NONLINEAR DIFFUSION IN POPULATION GENETICS,
COMBUSTION, AND NERVE PULSE PROPAGATION

by

D. G. ARONSON* and H. F. WEINBERGER*

School of Mathematics
University of Minnesota
Minneapolis, Minnesota 55455

1. INTRODUCTION

In this paper we shall investigate the behavior of solutions of the semilinear diffusion equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + f(u) \qquad (1.1)$$

for large values of the time t. Throughout this work we shall assume that $f(0) = f(1) = 0$ and consider only solutions $u(x,t)$ with values in $[0,1]$. The problems which we consider are the pure initial value problem in the half-space $\mathbb{R} \times \mathbb{R}^+$ and the initial-boundary value problem in the quarter-space $\mathbb{R}^+ \times \mathbb{R}^+$.

The equation (1.1) occurs in various applications, and we shall consider forms of the function $f(u)$ which are suggested by some of these applications.

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The classical application is to the following problem in population genetics, which was formulated by R. A. Fisher [4].

Consider a population of diploid individuals. Suppose that the gene at a specific locus in a specific chromosome pair occurs in two forms, called alleles, which we denote by a and A. Then the population is divided into three classes or genotypes. Two of these classes consist of individuals called homozygotes which carry only one kind of allele. The members of these classes are denoted by aa or AA, depending on the alleles they carry. The third class consists of individuals, called heterozygotes, which carry one of each allele. We denote these individuals by aA.

Let the population be distributed in a one-dimensional habitat. The linear densities of the genotypes aa, aA, and AA at the point x of the habitat at time t are denoted by $\rho_1(x,t)$, $\rho_2(x,t)$, and $\rho_3(x,t)$, respectively. We assume that the population mates at random, thereby producing offspring with a birth-rate denoted by r, and that the population diffuses through the habitat with diffusion constant 1. We further assume that the death rate depends only on the genotype with respect to the alleles a and A, and denote the death rates of the genotypes aa, aA, and AA by τ_1, τ_2, and τ_3, respectively. In general, these death rates differ slightly, so that some genotypes are more viable than others. Reproduction by cell division can be incorporated into this model by adding negative quantities to the death rates. Therefore we make no assumption about the signs of the τ_i.

Under the assumptions stated above the population densities satisfy the system of partial differential equations

$$\left.\begin{aligned}
\frac{\partial \rho_1}{\partial t} &= \frac{\partial^2 \rho_1}{\partial x^2} - \tau_1 \rho_1 + \frac{r}{\rho}\left(\rho_1 + \frac{1}{2}\rho_2\right)^2 \\
\frac{\partial \rho_2}{\partial t} &= \frac{\partial^2 \rho_2}{\partial x^2} - \tau_2 \rho_2 + \frac{2r}{\rho}\left(\rho_1 + \frac{1}{2}\rho_2\right)\left(\rho_3 + \frac{1}{2}\rho_2\right) \\
\frac{\partial \rho_3}{\partial t} &= \frac{\partial^2 \rho_3}{\partial x^2} - \tau_3 \rho_3 + \frac{r}{\rho}\left(\rho_3 + \frac{1}{2}\rho_2\right)^2
\end{aligned}\right\} \quad (1.2)$$

where

$$\rho(x,t) \equiv \rho_1(x,t) + \rho_2(x,t) + \rho_3(x,t) .$$

In the Appendix we show that if the derivatives of the initial data are small, if r is very large, and if the quantity

$$\varepsilon = |\tau_1 - \tau_2| + |\tau_3 - \tau_2|$$

is very small, then for times which are small relative to ε^{-1} the relative density

$$u(x,t) = \frac{\rho_3 + \frac{1}{2}\rho_2}{\rho_1 + \rho_2 + \rho_3} \quad (1.3)$$

can be expected to be close to the solution with the same initial values of the equation (1.1) with

$$f(u) = u(1-u)\{(\tau_1 - \tau_2)(1-u) - (\tau_3 - \tau_2)u\}. \quad (1.4)$$

Other heuristic derivations of this equation are given in [4] and [11]. In general, the equation (1.1) should be regarded as a highly idealized and simplified model of some qualitative features of the genetic processes rather than as a strict quantitative model. It is therefore of interest to study the relation between the qualitative form of the function $f(u)$ and the qualitative behavior of solutions of the equation (1.1).

Regardless of the values of the τ_i, the function $f(u)$ given by (1.4) has the properties

$$f \in C^1[0,1], \quad f(0) = f(1) = 0. \tag{1.5}$$

We shall always deal with functions $f(u)$ which satisfy these conditions. Additional assumptions on $f(u)$ which depend on the relative values of the τ_i are also suggested by the function (1.4). Since we can always interchange the labels of a and A and hence the values of τ_1 and τ_3, there is no loss of generality in assuming that $\tau_1 \geq \tau_3$, so that AA is at least as viable as aa. There are then three cases.

CASE 1. If $\tau_3 \leq \tau_2 < \tau_1$, the viability of the heterozygote is between the viabilities of the homozygotes, and we call this the <u>heterozygote intermediate</u> case. The relevant properties of the function (1.4) are

$$f'(0) > 0, \quad f(u) > 0 \quad \text{in} \quad (0,1). \tag{1.6}$$

This is the case which was considered in the classical studies of Fisher [4] and Kolmogoroff, Petrovsky, and Piscounoff [11].

CASE 2. If $\tau_2 < \tau_3 \leq \tau_1$, we have <u>heterozygote superiority</u>. The relevant features of $f(u)$ are

$$\left.\begin{array}{l} f'(0) > 0 \quad f'(1) > 0, \quad \text{and} \quad f(u) > 0 \\ \text{in} \quad (0,\alpha), \quad f(u) < 0 \quad \text{in} \quad (\alpha,1) \\ \text{for some} \quad \alpha \in (0,1). \end{array}\right\} \tag{1.7}$$

CASE 3. If $\tau_3 \leq \tau_1 < \tau_2$, we have heterozygote inferiority. The relevant features of $f(u)$ are

$$\left.\begin{array}{l} f'(0) < 0, \quad f(u) < 0 \text{ in } (0,\alpha), \quad f(u) > 0 \\ \text{in } (\alpha,1) \text{ for some } \alpha \in (0,1), \\ \int_0^1 f(u)\,du > 0. \end{array}\right\} \tag{1.8}$$

There are various other applications which lead to similar models. For example certain flame propagation problems in chemical reactor theory lead to equations of the form (1.1) with a function $f(u)$ which satisfies (1.5) and the generalization

$$\left.\begin{array}{l} f(u) \leq 0 \text{ in } (0,\alpha), \quad f(u) > 0 \text{ in } (\alpha,1) \\ \text{for some } \alpha \in (0,1), \ \int_0^1 f(u)\,du > 0 \end{array}\right\} \tag{1.8'}$$

of (1.8). (See, for example, the article of Gelfand [5]). Here u represents a normalized temperature and α represents a critical temperature at which an exothermic reaction starts.

A model for the propagation of a voltage pulse through the nerve axon of a squid has been proposed by Hodgkin and Huxley [6]. The voltage u satisfies an equation of the form

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + F[u]$$

where F is a certain rather complicated nonlinear functional. An electrical analogue which exhibits the qualitative features of the Hodgkin-Huxley model was proposed by Nagumo, Arimoto, and Yoshizawa [12]. This model leads to the equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + f(u) - \varepsilon \int_0^t u(x,\tau)\,d\tau \qquad (1.9)$$

where ε is a nonnegative parameter and

$$f(u) = u(1 - u)(u - \alpha)$$

for some $\alpha \in (0,\frac{1}{2})$. Note that this function satisfies the conditions (1.5) and (1.8). It has been suggested by Cohen [2, p. 35] that (1.9) with $\varepsilon = 0$ is a model for a nerve which has been treated with certain toxins. Moreover, a rescaled version of (1.9) with $\varepsilon = 0$ has been used by Nagumo, Yoshizawa, and Arimoto [13] as a model for a bistable active transmission line.

In their classical paper [11] Kolmogoroff, Petrovsky, and Piscounoff considered equation (1.1) in the heterozygote intermediate case. They proved the existence of a number $c^* > 0$ such that (1.1) possesses travelling wave solutions $u(x,t) = q(x - ct)$ for all velocities c with $|c| \geq c^*$. (These travelling wave solutions in the heterozygote intermediate case were also discussed by Fisher in [4].) Moreover, they proved that the solution of the special initial value problem with

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

converges (in a certain sense) to a travelling wave solution with speed c^*.

Kanel' [7, 8, 9, 10] has extended and generalized these results in the heterozygote inferior case (1.8) and the case of flame propagation (1.8'). Moreover, Kanel' has observed the occurrence of a threshold behavior with respect to the initial values $u(x,0)$ in these cases.

