounded solution with $p \to 0$ as $z \to \pm\infty$, then (20) has a nonstationary pulse solution, with speed $c = k$.

Proof. Rearranging (19) and using $p = u + Dv$, we obtain

$$u = \frac{-Dp' - cp}{c(D-1)} \quad \text{and} \quad v = \frac{p' + cp}{c(D-1)}, \tag{22}$$

or alternatively,

$$p = u + Dv \quad \text{and} \quad p' = -c(u+v). \tag{23}$$

Substituting (21) and (22) into (20) gives

$$Dp''' + c(D+1)p'' + c^2p' - c(D+1)Q + \frac{D[p'k^2 + cDQ]}{k^2(D-1)}\frac{\partial Q}{\partial u} - \frac{D[k^2p' + cQ]}{k^2(D-1)}\frac{\partial Q}{\partial v} - k^2p' = 0. \tag{24}$$

Using (23) we obtain

$$\frac{\partial Q}{\partial u} = \frac{\partial Q}{\partial p} - c\frac{\partial Q}{\partial p'},$$
$$\frac{\partial Q}{\partial v} = D\frac{\partial Q}{\partial p} - c\frac{\partial Q}{\partial p'}.$$

Substituting into Eq. (24) we may write

$$Dp''' + c(D+1)p'' + c^2p' - c(D+1)Q - Dp'\frac{\partial Q}{\partial p} - D\frac{c^2}{k^2}Q\frac{\partial Q}{\partial p'} - k^2p' = 0.$$

Rewriting using the total derivative, we obtain

$$Dp''' + c(D+1)(p'' - Q) - D\frac{dQ}{dz} + D\frac{\partial Q}{\partial p'}\left[p'' - \frac{c^2}{k^2}Q\right] + (c^2 - k^2)p' = 0.$$

Which can be expressed in the form

$$\left[D\frac{d}{dz} + c(D+1)\right](p'' - Q) + D\frac{\partial Q}{\partial p'}\left[p'' - \frac{c^2}{k^2}Q\right] + (c^2 - k^2)p' = 0.$$

Choosing the wave speed $c = k$, we obtain

$$\left[D\frac{d}{dz} + k(D+1) + D\frac{\partial Q}{\partial p'}\right](p'' - Q) = 0.$$

This is automatically satisfied because of our assumption that $p'' = Q$. Therefore, the solution of $p'' = Q$ that satisfies $p \to 0$ when $z \to \pm\infty$ is a nonstationary pulse solution of Eqs. (10)–(11). ■

Example: Nonstationary pulse solution. In order to illustrate the existence of a nonstationary pulse solution to systems of type (10)–(11), it is helpful to consider a particular example. One way to generate nontrivial examples is to adopt the ansatz that $Q(p, p')$ is a function of p only. Given a specific function form of $g(u, v)$, one can then determine conditions on $g(u, v)$ that are consistent with the ansatz. This allowed us to find the following quadratic example:

$$g(u, v) = 6(u^2 - D^2v^2) + \frac{(k^2 - 4)u + (k^2 - 4D^2)v}{1 - D},$$

where $k \neq 0$ is a constant.

The steady states of this system can be obtained by setting the z derivatives in (12) and (17) to zero. This gives $g(u, v) = 0$ and $u + v = 0$, which yields solutions

$$(u, v) = (0, 0), \quad \text{and} \quad (u, v) = \left(\frac{2}{3(1-D)}, -\frac{2}{3(1-D)}\right).$$

The stability of these uniform solutions may be analysed using the stability criterion derived in [16]. The steady state at $(u, v) = (0, 0)$ is stable for all $D > 0$ since $g_u - g_v = -4(D+1) < 0$ and $Dg_u - g_v = -(c^2 + 4D) < 0$. On the other hand, the second steady state is guaranteed to be unstable since $g_u - g_v = 4(D+1) > 0$.

