On a Nonlinear Diffusion Equation Describing Population Growth

Abstract: A nonlinear eigenvalue problem is solved analytically to obtain the shock-like traveling waves of Fisher's nonlinear diffusion equation, with which he described the wave of advance of advantageous genes. A phase-plane analysis of the wave profiles shows that the propagation speed of the waves is linearly proportional to their thickness. The analytic solution is asymptotically accurate in the limit of infinitely large characteristic speeds. However, as they have a minimum threshold value which is not zero, the asymptotic solution turns out to be highly accurate for all propagation speeds. The wave profiles of Fisher's equation are shown to be identical to the steady state solutions of the Korteweg-de Vries-Burgers equation that are obtained when dissipative effects are dominant over dispersive effects.

Introduction

This paper describes our study of the traveling wave solutions of

$$u_{\tau} = \nu u_{uu} + ku \ (1 - u), \tag{1}$$

a nonlinear equation of evolution of diffusive type used by Fisher [1] to describe the propagation of a virile mutant in an infinitely long habitat. The growth of the mutant population is due to diffusion and nonlinear local multiplication. In Eq. (1), ν is the diffusion coefficient, k is a positive multiplication factor, τ is time, y is distance, and the subscripts designate partial derivatives. With only an inconsequential variation, Eq. (1) becomes a model used to describe the evolution of the neutron population in a nuclear reactor, where the domain is obviously finite [2]. The use of the same model for both problems is not surprising because neutrons in a reactor evolve in time by the same physical processes as the population in Fisher's equation, that is, by diffusion and nonlinear local multiplication.

In the second section, we review the fundamental results obtained by Fisher [1] and by Kolmogoroff, Petrovsky, and Piscounoff (KPP) [3].

The phase-plane analysis of the traveling waves defined by Eq. (1) is carried out in the third section. This analysis yields the result that the propagation speed of the waves is linearly proportional to their thickness.

We obtain analytically in the fourth section the traveling wave profiles in the physical plane. Although the accuracy of the solution increases asymptotically with the propagation speed, the solution is highly accurate for all the characteristic speeds because these have a minimum threshold value which is not zero. This notable result is verified by the excellent agreement between the analytic solution for the traveling wave of minimum speed and the numerical solution of Fisher [1]. We also show that Fisher's population fronts are identical to some of the steady state solutions of the Korteweg-de Vries-Burgers equation.

The stability analysis of the fifth section shows that all the traveling waves are unstable for the case of small perturbations that vanish at infinity. This is true because an infinitesimally small perturbation can transform one wave into another, a property characteristic of problems with a continuous spectrum of wave fronts. However, if we restrict the perturbations so that they vanish at a finite distance in the wave frame, we can then prove stability.

Fisher's equation in infinite domains

It is convenient to remove dimensions from Eq. (1) by expressing time and length in the dimensionless units $t = k\tau$ and $x = (k/\nu)^{1/2}y$, so that Eq. (1) acquires the simpler form

$$u_t = u_{xx} + u(1 - u). (2)$$

Fisher's equation can be thought of as describing the nonlinear evolution of a population in a one-dimensional habitat. The habitat can support only a certain maximum population per unit length which, for convenience, we choose as unity. The initial condition for Fisher's equation must thus be restricted as follows:

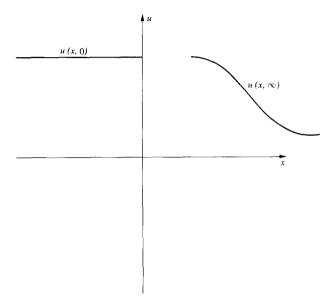


Figure 1 Qualitative plot of the profile of the minimum-speed traveling wave.