We study solutions of the equation (1.1) with $f(u)$ subject to (1.5) and (1.6), (1.7), (1.8) or (1.8'). In the applications to flame propagation and voltage pulse propagation it is natural to consider the initial-boundary value problem on the quarter plane $\mathbb{R}^+ \times \mathbb{R}^+$ as well as the pure initial value problem. We shall deal with both of these problems under rather mild restrictions on the data.

In the various cases under consideration we derive the limit behavior of the solution $u(x,t)$ as $t \to \infty$. We study the stability properties of the equilibrium states $u \equiv 0$, $u \equiv \alpha$, and $u \equiv 1$ in the initial value problem in Section 3. We show in Section 4 that in every case there exists a $c^* > 0$ with the property that in the pure initial value problem every disturbance which is initially confined to a bounded set and which is propagated at all is propagated at the asymptotic speed c^*. These results are extended to solutions of the initial-boundary value problem in Section 5.

Many of the results which we obtain here for functions $f(u)$ which satisfy (1.6), (1.7), (1.8), or (1.8') are valid in more general circumstances. These generalizations will be published elsewhere [1].

2. A MAXIMUM PRINCIPLE AND ITS APPLICATIONS

All the forcing functions $f(u)$ described in Section 1 satisfy the conditions

$$f(0) = f(1) = 0, \quad f \in C^1[0,1]. \tag{2.1}$$

In the remainder of this paper these conditions will be understood to hold even if they are not mentioned explicitly.

We begin our study of the equation (1.1) with a version of the maximum principle.

PROPOSITION 2.1. *Let* $u(x,t) \in [0,1]$ *and* $v(x,t) \in [0,1]$ *satisfy the inequalities*

$$u_t - u_{xx} - f(u) \geq v_t - v_{xx} - f(v) \quad \textit{in} \quad (a,b) \times (0,T],$$

$$0 \leq v(x,0) \leq u(x,0) \leq 1 \quad \textit{in} \quad (a,b)$$

where $-\infty \leq a < b \leq \infty$ *and* $0 < T \leq \infty$. *Moreover, if* $a > -\infty$, *assume that*

$$0 \leq v(a,t) \leq u(a,t) \leq 1 \quad \textit{on} \quad [0,T]$$

and if $b < \infty$ *assume that*

$$0 \leq v(b,t) \leq u(b,t) \leq 1 \quad \textit{on} \quad [0,T].$$

Then $u \geq v$, *and if* $u(x,0) > v(x,0)$ *in an open subinterval of* (a,b) *then* $u > v$, *in* $(a,b) \times (0,T]$.

PROOF. By the theorem of the mean we find that

$$(u-v)_t - (u-v)_{xx} \geq f(u) - f(v) = f'(v+\theta(u-v))(u-v)$$

for some $\theta \in (0,1)$. Let $\alpha = \max\limits_{[0,1]} f'(u)$, and define

$$w(x,t) = (u-v)e^{-\alpha t}.$$

Then

$$w_t - w_{xx} \geq \{f'(v + \theta(u-v)) - \alpha\}w.$$

Since the coefficient of w is nonpositive, our result follows from the strong maximum principle for linear parabolic inequalities. (See, for example, [14, p. 172].)

We now derive the principal tool for our investigation.

PROPOSITION 2.2. *Let* $q(x) \in [0,1]$ *be a solution of the ordinary differential equation*

$$q'' + f(q) = 0 \quad in \quad (a,b)$$

where $-\infty \le a < b \le \infty$. *If* $a > -\infty$ *assume that* $q(a) = 0$ *and if* $b < \infty$ *assume that* $q(b) = 0$. *Let* $v(x,t)$ *denote the solution of the initial value problem*

$$v_t = v_{xx} + f(v) \quad in \quad \mathbb{R} \times \mathbb{R}^+, \tag{2.2}$$

$$v(x,0) = \begin{cases} q(x) & in \quad (a,b) \\ 0 & in \quad \mathbb{R}\setminus(a,b). \end{cases}$$

Then $v(x,t)$ *is a nondecreasing function of* t *for each* x. *Moreover,*

$$\lim_{t\to\infty} v(x,t) = \tau(x)$$

uniformly in each bounded interval, where $\tau(x)$ *is the smallest nonnegative solution of the differential equation*

$$\tau'' + f(\tau) = 0 \tag{2.3}$$

on the whole real line $\mathbb{R}$ *which satisfies the inequality*

$$\tau(x) \ge q(x) \quad in \quad (a,b). \tag{2.4}$$

PROOF. By Proposition 2.1, $v(x,t) \ge 0$ in $\mathbb{R} \times \mathbb{R}^+$. Thus we can apply Proposition 2.1 with u replaced by the present $v(x,t)$ and v replaced by $q(x)$ to find that $v(x,t) \geq q(x)$ in $(a,b) \times \mathbb{R}^+$. We then see that for any $h > 0$ we have

$$v(x,h) \geq v(x,0) \quad \text{in } \mathbb{R}.$$

We now apply Proposition 2.1 to $v(x,t+h)$ and $v(x,t)$ to conclude that for any $h > 0$,

$$v(x,t+h) \geq v(x,t) \quad \text{in } \mathbb{R} \times \mathbb{R}^+.$$

Since $u \equiv 1$ is a solution of (1.1), Proposition 2.1 shows that $v(x,t) \leq 1$. Thus for each x, $v(x,t)$ is nondecreasing in t and bounded above. Therefore the limit $\tau(x)$ exists.

By applying the inverse of the heat operator to the equation (2.2) it is easy to show that v_x, v_{xx}, and v_t are uniformly bounded in $\mathbb{R} \times [1,\infty)$. It then follows from the Schauder-type theory for parabolic equations (see [3, p. 92]) that on each bounded x-interval the families of functions v_x, v_{xx}, and v_t, parametrized by t, are equicontinuous in x. Therefore on each bounded x-interval, v converges to τ and v_x, v_{xx}, and v_t converge to the corresponding derivatives of τ uniformly. It follows that τ satisfies the steady-state equation (2.3) in $\mathbb{R}$. Since $v(x,t) \in [0,1]$, $\tau(x) \in [0,1]$, and since $v(x,t) \geq q(x)$ in $(a,b) \times \mathbb{R}^+$, τ satisfies the inequality (2.4).

Finally, if $\sigma(x)$ is any nonnegative solution of (2.3) in all of $\mathbb{R}$ which satisfies the inequality (2.4), then $v(x,0) \leq \sigma(x)$. Hence by Proposition 2.1 $v(x,t) \leq \sigma(x)$ and therefore also $\tau(x) \leq \sigma(x)$. This shows that $\tau(x)$ is the minimal nonnegative solution of (2.3) with the property (2.4).

Note that Proposition 2.2 establishes the existence of a unique nonnegative solution of (2.3) which is minimal with respect to the condition (2.4).

3. STABILITY AND THRESHOLD RESULTS

Our first result establishes the stability of the equilibrium state $u \equiv 1$ in the heterozygote intermediate case and the state $u \equiv \alpha$ in the heterozygote superior case.

THEOREM 3.1. *Let* $u(x,t) \in [0,1]$ *be a solution of* (1.1) *in* $\mathbb{R} \times \mathbb{R}^+$.

(i) If $f(u)$ *satisfies* (2.1) *and* (1.6), *then either* $u(x,t) \equiv 0$ *or*

$$\lim_{t\to\infty} u(x,t) = 1.$$

(ii) If $f(u)$ *satisfies* (2.1) *and* (1.7), *then*

$$u(x,t) \equiv 0, \quad u(x,t) \equiv 1, \quad \textit{or}$$

$$\lim_{t\to\infty} u(x,t) = \alpha.$$

PROOF. The differential equation

$$q'' + f(q) = 0$$

has the first integral

$$\frac{1}{2} q'^2 + F(q) = k \tag{3.1}$$

where k is an arbitrary constant and

$$F(q) \equiv \int_0^q f(u)du.$$

Suppose first that $f(u)$ satisfies the conditions (2.1) and (1.7) of the heterozygote superior case. Then for any $\varepsilon \in (0,\alpha)$, $F(q)$ is increasing in $(0,\varepsilon)$ and in particular $F(\varepsilon) > 0$. Since $f(\varepsilon) > 0$, it is easily seen that $\{F(\varepsilon) - F(u)\}^{-1/2}$ is integrable on the interval $[0,\varepsilon]$. It follows that for each $\varepsilon \in (0,\alpha)$ the problem

$$\frac{1}{2} q'^2 + F(q) = F(\varepsilon)$$

$$q(0) = 0$$

$$q'(0) = \{2F(\varepsilon)\}^{1/2}$$

has a solution $q_\varepsilon(x)$ which is positive in the interval $(0,b_\varepsilon)$, where

$$b_\varepsilon = 2\int_0^\varepsilon [2\{F(\varepsilon) - F(u)\}]^{-1/2} du.$$

Moreover, $q_\varepsilon(x) \le q_\varepsilon(\frac{1}{2} b_\varepsilon) = \varepsilon$, and

$$q_\varepsilon(0) = q_\varepsilon(b_\varepsilon) = 0.$$

As ε decreases to zero, q_ε approaches the solution $\varepsilon \sin\{f'(0)\}^{1/2} x$ of the corresponding linearized problem, and b_ε approaches $\pi/\{f'(0)\}^{1/2}$.

