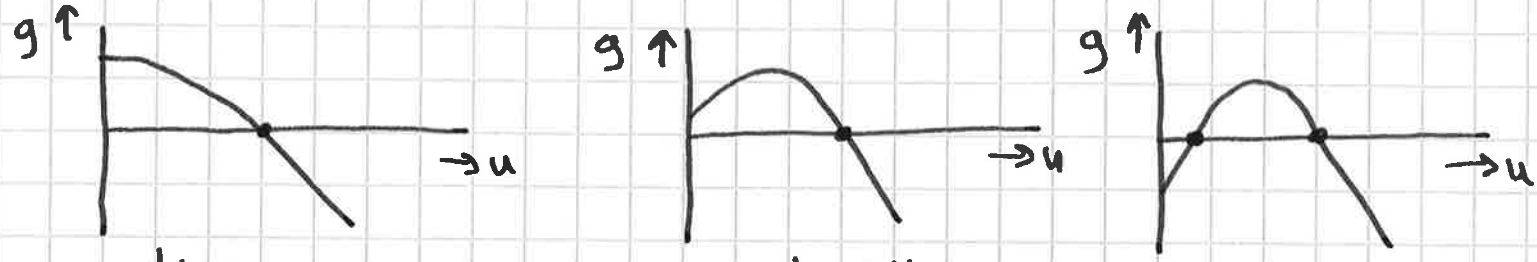
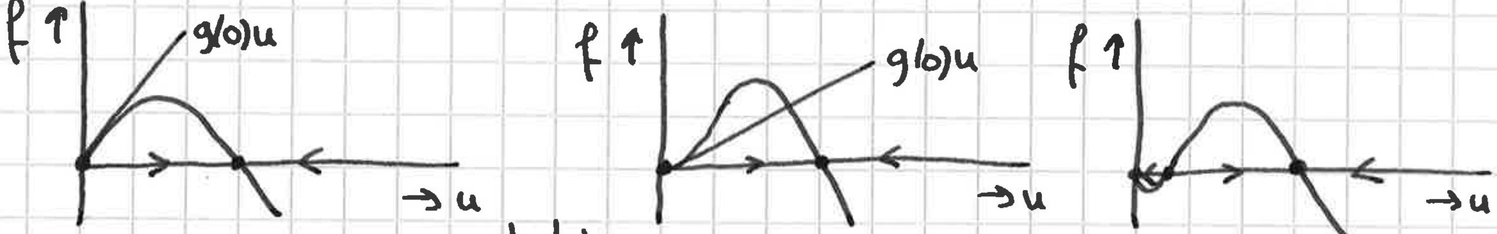
Travelling waves and the asymptotic speed of propagation

Section 1 Classification of growth functions for single species population dynamics:

$$\dot{u} = f(u) = u\,g(u)$$



negative density dependence | weak Allee effect | strong Allee effect



monostable | bistability

every introduction leads to establishment at carrying capacity

introduction triggers a transition

introduction only leads to establishment if a threshold is exceeded

Now add the spatial dimension, with movement described by diffusion. Introduction will be, as a rule, very localized. We therefore ask: how <u>fast</u> does establishment happen? Or, in otherwords: how fast does a successful invader spread?

Section 2 Travelling waves for the monostable case

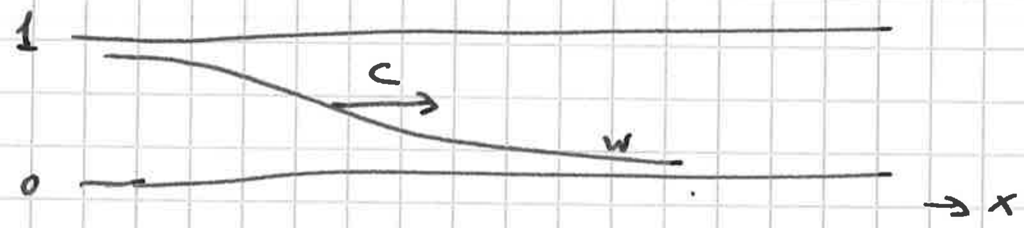
Consider (11.1) $\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + f(u) \quad , \; -\infty < x < \infty$

with $f \in C^1$, $f(0) = 0 = f(1)$, $f'(0) > 0$, $f > 0$ on $(0,1)$, $f'(1) < 0$