By examining (21), one can readily show that this form of g is compatible with the function Q given by

$$Q = 2p(2 - 3p).$$

Hence, if we can show that $p'' = Q$ has a solution that satisfies $p \to 0$ when $z \to \pm\infty$ we can obtain a traveling pulse solution. In this case, Q depends only on p, and so we may integrate twice with respect to z using the conditions $p' = p = 0$ when $z \to \pm\infty$ to obtain

$$p(z) = \text{sech}^2 z.$$

The expressions for $u(z)$ and $v(z)$ can then be obtained by setting $c = k$ in (22) to give

$$u(z) = -\frac{\text{sech}^2 z(2D\tanh z - k)}{k(1-D)},$$
$$v(z) = \frac{\text{sech}^2 z(2\tanh z - k)}{k(1-D)}, \tag{25}$$

where $z = x - kt$. This solution is shown in Fig. 1(a). It has the property that $(u, v) \to (0, 0)$ as $z \to \pm\infty$, so that it is indeed a pulse solution. In this solution, both dependent variables are negative for some regions in the domain shown. In order to apply these solutions to the modeling problems described in the Introduction where the quantities of interest are populations or concentrations, the functions u and v might be considered as deviations from some background level. In this way, a negative solution may be considered to be a concentration lower than the predefined background level.

The construction of a nonstationary pulse solution to a system of only two reaction-diffusion equations is of particular interest, since it demonstrates that the minimal model for a SD wave that was described in the introduction is a system of only

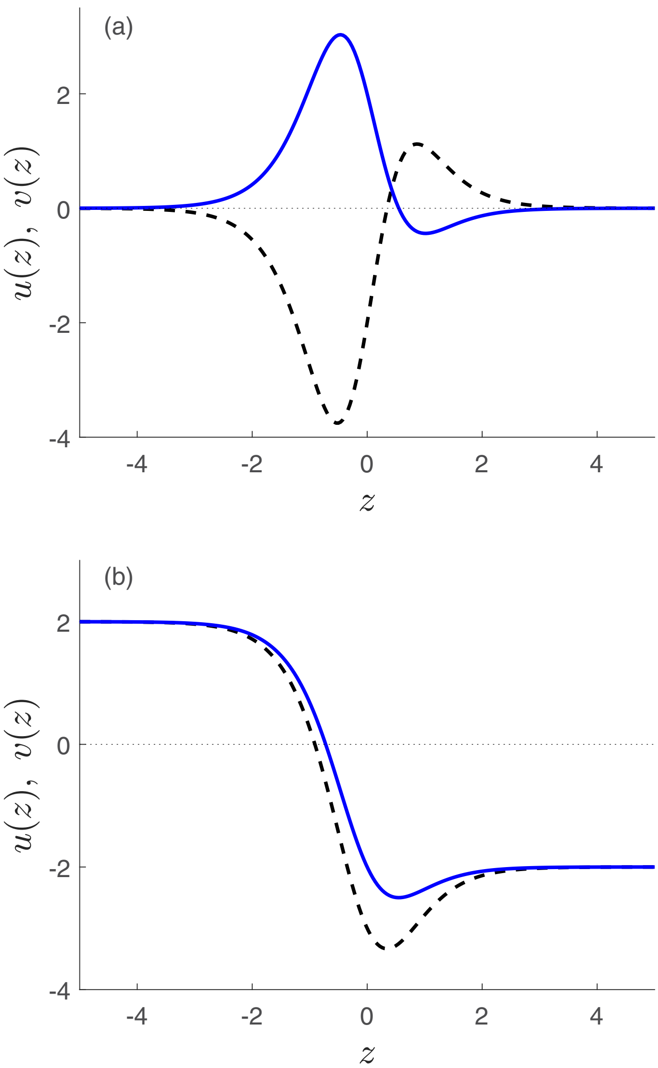

FIG. 1. Example nonstationary solutions in the generic case, $D \neq 0, 1$. (a) Nonstationary pulse solution given by (25). (b) Nonstationary front solution given by (27). In both cases, the black dashed line shows $u(z)$ and the blue solid line shows $v(z)$. Also, $D = 1.5,\ k = 1$.

two reaction-diffusion equations. We will further elaborate on this in Sec. IV.

