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BIOLOGICAL INVASIONS WITH FLUX-LIMITED DISPERSAL

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Abstract

We study traveling wave fronts in a population model that includes growth, advection, settlement, and dispersion. Unlike the classical Fickian model, the diffusive flux is assumed to be a nonlinear function of the gradient, and it remains bounded for all values of the gradient. When there is dispersion, settlement, and no growth, the model gives rise to both smooth wave fronts and shock-like fronts, depending upon the parameter values. When the model includes logistics growth, smooth wave front solutions exist. The model provides another theoretical framework in which to study the dispersal patterns of invading organisms.

Keywords: biological invasions, dispersal, settlement, traveling waves.
AMS Subject Classifications. 35K57, 92D25

1 Introduction

Traveling waves, i.e., signals of fixed shape that propagate at constant speed through a medium, model a variety of phenomena observed in biology, chemistry, geology, and in other physical sciences, and they have been studied extensively in the literature (see Britton 1986; Logan 1994; Volpert and Volpert 1994; Grindrod 1996; Shigesada and Kawasaki 1997; Kot 2001; Okobu and Levin, 2001; Murray 2002a, 2002b). In ecology, traveling waves often arise as solutions to nonlinear partial differential equations that model coupled reaction-diffusion-advection (growth-dispersion-advection) processes, and such solutions can elucidate the complex interactions among these various processes. For example, moving populations can disperse through diffusion, while subject to a growth law; traveling wave solutions are special solutions where growth and advective effects balance the dispersal effects. Such models have been the basis of study of the spread of animal populations, the spread of epidemics, the dispersal of genes throughout a population, seed dispersal, and other biological invasions. One prototype for such models is the well-known Fisher equation with advection and logistics growth,

$$u_t = Du_{xx} - vu_x + ru(1 - u/K),$$

where $u = u(x,t)$ is a population density, D is the diffusion constant, and v is the advection speed. The constants r and K are the growth rate and carrying capacity, respectively. Here, and in the sequel, we use subscripts for partial derivatives, i.e., $u_t = \partial u/\partial t$ and $u_{xx} = \partial^2 u/\partial x^2$. This model produces solutions that are smooth waves traveling with constant velocity and shape. Without the diffusion term, the traveling wave fronts can be discontinuous, exhibiting shock-like structure (Lika and Hallam 1999). Many other models have also been developed with density-dependent diffusion, e.g., $D = D(u)$ (e.g., see Murray 2002a, 2002b). These models have been used to study insect dispersion (but their suitability in this regard is "immature and awaits future investigation" (Okubo and Levin, 2001)).

Many of these traditional reaction-diffusion models having traveling wave solutions can underestimate the actual rate of invasion or actual speed of the wave front. Therefore other dispersion models have been proposed to improve upon the predictions. A particularly successful model is an integro-difference equation of the form

$$u_{n+1}(x) = \int_{-\infty}^{\infty} k(x,y)g(u_n(y))dy,$$

where the population density $u_n(x)$ at a discrete time n evolves into the density $u_{n+1}(x)$ in two stages. During the sedentary stage the local populations produce $g(u_n(x))$ progeny, and in stage two the progeny disperse with redistribution kernel $k(x,y)$, which is the probability of relocating from position x to position y. This model has been developed with respect to ecological applications by Kot *et al* (1996) and has been extended to problems with fluctuating environments (Neubert 2000) and age or stage structure (Neubert & Caswell 2000).

In this note we investigate the existence of traveling waves in an alternate model where the dispersive flux is limited. We abandon the usual assumption of Fickian diffusion, based on random motion, where the diffusive flux H is linear in the gradient and given by

$$H = -Du_x, \tag{1}$$

and we postulate a bounded flux of the form

$$H = -DF(u_x), \tag{2}$$

where $F = F(w)$, $w \in R$, is a given smooth, nonlinear, monotone function with the property that it remains bounded at $\pm\infty$. Specifically, we assume

