MOVEMENT OF A SESSILE CELL COLONY

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Abstract

Surface motion of an isolated sessile bacterial colony is described by a free surface condition known as the kinematic boundary condition. When the colony is attached to a surface which does not allow slip, a difficulty arises in describing the motion of the contact line at the boundary of the colony. Here we present a new theory which allows for a resolution of this difficulty, by allowing for a 'radiative' direction-dependent flux of the medium. In effect, this allows slip to occur near the contact line.

1. Introduction

Surface motion of a drop occurs in a number of situations. Most obviously, the motion of a drop of viscous fluid as it rolls down a plane is an example. In a number of situations, surfaces grow by accretion, or shrink through ablation; etching and melting are examples of the latter, while crystal growth, snowfall and ice sheet accumulation are examples of the former. Anderson and Davis (1995) study the spreading of a fluid drop which loses mass by evaporation at its surface [1]. We are particularly interested in situations where the interfacial motion is caused by growth of the medium. Most simply, this occurs in the growth of cell colonies, for example in a petri dish. The growth of biofilm on a wall, the growth of tumours, or the growth of plant leaves or roots are other examples. In particular, the growth of biofilm (Winstanley *et al.* 2011) ([6]) has been a primary motivation for the present study.

To provide a mathematical context for the situation of interest, consider first a free surface which grows (or decays) with a constant speed. By this we mean that the speed of the interface in the normal direction is constant. For simplicity,

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we will discuss only two-dimensional surfaces $z = s(x,t)$, where s is the interfacial elevation above a flat wall, $z = 0$ and x measures distance along the wall. If the normal (upwards) velocity of the interface is v_n, then the evolution equation for s is

$$s_t = v_n\sqrt{1+s_x^2}, \tag{1.1}$$

where s_t and s_x denote partial derivatives of s with respect to t and x, respectively. If v_n is negative, this describes etching, and an initially rough surface is smoothed; this is the basis for lead glass polishing by chemical etching or dissolution (Ward *et al.* 2011) ([5]).

The evolution equation (1.1) is easily solved by the method of characteristics. We write

$$s_x = p, \quad s_t = q, \quad F(p,q) = q - v_n\sqrt{1+p^2}. \tag{1.2}$$

Then the characteristic equations for x, p and s follow from Charpit's equations and take the form

$$\dot{x} = -\frac{v_n p}{\sqrt{1+p^2}},$$

$$\dot{p} = 0,$$

$$\dot{s} = \frac{v_n}{\sqrt{1+p^2}} \tag{1.3}$$

where the overdots denote differentiation with respect to t along the characteristics, and the solution can be written parametrically as

$$x = \xi - \frac{v_n s_0' t}{\sqrt{1+s_0'^2}}, \quad s = s_0 + \frac{v_n t}{\sqrt{1+s_0'^2}}, \tag{1.4}$$

where we assume the initial condition $s = s_0(\xi)$ at $t = 0$.

If $v_n < 0$ (the shrinking drop), this solution is perfectly fine. However, it is immediately evident that problems may arise if $v_n > 0$. If, for example, the contact angle $\theta = \tan^{-1}(s_0')$ is finite at the edge, i. e., p is finite, then the front elevation increases, and the interface balloons away from the surface. A physically sensible solution can be recovered by allowing $p = \infty$ at the front, which is then vertical; for example, if we take $s_0 = \sqrt{l^2 - x^2}$, then the solution is just

$$s = \sqrt{(l + v_n t)^2 - x^2}. \tag{1.5}$$

Nevertheless, the issue of what to do if the contact angle is finite remains.