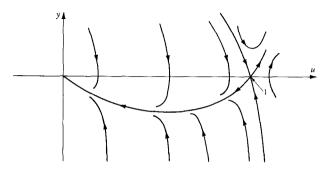


Figure 2 Qualitative plot of the trajectories of Eq.(9). The solution to the nonlinear eigenvalue problem defined by Eqs. (7) and (8) is given by the trajectory that intercepts the critical points. These are a saddle point at (u,y) = (1,0) and a stable node at (u,y) = (0,0).

$$0 \le u(x,0) \le 1, \qquad -\infty < x < \infty. \tag{3}$$

We shall be interested in the solutions of Eq. (2), subject to Eq. (3), such that all the x derivatives tend to zero as $x \to \pm \infty$ and that satisfy the conditions

$$\lim_{x \to -\infty} u(x,t) = 1, \qquad \lim_{x \to +\infty} u(x,t) = 0, \qquad t \ge 0. \tag{4}$$

The problem defined by Eqs. (2), (3), and (4) describes the advance of the population along a habitat that is saturated at the left and unoccupied at the right. In their basic paper, KPP [3] proved that, for each initial condition of the form (3), Eq. (2) has a unique solution that is bounded for all times as the initial distribution, i.e.,

$$0 \le \dot{u}(x,t) \le 1, \qquad -\infty < x < \infty, \qquad t > 0$$

Further, in a series of remarkable theorems, KPP showed that, for the following initial conditions satisfying Eqs. (4).

$$u(x,0) = \begin{cases} 1 & x < 0 \\ 0 & x > 0 \end{cases}$$
 (5a)

and

$$u(x,0) = \begin{cases} 1 & x < a \\ f(x) & a < x < b \\ 0 & x > b, \end{cases}$$
 (5b)

where f(x) is arbitrary, the solution becomes, in the limit $t \to \infty$, a shock-like traveling wave that satisfies Eq. (4) and propagates to the right with the *minimum* allowed characteristic speed $c_{\min} = 2$.

Both Fisher [1] and KPP [3] found that Eq. (2) has an infinite number of traveling wave solutions of characteristic speeds $c \ge 2$. Fisher also carried out a very accurate and detailed numerical computation of the shock-like profile of the traveling wave of minimum speed, which is indicated conceptually in Fig. 1.

Wave profiles in the phase plane

The phase-plane analysis given in this section shows that a traveling wave propagates with a speed linearly proportional to its thickness. We seek traveling wave solutions of Eq. (2) in the form

$$u(x,t) = u(x - ct) \equiv u(s), \tag{6}$$

where c is the speed of the wave or population front. Substitution of Eq. (6) into Eq. (2) gives an ordinary nonlinear differential equation for the shock-like wave profiles,

$$(d^{2}u/ds^{2}) + c(du/ds) + u - u^{2} = 0.$$
 (7)

The proper boundary conditions for Eq. (7) satisfying Eqs. (4) are

$$u(-\infty) = 1, \qquad u(+\infty) = 0. \tag{8}$$

Equations (7) and (8) define a nonlinear eigenvalue problem in an infinite domain, where the propagation speed c is the eigenvalue. The trajectories defined by Eq. (7) in the phase plane $[(u, du/ds) \equiv (u,y)]$ are given by

$$dy/du = [(u^2 - u) - cy]/y. (9)$$

The form of these trajectories, shown in Fig. 2, applies if and only if the origin is a stable node [4]. This condition requires that the propagation speeds of the traveling waves be given by the continuous spectrum

$$c \ge 2,\tag{10}$$

Table 1 Coordinates of the point of inflection of the wave profile of minimum speed.

		(u, du/ds) from Eq. (15)		Exact corresponding value from Ref. [1]
Value:	First order	Second order	Third order	
	(0.5,-0.125)	(0.437,-0.125)	(0.437,-0.123)	(0.442,-0.123)

which is the result reported by Fisher and KPP. Unless Eq. (10) is satisfied, the origin of the phase-plane would be a center or a focus [4], and this configuration would result in negative distributions u, which is a physical impossibility.

Figure 2 shows that only the trajectory going through the critical points gives the solution to the nonlinear eigenvalue problem defined by Eqs. (7) and (8). Therefore, for each eigenvalue c there is a unique corresponding wave profile. The profiles are obtained as follows. It is convenient to define a new variable $\bar{y} = cy$, in terms of which Eq. (9) becomes

$$\varepsilon(d\bar{y}/du) = (u^2 - u - \bar{y})/\bar{y},$$

$$\varepsilon = 1/c^2, \qquad \bar{y} = cy.$$
(11)

The solution of Eq. (11) is sought in the form of a series

$$\bar{y}(u,\varepsilon) = g_0(u) + \varepsilon g_1(u) + \varepsilon^2 g_2(u) + \cdots$$
 (12)

Substituting into Eq. (11) and grouping the like powers of ε , one obtains

$$O(1) g_0 = u^2 - u,$$

$$O(\varepsilon) g_1 = -g_0 g'_0,$$

$$O(\varepsilon^2) g_2 = -g_0 g'_1 - g'_0 g_1,$$

$$\vdots$$

where the prime indicates derivative with respect to u.