$$|F(w)| \le M, \quad F(0) = 0, \quad F'(0) = 1, \tag{3}$$

$$F'(w) > 0, \quad F'(w) \to 0 \quad \text{as } w \to \pm\infty. \tag{4}$$

Figure 1 shows a generic form for F. Examples of such functions are

$$F(w) = \arctan w, \quad F(w) = \tanh w, \quad F(w) = \frac{w}{\sqrt{1+w^2}}.$$

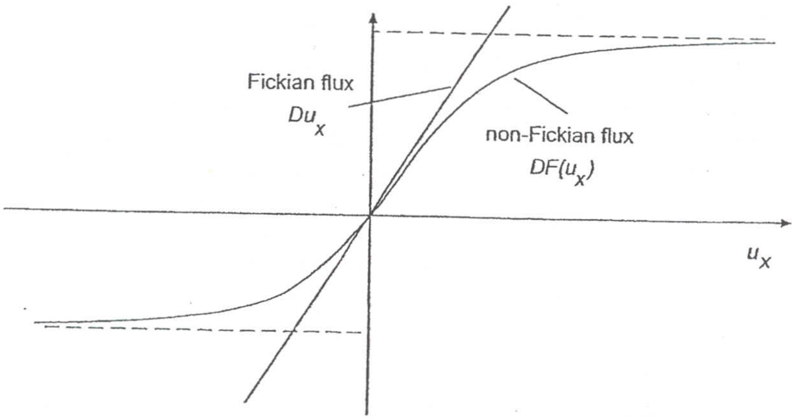

Figure 1: Schematic comparing a nonlinear, non-Fickian flux function $DF(u_x)$ and a Fickian flux function Du_x.

One motivation for this model can be described as follows. Fickian flux (1) is proportional to the gradient u_x and becomes arbitrarily large when steep fronts are present. In some dispersal problems this unbounded response to large gradients seems nonphysical. A flux of the form (2) will remain at a finite value even when the gradients become large, and this response could better describe some biological systems. At first it would appear that such an assumption would prevent steep gradients from forming, but in fact the opposite is true. This assumption can lead to both continuous and discontinuous (shocks) wave fronts, depending upon the value of a scaled dispersion constant, which acts as a bifurcation parameter in the system. Alternately, if we expand F in (2) in a Taylor series about zero, we obtain

$$\begin{aligned} H &= -D\left(F(0) + F'(0)u_x + \frac{1}{2}F''(0)u_x^2 + \cdots\right) \\ &= -Du_x + \cdots, \end{aligned}$$

which shows that the Fickian flux is just the first approximation of the general nonlinear flux (2). Thus, looked at in this manner, one might expect Fickian flux to more accurately model systems with small gradients. Okubo and Levin (2001) note that the Fickian model may not apply to turbulent diffusion. The flux (2) is not based on a random model like diffusion, and thus we will often refer to it as a dispersive model.

The idea of studying bounded fluxes in diffusion processes with nonlinear advection (Burgers-type equations) was introduced in Kurganov *et al* 1997,1998). A simple hydrogeological model involving solute transport in porous media is examined in Homp and Logan (1999)(also see Logan, 2001). Generally, these models present analytic difficulties because they lead to implicit differential equations for the wave fronts.

2 Limited Flux Models

In this section we set up a general one-dimensional model of population dynamics that includes advection (e.g., driven by wind or water motion) , limited flux, growth, and settlement. Let $u = u(x,t)$ denote the local population density of some mobile organism or propagule, measured in numbers per unit volume, and let $s = s(x,t)$ be the local density of the settled (non-mobile) organisms. Let $\phi = \phi(x,t)$ be the net flux of the advecting organisms (in organisms per unit area per time), and let $g = g(u)$ denote their growth rate, measured in organisms per volume per unit time. Then, in an arbitrary section $a \leq x \leq b$ of the domain, we have the usual balance law for the moving organisms in integral form:

$$\frac{d}{dt}\int_a^b u dx = \phi(a,t) - \phi(b,t) + \int_a^b g(u) dx - \frac{d}{dt}\int_a^b s dx. \tag{5}$$

This conservation law states that the rate of change of the number of advecting organisms in the arbitrary section equals the rate they flow in, minus the rate they flow out, plus the rate of growth, minus the rate of settlement. If the functions involved are sufficiently smooth, then the integral conservation law can be reformulated in the standard way (see, for example, Logan 1994) as a local law, the partial differential equation

$$u_t = -\phi_x + g(u) - s_t.$$

We take the net flux ϕ to be the sum of the bounded dispersive flux H given in (2) plus the migratory flux vu, where v is the advection speed. Thus

$$\phi = -DF(u_x) + vu.$$

Therefore,

$$u_t = DF(u_x)_x - vu_x + g(u) - s_t. \tag{6}$$

Note that the integral form (5) holds in all cases, even if u and s are discontinuous.

We next assume that the density of the settled organisms is algebraically related to the population density via

$$s = f(u), \tag{7}$$

where f is a given, positive function defined on $u \geq 0$. Thus, there is instant equilibrium between s and u. Generally, f satisfies the properties

$$f(0) = 0, \quad f'(u) \geq 0, \quad f''(u) \leq 0. \tag{8}$$

A typical example is a Holling type 2 (also hyperbolic or Michaelis-Menten) response, i.e.,

$$s = f(u) = \frac{k_1 u}{k_2 u + 1}.$$

For example, organisms advecting with the water in porous media often become attached to the porous fabric; there is often an equilibrium described by (2) (e.g., Langmuir or Freundlich models) between the migrating organisms and those attached (Logan 2001); nonequilibrium or dynamcial models have also been investigated where the rate of settlement is $s_t = G(u, s)$. In an ecological model, Neubert *et al* (1995) use a dynamic settlement equation of the form $s_t = h(t)u$ to model the dispersal of volant propagules; different choices of $h(t)$ generate different redistribution kernels.