In view of Proposition 2.1, if $u(x,t) \not\equiv 0$, $u(x,h) > 0$ for any $h > 0$. Since $b_\varepsilon < 2\pi/\{f'(0)\}^{1/2}$ when ε is sufficiently small, and since $q_\varepsilon(x) \le \varepsilon$, we can choose $\varepsilon > 0$ so small that $u(x,h) \ge q_\varepsilon(x)$ in $(0,b_\varepsilon)$. It then follows from Proposition 2.2 that

$$\liminf_{t\to\infty} u(x,t) = \liminf_{t\to\infty} u(x, t+h) \ge \tau(x)$$

where $\tau(x)$ is the smallest nonnegative solution of

$q'' + f(q) = 0$ which satisfies $q(x) \geq q_\varepsilon(x)$ in $(0, b_\varepsilon)$.

To show that $\tau(x) \geq \alpha$, we assume the contrary and show that a contradiction results. Suppose that there is an x_0 such that $\beta \equiv \tau(x_0) \in (0, \alpha)$. Then $\tau(x)$ satisfies the first order equation (3.1) with some $k \geq F(\beta)$. Hence $\{k - F(u)\}^{-1/2}$ is integrable on the interval $[0, \beta]$. Therefore $\tau(x)$ is implicitly determined by the equation

$$x = x_0 \mp \int_\tau^\beta [2\{k - F(u)\}]^{-1/2}\, du,$$

where the sign is determined by the sign of $\tau'(x_0)$. It follows that $\tau(x)$ becomes zero with $\tau' \neq 0$ at a finite value of x, so that τ cannot be a nonnegative solution of $q'' + f(q) = 0$ for all x. This contradiction shows that $\tau(x) \geq \alpha$ and hence that

$$\liminf_{t \to \infty} u(x,t) \geq \alpha.$$

If we apply this proof with $\alpha = 1$ when f satisfies (1.6) and recall that $u \leq 1$, we obtain the statement (i) of the Theorem.

We now let $v = 1 - u$ and note that v satisfies the equation (1.1) with $f(u)$ replaced by $-f(1 - v)$. If $f(u)$ satisfies (1.7), then $-f(1 - v) > 0$ for $v \in (0, 1-\alpha)$. Hence the same proof shows that if $u(x,t) \not\equiv 1$, then

$$\liminf_{t \to \infty} (1 - u(x,t)) \geq 1 - \alpha.$$

Hence we have proved statement (ii), and the Theorem is proved.

We remark that Theorem 3.1 not only proves the stability of the state $u \equiv 1$ in the heterozygote intermediate case but also the very strong instability of the state $u \equiv 0$. Similarly, statement (ii) shows that in the heterozygote superior case both the states $u \equiv 0$ and $u \equiv 1$ are very unstable.

We now turn to the case (1.8) of heterozygote inferiority. In this case we shall show that the equilibrium states $u \equiv 0$ and $u \equiv 1$ are stable while $u \equiv \alpha$ is unstable. As a consequence, we can expect threshold phenomena to be associated with this case.

We begin with the following elementary lemma.

LEMMA. *Let* $u(x,t) \in [0,1]$ *be a solution of* (1.1) *in* $\mathbb{R} \times \mathbb{R}^+$ *and let* $f(u) < 0$ *in the interval* $(0,\gamma]$. *If* $u(x,0) \in [0,\gamma]$, *then*

$$\lim_{t\to 0} u(x,t) = 0$$

uniformly on $\mathbb{R}$.

PROOF. Let v be the solution of the initial value problem

$$v_t = v_{xx} + f(v)$$

$$v(x,0) = \gamma.$$

Then v is independent of x and satisfies the relation

$$t = \int_v^\gamma [-f(u)]^{-1}\, du.$$

Hence v goes to zero as $t \to \infty$.

Since $v(x,0) \geq u(x,0)$, the Lemma follows from Proposition 2.1.

Our next theorem concerns the stability of the equilibrium state $u \equiv 0$ in the heterozygote inferior case. It is a generalization of a result proved by Kanel'[10]. In stating the theorem we shall use the following notation: For any $\rho \in [0,\alpha)$ we define

$$s(\rho) \equiv \sup\left\{\frac{f(u)}{u-\rho} : u \in (\alpha,1)\right\}.$$

Moreover, we shall use the notation

$$[\mu]^+ \equiv \max\{\mu,0\}.$$

THEOREM 3.2. *Let* $u(x,t) \in [0,1]$ *be a solution of equation* (1.1) *in* $\mathbb{R} \times \mathbb{R}^+$ *where* $f(u)$ *satisfies* (2.1) *and* (1.8). *If for some* $\rho \in [0,\alpha)$

$$\int_{-\infty}^{\infty} [u(x,0) - \rho]^+ \, dx < \left\{\frac{2\pi}{s(\rho)e}\right\}^{1/2} (\alpha-\rho), \qquad (3.2)$$

then

$$\lim_{t\to\infty} u(x,t) = 0$$

uniformly on $\mathbb{R}$.

PROOF. Fix ρ and write s for $s(\rho)$. Let $w(x,t)$ denote the solution of the problem

$$w_t = w_{xx} + sw$$

$$w(x,0) = [u(x,0) - \rho]^+.$$

By Proposition 2.1, $w \geq 0$ so that $w \equiv [w]^+$. Since $f(u) \leq 0$ on $[0,\alpha]$, it follows from the definition of $s(\rho)$ that

$$f(u) \leq s[u-\rho]^+.$$

Let

$$v(x,t) \equiv u(x,t) - \rho .$$

Then

$$\begin{aligned} v_t - v_{xx} - s[v]^+ &\le u_t - u_{xx} - f(u) \\ &= 0 \\ &= w_t - w_{xx} - s[w]^+ . \end{aligned}$$

In view of Proposition 2.1, $v(x,t) \le w(x,t)$ so that

$$u(x,t) \le w(x,t) + \rho .$$

The function we^{-st} satisfies the equation of heat conduction. Therefore

$$\begin{aligned} w(x,t) &= \frac{1}{2\sqrt{\pi t}} e^{st} \int_{-\infty}^{\infty} e^{-\frac{(x-\xi)^2}{4t}} [u(\xi,0) - \rho]^+ \, d\xi \\ &\le \frac{1}{2\sqrt{\pi t}} e^{st} \int_{-\infty}^{\infty} [u(\xi,0) - \rho]^+ \, d\xi . \end{aligned}$$

In particular, it follows from (3.2) that $u(x,(2s)^{-1})$ is bounded above by a constant $\gamma < \alpha$. Then the preceding Lemma proves Theorem 3.2.

Theorem 3.2 shows that the state $u \equiv 0$ is locally stable while the Lemma proves that the state $u \equiv \alpha$ is unstable in the case of heterozygote inferiority. We shall now show that the state $u \equiv 0$ is not globally stable, even with respect to disturbances of bounded support.

We observe that the hypotheses (1.8) or even (1.8') imply the existence of a unique $\kappa \in [\alpha,1)$ for which

$$F(\kappa) \equiv \int_0^\kappa f(u)\,du = 0. \tag{3.3}$$

Moreover, $F(q) > 0$ and $F'(q) = f(q) > 0$ for $q \in (\kappa,1)$. For any $\beta \in (\kappa,1)$ we define the length

$$b_\beta = 2\int_0^\beta \{2F(\beta) - 2F(u)\}^{-1/2}\,du,$$

and the solution $q_\beta(x)$ of $q'' + f(q) = 0$ which has the first integral

$$\frac{1}{2} q'^2 + F(q) = F(\beta)$$

and which satisfies $q(0) = 0$, $q'(0) = \{2F(\beta)\}^{1/2}$. Then $q_\beta > 0$ in $(0,b_\beta)$, $q_\beta(0) = q_\beta(b_\beta) = 0$, and

$$q_\beta(x) \leq q_\beta(\tfrac{1}{2} b_\beta) = \beta \quad \text{on} \quad [0,b_\beta].$$

With the aid of this function we state the following theorem.

THEOREM 3.3. *Let* $u(x,t) \in [0,1]$ *be a solution in the half-plane* $\mathbb{R} \times \mathbb{R}^+$ *of the equation* (1.1) *where* $f(u)$ *satisfies the conditions* (2.1) *and* (1.8) *or* (1.8').

If for some $\beta \in (\kappa,1)$ *and some* x_0

$$u(x,0) \geq q_\beta(x-x_0) \quad \textit{on} \quad (x_0,x_0 + b_\beta),$$

then

$$\lim_{t\to\infty} u(x,t) = 1.$$

PROOF. We apply Proposition 2.2 with $q(x) = q_\beta(x)$.