A further issue which confronts (1.5) is that it allows the front to move with a finite speed even where it is in contact with the wall, and this may be in conflict with many situations in which the drop is sessile, that is to say its material is attached to the wall and cannot slip there. This is the typical situation in fluid flows, and may also be appropriate in cell colony growth, where the cells adhere to the wall. Although we have as yet only discussed (1.1) as arising from interfacial motion, it is also the governing equation for s which arises from the kinematic condition for a material flow with a velocity field

$$\mathbf{v} = (u, w). \tag{1.6}$$

The condition that the velocity of the interface is also that of the particles which inhabit it is

$$s_t + \mathbf{v}.\boldsymbol{\nabla}(s - z) = 0, \tag{1.7}$$

and this is precisely (1.1), with $v_n = \mathbf{v}.\mathbf{n}$. Clearly, if we have a medium velocity $\mathbf{v}$ which satisfies the no-slip condition $\mathbf{v} = \mathbf{0}$ at $z = 0$, then the infinite slope solution (1.5) is inadmissible. In fact, $v_n = 0$ at the front and it cannot move. This is the celebrated contact line problem described by Dussan V. and Davis (1974) ([4]), who showed that contact line motion allied with a no-slip condition implies infinite force at the front. Resolutions of this dilemma have been described by Davis (2000) ([3]); either one poses a slip condition, typically of the form

$$u = \beta u_z, \tag{1.8}$$

where β is known as the slip length, or one assumes a thin precursor film, presumably maintained by molecular forces if the fluid is perfectly wetting. Neither of these fixes has much theoretical basis.

2. Flux intensity theory and effective slip

In dealing with the issue described above, we will focus on the case of a growing medium, such as a cell colony, since this provided the motivation for our study, and also because there is a clear physical interpretation of our theory. For a colony of cells, one can define both an average velocity $\mathbf{v}$ of the cells, but in addition there is a relative *flux intensity* I which represents the flux of newly created cells at $\mathbf{r}$. The flux intensity is taken to be a function both of position $\mathbf{r}$ and direction $\mathbf{s}$ ($\mathbf{s}$ is a unit vector). It is analogous to the radiative intensity defined in radiative transfer theory (Chandrasekhar 1960) ([2]). Relative to the mean velocity $\mathbf{v}$, I is the flux per unit area per unit solid angle of direction; thus I has units of m s^{-1} Ω^{-1}, where Ω represents the unit of solid angle (steradian).

This flux intensity defines an additional radiative cell flux $\mathbf{q}$ as

$$\mathbf{q} = \int_{\bigcirc} \mathbf{s} I(\mathbf{r}, \mathbf{s})\, d\omega, \tag{2.1}$$

where $d\omega = \dfrac{\mathbf{r}\,.\,d\mathbf{S}}{r^3}$ is the element of solid angle. If ϕ is the cell volume fraction, then the radiative cell flux defines a second velocity $\mathbf{v}_E$ as

$$\mathbf{q} = \phi(\mathbf{v}_E - \mathbf{v}). \tag{2.2}$$

This second velocity is not necessarily the same as the material averaged velocity $\mathbf{v}$ because the extruded cells may have a relative velocity (for example, if they are all extruded in one direction).

Conservation of cell mass properly involves the velocity $\mathbf{v}_E$, and takes the form

$$\phi_t + \boldsymbol{\nabla}.\,(\phi \mathbf{v}_E) = \phi g, \tag{2.3}$$

where g is the specific cell production rate. Similarly the kinematic condition (1.7) becomes

$$s_t + \mathbf{v}_E.\boldsymbol{\nabla}(s - z) = 0; \tag{2.4}$$

however, we propose that the mechanics of the medium (for example, a viscous stress tensor) should involve the material velocity, and in particular the no slip condition at the wall is still $\mathbf{v} = \mathbf{0}$ at $z = 0$.[1]

It remains to propose a model for the relative flux intensity. While there is variability of I with direction, it is natural to suppose that a newly-produced cell is braked by its external environment towards a background equilibrium. By analogy with radiative transfer theory, we propose the *flux intensity equation*

$$\mathbf{s}.\boldsymbol{\nabla}_{\mathbf{r}} I = \frac{\partial I}{\partial s} = -\frac{I - B}{l_p}, \tag{2.5}$$

where l_p is a measure of cell spacing. This equation states that I relaxes to the background level over a distance of order l_p, due to the braking effect of the environment. Generally, we assume $B = B(\mathbf{r})$ (the medium is isotropic); it also depends on I, and so the equation is not necessarily simple to solve. The only obvious suitable boundary condition is to specify no flux intensity downwards through the wall. Since the cells are presumed attached to the wall, this implies

$$I = 0 \quad \text{for} \quad \mathbf{s}.\mathbf{k} < 0 \quad \text{at} \quad z = 0, \tag{2.6}$$

where $\mathbf{k}$ is the unit normal in the z direction.