We look for solutions of the form

$$(11.2) \quad u(t,x) = w(x - ct)$$

with both the speed c and the profile w to be determined. (Note that the equation is invariant under both time translation and space translation. We are looking for a solution where a time translation



amounts to a space translation. Solutions which are invariant under a transformation group are often called self-similar solutions.)

Such solutions have to satisfy

$$(11.3) \qquad w'' + c w' + f(w) = 0$$

where $'$ indicates differentiation with respect to the moving coordinate $\qquad \xi = x - ct \qquad (11.4)$

Equation (11.3) is invariant under

$$\xi \longmapsto -\xi \qquad\qquad c \longmapsto -c$$

11.3/ that transforms  into 

so without loss of generality we restrict to $c > 0$.

We rewrite (11.3) as the two-dimensional first order system

$$
(11.5) \qquad \begin{aligned} w' &= v \\ v' &= -cv - f(w) \end{aligned}
$$

For $c \neq 0$ this is not a Hamiltonian system.

The Jacobi matrix for the equilibria

$$(0,0) \quad \text{and} \quad (1,0)$$

is of the form $\begin{pmatrix} 0 & 1 \\ -f' & -c \end{pmatrix}$

and so has eigenvalues

$$
(11.6) \qquad \lambda_{\pm} = \frac{-c \pm \sqrt{c^2 - 4f'}}{2}
$$

with corresponding eigenvectors

$$
(11.7) \qquad \begin{pmatrix} 1 \\ \lambda_{\pm} \end{pmatrix}
$$

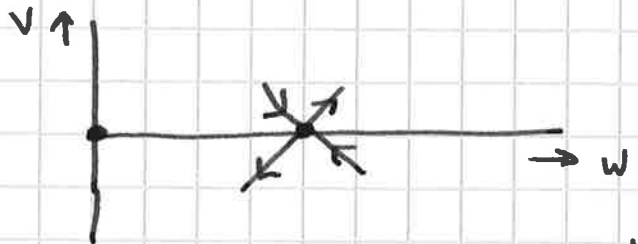
Since $f'(0) > 0$ we have for $(0,0)$:

$$
\operatorname{Re} \lambda_{\pm} < 0 \qquad \begin{aligned} c &< 2\sqrt{f'(0)} \quad \text{stable spiral point} \\ c &> 2\sqrt{f'(0)} \quad \text{stable node} \end{aligned}
$$

Since $f'(1) < 0$ we have for $(1,0)$:

$$\lambda_{-} < 0 < \lambda_{+} \quad \Rightarrow \text{saddle point}$$

11.4/ From these facts we conclude: for $c>0$ the only candidate for a solution of (11.3) that satisfies $0 \le w \le 1$ is the part of the unstable manifold of $(1,0)$ with $v<0$



and we do indeed get such a solution if the corresponding orbit has $(0,0)$ as its ω-limit set (= its "destination"), without crossing the v-axis (since then w assumes negative values). So we need to require

$$c \geqslant 2\sqrt{f'(0)} \qquad (11.8)$$

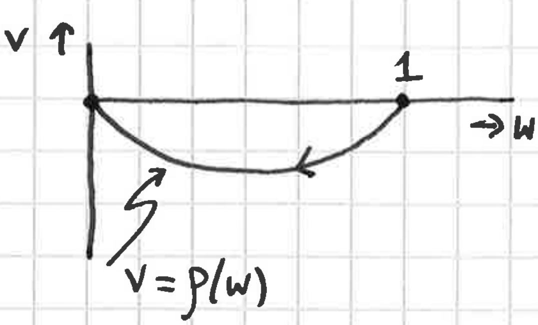
Moreover, the observation that only the part of the unstable manifold of $(1,0)$ with $v<0$ yields a candidate solution establishes at once that, for fixed c, there is, modulo translation at most one solution, so uniqueness.