4. Nonstationary fronts, $c \neq 0$

In the case of unequal diffusivities ($D \neq 0, 1$), by adding Eqs. (10) and (11), integrating once and making use of the boundary conditions at $z \to -\infty$, we find

$$u_z + Dv_z + c(u + v) = 0. \tag{26}$$

Evaluating (17) in the limit $z \to \infty$ and making use of the condition on the flux, we find that $c(u_+ + v_+) = 0$. In the nonstationary case for which $c \neq 0$, we conclude that $u_+ + v_+ = 0$. Therefore, the rest states far ahead of the wave must satisfy $g(u_+, v_+) = 0$ and $u_+ + v_+ = 0$. It follows from this that nonstationary front solutions of the system (10)–(11) exist only if the curves $g(u, v) = 0$ and $u + v = 0$ have multiple intersections. This was also noted by Wylie and Miura [16].

In order to find a nonstationary front solution, a heteroclinic orbit that links the two rest states must be found by solving the third-order dynamical system represented by (10) and (26). Following the same procedure explained above, this dynamical system can again be rewritten in the form (20). So finding a traveling front requires finding a value of the wave speed c such that a heteroclinic orbit exists. Although Wylie and Miura [16] were able to obtain traveling front solutions for both the cases $D = 0$ and $D = 1$, they did not present traveling front solutions for the case $D \neq 0, 1$. Below, we provide exactly such solutions.

Example: Nonstationary front solution. We consider a cubic reaction term of the form

$$g(u, v) = \frac{1}{1 - D}(u + v)(4Du^2 + 4D^3v^2 + 8D^2uv - 2ku - 2kD^2v + k^2),$$

where $k \neq 0$ is a constant.

By examining (21), one can readily show that this form of g is compatible with the function Q given by

$$Q = -2p'p.$$

We choose to find a solution to $p'' = Q$ that satisfies $p \to -1$ when $z \to -\infty$ and $p \to 1$ when $z \to \infty$. This will correspond to a traveling front solution. In this case, the equation $p'' = Q$ can be integrated twice with respect to z to obtain

$$p(z) = \tanh z.$$

The expressions for $u(z)$ and $v(z)$ can then be obtained by setting $c = k$ in (22) to give

$$u(z) = \frac{D\tanh^2 z - k\tanh z - D}{k(D - 1)},$$
$$v(z) = \frac{\tanh^2 z - k\tanh z - 1}{k(D - 1)}, \tag{27}$$

where $z = x - kt$. This solution is shown in Fig. 1. It has the property that $(u, v) \to (\mp 1/(D - 1), \pm 1/(D - 1))$ as $z \to \pm\infty$ and so that it is indeed a pulse solution.

B. Equal diffusivities, $D = 1$

Here we examine the behavior when $D = 1$. By adding Eqs. (10) and (11), integrating and making use of the boundary conditions, it can be shown that $u + v \equiv 0$. The problem can then be reduced to solving a single reaction-diffusion equation

$$v'' + cv' - g(-v, v) = 0.$$

This is precisely the problem that we considered in Sec. II, and hence the behavior observed in the case of a single equation is reflected here in the case $D = 1$. Following precisely the approach used in Sec. II, we can integrate this equation to find

$$c\int_{-\infty}^{\infty}(v_z)^2\,dz = G_2(-v_+, v_+) - G_2(-v_-, v_-), \tag{28}$$

where $G_2(-v, v) = \int_0^v g(-v', v')\,dv'$.

For a pulse solution, $v_+ = v_-$, so that any pulse must be stationary, $c = 0$ (since the integral on the left hand side is strictly positive).

For front solutions, $v_+ \neq v_-$ so that, in general, front solutions have a nonzero wave speed, except in the nongeneric case where $G_2(-v_+, v_+) = G_2(-v_-, v_-)$.