Next, we assume the mobile organisms grow logistically, while settled organisms cease to grow. In general, therefore, the governing equation for the population density is

$$(u + f(u))_t = DF(u_x)_x - vu_x + r_0 u(1 - u/K). \tag{9}$$

We can always eliminate the advection speed v by scaling time by L/v, where L is any length scale. Also, the densities u and s can be scaled by the carrying capacity K, and the equation can be written in dimensionless form as

$$(u + f(u))_t = aF(u_x)_x - u_x + ru(1 - u), \tag{10}$$

where a and r are dimensionless constants.

We are interested in the problem of finding traveling wave solutions (wavefront solutions) to (10) that approach constant states at plus and minus infinity. One can see the difficulty in (10) when dimensionless dispersion constant a is small; if the gradients are steep, then the dispersion term may not be able to compensate in order to maintain a smooth wave front with respect to the advection, growth, and settlement terms. In the sequel we develop the analysis in special cases.

In summary, we look for solutions of the form

$$u = u(z), \quad x = x - ct, \tag{11}$$

where c is the unknown wave front speed and $u(z)$ is the density wave form. It should cause no confusion to use the same symbol u for the wave form as for the density $u(x, t)$. We impose boundary conditions

$$u(-\infty) = u_0, \quad u(+\infty) = 0. \tag{12}$$

Thus, we seek traveling waves moving from a constant, given, positive density u_0 into the zero density state ($u_0 = 1$ for the logistics growth law, which corresponds to the carrying capacity). Substitution of (11) into (10) gives and ordinary differential equation for the density $u(z)$, namely

$$-c(u + f(u))' = aF(u')' - u' + ru(1 - u). \tag{13}$$

As a notational comment, in the sequel we use primes for derivatives. It will be clear from the context if the prime is a derivative with respect to z or a derivative with respect to u.

3 A Settlement Model Without Growth

3.1 Smooth wave fronts

We first examine an advection-dispersal-settlement model with no growth. The underlying ecological motivation is to present an alternate theoretical framework for problems involving wind-blown propagules, or any advecting organism whose growth in numbers or biomass can be ignored.

When the model has no growth, the wave front equation (13) for assumed smooth solutions becomes

$$-c(u+f(u))' = aF(u')' - u'.$$

This equation can be integrated immediately to obtain

$$-c(u+f(u)) = aF(u') - u,$$

where we have set the constant of integration equal to zero to satisfy the boundary condition at $z = +\infty$. Therefore we obtain the implicit differential equation

$$F(u') = a^{-1}(u - cu - cf(u)). \tag{14}$$

Note that if a is small, then the right hand side is large and possibly out of the range of F, which is bounded. If a smooth solution exists, then we can compute the wave speed by letting $z \to -\infty$ in (14) to obtain

$$c = \frac{u_0}{u_0 + f(u_0)}. \tag{15}$$

Therefore there is a relation between the signal speed c and the original state u_0, and $0 < c < 1$. We regard u_0 as being given.

To simplify the notation we define

$$G(u,a) = a^{-1}(u - cu - cf(u)),$$

where c is given by (15). Equation (14) is simply

$$F(u') = G(u,a). \tag{16}$$

We have $G(0,a) = G(u_0,a) = 0$, $G'(u,a) = a^{-1}(1 - c - cf'(u))$, and $G''(u,a) = -cf''(u) > 0$. Therefore, for any $a > 0$, the graph of G is strictly concave up on the interval $0 \leq u \leq u_0$. Its minimum occurs at the value $u = u_*$ for which $f'(u_*) = (1-c)/c$.