Solutions of (11.5) with $v<0$ are monotone decreasing functions of x, so we can invert $x \mapsto w(x)$ and look at v as a function of w rather than of x. If we put

$$v = \rho(w) \quad \text{then, using (11.5)}$$

$$\left.\begin{aligned} v' &= \rho'(w)\, w' = \rho'(w)\rho(w) \\ v' &= -c\rho(w) - f(w) \end{aligned}\right\} \Rightarrow \rho' = -c - \frac{f(w)}{\rho}$$

11.5/ So the solutions that we are looking for correspond to curves in the (w,v)-plane that connect $(0,0)$ and $(1,0)$ and that lie in the strip $\{(w,v) : 0 \le w \le 1, \; v \le 0\}$



Now suppose that for some value of c, say $\tilde{c}$, we do have a solution of this kind, so a curve $v = \rho(w)$ satisfying

$$\rho(0) = 0 = \rho(1)$$

$$\rho' = -\tilde{c} - \frac{f(w)}{\rho} \qquad (11.9)$$

From (11.6) we deduce (recall $f'(1) < 0$)

$$2 \frac{d}{dc} \lambda_+ \Big|_{(1,0)} = -1 + \frac{c}{\sqrt{c^2 - 4f'(1)}} < 0$$

So for $c > \tilde{c}$ the relevant part of the unstable manifold at $(1,0)$ enters the region bounded by ρ and the w-axis. On the w-axis the vector field defined by the right hand side of (11.5) points into this region (indeed, $v' = -f(w) < 0$), so <u>if</u> also ~~for~~ along the curve ρ the vector field points, for $c > \tilde{c}$, into the region, we know that the orbit is trapped inside this region and therefore has to converge to $(0,0)$, thus yielding a solution of the desired type for $c > \tilde{c}$. If we follow the curve $(w, \rho(w))$ in the direction of the flow defined by (11.5), the tangent vector is

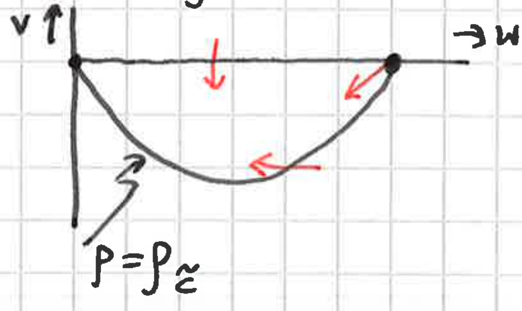
11.6/ $\begin{pmatrix} \rho \\ -\tilde{c}\rho - f(w) \end{pmatrix}$ and the normal pointing into the region between the curve and the w-axis is accordingly $\begin{pmatrix} -\tilde{c}\rho - f(w) \\ -\rho \end{pmatrix}$

The inner product of this normal vector and the vector field (11.5) for parameter c (rather than $\tilde{c}$) is accordingly

$$\rho(-\tilde{c}\rho - f(w)) - \rho(-c\rho - f(w)) = (c - \tilde{c})\rho^2$$

so positive for $c > \tilde{c}$

arrows correspond to $c > \tilde{c}$



We formulate a first conclusion:

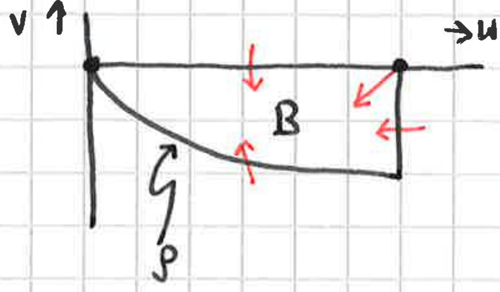
Lemma 1 The set of possible speeds is an upper half line or empty

Lemma 2 The set of speeds is non-empty

Proof Let $\rho : [0,1] \to (-\infty, 0]$ be a C^1-function with $\rho(0) = 0$, $\rho'(0) < 0$, $\rho(w) < 0$ for $0 < w < 1$. Let

$$c > \sup_{0 < w < 1} \left\{ -\rho'(w) - \frac{f(w)}{\rho(w)} \right\}$$

We claim that c is a speed.