Solutions for some example reaction-diffusion systems (10)–(11) with $D = 1$ were constructed by Wylie and Miura [16].

C. One species not diffusing, $D = 0$

We now turn our attention to the case $D = 0$ in which v does not diffuse. As we mentioned earlier, this is important for models of ionic transport in cellular media in which the two species u and v represent the concentration of a particular ion in the extracellular and intracellular spaces, respectively. On the continuum scale, ions that are inside a cell cannot diffuse. However, ions can move from the intracellular space to the extracellular space where they are free to diffuse. Note that the process of ions moving from the intracellular space to the extracellular space is represented by the cross-membrane flux terms $g(u, v)$. As a result of its importance in biological applications, the case $D = 0$ is a highly significant special case. As in the general case, the behavior of stationary and nonstationary solutions is quite different, and so we will study them separately.

1. Stationary pulses and fronts, $c = 0$

From Eq. (11) with $D = c = 0$, we see that in the stationary case, $g(u, v) = 0$. Substituting this into (10) with $c = 0$, we find $u_{zz} = 0$. Upon integrating and making use of the boundary conditions, we find that $u(z) \equiv 0$ is the only solution. It follows that $g(0, v(z)) = 0$. By definition, $g(0, 0) = 0$ and so the $u(z) = v(z) = 0$ is clearly a solution. However, it is possible that the function g is such that there are other constants v_* such that $g(0, v_*) = 0$. Therefore, a nontrivial solution can be constructed of piecewise constants in which $v(z)$ takes any of the constant values that correspond a subset of the steady states. Such solutions are clearly not unique.

In Fig. 2 we show the numerical results of a simulation with the reaction term $g(u, v) = v(v - \gamma)(v - 1) - u$. For this function g, the solutions of $g(0, v) = 0$ are $v = 0, \gamma, 1$. If $0 < \gamma < 1$, then $v = 0, 1$ are stable and $v = \gamma$ is unstable. The initial condition is chosen to be zero in u, while v has a double peaked function with the left peak broader than the right one. The numerical technique that we applied was a standard Crank-Nicolson algorithm for time stepping with a Newton-Raphson method to solve the resulting algebraic equations. As one can see from Fig. 2, the evolution of v is such that regions where v was initially large tend to evolve towards $v = 1$, whereas the regions where v was initially close to zero tend to evolve towards $v = 0$. The evolution of u is such that it starts from $u = 0$ but is driven away from zero by the flux terms. However, u eventually diffusively returns to the zero solution. Eventually, v evolves towards a piecewise constant solution with the two regions of $v = 1$ separated by regions of $v = 0$. The left region in which $v = 1$ is wider than the right one reflecting the widths of the initial disturbances. In Fig. 3 we plot the late-time solutions for u and v, and we clearly see that the solution is tending towards a piecewise constant function.