We consider the case that $G(u,a)$ is in the range of F, that is

$$G(u_*,a) \equiv \min_{0 \leq u \leq u_0} G(u,a) > \inf_{-\infty < w < \infty} F(w) \equiv -F_0. \tag{17}$$

See figure 2. Then we can put (16) in normal form as

$$u' = F^{-1}(G(u,a)). \tag{18}$$

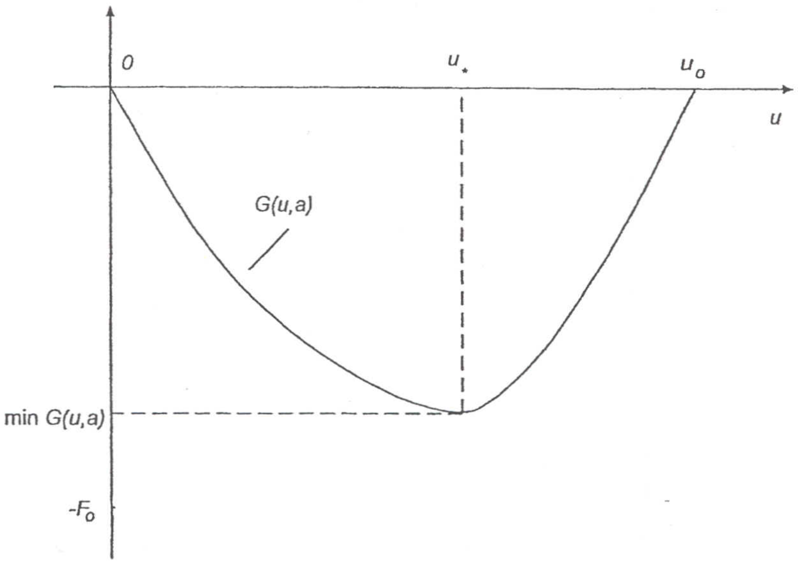

Figure 2: Graph of the function $G(u, a)$, the right side of the implicit equation (16), in the case that smooth wave fronts exist.

and the right side is continuous. Both end states $u = 0$ and $u = u_0$ are equilibrium solutions. We can check stability by examining the u-derivative of the right side of (18), evaluated at the end states. By the chain rule we have

$$\frac{\partial}{\partial u}F^{-1}(G(u,a)) = \frac{dF^{-1}}{dw}(G(u,a))G'(u,a).$$

The first factor is positive since F, and hence F^{-1}, is increasing, so the sign of the right side depends on the sign of $G'(u,a)$. Clearly $G'(0,a) < 0$ and $G'(u_0,a) > 0$, and therefore $u = 0$ is stable and $u = u_0$ is unstable. Consequently, when (17) holds, there is a unique, monotone decreasing, solution $u = u(z)$ to (18) that satisfies the boundary conditions (12). Of course, the uniqueness is up to a shift in z since the problem is autonomous. We observe that the validity of condition (17) depends on the value of the diffusion constant a. As a gets smaller, the minimum of $G(u,a)$ decreases because the value of u_* is independent of a. Therefore there is a critical value of a above which a smooth traveling wave exists. If $a = a_c$, then the wave front is smooth but has an infinite slope at a point. In summary, we have the following theorem.

Theorem 1 *Consider the advection-dispersion-settlement model*

$$(u + f(u))_t = aF(u_x)x - u_x, \tag{19}$$

where F satisfies conditions (3)-(4) and f satisfies (8). If

$$a > a_c,$$

where a_c is the value for which $\min G(u,a_c) = \inf F(w) = -F_0$, then there exists a unique smooth, monotone decreasing traveling wave solution $u = u(z)$,

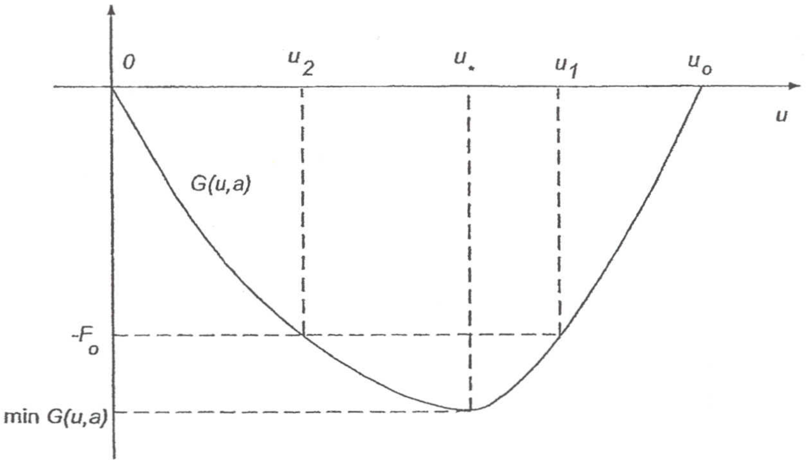

Figure 3: Graph of the function $G(u, a)$, the right side of the implicit equation (16), in the case of discontinuous wave fronts; its minimum lies below the minimum possible flux.