A very useful approximation follows from the reasonable assumption that l_p is small relative to the dimension of the colony. In that case, the solution of (2.5) is approximately

$$I \approx B(\mathbf{r}) - l_p \mathbf{s}.\boldsymbol{\nabla}_{\mathbf{r}} B, \tag{2.7}$$

and, in particular, we have the approximate local equilibrium approximation

$$B \approx \frac{1}{4\pi} \int_{\bigcirc} I \, d\omega. \tag{2.8}$$

[1] A useful insight into the difference between $\mathbf{v}$ and $\mathbf{v}_E$ lies in consideration of the cells at the wall. If attached, then certainly $\mathbf{v}.\mathbf{k} = 0$, but new cell production will ensure that $\mathbf{v}_E.\mathbf{k} > 0$.

It follows from (2.7) that the relative flux is

$$\int_{\bigcirc} \mathbf{s}I(\mathbf{r},\mathbf{s})\,d\omega = -\frac{4\pi l_p}{3}\boldsymbol{\nabla}B, \tag{2.9}$$

and we see that, as for radiative transfer, it is necessary to constitute B in terms of the variables of the medium. We do this by relating B to the net cell production rate. Note that (2.5) is a singular perturbation problem, where we might expect boundary layers to occur. However, a boundary layer structure is not possible for (2.6) (there is no exponential decay away from the boundary), which suggests that (2.7) must be uniformly valid. As we shall see later, this is not true at the margins.

The determination of B follows from the use of (2.8), together with the following considerations. If each cell, having volume V_c and surface area A_c, produces new cells at a rate G ($\mathrm{m}^3\ \mathrm{s}^{-1}$), then the source term in (2.3) is

$$g = \frac{G}{V_c}; \tag{2.10}$$

on the other hand, the total radiative flux is just

$$\int_{\bigcirc} I\,d\omega = \frac{G}{A_c}; \tag{2.11}$$

it follows that

$$B \approx \frac{G}{4\pi A_c} = \frac{V_c g}{4\pi A_c} \approx \frac{d_c g}{24\pi}, \tag{2.12}$$

where d_c is cell diameter.

We use (2.12) and (2.9) in (2.2) and (2.3), which leads to

$$\begin{aligned} \phi(\mathbf{v}_E - \mathbf{v}) &= -D\boldsymbol{\nabla}g, \\ \phi_t + \boldsymbol{\nabla}.(\phi\mathbf{v}) &= \phi g + D\nabla^2 g, \end{aligned} \tag{2.13}$$

where

$$D = \frac{l_p d_c}{18}. \tag{2.14}$$

The term in D is small and generally represents a regular perturbation of the equations, since typically g will depend on a nutrient c which is also determined by an elliptic equation.

3. Interfacial boundary condition

We now consider the adjusted kinematic boundary condition in (2.4). However, we cannot use (2.9) there. This is because there is a discontinuity in the flux at the surface. In the interior, the net flux $\mathbf{q}$ arises through a weak imbalance in the radiative flux in opposite directions. At the surface there is no such imbalance, and so we must consider the surface flux balances separately. We argue as follows: we measure arc length clockwise from the left margin and denote it as σ. In an

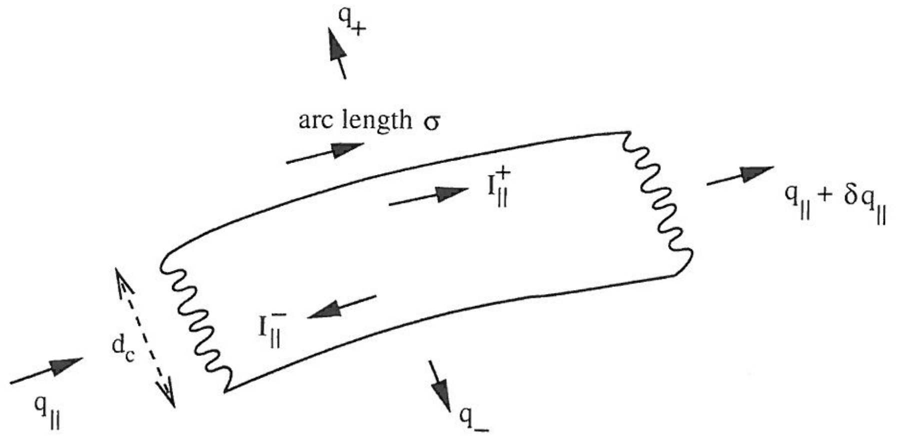

FIG. 1—Schematic of surface flux layer.