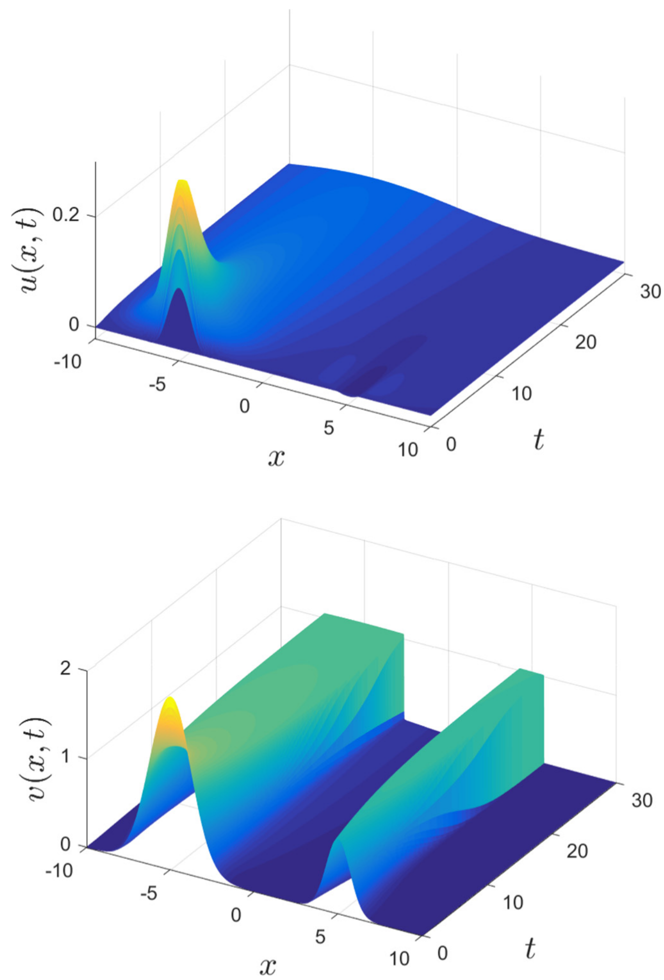

FIG. 2. Numerical results for an example reaction term $g(u, v) = v(v - \gamma)(v - 1) - u$. The solutions for both u and v evolve to a stationary pulse, which is piecewise constant. Here $\gamma = 0.5$.

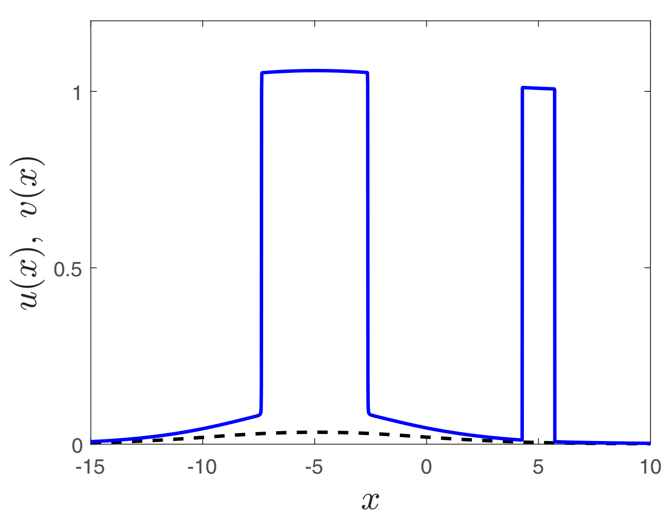

FIG. 3. The late time ($t = 30$) stationary pulse for the solution shown in Fig. 2. At this late time, both $u(x, t)$ and $v(x, t)$ have evolved to almost piecewise constant functions. The black dashed line shows $u(x, t)$, while the blue solid line shows $v(x, t)$. As before, $\gamma = 0.5$.

In the above numerical example, we have shown an example of a stationary pulse built from piecewise constants. In fact, we can also construct stationary front solutions from piecewise constants in a similar way. The only difference is that for a front we require that $v(-\infty) \neq v(\infty)$, meaning that the far fields must tend to different constant values far ahead of and far behind the front. In Sec. III A 2, we noted that for $D \neq 0$ that stationary fronts can exist, but that the global conservation law (16) implies that such solutions cannot be accessed if one perturbs a uniform rest state with a localized disturbance. This property is clearly also true for $D = 0$ for precisely the same reason.

2. Nonstationary pulses and fronts, $c \neq 0$

To investigate nonstationary pulses and fronts in the case when $D = 0$, we first add Eqs. (10) and (11), integrate, and make use of the boundary conditions to obtain $v = -(u' + cu)/c$, so that

$$u_{zz} + cu_z + g\left(u, -\frac{u' + cu}{c}\right) = 0. \tag{29}$$

While the system of equations can be reduced to a single equation in this case, the behavior is not analogous to that described in Sec. II because of the appearance of the derivative, u', in the reaction term. It is also worth noting that since $v = -(u' + cu)/c$, in the limit as $c \to \infty$ we find that $v = -u$.