The proof of the fact that the minimal nonnegative solution τ of the equation $q'' + f(q) = 0$ on $\mathbb{R}$ which satisfies $q \geq q_\beta(x-x_0)$ in $(x_0,x_0 + b_\beta)$ is identically one is the same as that of the fact that $\tau \equiv \alpha$ in the proof of Theorem 3.1. Thus the theorem is proved.

We note that Theorem 3.3 not only shows that the state $u \equiv 0$ is unstable with respect to disturbances with bounded support but also that the state $u \equiv 1$ is globally stable with respect to such disturbances.

Theorems 3.2 and 3.3 together exhibit a threshold phenomenon. A disturbance of bounded support of the state $u \equiv 0$ which is sufficiently large on a sufficiently large interval grows to one, while a disturbance which is not sufficiently large on a sufficiently large interval dies out.

If $f(u)$ satisfies only (1.8'), the Lemma does not apply. However, if (3.2) holds, then from the proof of Theorem 3.2 we find that $u < \alpha$ for $t \geq 1/2s(\rho)$ and that $[u(\cdot,1/2s(\rho)) - \rho]^+ \in L^1(\mathbb{R})$. A comparison with the equation of heat conduction then yields $\limsup u(x,t) \leq \rho$ as $t \to \infty$. Since Theorem 3.3 is valid when (1.8') holds, there are also threshold effects in this case.

4. PROPAGATION

In this section we investigate how the solution $u(x,t)$ of (1.1) behaves as a function of time. For this purpose we introduce the moving coordinate

$$\xi = x - ct, \quad c > 0.$$

If we define

$$v(\xi,t) \equiv u(\xi+ct,t),$$

the equation (1.1) becomes

$$v_t = v_{\xi\xi} + cv_\xi + f(v). \tag{4.1}$$

We note that the maximum principle, Proposition 2.1, and the convergence result, Proposition 2.2, are immediately extendable to this equation. Since the proofs are identical to those given in Section 2, we shall simply use these results without further comment.

The steady state equation which corresponds to (4.1) is, of course,

$$q'' + cq' + f(q) = 0. \tag{4.2}$$

This equation is equivalent to the system

$$q' = p$$
$$p' = -cp - f(q).$$

The functions $p(\xi)$, $q(\xi)$ corresponding to a solution of (4.2) give a trajectory in the q-p plane or, as it is usually called, the phase plane. Such a trajectory has the slope

$$\frac{dp}{dq} = -c - \frac{f(q)}{p} \tag{4.3}$$

for $p \neq 0$.

When $c = 0$, each trajectory satisfies an equation of the form

$$\frac{1}{2}p^2 + F(q) = \text{constant}.$$

Under our hypotheses on $f(u)$ there is an $\eta \in (0,1)$ such that $F(\eta) > 0$. For any ν such that $0 < \nu < [2F(\eta)]^{1/2}$ the trajectory through $(0,-\nu)$ lies in the strip $q \in [0,1)$ and contains a point of the positive p-axis. By continuity there is a $\tilde{c} = \tilde{c}(\nu) > 0$ such that the same is true for all $c \in [0,\tilde{c})$. Hence for $c \in [0,\tilde{c})$ there is no trajectory joining the origin and the line

$q = 1$.

We now consider $c > 0$. If $c^2 > 4f'(0)$, there is a nontrivial trajectory from the origin [15,§56]. The unique trajectory in the strip $q \in [0,1]$ that goes to the point $(0,-\nu)$ with $\nu > 0$ cannot cross any trajectory that goes to the origin. Hence if we take the limit as $\nu \downarrow 0$ of the trajectory that goes to $(0,-\nu)$ and if $c^2 > 4f'(0)$, we obtain a nontrivial extremal trajectory going to the origin. We denote this extremal trajectory by T_c.

We define

$$\sigma = \sup_{u \in [0,1]} \frac{f(u)}{u} ,$$

so that

$$f(u) \le \sigma u \quad \text{for} \quad u \in [0,1].$$

It follows that if T is any trajectory of (4.3), then

$$\frac{dp}{dq} \le -c - \sigma \frac{q}{p}$$

at every point of T where $q \in [0,1]$ and $p < 0$. On the other hand if $c^2 > 4\sigma$, the line through the origin

$$p = -\frac{1}{2}\left(c + \sqrt{c^2 - 4\sigma}\right) q \tag{4.4}$$

satisfies the differential equation

$$\frac{dp}{dq} = -c - \sigma \frac{q}{p} .$$

Consequently, the trajectory through $(0,-\nu)$ with $\nu > 0$ cannot cross this line for $q \in [0,1]$. It must therefore lie below it. Taking the limit as $\nu \downarrow 0$, we see that for $c^2 > 4\sigma$, T_c is bounded above by the line (4.4). In particular, T_c connects the origin with a point of the form $(1,-\nu)$ with $\nu > 0$.

In view of the above observations, the number

$$c^* = \inf\{c: c^2 > 4f'(0), \text{ there exists } \nu > 0 \text{ such that } (1,-\nu) \in T_c\}$$

is well-defined and positive. In the remainder of this section we shall exhibit various properties of c^*. In particular, we shall show that c^* is the asymptotic speed of propagation associated with the equation (1.1).

THEOREM 4.1. *Let* $u(x,t) \in [0,1]$ *be a solution of equation* (1.1), *where* $f(u)$ *satisfies* (1.6), (1.7), (1.8), *or* (1.8'), *in* $\mathbb{R} \times \mathbb{R}^+$. *If for some* x_0

$$u(x,0) \equiv 0 \quad \text{in} \quad (x_0, \infty), \tag{4.5}$$

then for each ξ *and each* $c > c^*$,

$$\lim_{t\to\infty} u(\xi+ct,t) = 0. \tag{4.6}$$

PROOF. Let $q_c(x)$ denote the solution of the steady state equation (4.2) in $\mathbb{R}^+$ which corresponds to the trajectory T_c and for which $q_c(0) = 1$. q_c is decreasing and approaches zero as $x \to \infty$.

We observe that the function $w \equiv 1 - u$ satisfies an equation like (1.1) but with $f(u)$ replaced by $-f(1 - w)$. We apply the extension of Proposition 2.1 with $q = 1 - q_c(x - x_0)$ in (x_0, ∞) to the equation

$$w_t = w_{\xi\xi} + cw_\xi - f(1 - w).$$

We note that $1 - u(x,0) \geq 1 - q_c(x - x_0)$. Hence by the extensions of Propositions 2.1 and 2.2

$$\liminf_{t \to \infty} (1 - u(\xi+ct,t)) \geq 1 - \tau(\xi) \tag{4.7}$$

where $\tau(\xi)$ is the solution of equation (4.2) which is maximal with respect to the properties

$$\tau(\xi) \leq 1 \quad \text{in} \quad \mathbb{R} \tag{4.8}$$

and

$$\tau(\xi) \leq q_c(\xi - x_o) \quad \text{in} \quad (x_o, \infty). \tag{4.9}$$

We must now show that $\tau(\xi) \equiv 0$.

For any $c > 0$ such that $c^2 > 4f'(0)$ the trajectory T_c has slope S^- at the origin, where

$$S^{\pm} = \frac{1}{2}\left\{-c \pm \sqrt{c^2 - 4f'(0)}\right\} .$$

Moreover, T_c is the unique trajectory with this slope at the origin. Any other trajectory which approaches the origin with $q > 0$ must do so with the slope S^+. These statements can be proved by the methods used by Petrovski [15, §56].

Since $c > c^*$, the trajectory T_c lies in the half-plane $p < 0$ for $q \in (0,1]$ and contains a point $(1,-\nu)$ with $\nu > 0$. If $\tau(\xi) \not\equiv 0$, then the corresponding trajectory T has slope S^+ or S^- at the origin. Since the slope of T_c at $(0,0)$ is S^-, it follows from (4.9) that T cannot have slope S^+ at $(0,0)$. Therefore $T \equiv T_c$, and there exists $\zeta \in \mathbb{R}$ such that $\tau(\zeta) = 1$ and $\tau'(\zeta) = -\nu < 0$. Hence $\tau(\xi) > 1$ for some $\xi < \zeta$. This contradicts (4.8), and we conclude that $\tau \equiv 0$. Since $u(x,t) \geq 0$ the assertion of the theorem follows from (4.7).

In view of (4.3) and the uniqueness property of T_c it can be shown that for $\bar{c}^2 > 4f'(0)$, T_c approaches $T_{\bar{c}}$ as $c \to \bar{c}$. That is, T_c is continuous in c.