element of the surface of width W and length $\Delta\sigma$, there are $\sim \phi W \Delta\sigma/d_c^2$ cells, each producing new material at a rate $G = V_c g$; thus the surface production rate per unit area is $\dfrac{\phi V_c g}{d_c^2} \approx \frac{1}{6}\pi\phi d_c g$, and this must be equal to the sum of the net flux up, q^+, the net flux down, q^-, and the net flux along the surface, j:

$$q^+ + q^- + j = \tfrac{1}{6}\pi\phi d_c g; \tag{3.1}$$

note that the flux vector at the upper surface is

$$\mathbf{q} = q_+\mathbf{n} + j\mathbf{T}, \tag{3.2}$$

where $\mathbf{T}$ is the tangent unit vector (in the direction of σ). The net flux down is still determined from $(2.13)_1$, thus

$$q^- = D\frac{\partial g}{\partial n}. \tag{3.3}$$

The kinematic condition (2.4) can be written in the form

$$\phi[s_t + \mathbf{v}.\boldsymbol{\nabla}(s-z)] = q_+\sqrt{1+s_x^2}, \tag{3.4}$$

which can be compared with (1.1); q_+ is determined from (3.1), and it only remains to determine the surface flux j. As it turns out , this is essential for the regularisation of the margin movement.

3.1. Surface flux

The production of new cells by the cells in the surface layer induces a tangential surface radiative flux intensity, as indicated in Fig. 1. We denote the component in the positive σ direction as $I_{\|}^+$, and that in the negative σ direction as $I_{\|}^-$. Integrating over all forward and backward directions, and over the surface layer thickness, we find the corresponding fluxes to be

$$q_{\|}^+ = \pi d_c I_{\|}^+, \quad q_{\|}^- = \pi d_c I_{\|}^-, \tag{3.5}$$

having units of m^2 s^{-1}. In addition, the components of the radiative transfer equation take the form

$$I_{\|}^{+} = B - l_p \frac{\partial I_{\|}^{+}}{\partial \sigma},$$
$$I_{\|}^{-} = B + l_p \frac{\partial I_{\|}^{-}}{\partial \sigma}, \tag{3.6}$$

from which we deduce

$$q_{\|}^{+} = \pi d_c B - l_p \frac{\partial q_{\|}^{+}}{\partial \sigma},$$
$$q_{\|}^{-} = \pi d_c B + l_p \frac{\partial q_{\|}^{-}}{\partial \sigma}. \tag{3.7}$$

If we define the net surface flux in the positive σ direction as

$$q_{\|} = q_{\|}^{+} - q_{\|}^{-}, \tag{3.8}$$

then we can deduce from (3.7) that $q_{\|}$ satisfies the equation

$$q_{\|} = -2\pi d_c l_p \frac{\partial B}{\partial \sigma} + l_p^2 \frac{\partial^2 q_{\|}}{\partial \sigma^2}. \tag{3.9}$$

We assume that the first term on the right hand side is very small, if not actually zero. From (2.12), this is justified if

$$|q_0| \gg \frac{l_p d_c^2 g}{12d}, \tag{3.10}$$

where d is the drop size, and q_0 is defined below (see (3.13)). In this case we may approximate (3.9) as

$$q_{\|} = l_p^2 \frac{\partial^2 q_{\|}}{\partial \sigma^2}. \tag{3.11}$$

The second derivative term is also small (because $l_p \ll d$), but is crucially retained as it provides a singular correction which will be important at the margins (where it is essential that $q_{\|}$ be non-zero). Note that the *net* flux j in (3.1) leaving the surface segment is just

$$j = \frac{\partial q_{\|}}{\partial \sigma}, \tag{3.12}$$

and has units of m s^{-1}. The approximate solution of (3.11) near the left margin ($\sigma = 0$) is just

$$q_{\|} = q_0 \exp\left(-\frac{\sigma}{l_p}\right), \tag{3.13}$$

so that

$$j = -\frac{q_0}{l_p}\exp\left(-\frac{\sigma}{l_p}\right). \tag{3.14}$$

We allow the coefficient q_0 to depend on local slope $p = s_x$ and time t, but it is as yet undetermined. We expect $q_0 < 0$ so that there is a surface flux towards the margin, allowing it to move.