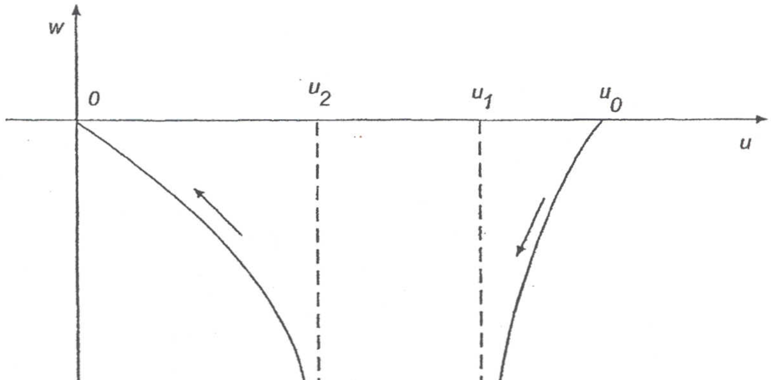

Figure 4: The uw phase plane ($w = u'$) for the case of nonsmooth solutions. The two branches are joined at $w = -\infty$ by a jump of magnitude $u_1 - u_2$.

$z = x - ct$ of (19), satisfying the boundary conditions (12) for any u_0. The wave speed is given by (15). If $a = a_c$ the the traveling wave has an infinite slope at a single point, but is otherwise smooth.

We consider a simple example with hyperbolic uptake and an arctangent flux. Let $f(u) = \frac{u}{u+1}$ and $F(w) = \arctan w$ so that (10) is

$$(u + \frac{u}{u+1})_t = a(\arctan u_x)_x - u_x.$$

Then $-F_0 = \inf F(w) = -\pi/2$ and $G(u,a) = a^{-1}(u - cu - \frac{cu}{1+u})$. Then the minimum of G occurs at $u_* = -1 + \sqrt{\frac{c}{1-c}}$, where the wave speed c is given by

$$c = \frac{1+u_0}{2+u_0}.$$

The critical value a_c satisfies $G(u_*, a_c) = -\pi/2$, or

$$a_c = -\frac{2}{\pi}(u_* - cu_* - \frac{cu_*}{1+u_*}).$$

For $a > a_c$ there will be a unique traveling wave solution to (19). Specifically, if $u_0 = 1$ then $c = \frac{2}{3}$ and $u_* = \sqrt{2} - 1 \simeq 0.414$. Then $a_c \simeq 0.036$.

A similar analysis can be carried out if the the model contains nonlinear advection terms, e.g.,

$$(u + f(u))_t = aF(u_x)_x - (\frac{1}{2}u^2)_x.$$

3.2 Discontinuous wave fronts

If $a < a_c$ then the range of G lies outside the domain of F and the minimum of G is below the value $F_0 = \inf F(w)$. A schematic of this situation is shown in figure 3. In this case the implicit differential equation (14) cannot be put in normal form. Because of the strict concavity of G, the horizontal line $y = -F_0$ intersects $G(u,a)$ in exactly two points whose u-values are $u = u_1$, and $u = u_2$, with $0 < u_2 < u_* < u_1 < u_0$. Observe that u_1 and u_2 depend upon the value of a. If we plot the locus $F(w) = G(u,a)$ in a uw-phase plane (here $w = u'$) we obtain a typical graph shown in figure 4; the function $w = F^{-1}(G(u,a))$, which is the derivative of u, is defined only in the intervals $0 \leq u < u_2$ and $u_1 < u \leq u_0$. We also have the loci asymptotic to the vertical lines $u = u_2$ and $u = u_1$. Therefore there is no smooth connection between the end states $u = 0, w = 0$, and $u = u_0, w = 0$. This opens the possibility of connecting the two branches at $w = -\infty$ with a jump condition in u of magnitude $u_1 - u_2$ and obtaining a discontinuous traveling wave solution, or shock shock solution. The diagram is shown in figure 5 where, without loss of generality, we have placed the discontinuity at $z = 0$. To show that this is a consistent picture, we must show that the speed $\widehat{c}$ that shock progresses, as determined by the

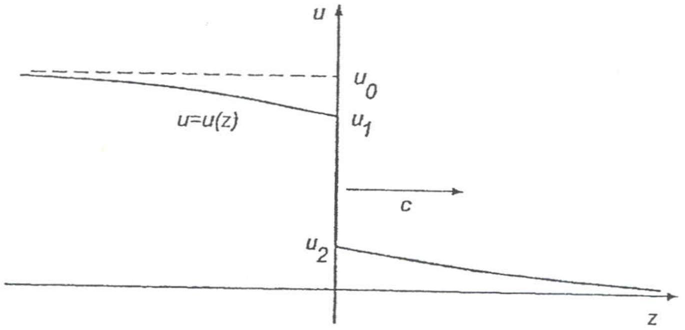

Figure 5: A discontinuous wave front solution propagating at speed c with jump $u_1 - u_2$, where u_1 and u_2 are the roots of $G(u,a) = -F_0$.

