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A continuum model for the growth of bacterial colonies on a surface

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Abstract. A model for the spatio-temporal growth of a bacterial colony on the flat surface of a solid medium is introduced based on a reaction-diffusion equation with vertical and lateral growth components. If the colony height is restricted to some maximum value, the colony morphology corresponds to solitary wave propagation in the radial direction. However, if colony growth is flux limited by the diffusion of initially separated components into the colony, vertical colony growth results from a steady state, finite sized reaction zone within the colony. In the flux-limited growth regime a more general colony morphology is obtained with constant velocity propagation of the colony radius and central height in qualitative agreement with experiment.

1. Introduction

The growth of bacterial colonies on the surface of a solid medium is a common process and by appropriate variation of the environmental conditions a wide variety of colony morphologies can be observed. Extensive experimental studies have been made of the colony morphologies for *Bacillus subtilus* growing on the surface of a thin agar plate as a function of the gel strength, nutrient concentration, temperature and humidity [1, 2]. In the absence of mutations, three basic colony morphologies were observed corresponding to compact growth, tip-splitting growth and fractal growth. Although for colonies of an immotile strain of *Bacillus subtilus* only compact and fractal growth morphologies were found [1]. In general terms, bacterial colonies grown from single cells on nutrient-poor media show ramified structures, whilst on nutrient-rich media the compact colonies have an overall circular shape with a rough edge. Other experimental studies of the growth of compact colonies of *Escherichia coli* and *Bacillus subtilus* on agar plates also shown kinetic roughening at the colony edge [3]. Unfortunately, all of these studies concentrate on the analyis of a two-dimensional projection of the colony on to the flat surface whereas in general, bacterial colonies grown on the surface of a growth medium will not be a single cell deep. The three-dimensional form of the colonies as function of time is less well understood.

In a pioneering study of the growth kinetics of surface colonies of bacteria, Pirt [4] observed a virtual constant rate of radial growth for colonies of *Escherichia coli*, *Klebsiella aerogenes* and *Streptococcus faecalis*. Wimpenny [5] later determined the radial height profile for colonies of *Bacillus cereus*, *Escherichia coli* and *Staphylococcus albus* of different ages on nutrient agar. In spite of the differences in cell types, the colony profiles were seen to have a common basic structure. A steeply rising leading

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edge and a flat or domed centre whose height grows linearly with time. However, the vertical growth rate of the colony at its centre is at least an order of magnitude smaller than the radial growth rate of the colony. Subsequently similar observations were also made by Kamath and Bungay [6] for the growth of yeast colonies on solid media.

In the following section we introduce a model for the spatio-temporal evolution of bacterial colonies grown from a localized inoculation on a flat surface. Colony expansion results from structural reorganization following the growth and division of cells within the colony. Thus the model is based upon a reaction-diffusion equation which includes a reaction term that allows for colony expansion which is locally normal to the suface and for lateral growth anisotropy. A key component of the model is the functional form of the normal growth velocity. In section 3 growth is subject to a simple restriction of the maximum height of the colony and connection is made with a model introduced by Pirt [4]. However, in general, colony growth is limited by the flux of oxygen and nutrient into the colony. In section 4 a microscopic model is introduced to characterize the flux limited growth of biofilms and support a more general form for the normal growth velocity used in section 5 to model the flux limited growth of surface colonies. The paper concludes with a discussion.

2. Model

In unstirred media, since the growth in microbial numbers occurs by cell division, spatial variations of the microbial population can be expected. For compact bacterial colonies growing on the surface of a solid growth medium, the colony morphology can be described by its height $h(\boldsymbol{r}, t)$ above the surface. Since we will work in the continuum limit, $h(\boldsymbol{r}, t)$ represents a course-grained description of the colony's height profile. Thus it is reasonable, and convenient, to ignore any overhangs in the colony surface and assume that $h(\boldsymbol{r}, t)$ is a single-valued function of the position of $\boldsymbol{r}$ in the surface.