Near $\sigma = 0$, we have (assuming a locally linear drop profile)

$$\sigma \approx \frac{s\sqrt{1+s_x^2}}{s_x}, \tag{3.15}$$

so that we can write

$$j = -\frac{q_0}{l_p}\exp(-\Lambda s), \tag{3.16}$$

where

$$\Lambda = \frac{\sqrt{1+p^2}}{l_p p}. \tag{3.17}$$

Thus we have, from (3.1), (3.3) and (3.16),

$$q_+ = \tfrac{1}{6}\pi\phi d_c g - D\frac{\partial g}{\partial n} + \frac{q_0}{l_p}e^{-\Lambda s}. \tag{3.18}$$

The second term is negligible and will be neglected. It is much less than the final term providing, using (2.14),

$$|q_0| \gg \frac{Dgl_p}{d} = \frac{l_p^2 d_c g}{18d}, \tag{3.19}$$

which is essentially the same as (3.10). The kinematic condition (3.4) can now be written in the form

$$\phi[s_t + \mathbf{v}.\boldsymbol{\nabla}(s-z)] = q_+\sqrt{1+s_x^2}. \tag{3.20}$$

4. Droplet evolution

In order to illustrate the use of this condition, we consider the particular case where $\mathbf{v} = \mathbf{0}$. This is in any case true near the margin, which is our main concern, and more elaborate prescription of $\mathbf{v}$ involves discussion of cell rheology and so on, which is beyond the scope of our focus.

In this case, the droplet shape is determined by the evolution equation

$$s_\tau = f(s,p) = \left(1 + Qe^{-\Lambda s}\right)\sqrt{1+p^2}, \tag{4.1}$$

where $p = s_x$,

$$t = \frac{6\tau}{\pi d_c g}, \quad Q = \frac{6q_0}{\pi\phi d_c l_p g}, \tag{4.2}$$

and Λ is given by (3.17). Note that τ has units of length, while Q is dimensionless. Note further that the assumption (3.10) (and thus also (3.19)) is equivalent to

$$|Q| \gg \frac{d_c}{2\pi\phi d}. \tag{4.3}$$

Charpit's characteristic equations for the solution are now

$$\begin{aligned} \dot{x} &= -f_p, \\ \dot{p} &= pf_s, \\ \dot{s} &= f - pf_p, \end{aligned} \tag{4.4}$$

where the overdot denotes differentiation with respect to τ. The function $Q(p,\tau)$ must be chosen in order that the margin of the drop remain at the wall, i. e., so that $\dot{s} = 0$ when $s = 0$. The dependence of Q on τ does not affect the form of (4.4). From (4.1), we have

$$\begin{aligned} f_s &= -\Lambda Q e^{-\Lambda s}\sqrt{1+p^2}, \\ f_p &= \frac{p}{\sqrt{1+p^2}}\left(1 + Qe^{-\Lambda s}\right) + \left(Q_p - sQ\Lambda_p\right)e^{-\Lambda s}\sqrt{1+p^2}, \end{aligned} \tag{4.5}$$

and thus at $s = 0$,

$$(f - pf_p)|_{s=0} = \frac{1+Q}{\sqrt{1+p^2}} - pQ_p\sqrt{1+p^2} = 0, \tag{4.6}$$

of which the solution is

$$Q = \frac{V(\tau)p}{\sqrt{1+p^2}} - 1, \tag{4.7}$$

whence the partial differential equation (4.1) for s is

$$s_\tau = Vpe^{-\Lambda s} + \left(1 - e^{-\Lambda s}\right)\sqrt{1+p^2}, \tag{4.8}$$