Equations (13) show that the series (12) is obtained merely by a substitution process, without the need for solving any differential equation at any order in ε . After transforming to the variable y, we explicitly get

$$y(u,\varepsilon) = \varepsilon^{1/2}(u^2 - u) - \varepsilon^{3/2}(2u^3 - 3u^2 + u) + 2\varepsilon^{5/2}(5u^4 - 10u^3 + 6u^2 - u) + O(\varepsilon^{7/2}).$$
 (14)

The result given by Eq. (14) has two notable properties. First, the limit as $\varepsilon \to 0$ is uniform, i.e., to any order in ε the series (14) gives approximations to the trajectory that intercepts both critical points [Fig. 2], as can be seen by inspection of Eq. (14). Second, the series (14) is asymptotically accurate in the limit of infinitely large propagation speeds $[\varepsilon \to 0, c \to \infty]$; see Eq. (11)]; how-

ever, because the minimum speed is sufficiently high so that the expansion parameter ε is always "small" (i.e., its maximum allowed value is 0.25) we expect that the accuracy of Eq. (14) will be good for *all* traveling waves defined by Eqs. (2), (3), and (4). It will be shown that this is indeed the case.

Equation (14) is now used to obtain the propagation speed of the waves. The coordinates of the minimum of the trajectory that intercepts the critical points are obtained by an elementary calculation using Eq. (14). The result is

$$(u,y) \equiv (u,du/ds) = [1/2 - \varepsilon/4, -(1 - \varepsilon^2/4)/4c],$$
 (15) which gives the coordinates of the inflection point of the wave profile in the physical plane, as indicated in Fig. 1 and Table 1. We define the steepness S of the profile as the magnitude of the slope of its point of inflection; Eq. (15), then, shows that, for all quantitative purposes,

$$S = 1/4c, \tag{16}$$

because the error in Eq. (16) is $O(\varepsilon^2)$. The maximum error, which occurs for the minimum-speed wave, is less than two percent, as is indicated by the data in Table 1. For the faster waves, this error decays as the fourth power of the speed [see Eqs. (15) and (11)]. Because the profile half-thickness L is inversely proportional to the steepness, Eq. (16) yields the fundamental result

$$c = L/4, (17)$$

i.e., the propagation speed of the wave is linearly proportional to its thickness. An interesting consequence of this result is that all the waves, regardless of their thicknesses, would take the same time to pass before a stationary observer.

Kendall's numerical solution (Figs. 5 and 6 of Ref. 5) of an equation similar to Fisher's showed the linear dependence between the propagation speed and the wave thickness. In a recent paper, Montroll [6] studied a nonlinear equation of evolution that is similar to Fisher's equation. Montroll solved the partial nonlinear differential equation exactly by transforming it into the linear heat equation, a technique similar to that used by Hopf [7] and Cole [8] for Burgers' equation. Montroll argued that the solution of his equation closely resembles that of Fisher's equation. Although there are some formal similarities between Fisher's and Montroll's equations,

the qualitative behavior of their solutions is in fact quite different. For the traveling waves corresponding to our initial conditions [Eqs. (3) and (4)], Montroll's equation admits arbitrarily steep profiles [Eq. (31) of Ref. 6], but, as shown by Eqs. (16) and (10), diffusion prevents the steepness of the profiles of Fisher's equation from exceeding the maximum value

$$S_{\text{max}} = 1/8$$
.

In dimensionless units, the wave speed for Montroll's equation [9] is given by

$$c = 4S + (1/4S) = (4/L) + (L/4),$$
 (18)

which shows a nonlinear dependence between the wave speed and its thickness. In Fisher's equation, on the other hand, the speed is linearly proportional to the thickness [see Eq. (17)].