Rankine-Hugoniot jump condition from the differential equation, coincides with the wave speed c already determined from the traveling wave analysis. The jump condition associated with the partial differential equation (10) is (e.g., see Logan 1994)

$$-\widehat{c}[u + f(u)] = [aF(u_x)] - [u],$$

where the square bracket denotes the jump across the front, that is, the value just behind the front minus the value just ahead of the front. Therefore we have

$$-\widehat{c}(u_1 + f(u_1) - u_2 - f(u_2)) = [aF(u_x)] - (u_1 - u_2),$$

because $[aF(u_x)] = 0$. Therefore

$$\widehat{c} = \frac{u_1 - u_2}{u_1 + f(u_1) - u_2 - f(u_2)}.$$

But we also have $G(u_1, a) = G(u_2, a)$, which, when written out, gives c equal to the same expression as above. Therefore $c = \widehat{c}$, and it is consistent to insert a shock of magnitude $u_1 - u_2$ as illustrated in figure 5. Other than at the front, the solution is smooth. We have demonstrated the following theorem.

Theorem 2 *Consider the advection-dispersion-settlement model*

$$(u + f(u))_t = aF(u_x)x - u_x, \tag{20}$$

where F satisfies conditions (3)-(4) and f satisfies (8). If

$$0 < a < a_c,$$

where a_c *is the value for which* $\min G(u_*, a_c) = \inf F(w) = -F_0$, *then there exists a discontinuous traveling wave solution* $u = u(z)$, $z = x - ct$ *of (20), satisfying the boundary conditions (12) for any* u_0. *The wave speed is given by (15) and the magnitude of the jump is* $u_1 - u_2$, *where* u_1 *and* u_2 *are the two solutions to* $G(u, a) = -F_0$.

In summary, under the stated assumptions, for problems with limited flux there are both continuous and discontinuous wave fronts, depending upon the value of the scaled dispersion constant a. For larger a, above the critical value, there is enough dispersion in the problem to smooth out wave fronts; for small values of a, below the critical value, there is not enough dispersion and the nonlinearity in the settlement term dominates and smooth wave fronts are excluded. We can view this problem as a bifurcation. There are three parameters in the problem, a, c, and u_0. The latter two are connected. Therefore, given c or u_0, we can determine the critical value of the parameter a for which smooth wave fronts exist. A different view that one could take is to regard a as a fixed parameter and determine possible wave speeds c, or end states u_0, for which smooth wave fronts exist. It is well known that problems of these types with a Fickian flux do not permit discontinuous fronts.

Finally, we note that the limited flux model predicts the same wave front speed as the Fickian flux model; it is the pattern of dispersion that is affected.

4 A Growth Model with Settlement

We now examine a problem when the propagules are subject to logistics growth, but after settlement, there is no growth. As we shall observe, the existence of two equilibrium populations (zero and one) will have a smoothing effect on the wave fronts. When growth is present we have the traveling wave differential equation given as (see (13))

$$-c(u + f(u))' = aF(u')' - u' + ru(1-u)$$

or

$$F(u')' = a^{-1}((1 - c - cf'(u))u' - ru(1-u)).$$

The boundary conditions are

$$u(-\infty) = 1, \quad u(+\infty) = 0. \tag{21}$$

A traveling wave will correspond to a wave front with constant velocity moving from a region of saturated population $u = 1$, corresponding to the carrying capacity, into a region with zero population. With the presence of the growth term we cannot integrate the last equation directly, as in the previous case. Therefore we analyze the problem in a uw phase plane where $w = u'$. Thus we obtain the implicit dynamical system

$$\begin{aligned} u' &= w \\ F(w)' &= a^{-1}\left((1 - c - cf'(u))w - ru(1-u)\right). \end{aligned}$$

We apply the chain rule to obtain $F(w)' = F'(w)w'$. Consequently, the system becomes

$$\begin{aligned} u' &= w \\ w' &= \tfrac{1}{aF'(w)}\left((1-c-cf'(u))w - ru(1-u)\right). \end{aligned} \tag{22}$$

Observe that the assumptions on F imply $F'(w) > 0$.

The two critical points are $(0,0)$ and $(1,0)$. Existence of a traveling wave solution is equivalent to existence of a heteroclinic orbit connecting the two critical points, $(1,0)$ at $z = -\infty$, to $(0,0)$ at $z = +\infty$. The vertical nullcline is the curve $w = 0$ and the horizontal nullcline is

$$(1-c-cf'(u))w = ru(1-u).$$

Note also that $u' > 0$ in the upper half plane ($w > 0$), and $u' < 0$ in the lower half plane ($w < 0$). Thus, if there is a connecting orbit from $(1,0)$ to $(0,0)$, then it must lie entirely in the lower half plane.