and calculation of $\dot{x}_f$ at $s = 0$ shows that $\dot{x}_f = -V$, i. e., V is (minus) the front speed (in terms of τ). In terms of t, the actual front speed is

$$-\frac{dx_f}{dt} = V_f = \tfrac{1}{6}\pi d_c g V. \tag{4.9}$$

The determination of V is a consequence of a mass flux continuity condition at the front, somewhat analogous to Dussan V. and Davis's (1974) ([4]) discussion of the kinematics at the contact line. The flux $-q_{\|}$ towards the (left hand) margin must equal the relative flux away from the margin, thus

$$q_{\|} = -V_f d_c \quad \text{at} \quad s = 0 \quad (p > 0). \tag{4.10}$$

From (3.13), (4.2) and (4.7), this leads to the prescription of V as

$$V = \frac{1}{\beta + \dfrac{p_f}{\sqrt{1+p_f^2}}}, \tag{4.11}$$

where

$$\beta = \frac{d_c}{\phi l_p}, \tag{4.12}$$

and we suppose $\beta \sim O(1)$. From (4.7) and (4.11), we have

$$-Q = \frac{\beta}{\beta + \sin\theta_f}, \tag{4.13}$$

where $p_f = \tan\theta_f$, and using (4.12) and (4.3), we see that the assumption (3.10) is justified if

$$l_p \ll \frac{2\pi d}{\beta + \sin\theta_f}, \tag{4.14}$$

which is certainly valid for $\beta \sim O(1)$. This justifies our sequence of approximate solutions.

This gives V in terms of p_f, the value of p at $s = 0$, and an evolution equation for p_f follows from (4.4) and (4.5), which leads to

$$\dot{p}_f = \frac{\Lambda\beta p_f(1+p_f^2)}{\beta\sqrt{1+p_f^2} + p_f}. \tag{4.15}$$

The characteristic equations take the form

$$\begin{aligned} \dot{x} &= -\frac{p}{\sqrt{1+p^2}}\left(1 - e^{-\Lambda s}\right) - Ve^{-\Lambda s}, \\ \dot{p} &= \Lambda p e^{-\Lambda s}\left[\sqrt{1+p^2} - Vp\right], \\ \dot{s} &= \frac{\left(1 - e^{-\Lambda s}\right)}{\sqrt{1+p^2}}. \end{aligned} \tag{4.16}$$

It is evident from (4.15) that p_f reaches infinity in finite time, at which point $V < 1$. Consequently, $(4.16)_2$ implies that p also reaches infinity in finite time. At this point the slope becomes infinite, and in fact the drop continues to roll round until the contact angle at the front becomes π. To see this, we write

$$p = \tan\theta, \tag{4.17}$$

so the equations (4.16) become

$$\dot{x} = -\left(1 - e^{-\Lambda s}\right)\sin\theta - Ve^{-\Lambda s},$$
$$\dot{\theta} = \Lambda e^{-\Lambda s}\sin\theta\,[1 - V\sin\theta],$$
$$\dot{s} = \left(1 - e^{-\Lambda s}\right)\cos\theta, \tag{4.18}$$

and the velocity V and the front slope angle θ_f are given by

$$V^L = \frac{1}{\beta + \sin\theta_f^L}, \quad \dot{\theta}_f^L = \frac{\beta\Lambda\sin\theta_f^L}{\beta + \sin\theta_f^L}, \tag{4.19}$$

where the superscript L denotes the left hand front; from this we can see that $\theta_f^L \to \pi$ and thus $V^L \to 1/\beta$ as $\tau \to \infty$.

This describes the evolution of the colony in the vicinity of the left hand margin. Evidently the right hand margin is described by the same equations, but with the signs of V, θ, θ_f and x changed. We can see that the equations (4.18) are unchanged under this change of sign, as are both equations in (4.19) providing β has the same sign as θ_f. We thus obtain a description for the right hand front by prescribing V^R and θ_f^R as the following replacement of (4.19):

$$V^R = \frac{1}{-\beta + \sin\theta_f^R}, \quad \dot{\theta}_f^R = \frac{\beta\Lambda\sin\theta_f^R}{\beta - \sin\theta_f^R}. \tag{4.20}$$

This gives us two expressions for the left and right front speeds, V^L and V^R, but in practice, we need a uniform expression for V in (4.18), which has to switch smoothly between the values at the two fronts. This is possible because for $s = O(1)$, the value of V is irrelevant. A uniform expression can thus be obtained by defining V in (4.18) as

$$V = V^L H(\theta) + V^R[1 - H(\theta)], \tag{4.21}$$

where

$$H(\theta) = \tfrac{1}{2}(1 + \tanh K\theta), \tag{4.22}$$

where K is positive and large, though in practice it need not be very large.