Wave profiles in the physical plane

The wave profiles in the physical plane are now obtained using the results of the phase-plane analysis. When a new unit of length is defined by

$$z \equiv \frac{s}{c},\tag{19}$$

Eq. (7) becomes

$$\varepsilon(d^2u/dz^2) + du/dz + u - u^2 = 0,$$

$$u(-\infty) = 1$$
, $u(+\infty) = 0$, $\varepsilon = 1/c^2 \le 1/4$. (20)

Since there is a uniform limit as $\varepsilon \to 0$ for Eq. (20), a valid solution in all the domain is obtained simply by expanding

$$u(z;\mathbf{\varepsilon}) = u_0(z) + \mathbf{\varepsilon} u_1(z) + \cdots \tag{21}$$

Substituting Eq. (21) into Eq. (20) and grouping like powers of ε , one obtains

$$O(1) \quad u_0' + u_0 - u_0^2 = 0, \tag{22}$$

O(1)
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 (22)
O(ϵ) $u_1' + (1 - 2u_0)u_1 = -u_0''.$ (23)

The initial conditions for u_0 and u_1 are given by Eq. (15), with the origin of distance in the wave frame being the point of inflection of the wave [see also Eq. (21)]; i.e.,

$$u_0(0) = 1/2, u_1(0) = -1/4.$$
 (24)

Therefore, solving successively Eqs. (22) and (23), with their respective initial conditions given in Eq. (24), and transforming back to the variable s [Eq. (19)], we finally obtain the wave profiles:

$$u(s;\varepsilon) = \frac{1}{1 + \exp(s/c)} - \varepsilon \frac{\exp(s/c)}{[1 + \exp(s/c)]^2} \times \left[1 - \ln \frac{4 \exp(s/c)}{\{1 + \exp(s/c)\}^2}\right] + O(\varepsilon^2).$$
 (25)

It should be noticed that the profile half-thickness, defined as the reciprocal of the steepness S[Eqs.(16)]and (17)}, is L = 4c, which is four times the relaxation length or e-folding distance of the wave given by Eq. (25). Therefore, in the wave frame with the origin at the point of inflection, the main part of the wave extends over one full thickness from -L to +L. As discussed previously, the accuracy of the asymptotic expansion for the wave profiles is least for the minimum-speed wave. where $\varepsilon = 1/4$. For the faster waves, the accuracy of the result (25) increases as the fourth power of the propagation speed. A comparison of the profiles given by Eq. (25) for the minimum-speed wave with the numerical solutions obtained by Fisher [1] is shown in Table 2. The origin of distance used by Fisher in the wave frame was different from ours; the correspondence between his abscissas and ours is $s = s_F - 0.765$.

In Table 2 the wave profile is given as a function of distance in Fisher's coordinate system. The agreement between the second-order asymptotic solution and the numerical solution is uniformly good over the whole thickness of the wave. Therefore we could use the profiles (25) in conjunction with the KPP initial condition given by Eq. (5a) as a standard for comparison of numerical methods for solving time-dependent viscous flow problems [10]. It should be recalled that the accuracy of Eq. (25) is independent of the values of the diffusion coefficient ν and the multiplication factor k.

We conclude by pointing out an interesting result. The diffusive waves of Fisher's equation are identical to the steady state solutions of the Korteweg-de Vries-Burgers equation,

$$u_t + uu_x - \nu u_{rr} + \mu u_{rrr} = 0, \qquad \nu > 0, \quad \mu > 0, \quad (26)$$

which are obtained when the diffusive effects (determined by the magnitude of ν) dominate over the dispersive effects (determined by the magnitude of μ). The Korteweg-de Vries-Burgers equation has been used by Johnson [11] for the description of shallow water waves on a viscous fluid [11]. Numerical computations of the steady-state solutions have been done by Johnson. who also obtained an asymptotic solution for the case in which the dispersive effects dominate the dissipative effects [11,12], and by Grad and Hu [13] for a problem of weak plasma shocks propagating perpendicularly to a magnetic field. The steady state solutions of (26) are given [Eq.(35) of Ref. 11] by

$$H^{2} - H + H'' = \sigma H', \qquad \sigma > 0$$

$$H(-\infty) = 1, \qquad H(+\infty) = 0.$$
(27)

where the primes denote derivatives relative to the independent variable x, and the parameter σ is defined in terms of the diffusion and dispersion coefficients ν and μ [11,14]. With the new independent and dependent vari-

ables defined as s = -x and u = 1 - H, respectively, Eq. (27) becomes

$$u'' + \sigma u' + u - u^2 = 0,$$

$$u(-\infty) = 1, \qquad u(+\infty) = 0,$$
(28)

which is exactly our Eq. (7) if we reinterpret σ as the propagation speed of the Fisher-equation waves.