REMARKS. 1. Because the trajectory T_c has slope $-\frac{1}{2}\left(c + \sqrt{c^2 - 4f'(0)}\right)$, the function q_c has the property

$$\lim_{x\to\infty} q_c(x)^{1/x} = e^{-\frac{1}{2}\left(c+\sqrt{c^2-4f'(0)}\right)}.$$

One can then see from the proof that the condition (4.5) can be replaced by

$$\lim_{x\to\infty} u(x,0)^{1/x} = 0.$$

2. Since the equation (1.1) is invariant when x is replaced by $-x$, the conclusion (4.6) holds for $c < -c^*$ if (4.5) is replaced by

$$u(x,0) \equiv 0 \text{ in some interval } (-\infty, x_0)$$

or by

$$\lim_{x\to-\infty} u(x,0)^{-1/x} = 0.$$

3. If $u(x,0) \equiv 0$ outside a bounded interval, we have (4.6) for $|c| > c^*$. Moreover, it can be shown that the convergence is uniform in this case.

Next we show that there always exists a travelling wave solution with velocity c^*.

THEOREM 4.2. *If* $f(u)$ *satisfies* (1.6), (1.7), (1.8), *or* (1.8'), *there exists a travelling wave solution* $u = q^*(x - c^*t)$ *of* (1.1). *Moreover,* $q^{*\prime}(\xi) < 0$,

$$\lim_{\xi\to\infty} q^*(\xi) = 0$$

and

$$\lim_{\xi\to-\infty} q^*(\xi) = \begin{cases} 1 & \textit{if } f(u) \textit{ satisfies } (1.6), (1.8), \textit{or } (1.8') \\ \alpha & \textit{if } f(u) \textit{ satisfies } (1.7). \end{cases}$$

PROOF. If ${c^*}^2 > 4f'(0)$, then the trajectory T_{c^*} exists and lies in the half-strip $q \in [0,1]$, $p \le 0$ at least in a relative neighborhood of the origin. T_{c^*} is minimal in the sense that there is no other trajectory which lies below T_{c^*} and approaches the origin.

If ${c^*}^2 > 4f'(0)$ and T_{c^*} does not intersect the positive q-axis, then by continuity the same will be true of T_c for a slightly smaller value of c, which contradicts the definition of c^*. Therefore T_{c^*} intersects the q-axis at a point $(\eta,0)$ with $\eta \in (0,1]$. If $f(\eta) \neq 0$, then since T_{c^*} must go in the negative q-direction for $p < 0$, (4.3) implies that $f(\eta) > 0$. But then there is a number $\eta_1 > \eta$ such that $f(\eta_1) > 0$. The part of the trajectory through $(\eta_1, 0)$ on which $p < 0$ lies below T_{c^*}, and must go to the negative p-axis. By continuity, the same will be true for sufficiently small $c > c^*$, and the resulting trajectory through $(\eta_1, 0)$ bounds T_c away from $q = 1$. This again contradicts the definition of c^*. We conclude that T_{c*} must hit the q-axis at a point $(\eta,0)$ where $f(\eta) = 0$.

According to (4.3), if $f(q) < 0$, the slope of T_{c*} is negative. Therefore, T_{c*} cannot hit the q-axis at a zero η of $f(u)$ which is the right endpoint of an interval where $f(u)$ is negative. Thus if $c^{*2} > 4f'(0)$, then T_{c*} must hit the q-axis at $(1,0)$ in the cases (1.6), (1.8), and (1.8') and at $(\alpha,0)$ in the case (1.7).

If, on the other hand, $c^{*2} = 4f'(0)$, then since $c^* > 0$, $f'(0)$ must be positive. Hence $f(u)$ satisfies (1.6) or (1.7). In particular, $f(u) > 0$ in an interval $(0,\alpha)$, where we set $\alpha = 1$ in the case (1.6). The trajectories through the points of the interval $(0,\alpha)$ of the q-axis go downward and to the left in the half-strip $q \in [0,1]$, $p < 0$. Hence they cannot recross the positive q-axis. On the other hand, suppose that a trajectory $S_{c*}(\eta)$ through some point $(\eta,0)$ with $\eta \in (0,\alpha)$ went to a point $(0, -\nu)$ on the negative p-axis. By continuity the trajectory $S_c(\eta)$ through $(\eta,0)$ would still go to the negative p-axis for any sufficiently small $c > c^*$. Since $S_c(\eta)$ would bound T_c away from the q-axis, we would again find a contradiction with the definition of c^*. We conclude that every trajectory $S_{c*}(\eta)$ through a point $(\eta,0)$ with $\eta \in (0,\alpha)$ must go to the origin. By continuity the same is true of the limit of these trajectories as η approaches α. This limiting trajectory connects the point $(\alpha,0)$ with the origin.

We have shown that there is always a trajectory in the phase plane that connects $(1,0)$ to the origin in the cases (1.6), (1.8), and (1.8') and that connects $(\alpha, 0)$ to the origin in the case (1.7). Any solution $q^*(\xi)$ corresponding to this trajectory clearly has the properties stated in the theorem.

REMARKS. 1. If $c^{*2} = 4f'(0)$ the trajectory corresponding to q^* may not be the minimal trajectory through the origin, which we have called T_{c^*}. For example, if $f(u)$ has the property $f(u) \leq f'(0)u$, then $\sigma = f'(0)$. Hence T_{c^*} lies below the line (4.4) with $c = c^*$. Thus T_{c^*} goes to the negative half-line $q = 1$. Since $f'(0) > 0$ in this case, the proof of Theorem 4.1 works with $c = c^*$.

2. If $f'(0) > 0$, the above proof can be extended to show that there is a travelling wave solution with the properties stated in Theorem 4.2 for every $c \geq c^*$. The problem treated by Kolmogoroff, Petrovsky, and Piscounoff [11] has the properties of Remarks 1 and 2.

3. The function $q^*(-x - c^*t)$ gives a travelling wave with velocity $-c^*$.

Finally, we consider the behavior of $u(\xi+ct,t)$ for $|c| < c^*$. Here we shall have to consider the three cases separately.

THEOREM 4.3. *Let* $u(x,t) \in [0,1]$ *be a solution of* (1.1) *in* $\mathbb{R} \times \mathbb{R}^+$ *where* $f(u)$ *satisfies* (1.6). *If* $u(x,t) \not\equiv 0$, *then for each* c *with* $|c| < c^*$ *and each* ξ

$$\lim_{t\to\infty} u(\xi+ct, t) = 1.$$

PROOF. If $c \in (0,\{4f'(0)\}^{1/2})$, then the origin in the phase plane is a spiral point. This means that there are trajectories in the strip $q \in [0,1]$ which connect the positive p-axis to the negative p-axis.

If $c^{*2} > 4f'(0)$, the proof of Theorem 4.2 shows that T_{c^*} goes from $(1,0)$ to $(0,0)$ in the lower half plane. Consider any $c \in (\{4f'(0)\}^{1/2}, c^*)$. Because of equation (4.3), the trajectory T_c lies above T_{c^*}. Hence T_c crosses the q-axis at a point $(\eta,0)$ with $\eta \in (0,1)$. Then if $\beta \in (\eta,1)$ the lower part of the trajectory T through $(\beta,0)$ stays below T_c. Therefore, T goes to the negative p-axis. Since $f(u) > 0$ in $(0,1)$, we see from (4.3) that the slope of T is negative in the upper half-plane. Moreover, the slope is bounded below when p is bounded away from zero. Therefore, T goes from a point on the positive p-axis to $(\beta,0)$ and from there to a point on the negative p-axis.

We have shown that for each $c \in (0, c^*)$ there is a trajectory T which connects the positive p-axis to the negative p-axis. T crosses the q-axis at a point $(\beta,0)$ with $\beta \in (0,1)$, and lies in the strip $q \in [0,\beta]$. Let q_β be the corresponding solution of $q'' + cq' + f(q) = 0$ for which $q_\beta(0) = 0$, $q_\beta'(0) > 0$. This solution is positive on a finite interval $(0,b)$ and vanishes at its ends. Moreover, $q_\beta(x) \le \beta < 1$.

According to Theorem 3.1, $u(x,t)$ converges to 1 as $t \to \infty$. Moreover, this theorem was proved by using Proposition 2.2, which states that the convergence is uniform on every bounded x-interval. In particular, there is a time T so that

$$u(x,T) \geq \beta \geq q_\beta(x) \text{ on } [0,b].$$

Theorem 4.3 for $c \in [0,c^*)$ now follows from applying the extensions of Propositions 2.1 and 2.2 to the solution v of (4.1) and recalling that $v(\xi,t) = u(\xi+ct,t)$. Since replacing x by $-x$ replaces c by $-c$, the Theorem is also true for $c \in (-c^*,0]$.

In exactly the same manner we can prove:

THEOREM 4.4. *Let* $u(x,t) \in [0,1]$ *be a solution of* (1.1) *in* $\mathbb{R} \times \mathbb{R}^+$ *where* $f(u)$ *satisfies* (1.7). *If* $u(x,0) \not\equiv 0$ *then for each* c *such that* $|c| < c^*$ *and each* ξ

$$\liminf_{t \to \infty} u(\xi+ct, t) \geq \alpha.$$

We remark that in this case there will in general be another propagation speed at which the decrease of u to α travels.