In solving the problem numerically, we prescribe $s(x,0) = s_0(x)$, from which we have the initial values of $\theta_f^{L,R}$ (left and right fronts, defined by $\tan\theta_f = s_x|_{s=0}$, $\theta_f^L > 0$, $\theta_f^R < 0$). (4.19) and (4.20) thus provide for the solution of $\theta_f^{L,R}(\tau)$ and thus $V^{L,R}$, from which, using (4.21), we can then solve (4.18) to find x, θ and s. Starting from an initial parabolic profile, Fig. 2 shows the evolution to an advancing profile with contact angle π.

5. Discussion

Faced with the contact line problem of the inconsistency of a no slip condition with a moving contact line, we have posed a resolution in the particular context of the

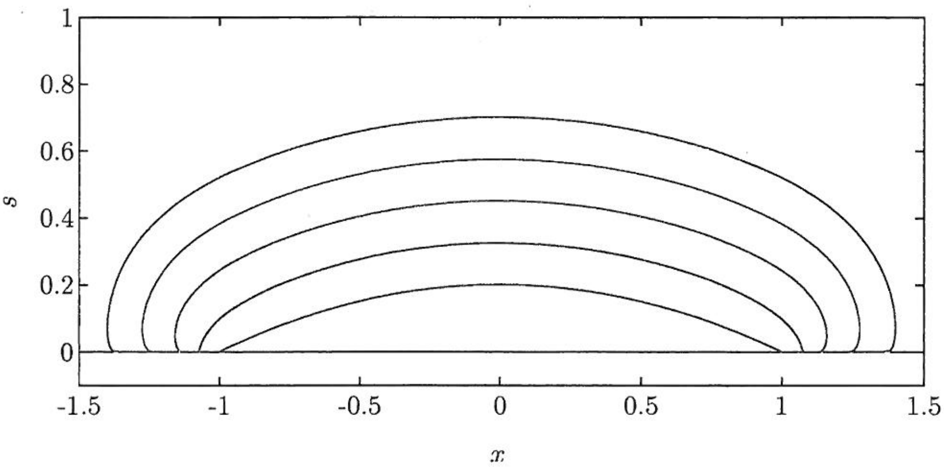

FIG. 2—Evolution of an initially parabolic cell colony, and the formation of a rolling front. The solution of (4.8) is constructed using the characteristic equations (4.18), with V defined by (4.21) and (4.22), and with $K = \infty$ (meaning that the symmetry of the solution was used). The other parameter values are $\Lambda = 20$ and $\beta = 1$.

growth of a colony of attached cells. The growth of the cells induces an extra cell flux, which is described by a direction-dependent flux intensity, analogous to the radiative flux intensity of radiative transfer theory.

For a 'dense' medium, we can approximately solve this to provide an explicit representation for the extra induced flux. However, this expression is inappropriate at a free surface, because there is a jump in the flux at the surface. By detailed consideration of the flux in a surface layer, we are led to an expression for the tangential surface flux, and this finally leads us to a corrected form of the surface kinematic condition.

The tangential surface flux decays exponentially away from the attached surface, but has an unknown dependence on the free surface slope and time. The slope dependence is determined by the requirement that the drop remain attached to the surface, while the time dependence is determined by a tangential surface flux continuity condition at the margin.

With these conditions in place, a closed set of characteristic equations is found for the interface, whose solution shows that an initially concave surface will roll up so that the margins advance with a contact angle of π, consistent with kinematic considerations. Although our specific application has been to sessile cell colonies, these results raise the interesting possibility of applying a similar theory to contact line problems in fluid mechanics.

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