The Fisher and KPP condition $\sigma = c \ge 2$ [see Eq. (10)] leads to the shock profiles of Johnson, which are monotonic both upstream and downstream. For $\sigma < 2$, the second class of steady state solutions of (26) is obtained, i.e., shocks that are oscillatory and damped upstream, and monotonic downstream [11].

Stability

The question of the stability of the traveling waves has not been resolved in the literature [1,3,5,6]. We now show that all the waves are unstable against small perturbations that vanish at infinity. When we restrict the perturbations so that they vanish at a finite distance, then, we prove stability. By using this stability analysis, in conjunction with a monotonicity result of KPP[3], we prove that the superspeed waves do not evolve necessarily into the minimum speed wave, when subject to arbitrary perturbations.

We define a coordinate system moving in the positive x-direction with a speed c, i.e., s = x - ct; Eq. (2) then becomes

$$u_t = u_{ss} + cu_s + u(1 - u).$$
 (29)

We now use the standard stability formalism discussed by Jeffrey and Kakutani [14] for Burgers' equation, and by Cohen for boundary value problems in finite domains [15]. We superimpose a small disturbance v(s,t) on the traveling wave u(s;c), i.e.,

$$u(s,t) = u(s,c) + \varepsilon v(s,t). \tag{30}$$

Substituting (30) into (29) and keeping only terms of the first order in ϵ , we obtain the time-dependent equation for the perturbation

$$v_t = v_{ss} + cv_s + [1 - 2u(s;c)]v. (31)$$

We say that the wave u(s;c) is stable if all solutions of (31) decay in time as follows:

$$\lim_{t \to \infty} v(s,t) = 0, \qquad \text{or } \lim_{t \to \infty} v(s,t) = u_s(s;c). \tag{32}$$

The first limit has an obvious meaning. The second would result in an infinitesimally small translation of the wave along the axis because

$$u(s - \delta s; c) = u(s; c) - u_s \delta s.$$

It is shown below that $u_s(s;c)$ is a stationary solution of (31), as required.

If we now look for solutions of (31) in the form

Table 2 Profile of the wave of minimum speed: asymptotic and numerical solutions.*

	Asymptotic solution, Eq. (25)		Fisher's numerical solution. Table IV
s_{F}	First order	Second order	of Ref. 1
-10.3480	1.0	0.99	0.99
-5.9205	0.96	0.94	0.94
-3.3525	0.89	0.84	0.84
-1.9572	0.79	0.74	0.74
-0.9191	0.70	0.64	0.64
-0.0360	0.60	0.54	0.54
0.765	0.50	0.44	0.44
1.5224	0.41	0.34	0.35
2.4101	0.30	0.24	0.25
3.5053	0.20	0.14	0.15
5.3693	0.09	0.05	0.05
7.6061	0.03	0.01	0.01

^{*}Fisher used the parameter values $\nu=k=1$, and c=2 for the minimum-speed profile.

$$v(s,t) = f(s) \exp(-\lambda t), \tag{33}$$

we find that λ and f are given by the following eigenvalue problem, which is not self-adjoint:

$$f'' + cf' + (\lambda + 1 - 2u)f = 0$$
 $f \to 0 \text{ as } s \to \pm \infty.$ (34)

Just as for the case of the Burgers and Korteweg-de Vries equations [14], the fundamental eigenvalue and eigenfunction of (34) are

$$\lambda = 0, \qquad f(s) = u_s(s;c), \tag{35}$$

as can be seen by substituting (35) into (34). This gives the s-derivative of Eq. (7). The result (35) is characteristic of all traveling wave problems and has the physically obvious meaning that a traveling wave is invariant under translation along the axis. It is also known that all other eigenvalues of (34) satisfy $Re(\lambda) > 0$, which is sufficient to prove stability in problems such as Burgers' equation, where there is a unique traveling wave solution [14,16]. However, we now show that, because of the existence of a continuous spectrum of traveling waves, not all solutions of (31) are of the form (33).