In the heterozygote inferior case we have seen that $u(x,t) \to 1$ if and only if the initial conditions exceed some threshold value. Thus we cannot expect the analogue of Theorems 4.3 and 4.4 to hold without some conditions such as those of Theorem 3.3 on $u(x,0)$. With this in mind we can carry through the argument used above to obtain the following result.

THEOREM 4.5. *Let* $u(x,t) \in [0,1]$ *be a solution of* (1.1) *in* $\mathbb{R} \times \mathbb{R}^+$ *where* $f(u)$ *satisfies* (1.8) *or*

(1.8'). *Suppose that*

$$\lim_{t\to\infty} u(x,t) \equiv 1.$$

Then for every c *with* $|c| < c^*$ *and each* ξ

$$\lim_{t\to\infty} u(\xi+ct,\, t) = 1.$$

We see from Theorems 4.1, 4.3, 4.4, and 4.5, that a disturbance which is initially confined to a half-line $x < x_0$ and which increases to either 1 or α is propagated with the asymptotic speed c^*. More precisely, if β is any constant such that $\beta \in (0,1)$ in cases (1.6), (1.8), or (1.8') or $\beta \in (0,\alpha)$ in case (1.7), and if we define

$$\overline{x}(t) = \max\,\{x\colon u(x,t) = \beta\},$$

$$\underline{x}(t) = \min\,\{x > 0\colon u(x,t) = \beta\},$$

then

$$\lim_{t\to\infty} \overline{x}/t = \lim_{t\to\infty} \underline{x}/t = c^*.$$

5. THE INITIAL-BOUNDARY VALUE PROBLEM

We now consider the initial-boundary value problem

$$\left.\begin{aligned} &u_t = u_{xx} + f(u) && \text{in } \mathbb{R}^+ \times \mathbb{R}^+, \\ &u(x,0) = 0 && \text{in } \mathbb{R}^+, \\ &u(0,t) = \psi(t) && \text{in } \mathbb{R}^+, \end{aligned}\right\} \tag{5.1}$$

where $\psi(t)$ is a given function with values on the interval $[0,1]$. Since both the results for this problem and their derivations are very similar to those for the initial value problem, we shall only sketch the proofs.

The analog of Proposition 2.2 is the following proposition, which is proved in the same manner.

PROPOSITION 5.1. *Let* $q(x) \in [0,1]$ *be a solution of the equation* $q'' + f(q) = 0$ *in* (a,b) *with* $a > 0$, *and let* $q(a) = q(b) = 0$.

Let $v(x,t)$ *denote the solution of the initial-boundary value problem*

$$v_t = v_{xx} + f(v) \quad \textit{in} \quad \mathbb{R}^+ \times \mathbb{R}^+,$$
$$v(x,0) = \begin{cases} q(x) & \textit{in} \quad (a,b) \\ 0 & \textit{in} \quad \mathbb{R}^+ \backslash (a,b), \end{cases}$$
$$v(0,t) = \phi(t) \quad \textit{in} \quad \mathbb{R}^+.$$

Suppose that $\phi(t)$ *is nondecreasing,* $\phi(0) = 0$, *and* $\phi(t) \in [0,1]$.

Then $v(x,t)$ *is nondecreasing in* t *and*

$$\lim_{t\to\infty} v(x,t) = \tau(x)$$

where $\tau(x)$ *is the smallest nonnegative solution of the equation*

$$\tau'' + f(\tau) = 0 \quad \textit{in} \quad \mathbb{R}^+$$

which satisfies the inequalities

$$\tau(0) \geq \lim_{t\to\infty} \phi(t)$$

and

$$\tau(x) \geq q(x) \quad \textit{in} \quad (a,b).$$

Moreover, the convergence of v *to* τ *is uniform on each closed bounded interval in the interior of* $\mathbb{R}^+$.

If $f(u)$ satisfies the conditions (1.6) of the heterozygote intermediate case, we see from the first integral (3.1) that the initial value problem

$$\left.\begin{array}{l} q'' + f(q) = 0 \quad \text{in } \mathbb{R}^+ \\ q(0) = \beta \end{array}\right\} \tag{5.2}$$

has a unique solution in $[0,1]$ for each $\beta \in (0,1]$ and two such solutions for $\beta = 0$. All these solutions other than $q \equiv 0$ approach 1 as $x \to \infty$. By employing Proposition 2.1 and Proposition 5.1 in a proof like that of Theorem 3.1 we find the following result:

THEOREM 5.1. *Let* $u(x,t) \in [0,1]$ *be the solution of the problem* (5.1) *where* $f(u)$ *satisfies* (1.6). *If* $u(x,t) \not\equiv 0$, *then*

$$\liminf_{t \to \infty} u(x,t) \geq \tau(x)$$

where $\tau(x)$ *is the unique positive solution of the problem* (5.2) *with*

$$\beta = \liminf_{t \to \infty} \psi(t).$$

In particular,

$$\lim_{x \to \infty} \liminf_{t \to \infty} u(x,t) = 1.$$

Thus if $\psi(t) \not\equiv 0$, $u(x,t)$ approaches values near one far from the boundary regardless of the behavior of $\psi(t)$.

In the same manner we find that if $f(u)$ satisfies the conditions (1.7) of the heterozygote superior case, then

$$\lim_{x\to\infty} \liminf_{t\to\infty} u(x,t) = \lim_{x\to\infty} \limsup_{t\to\infty} u(x,t) = \alpha$$

unless $\psi(t) \equiv 0$.

In the heterozygote inferior case (1.8) or the combustion case (1.8'), it is easily seen from (3.1) that for $\beta \in [0,\kappa)$, with κ defined by (3.3), there is a solution $q_\beta(x)$ of the problem (5.2) such that

$$\lim_{x\to\infty} q_\beta(x) = 0.$$

(There is another solution which approaches 1, but we shall not use it.)

We then find the following result from Proposition 2.1.

THEOREM 5.2. *Let* $u(x,t) \in [0,1]$ *be the solution of the problem* (5.1) *and let* $f(u)$ *satisfy* (1.8). *If*

$$\beta = \sup_{t\in\mathbb{R}^+} \psi(t) < \kappa,$$

then $u(x,t) \le q_\beta(x)$. *In particular,*

$$\lim_{x\to\infty} \limsup_{t\to\infty} u(x,t) = 0.$$

One can, in fact, obtain the following analogue of Theorem 3.2.

THEOREM 5.3. *Let* $u(x,t) \in [0,1]$ *be the solution of the problem* (5.1) *with* $f(u)$ *subject to the conditions* (1.8).

Suppose that for some $T \in \mathbb{R}^+$ *and some* $\rho \in (0,\alpha)$

$$\psi(t) \le \rho \quad \text{in} \quad (T,\infty)$$

and

$$\int_0^T e^{s(\rho)(T-t)} [\psi(t) - \rho]^+ \, dt < \sqrt{2\pi/e}\,(\alpha - \rho)/s(\rho),$$

where $s(\rho)$ *and* $[\mu]^+$ *are defined as in Theorem* 3.2. *Then*

$$\lim_{x\to\infty} \limsup_{t\to\infty} u(x,t) = 0.$$

REMARK. If $f(u)$ only satisfies (1.8'), we can still show that under the conditions of Theorem 5.3 $\limsup_{t\to\infty} u(x,t) \le \rho$.

The following result, together with the two preceding theorems, shows that there is a threshold effect in the initial-boundary value problem.

THEOREM 5.4. *Let* $u(x,t) \in [0,1]$ *be the solution of the initial-boundary value problem* (5.1) *and let* $f(u)$ *satisfy* (1.8) *or* (1.8'). *Let* κ *be defined by* (3.3).

For any $\beta \in (\kappa,1)$ *there is a positive time* T_β *with the property that the condition*

$$\psi(t) \ge \beta \quad \text{on} \quad (t_0, t_0 + T_\beta) \tag{5.3}$$

for some nonnegative t_0 *implies*

$$\lim_{x\to\infty} \liminf_{t\to\infty} u(x,t) = 1. \tag{5.4}$$

PROOF. Let $\chi(t)$ be a smooth nondecreasing function which satisfies the conditions

$$\chi(t) = \begin{cases} 0 & \text{in } (-\infty,0) \\ \beta & \text{in } (1,\infty). \end{cases}$$

Let $w(x,t)$ denote the solution of the problem

$$w_t = w_{xx} + f(w) \quad \text{in } \mathbb{R}^+ \times \mathbb{R}^+,$$

$$w(x,0) = 0 \quad \text{in } \mathbb{R}^+,$$

$$w(0,t) = \chi(t) \quad \text{in } \mathbb{R}^+.$$

By Proposition 5.1

$$\lim_{t\to\infty} w(x,t) = \tau(x)$$

where $\tau(x)$ is the smallest nonnegative solution of the problem (5.2). Since $\beta > \kappa$, the problem (5.2) has only one nonnegative solution, and this solution is increasing, so that

$$\tau(x) > \beta \quad \text{in } \mathbb{R}^+.$$

Moreover, the convergence of $w(x,t)$ to $\tau(x)$ is uniform on each bounded interval.