In fact, the techniques that we developed for $D \neq 0$ in Sec. III A 3 can also be directly applied to the case $D = 0$, and we can use exactly the same methods to find families of functions $g(u, v)$ for which nonstationary pulses and fronts exist. In fact, (29) corresponds to (21) since $u(z) = p(z)$ in the case $D = 0$. We note that Wylie and Miura [16] found an exact nonstationary front solution for a particular cubic function g when $D = 0$. They did this by essentially guessing that the form of solution could be expressed in terms of hyperbolic functions. However, we can use our approach to find both nonstationary pulses and nonstationary fronts for a much broader range of functional forms of g. Below we give an example of a function g that has nonstationary pulse solutions.

Example: Nonstationary pulse solution with $D = 0$. We consider a cubic reaction term of the form

$$g(u, v) = g(u, v) = 8u^3 - 6u^2 + k^2(u + v),$$

where $k \neq 0$ is a constant. Examining (21), one can readily show that this form of g corresponds to the function Q given by

$$Q = 6p^2 - 8p^3,$$

Integrating the equation $p'' = Q$ twice with respect to z and applying the boundary conditions at $z \to \pm\infty$ we obtain

$$p(z) = \frac{1}{z^2 + 1}.$$

The expressions for $u(z)$ and $v(z)$ can then be obtained by setting $c = k$ in (22) to give

$$u(z) = \frac{1}{z^2 + 1}, \quad v(z) = \frac{-kz^2 + 2z - k}{(z^2 + 1)^2 k}, \tag{30}$$

where $z = x - kt$. This solution is shown in Fig. 4. As expected, in the limit $c = k \to \infty$, we see that $v(z) = -u(z)$.

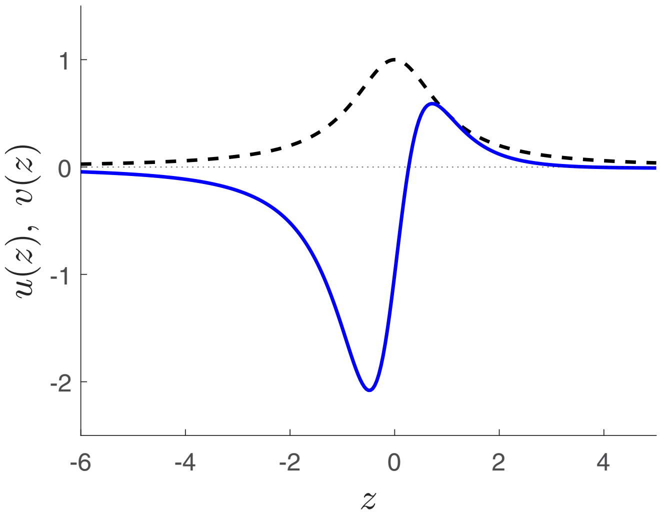

FIG. 4. Example nonstationary pulse solution in the case when $D = 0$, solution (30). The black dashed line shows $u(z)$ and the blue solid line shows $v(z)$. Here $k = 0.5$.

IV. FINAL REMARKS

In this discussion, we summarize the new results presented in this paper, highlight the differences between a single reaction-diffusion equation and a system of reaction-diffusion equations with degenerate source terms, and discuss some of the possible implications for CSD waves.

We have shown that there is a fundamental difference in the types of pulse solutions that may exist for a single reaction-diffusion equation and a system of two reaction-diffusion equations (in the most general case, $D \neq 0, 1$). While

TABLE I. Summary of the types of pulse solutions permitted by a single reaction-diffusion equation, and a degenerate reaction-diffusion system (1)–(2).

	Pulse solutions			
	RD equation	RD system, $D \neq 1, 0$	RD system, $D = 1$	RD system, $D = 0$
Stationary ($c = 0$)	Can exist	Can exist	Can exist	Discontinuous solutions can exist
Nonstationary ($c \neq 0$)	Never exist	Can exist	Never exist	Can exist for g with certain properties, e.g., $g = f(u) + v$

TABLE II. Summary of the types of front solutions permitted by a single reaction-diffusion equation, and a degenerate reaction-diffusion system (1)–(2).