Consider an infinitesimally small perturbation that changes the wave having velocity c into a neighboring one of speed $c + \delta c$; in this case, the initial condition for Eq. (31) is

$$v(s,0) = u(s;c + \delta c) - u(s;c).$$
 (36)

One should keep in mind that Eq. (31) is expressed in a coordinate system moving with a speed c; in this frame, the wave $c + \delta c$ moves with speed δc and the wave having velocity c is stationary. Therefore, the solution of (31) with the initial condition (36) is

$$v(s,t) = u(s - \delta ct; c + \delta c) - u(s;c)$$

$$= u(s;c + \delta c) - u_s(s;c + \delta c)\delta ct - u(s;c)$$

$$= u(s;c) + u_c(s;c)\delta c - u_s(s;c + \delta c)\delta ct - u(s;c)$$

$$= \delta c(u_c - tu_s).$$
(37)

That (37) is an exact solution of (31) can be verified by direct substitution. The result (37) has the following physical meaning. Relative to an observer riding the wave of velocity c, the faster wave will start moving away to a distance which is linearly proportional to the time elapsed since the instant of the perturbation. In the precise sense of this discussion, we can say that all traveling waves of Fisher's equation are unstable.

If the perturbations are restricted so that they vanish at a finite distance in the wave frame, this precludes the transformation of one wave into another and stability results. This can be shown by a study of the eigenvalue equation (34) with the boundary conditions $f(\pm L) = 0$. In this case, the problem is made self-adjoint by the transformation $f(s) = \exp(-cs/2) \ y(s)$, so that it becomes

$$y'' + [\lambda - q(s)]y = 0,$$

 $y(\pm L) = 0,$
 $q(s) \equiv c^2/4 - (1 - 2u) \ge 2u(s;c) > 0,$ (38)

because $c \ge 2$. Since the traveling waves u(s;c) are everywhere positive, q(s) is larger than 0 also; it is then known that all eigenvalues of (38) are real and positive, which means that all finite extent perturbations of the wave decay exponentially in time.

The precise time evolution of different initial conditions and the main stability results obtained here will be studied further in a forthcoming paper, where Fisher's equation is solved numerically.

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Note added in proof

We demonstrate that the superspeed waves (c > 2) do not necessarily evolve into the minimum speed wave when subject to arbitrary perturbations of infinite extent. To prove this, we consider an initial condition [see Eq. (30)]:

$$u(s,0) = u(s;c) + \varepsilon v(s,0), \tag{39}$$

where the perturbation satisfies

$$v(s,0) > 0. \tag{40}$$

KPP obtained a monotonicity result (Theorem 3 of [3]) which shows that, in a fixed laboratory frame, the distribution resulting from the initial condition (39) and (40) satisfies

$$u(x,t) > u(x;c,t). \tag{41}$$

The result (41) has an obvious physical meaning in the context of heat conduction, namely, the temperature distribution in a rod resulting from an instantaneous temperature increase superimposed on the traveling heat wave u(x;c,t) must be everywhere higher than the temperature given by the unperturbed heat wave [17]. Let us now assume that the initial condition (39) and (40) evolves into a wave. We now show that this wave cannot have a speed smaller than c; if it had a speed smaller than c then, after a sufficiently long time, the distribution resulting from the slower wave would satisfy

$$u(x;c-\delta c,t) < u(x;c,t), \tag{42}$$

which is in contradiction with the monotonicity result of KPP [Eq. (41)]. Therefore, a necessary condition for the slowing down of the waves is that the perturbations satisfy v(s,0) < 0. When the perturbations are of the class (40) but of finite extent, we have proved [see Eq. (38)] that the initial condition (39) reverts again into the wave u(s;c) in the wave frame. However, in order to satisfy the KPP condition (41), the initial condition must asymptotically evolve into a wave u(s;c) which, in the laboratory frame, is translated to the right with respect to the original wave. If the finite-extent perturbation were negative, the original wave would be instead translated to the left.

In conclusion, even if we assume that all initial conditions of Fisher's equation evolve into traveling waves, the stability analysis shows that the minimum speed wave is *not* the unique time-asymptotic steady state.

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- 16. That is, unique for fixed upstream $(x \to -\infty)$ and downstream $(x \to +\infty)$ values of the distribution.
- 17. We note here that s is the distance in the wave frame, x is the distance in a fixed laboratory frame, u(x,t) is any solution of the partial differential equation (3), and u(x;c,t) is a traveling wave solution with velocity c.

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