Let B be the region bounded by the curve ρ, the w-axis and, if $\rho(1) < 0$, the piece of the line $w = 1$ with $\rho(1) \leq v \leq 0$.

11.7/ Along such a piece of the line $w=1$ we have, for $v<0$ and according to (11.5), $w'=v<0$, so orbits can enter but not leave B. Along the curve ρ the inner product of inward pointing normal and vector field corresponding to (11.5) equals

$$-\rho\rho' - c\rho - f(w) = -\rho\left(c+\rho' + \frac{f(w)}{\rho}\right)$$

and the condition that we imposed on c guarantees that this is negative for $0<w<1$, so also along this part of ∂B orbits of (11.5) can enter B but not leave. It remains to show that the relevant part of the unstable manifold of $(1,0)$ enters B. If $\rho(1)<0$ this is immediately clear. If $\rho(1)=0$ and $\rho'(1)=0$ we actually have that

$$\lim_{w\uparrow 1} -\rho'(w) - \frac{f(w)}{\rho(w)} = +\infty$$

and our assertion about c becomes meaningless, so we should not consider such ρ. If $\rho(1)=0$ and $\rho'(1)>0$ then our condition on c guarantees that

$$c \geq \lim_{w\uparrow 1}\left(-\rho'(w) - \frac{f(w)}{\rho(w)}\right) = -\rho'(1) - \frac{f'(1)}{\rho'(1)}$$

and hence also that

$$(\rho'(1))^2 + c\rho'(1) + f'(1) > 0$$

The function $\lambda \mapsto \lambda^2 + c\lambda + f'(1)$ is negative for $\lambda=0$ and equal to zero for $\lambda=\lambda_+$ so the above inequality guarantees that $\rho'(1) > \lambda_+$ or, in other words, that the relevant part of the unstable manifold of $(1,0)$ enters B. $\square$

<u>Definition 3</u> $c_0 = \inf \{ c : c \text{ is a speed} \}$

Here "c is a speed" means that (11.5) has an orbit connecting $(1,0)$ and $(0,0)$ while residing in the region $0 \leq w \leq 1$, $v \leq 0$. (Orbits connecting different equilibrium points are called <u>heteroclinic orbits</u>.)

<u>Lemma 4</u> c_0 is a speed

"<u>Proof</u>" The relevant part of the unstable manifold of $(1,0)$ cannot leave the strip $0 \leq w \leq 1$, $v \leq 0$ through the line $w=1$ or through the w-axis. By (11.8) we know that $c_0 > 0$. From the second equation in (11.5) we deduce that $v' > 0$ if $v < -\frac{1}{c_0} \sup_{0 \leq w \leq 1} f(w)$. So the orbit cannot go to infinity in this strip. Hence either the orbit has $(0,0)$ as its limit point or it leaves the strip in a point $(0,v)$ for some $v<0$. In the latter case a continuity argument (that is not easily made precise; in particular, I would not know a reference) shows that for slightly higher values of c the unstable manifold would also hit the negative v-axis. As we know that this does <u>not</u> happen, we conclude that also for $c = c_0$ there is a heteroclinic orbit.