To determine the nature and stability of the critical points we compute the linearization (defined by the Jacobian matrix) at each of the critical points. For convenience, we define

$$s = 1-c-cf'(0),\ t = 1-c-cf'(1).$$

It is straightforward to determine that the Jacobian matrices are

$$J(0,0) = \begin{bmatrix} 0 & 1 \\ -\frac{r}{a} & \frac{s}{a} \end{bmatrix} \text{ and } J(1,0) = \begin{bmatrix} 0 & 1 \\ \frac{r}{a} & \frac{t}{a} \end{bmatrix}.$$

The eigenvalues, eigenvectors of $J(0,0)$ are

$$\lambda_{\pm} = \frac{s \pm \sqrt{s^2-4ar}}{2a},\ \mathbf{u}_{\pm} = \begin{bmatrix} 1 \\ \frac{s\pm\sqrt{s^2-4ar}}{2a} \end{bmatrix}. \tag{23}$$

and the eigenvalues, eigenvectors of $J(1,0)$ are

$$\mu_{\pm} = \frac{t \pm \sqrt{t^2+4ar}}{2a},\ \mathbf{v}_{\pm} = \begin{bmatrix} 1 \\ \frac{t\pm\sqrt{t^2+4ar}}{2a} \end{bmatrix}. \tag{24}$$

It is clear that the eigenvalues $\mu_{\pm}$ at $(1,0)$ are always real and of opposite sign, so that $(1,0)$ is a saddle point. In order to have a stable node at the origin (a spiral is rejected because it will lead to negative values of the density u) we must have $s < 0$ and $s^2 \geq 4ar$. Both of these conditions are satisfied provided that

$$s = 1-c-cf'(0) \leq -2\sqrt{ar}. \tag{25}$$

Equation (25) gives a lower bound for the possible wave speeds, namely

$$c \geq \frac{1+2\sqrt{ar}}{1+f'(0)}. \tag{26}$$

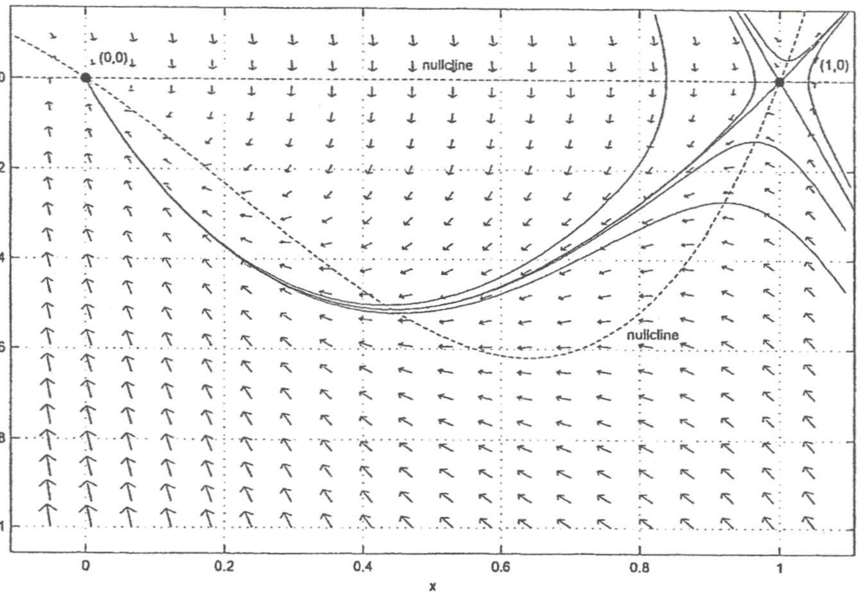

Figure 6: The uw phase plane in the case $h(1) < 0$.

This is the same lower bound that one would obtain if the diffusive flux were Fickian. What changes in the limited flux model is the dispersal pattern. The difference is the factor $1/F'(w)$ in (22). For larger gradients this factor causes w' to increase in the limited flux model, giving rise to steeper fronts for a given wave speed.

The eigenvector $\mathbf{v}_+$ at $(1,0)$ gives the local direction of the two unstable manifolds leaving $(1,0)$ and has positive slope, and the eigenvector $\mathbf{v}_-$ gives the local direction of the two stable manifolds at $(1,0)$ and has negative slope. The two eigenvectors $\mathbf{u}_\pm$ corresponding to the two negative eigenvalues $\lambda_\pm$ at $(0,0)$ define the local directions of the two stable manifolds entering $(0,0)$. Both eigenvectors lie in the third quadrant ($u > 0$, $w < 0$), and one can check that their slopes are greater (negatively) than the slope of the nullcline at $(0,0)$.