We recall the solution $q_\beta(x)$ of $q'' + f(q) = 0$ which was used in the proof of Theorem 3.3. It is defined and positive in an interval $(0,b_\beta)$, vanishes at the ends of this interval, and satisfies the inequality

$$q_\beta(x) \le q_\beta(\tfrac{1}{2}b_\beta) = \beta \quad \text{on} \quad (0,b_\beta).$$

Thus $q_\beta(x-1) < \tau(x)$ on $(1,b_\beta+1)$.

Since $w(x,t)$ converges to $\tau(x)$ uniformly on $[1,b_\beta+1]$, there is a time T_β for which

$$w(x,T_\beta) \ge q_\beta(x-1) \quad \text{on} \quad [1,b_\beta+1].$$

We now apply Proposition 2.1 to see that because of (5.3),

$$u(x, t+t_0) \geq w(x,t) \quad \text{in} \quad \mathbb{R}^+ \times [0,T_\beta].$$

Hence

$$u(x, T_\beta+t_0) \geq q_\beta(x - 1) \quad \text{in} \quad (1, b_\beta+1).$$

Because of Propositions 2.1 and 5.1, $\liminf_{t \to \infty} u(x,t)$ is bounded below by a nonnegative solution τ^* in $\mathbb{R}^+$ of $q'' + f(q) = 0$ which, in turn, is bounded below by $q_\beta(x - 1)$ in $(1, b_\beta+1)$. In particular $\tau^*(\frac{1}{2} b_\beta + 1) \geq \beta > \kappa$. The first integral (3.1) then shows that $\tau(x) \to 1$ as $x \to \infty$, which proves (5.4).

If, as in Section 4, we introduce the coordinate $\xi = x - ct$, the set $\mathbb{R}^+ \times \mathbb{R}^+$ is mapped onto the set $\{(\xi,t) : \xi > -ct, t > 0\}$. If $c > 0$, we can prove an extension of Proposition 2.2 for solutions $v(\xi,t)$ of $v_{\xi\xi} + cv_\xi + f(v) = 0$ which vanish on the boundary $\xi = -ct$. The limit $\tau(\xi)$ is a nonnegative solution of $\tau'' + c\tau' + f(\tau) = 0$ in all of $\mathbb{R}$. The proofs of Theorems 4.1, 4.3, 4.4, and 4.5 now yield the following result, with c^* defined as before.

THEOREM 5.5. *Let* $u(x,t) \in [0,1]$ *be the solution of the problem* (5.1) *and let* $f(u)$ *satisfy one of the conditions* (1.6), (1.7), (1.8), *or* (1.8').

(a) Then for any $c > c^*$ *and any real* ξ

$$\lim_{t\to\infty} u(\xi+ct, t) = 0.$$

(b) If $\lim_{x\to\infty} \liminf_{t \to \infty} u(x,t) = 1$, *then for any*

$c \in (0,c^*)$ *and any real* ξ

$$\lim_{t\to\infty} u(\xi+ct,\ t) = 1.$$

(c) *If* $f(u)$ *satisfies* (1.7) *and* $u(x,t) \not\equiv 0$, *then for any* $c \in (0,c^*)$ *and any real* ξ

$$\liminf_{t \to \infty} u(\xi+ct,\ t) \geq \alpha.$$

Thus c^* is also the asymptotic propagation velocity associated with the initial-boundary value problem (5.1).

6. APPENDIX: REDUCTION OF THE SYSTEM (1.2) TO A SINGLE EQUATION

In this section we shall indicate how the initial value problem for the equation (1.1) with $f(u)$ given by (1.4) is related to the initial value problem for the system (1.2).

We first consider the initial value problem which consists of finding a solution of the system (1.2) in $\mathbb{R}\times\mathbb{R}^+$ subject to the initial conditions

$$\rho_j(x,0) = \gamma_j(x) \quad \text{in } \mathbb{R}, \quad (j = 1,2,3). \tag{6.1}$$

The functions γ_j are assumed to be smooth and nonnegative. Moreover, we assume that there exist positive constants a and b such that

$$0 < a \leq \gamma(x) \equiv \sum_{j=1}^{3} \gamma_j(x) \leq b. \tag{6.2}$$

The solution of the problem (1.2), (6.1) is obtained by inverting the linear part of the operator and applying the method of successive approximations. Let $\rho_j^{(\ell)}$ denote the j-th component of the ℓ-th iterate, where $\rho_j^{(0)}$ is the j-th component of the solution of the uncoupled system

$$\frac{\partial \rho_j}{\partial t} = \frac{\partial^2 \rho_j}{\partial x^2} - \tau_j \rho_j \qquad (j = 1,2,3)$$

with the initial data (6.1). By the maximum principle [14], $\rho_j^{(0)} \geq 0$. Let

$$\nu = \max\ (\tau_1 , \tau_2 , \tau_3)$$

and

$$\rho^{(\ell)} = \rho_1^{(\ell)} + \rho_2^{(\ell)} + \rho_3^{(\ell)} .$$

Using (6.2) in a standard comparison argument, we obtain the estimate

$$\rho^{(0)}(x,t) \geq ae^{-\nu t} \quad \text{in } \mathbb{R} \times \mathbb{R}^+ .$$

Since the nonlinear terms in (1.2) are nonnegative when the ρ_j are nonnegative and their sum ρ is positive, it follows that $\rho_j^{(\ell)} \geq \rho_j^{(0)}$ and hence also that $\rho^{(\ell)} \geq \rho^{(0)} \geq ae^{-\nu t}$ for all ℓ. It is then a routine matter to show that the $\rho_j^{(\ell)}$ converge to the unique bounded solution of the problem (1.2), (6.1) in $\mathbb{R} \times (0,T]$ for any $T \in \mathbb{R}^+$. In particular, the components ρ_j of the solution are nonnegative and

$$\rho(x,t) \geq ae^{-\nu t} \quad \text{in } \mathbb{R} \times \mathbb{R}^+ . \qquad (6.3)$$

Moreover, in carrying through the details of the successive approximations, one also obtains the bounds

$$\rho(x,t) \leq be^{(r-\lambda)t}$$

and

$$\left|\frac{\partial\rho}{\partial x}(x,t)\right| \le e^{-\lambda t}\sum_{j=1}^{3}\sup_{\mathbb{R}}|\gamma_j'| + 2br\sqrt{\frac{t}{\pi}}\,e^{(r-\lambda)t} \tag{6.4}$$

where

$$\lambda = \min(\tau_1, \tau_2, \tau_3).$$

If we introduce the new dependent variables

$$\left.\begin{aligned} v &= \frac{1}{\rho}\left(\rho_3 + \frac{1}{2}\rho_2\right) \\ \sigma &= \frac{1}{\rho^2}\left(\rho_2^2 - 4\rho_1\rho_3\right) \\ \mu &= \frac{\partial}{\partial x}(\log\rho), \end{aligned}\right\} \tag{6.5}$$

the system (1.2) becomes

$$\frac{\partial v}{\partial t} - \frac{\partial^2 v}{\partial x^2} - f(v) = 2\mu\frac{\partial v}{\partial x} + \frac{1}{4}\{(\tau_2-\tau_1)v - (\tau_2-\tau_3)(1-v)\}\sigma \tag{6.6a}$$

$$\left.\begin{aligned} \frac{\partial\sigma}{\partial t} - \frac{\partial^2\sigma}{\partial x^2} - 2\mu\frac{\partial\sigma}{\partial x} + \{r - (\tau_1-\tau_3)(1-2v) + \frac{\tau^*}{4}\sigma\}\sigma \\ = 4\tau^* v^2(1-v)^2 - 8\left(\frac{\partial v}{\partial x}\right)^2 \end{aligned}\right\} \tag{6.6b}$$

$$\frac{\partial\mu}{\partial t} - \frac{\partial^2\mu}{\partial x^2} = \frac{\partial}{\partial x}\{\mu^2 + \frac{\tau^*}{4}\sigma + (\tau_2-\tau_3)v^2 + (\tau_2-\tau_1)(1-v)^2\} \tag{6.6c}$$

where f is defined by (1.4) and

$$\tau^* = \tau_1 - 2\tau_2 + \tau_3.$$

Note that v represents the relative density of the allele A in the population. The quantity σ measures the deviation of the system from the Hardy-Weinberg equilibrium, while μ measures its deviation from uniform population density.

To establish a relationship between the equation (1.1) and the system (1.2) we must find conditions which guarantee that the right-hand side of (6.6a) is negligible relative to f. In the usual derivations of equation (1.1) in population genetics it is tacitly assumed that $\sigma \equiv \mu \equiv 0$. However, (6.6c) shows that this assumption implies $\partial v/\partial x \equiv 0$. Thus, if $\sigma \equiv \mu \equiv 0$, there is no spacial variation, and, in particular, no diffusion. Here we shall only assume that $\partial v/\partial x$ and μ are <u>initially</u> small.