11.9/ An alternative proof begins by fixing for $c > c_0$ the translate of the solution by requiring that for $x = 0$ it has value $\frac{1}{2}$. Next one checks ~~con~~ that there is a uniform bound for the derivative, in particular uniform in c for c in an interval (c_0, c_0+1). The Arzela - Ascoli Theorem then guarantees that there is a sequence $c_n = c_0 + \gamma_n$, with $\gamma_n \downarrow 0$ as $n \to \infty$, such that the solutions with parameter c_n converge uniformly on compact intervals. Obviously the limit takes the value $\frac{1}{2}$ for $x = 0$, so is neither identically zero nor identically one. Finally one rewrites the equation in integral form and checks that one can pass to the limit in the equation. $\square$

Combining the proof of Lemma 2 with Lemma's 1, 4 and (11.9) we obtain the following <u>variational characterization</u> of the minimal speed:

<u>Lemma 5</u> Define

$$P = \left\{ \rho \in C^1([0,1];\mathbb{R}) : \rho(0) = 0, \rho'(0) < 0, \rho < 0 \text{ on } (0,1) \right\}$$

Then

$$c_0 = \min_{\rho \in P} \sup_{0 < w < 1} \left\{ -\rho'(w) - \frac{f(w)}{\rho(w)} \right\} \qquad (11.10)$$

<u>Proof</u> Call the right hand side of (11.10) c_P, where, at first, we replace min by inf as we are not yet sure that the inf is achieved. The proof of Lemma 2 establishes that $c_0 \leq c_P + \varepsilon$ for every $\varepsilon > 0$, hence $c_0 \leq c_P$.

According to Lemma 4, there exists a curve ρ satisfying (11.9) for $\tilde{c} = c_0$. Clearly $\rho'(0) \leq 0$ and $\rho'(0) = 0$ is incompatible with the equation, so $\rho'(0) < 0$ and accordingly this ρ belongs to P. We conclude that $c_0 \geqslant c_p$. □

<u>Lemma 6</u> $$2\sqrt{f'(0)} \leqslant c_0 \leq 2\sqrt{\sup_{0<w<1} \frac{f(w)}{w}}$$

<u>Proof</u> The left inequality simply reflects that we restrict our attention to heteroclinic orbits that satisfy $w \geqslant 0$, recall (11.8). Choose, for $\varkappa > 0$, $\rho(w) = -\varkappa w$, then

$$-\rho'(w) - \frac{f(w)}{\rho(w)} = +\varkappa + \frac{1}{\varkappa}\frac{f(w)}{w}$$

and Lemma 5 implies that $$c_0 \leqslant \varkappa + \frac{1}{\varkappa} L$$

where $L = \sup_{0<w<1} \frac{f(w)}{w}$. By choosing $\varkappa = \sqrt{L}$ we minimize the righthand side. This leads to $c_0 \leq 2\sqrt{L}$ □

<u>Corollary 7</u> In case of negative density dependence we have $c_0 = 2\sqrt{f'(0)}$

<u>Example 8</u> Consider for $\nu > -1$

$$f(w) = w(1-w)(1+\nu w) \qquad (11.11)$$

then

$$c_0 = \begin{cases} 2, & -1 < \nu \leq 2 \\ \frac{\nu+2}{\sqrt{2\nu}}, & \nu \geqslant 2 \end{cases}$$

11.11/ To show this, note first that $f'(0) = 1$ and that, for $\nu > -1$, indeed $f(w) > 0$ for $0 < w < 1$. Next note that
$$\frac{f(w)}{w} = (1-w)(1+\nu w)$$
achieves its maximum in $w = 0$ if $-1 < \nu \leq 1$ and in $w = \frac{\nu - 1}{2\nu}$ if $\nu > 1$. In the first case the maximum equals 1 and in the second case $(\nu+1)^2/4\nu$. At this point we can only conclude that $c_0 = 2$ for $-1 < \nu \leq 1$.