There are basically two special cases to consider, depending upon the sign of the function

$$h(u) = 1 - c - cf'(u).$$

Note that $h(0) < 0$ and $h''(u) = -cf''(u) > 0$, which implies that h is increasing; also $h(0) = s$, $h(1) = t$, and $s < t$. When h has a zero in the interval $0 < u < 1$, the horizontal nullcline has a vertical asymptote at that value. If there is no zero, then the nullcline is continuous and lies entirely in the lower plane, connecting the two critical points.

The actual existence proof for traveling waves in both cases follows exactly the same idea as is commonly given in the case of the Fisher equation, namely to show the existence of a heteroclinic orbit connecting $(1,0)$ to $(0,0)$. This is done by constructing a basin of attraction for the critical point $(0,0)$ (see Kot, 2001, for a highly readable presentation).

We summarize the result in a theorem.

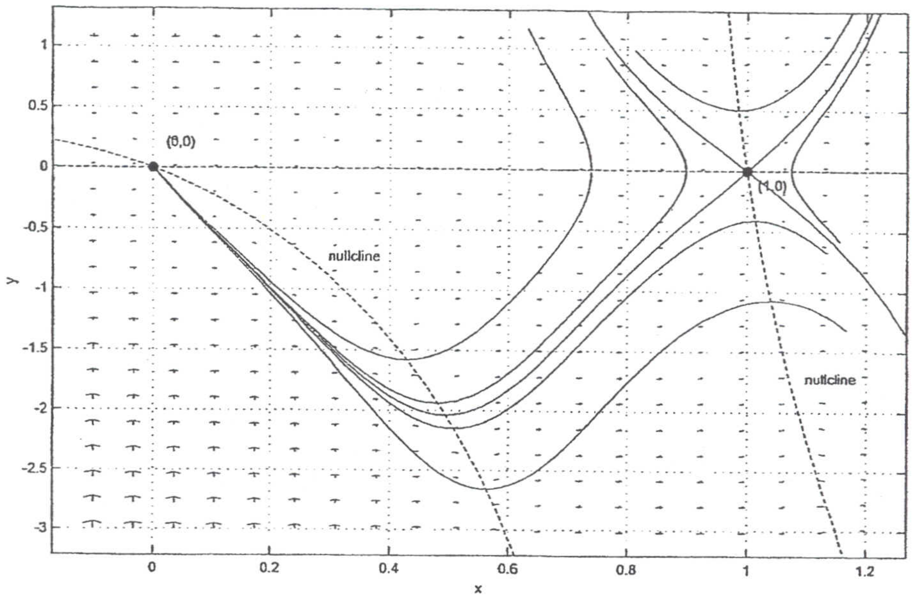

Figure 7: The uw phase plane in the case $h(1) \geq 0$ where the nullcline has an asymptote.

Theorem 3 *Consider the advection-dispersion-growth-settlement model (10) where F and f satisfy (3)-(4) and (8) respectively. Let $h(u) = 1 - c - cf'(u)$ where c satisfies (26). Then there exists a unique, monotone decreasing, smooth traveling wave solution with wave speed c to (10) satisfying the boundary conditions (21).*

Figures 6 and 7 show simulations in the phase plane for the cases $h(1) < 0$ and $h(1) \geq 0$. In both cases the diffusive flux is $F(u_x) = \arctan(u_x)$, the settlement functional response is $f(u) = u/(u+1)$, and the growth rate is $r = 1$. For the case $h(1) < 0$ the dispersion constant is $a = 0.25$, and the wave speed is $c = 1$. The full partial differential equation in this case is

$$u_t = 0.25 \arctan(u_x)_x - u_x + u(1-u) - (\frac{u}{u+1})_t$$

For the case $h(1) \geq 0$ the diffusion constant is $a = 1/16$ and the wave speed is $c = 31/40$.

5 Discussion

Because of the environmental and economic importance of understanding biological invasions, ecologists have collected large amounts of data on dispersal patterns and propagation speeds of spreading organisms, and many models have been developed to fit the data (Kot, 2002). In this note we have posed another theoretical framework to model the dispersal and settlement of propagules based on a bounded flux hypothesis. The bounded flux model, which is not based on probability distributions or random motion assumptions, gives the same wave front speeds as would be obtained using a Fickian assumption, but the dispersal pattern is different. When no biomass growth is included, propagules can spread with a sharp wave front or a continuous wave front, depending upon the relative values of the dispersion constant and the minimum possible flux in the model. When logistics growth is included, smooth traveling waves exist.

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