The solution of the initial value problem (1.2), (6.1) generates a solution of the system (6.6) with initial data

$$v(x,0) = v_o(x), \quad \sigma(x,0) = \sigma_o(x), \quad \mu(x,0) = \mu_o(x) \quad \text{in } \mathbb{R}$$

where, for example,

$$v_o(x) = \frac{\gamma_3(x) + \frac{1}{2}\gamma_2(x)}{\gamma_1(x)+\gamma_2(x)+\gamma_3(x)} .$$

Since $\rho_j \geq 0$ and $\rho > 0$, we have

$$v \in [0, 1], \quad \sigma \in [-1, 1] \quad \text{in } \mathbb{R} \times \mathbb{R}^+. \tag{6.7}$$

Moreover, by (6.3) and (6.4), μ is bounded in every strip $\mathbb{R} \times [0,T]$.

We shall assume for simplicity that

$$\mu_o \equiv 0 \quad \text{in } \mathbb{R}. \tag{6.8}$$

In view of (6.7) the term in braces on the right-hand side of (6.6c) is bounded by $\mu^2 + \frac{5}{4}\varepsilon$, where

$$\varepsilon = |\tau_1 - \tau_2| + |\tau_3 - \tau_2|$$

is a small parameter. It follows from (6.6c) that

$$|\mu(x,t)| \le \int_0^t \int_{\mathbb{R}} \left|\frac{\partial G}{\partial x}(x-\xi, t-\eta)\right| \{\mu(\xi,\tau)^2 + \frac{5}{4}\varepsilon\} d\xi d\eta, \quad (6.9)$$

where $G(x,t)$ denotes the fundamental solution of the equation of heat conduction. Let

$$M(t) = \sup_{\mathbb{R}\times[0,t]} |\mu(\xi,\eta)|. \qquad (6.10)$$

Then (6.9) implies that

$$M(t) \le 2\sqrt{\frac{t}{\pi}}\left\{M(t)^2 + \frac{5}{4}\varepsilon\right\}.$$

Therefore

$$M(t) \le \frac{1}{4}\sqrt{\frac{\pi}{t}}\left\{1 - \left(1 - \frac{20\varepsilon t}{\pi}\right)^{1/2}\right\},$$

provided $20t\varepsilon \le \pi$. In particular, if $\varepsilon t \in [0, 3\pi/80]$, then $1 - (20\varepsilon t/\pi) \ge 1/4$. It follows from the mean value theorem that

$$|\mu(x,t)| \le M(t) \le 5\varepsilon\sqrt{\frac{t}{\pi}} \text{ in } \mathbb{R}\times\left[0, \frac{3\pi}{80\varepsilon}\right]. \quad (6.11)$$

In order to estimate the product $\mu \cdot \partial v/\partial x$ we need a suitable bound for $|\partial v/\partial x|$. For this purpose we assume that there is a constant k_1 such that

$$|v_o'(x)| \le k_1 \varepsilon^{1/2}. \qquad (6.12)$$

Here and in the sequel we denote by k, with or without subscript, a constant which does not depend on ε or r.

From (6.6a) we obtain the integral identity

$$\left.\begin{aligned}\frac{\partial v}{\partial x}(x,t) &= \int_{\mathbb{R}} G(x-\xi,\ t)\,v_o'(\xi)\,d\xi \\ &+ \int_o^t\int_{\mathbb{R}} G_x(x-\xi,\ t-\eta)\Big\{2\mu\,\frac{\partial v}{\partial x} + f(v) \\ &+ \frac{1}{4}\,[(\tau_2-\tau_1)v - (\tau_2-\tau_3)(1-v)]\sigma\Big\}\,d\xi\,d\eta.\end{aligned}\right\} \tag{6.13}$$

Let

$$m(t) = \sup_{\mathbb{R}\times[0,t]} \left|\frac{\partial v}{\partial x}(\xi,\eta)\right|.$$

In view of (1.4), we have $f(v) = O(\varepsilon)$. Thus by (6.7), (6.11), (6.12), and (6.13) we find that

$$m(t) \le k_1\varepsilon^{1/2} + 5\varepsilon t m(t) + k_2\varepsilon t^{1/2} \quad \text{in} \quad \left[0,\ \frac{3\pi}{80\varepsilon}\right].$$

Thus

$$\left|\frac{\partial v}{\partial x}(x,t)\right| \le m(t) \le k\varepsilon^{1/2} \quad \text{in}\ \ \mathbb{R}\times\left[0,\ \frac{3\pi}{80\varepsilon}\right]. \tag{6.14}$$

Moreover, for $t \in [0,\ 3\pi/80\varepsilon]$, equation (6.6b) has the form

$$\frac{\partial\sigma}{\partial t} - \frac{\partial^2\sigma}{\partial x^2} - 2\mu\,\frac{\partial\sigma}{\partial x} + (r-c)\sigma = g,$$

where, in view of (6.7) and (6.14), $c \le k_3\varepsilon$ and $|g| \le k_4\varepsilon$. If $r > 2\varepsilon k_3$, a standard comparison argument shows that

$$|\sigma(x,t)| \le s e^{-\frac{1}{2}rt} + \frac{2\varepsilon k_4}{r} \quad \text{in}\ \ \mathbb{R}\times\left[0,\ \frac{3\pi}{80\varepsilon}\right], \tag{6.15}$$

where s is an upper bound for $|\sigma_o(x)|$. (Note that by (6.7), $s \le 1$.)

Let u denote the solution of the equation (1.1) with

$u(x,0) = v_o(x)$. By the mean value theorem and (6.6a), the difference

$$w = v - u$$

satisfies the equation

$$\frac{\partial w}{\partial t} - \frac{\partial^2 w}{\partial x^2} - f'(\eta)w = 2\mu \frac{\partial v}{\partial x} + \frac{1}{4}\{(\tau_2-\tau_1)v - (\tau_2-\tau_3)(1-v)\}\sigma,$$

where $\eta(x,t)$ lies between $u(x,t)$ and $v(x,t)$ and hence between 0 and 1. We see from (6.7), (6.11), (6.14), and (6.15) that

$$\left|\frac{\partial w}{\partial t} - \frac{\partial^2 w}{\partial x^2} - f'(\eta)w\right| \leq k\varepsilon\left(se^{-\frac{1}{2}rt} + \sqrt{\varepsilon t} + \frac{\varepsilon}{r}\right)$$

$$\text{in } \mathbb{R} \times \left[0, \frac{3\pi}{80\varepsilon}\right].$$

According to (1.4), $f'(u) = O(\varepsilon)$ so that $tf'(\eta)$ is uniformly bounded for $t \in [0, 3\pi/80\varepsilon]$. Since $w(x,0) = 0$, a standard comparison argument shows that

$$|w(x,t)| \leq k\varepsilon t\left[\frac{s}{rt}\left(1 - e^{-\frac{1}{2}rt}\right) + \sqrt{\varepsilon t} + \frac{\varepsilon}{r}\right] \quad \text{in } \mathbb{R} \times \left[0, \frac{3\pi}{80\varepsilon}\right]. \tag{6.16}$$

Therefore, the difference $|u - v|$ is very small compared to εt, provided that ε/r is sufficiently small and $\frac{1}{r} \ll t \ll \frac{1}{\varepsilon}$.

Since $f(u)/\varepsilon$ is bounded below on any closed interval which does not contain 0, α, or 1, we can expect the effect of $f(u)$ on the solution of (1.1) to be of the order εt. Thus for t which are large compared to r^{-1}, but small compared to ε^{-1}, the error made by replacing the system (1.2) by the single equation (1.1) is small compared to the effect of f.

REMARKS. 1. The estimate (6.15) shows that $\sigma = O(\varepsilon r^{-1})$ for $t \geq r^{-1} \log(r\varepsilon^{-1})$. Thus any deviation from the Hardy-Weinberg law is damped out in time $r^{-1} \log(r\varepsilon^{-1})$. For a system which has been in operation for at least this long before $t = 0$, we can assume that $s = O(\varepsilon r^{-1})$. It then follows from (6.16) that $|u-v| = t\,o(\varepsilon)$ for all $t << \varepsilon^{-1}$.

2. The assumption that $\mu_o \equiv 0$ is not necessary. The inequality (6.16) is still valid if $\mu_o = o(\varepsilon^{1/2})$.

3. By simple dimensional considerations, it follows that the propagation speed c^* associated with equation (1.1) is of order $\varepsilon^{1/2}$ when $f(u)$ is given by (1.4). Thus the time it takes a pulse to reach a particular point is of order $\varepsilon^{-1/2}$, which may be small relative to ε^{-1}.

4. Since the bounds (6.11) and (6.14) do not depend upon a or b, a simple limiting process shows that the condition (6.2) may be replaced by the condition $\gamma(x) > 0$.

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