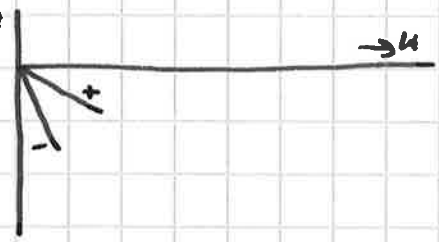
Remarkably, for this particular function f an explicit solution, the so-called Huxley pulse is known. It is given by
$$w_H(\xi) = \frac{1}{1 + e^{\sqrt{\frac{\nu}{2}}\,\xi}} \qquad (11.12)$$

Exercise 9 Verify that w_H satisfies (11.3) with
$$c = \frac{\nu + 2}{\sqrt{2\nu}} \qquad (11.13)$$

As this speeds equals 2 for $\nu = 2$ and, by Lemma 6, $c_0 \geqslant 2$, we now know that $c_0 = 2$ for $\nu = 2$. It is not difficult to show that, since f increases with ν, so does c_0 (indeed, just look at (11.10) and take into account that $\rho < 0$). Hence $c_0 = 2$ for $-1 < \nu \leq 2$. In order to verify that c_0 is given by (11.13) for $\nu \geqslant 2$ we need to show that (11.12) is the solution with minimal speed. How can we possibly do that?

If $c_0 = 2\sqrt{f'(0)}$ we know that it is "minimal" because the equilibrium $(0,0)$ changes from a stable

11.12/ node into a stable spiral point. But what characterizes "minimality" if $(0,0)$ remains a stable node? For the eigenvalues of the Jacobi matrix for $(0,0)$ we have $\lambda_- < \lambda_+ < 0$ and the corresponding directions are as shown in the figure →



For large x the solutions converging to $(0,0)$ behave as

$$c_+ e^{\lambda_+ x} + c_- e^{\lambda_- x}$$

and since $\lambda_- < \lambda_+$ this means geometrically that, except for one exceptional orbit corresponding to $c_+ = 0$, orbits are tangent to the + eigenvector. So for $c > c_0$ the heteroclinic orbit "comes in" along the + direction. But for the exceptional c_0, it comes in along the − direction. For $c < c_0$ the orbit originating in $(1,0)$ first intersects the v-axis before coming in along the + direction <u>from the other side</u>.

From (1.12) we compute $V_H(\xi) = W_H'(\xi)$ and next compute the limit of $\frac{V_H(\xi)}{W_H(\xi)}$ for $\xi \to \infty$. The result is $-\sqrt{\frac{\nu}{2}}$. We also compute $\lambda_- = \frac{-c - \sqrt{c^2 - 4f'(0)}}{2}$ for c given by (11.13). The result is $-\sqrt{\frac{\nu}{2}}$. We conclude that the Huxley pulse comes in at $(0,0)$ along the exceptional − direction, hence must be the critical heteroclinic connection corresponding to the minimal wave speed c_0.

<u>End of Example 8</u>

Because of their form  these wave solutions are called <u>travelling fronts</u> (while solutions of the form  are called <u>travelling pulses</u>)

If $c_0 = 2\sqrt{f'(0)}$, like in the case of negative density dependence, we speak about <u>pulled fronts</u>, since it is the linearized dynamics at the front of the invasion that determines the speed (recall Section 5.3 of syllabus_chs.pdf)

If $c_0 > 2\sqrt{f'(0)}$, like in the case of a weak Allee effect, we speak about <u>pushed fronts</u>, since higher population densities are involved in determining the speed (and, of course, the shape).

See J. Garnier, T. Giletti, F. Hamel, L. Roques, Inside dynamics of pulled and pushed fronts, Journal de Mathématiques Pures et Appliquées (2012) <u>98</u>: 428–449 for a recent characterization of the difference between those two kinds of fronts.

If we consider $\dfrac{\partial u}{\partial t} = \Delta u + f(u)$, $x \in \mathbb{R}^n$, we may choose any unit vector $\nu \in \mathbb{R}^n$ and look for travelling <u>planar waves</u>, i.e., solutions of the form

$$u(t,x) = w(x \cdot \nu - ct)$$

which travel in the <u>direction</u> ν and are constant on lines orthogonal to ν. The function w has to satisfy (11.3).