Front solutions				
	RD equation	RD system, $D \neq 1, 0$	RD system, $D = 1$	RD system, $D = 0$
Stationary ($c = 0$)	Can exist [only if $F(u_+) = F(u_-)$]	Can exist, but not accessible by perturbing arbitrary initial condition	Can exist	Discontinuous solutions can exist
Nonstationary ($c \neq 0$)	Can exist	Can exist	Can exist	Can exist

nonstationary pulses may exist for a system of two equations, they never exist for a single equation. The fact that nonstationary pulses may never exist for a single equation is perhaps known colloquially, but it seems not to have been reported in the literature, and indeed, incorrect examples of nonstationary pulses may be found. On the other hand, the proof that nonstationary pulses may exist for a system of two reaction-diffusion equations is important because it demonstrates that the minimal degenerate system that will admit nonstationary pulses consists of two reaction-diffusion equations.

This conclusion has important consequences for the modeling of CSD waves. It was previously believed that in order to exhibit nonstationary pulses, a CSD model would need to explicitly account for the intracellular and extracellular concentrations of two ion species, resulting in a system of four reaction-diffusion equations [9]. The results derived here show that the nonstationary pulses typically observed during a CSD episode may be replicated by taking into account the intracellular and extracellular concentrations of just one ion species, resulting in a system of two reaction-diffusion equations.

We have also investigated front solutions of degenerate systems in the case ($D \neq 1$). We found that stationary fronts can exist; however, they cannot be accessed by perturbing a uniform rest state. Consequently, they would not be observed in a CSD model that consisted of only two reaction-diffusion equations describing the intracellular and extracellular concentrations of just one ion species. Conversely, nonstationary fronts can exist, providing the curves $g(u, v) = 0$ and $u + v = 0$ have multiple intersections.

For a system of two reaction-diffusion equations in the case of equal diffusivities, $D = 1$, we have shown that the system (10)–(11) can be reduced to a single reaction-diffusion equation (8), and therefore the conclusions about the types of solutions that may exist for a single equation hold for a system in the case $D = 1$. With regard to modeling CSD waves, this implies that in order to obtain nonstationary pulses, the diffusivities in the intracellular and extracellular space must be different. This is inherently true of the type of model proposed by Tuckwell and Miura [9] since the ions in the intracellular space cannot diffuse over the same length scales as those in the extracellular space.

When one species cannot diffuse ($D = 0$), a reaction-diffusion system such as that examined here can admit stationary piecewise constant solutions, where $u(x) \equiv 0$ and the solution for $v(x)$ is composed of regions of constant values that satisfy $g(0, v) = 0$. Such a solution can evolve from a disturbance to the localized rest state to produce a stationary pulse.

In this paper, we also describe a method that can be used to produce nonstationary pulse and front solutions to a degenerate reaction-diffusion system for a large family of functions $g(u, v)$, and for all values of the diffusion constant, $D \neq 1$. Several examples have been provided.

The potential for a reaction-diffusion equation or system to allow stationary or nonstationary fronts or pulses is summarized in Tables I and II.

An important question that remains open is the relationship between the example fronts and pulses presented here and the pushed and pulled fronts as described by van Saarloos [20]. In this paper we have not investigated the relevance of the linear spreading speed to solutions of this type and leave this to future work.

The question of stability also remains open; however, it is an important consideration, particularly in the application of solutions to real-world problems such as those described in the Introduction. The solutions shown in Figs. 2 and 3 appear (numerically) to be stable. Numerical evidence indicates that there does exist stable traveling pulse solutions to the Tuckwell-Miura model equations [9]; however, a more general stability theory is beyond the scope of this paper and is left to future work. While unstable waves are less likely to be observed in real situations, it has been suggested that they may be important in some cellular pathways [21] and as a mechanism to generate chaos in the wake of an invasion [22].

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