Consider the growth of a compact bacterial colony which occurs by the expansion and division of cells within the colony. The colony will grow in volume by expansion in a direction which is locally normal to the surface. Let the normal growth velocity of the colony be $v\boldsymbol{n}$, where $\boldsymbol{n}$ is the unit vector which is locally normal to the colony surface. The incremental change in height in time δt projected along the vertical axis is then $\delta h = v\,\delta t[1+(\nabla h)^2]^{1/2}$, giving in the limit $\delta t \to 0$

$$\partial h/\partial t = v[1+(\nabla h)^2]^{1/2} \approx v(1+(1/2)(\nabla h)^2+\ldots). \tag{2.1}$$

After the inclusion of a term to account for the relaxation of the colony surface and allowing for the possibility of a lateral growth anisotropy, the simplest nonlinear partial differential equation for the spatio-temporal growth kinetics of the colony surface in the absence of fluctuations can be written as

$$\partial h(\boldsymbol{r}, t)/\partial t = \nu\nabla^2 h(\boldsymbol{r}, t) + v(\boldsymbol{r}, h(\boldsymbol{r}, t), t)[1+(\Lambda/2)(\nabla h(\boldsymbol{r}, t))^2] \tag{2.2}$$

where ν is a mobility coefficient which can be identified with the surface tension and ∇^2 is the Laplacian operator. The second term on the right-hand side of equation (2.2) represents the lowest order of growth term that can appear in a surface growth model. Such a nonlinear term must be expected in all situations where lateral growth is allowed and Λ characterizes the lateral growth anisotropy [7]. If the normal growth velocity v was a constant, then equation (2.2) would be equivalent to the KPZ equation for surface growth in the absence of fluctuations [7]. However in a bacterial colony v will, in

general, be a function of the time t, location r and local height $h(r, t)$. In the following we will investigate colony evolution with model forms of $v(r, h(r, t), t)$ which correspond to different realizations of the physical processes controlling bacterial colony growth.

For the growth of a colony with circular symmetry on a flat two-dimensional surface from an inoculum located at the origin equation (2.2) reduces to

$$\partial h(r, t)/\partial t = (v/r)\partial/\partial r(r\,\partial h/\partial r) + v(1 + (\Lambda/2)(\partial h/\partial r)^2) \tag{2.3}$$

which must be supplemented by the initial condition that $h(r=0, t=0)>0$ and the boundary condition $(\partial h/\partial r)_{r=0}=0$. These initial and boundary conditions are conveniently met by assuming that the inoculation is in the form of a Gaussian located at the origin with

$$h(r, 0)/h(0, 0) = I(r, \sigma) = \exp(-r^2/2\sigma^2) \tag{2.4}$$

where $h(0, 0)$ and σ characterize the height and width of the colony at inoculation.

3. The Pirt model

In a pioneering study of the growth of bacterial colonies on the surface of a solid nutrient medium [4], Pirt noted, over a wide variety of conditions, a constant rate of increase of the colony radius while the thickness of the colony away from its outer periphery was approximately constant. To reconcile this observation with the well known exponential growth of cell number in liquid cultures Pirt introduced a geometric model for bacterial colony evolution. In this model the colony grows exponentially in a growth zone at its outer edges up to a maximum colony height, resulting in a flat central region. This model can be quantified within the context of equation (2.3) by writing the normal growth velocity as

$$v(h(r, t)) = \lambda h(r, t)(1-h(r, t)/h_m) \tag{3.1}$$

where λ is a growth coefficient and h_m is the maximum height obtained by the colony. A logistic form has been assumed for the normal growth velocity as a simple functional form that defines a maximum colony height and gives locally exponential growth ($\partial h/\partial t \propto h$) for the leading edges of the colony where h is small ($h \ll h_m$). Substituting equation (3.1) into equation (2.3) gives

$$\partial u/\partial t^* = (1/x)\,\partial/\partial x\,(x\,\partial u/\partial x) + u(1-u)[1 + (\xi/2)(\partial u/\partial x)^2] \tag{3.2}$$

where $u = u(x, t^*) = h(x, t^*)/h_m$, $x = (\lambda/v)^{1/2} r$, $t^* = \lambda t$ and $\xi = (\lambda\Lambda h_m{}^2/v)$. This equation is supplemented by the initial condition that $u(r=0, t=0)>0$ and the boundary condition $(\partial u/\partial r)_{r=0}=0$, both of which are satisfied by the Gaussian inoculation of equation (2.4).

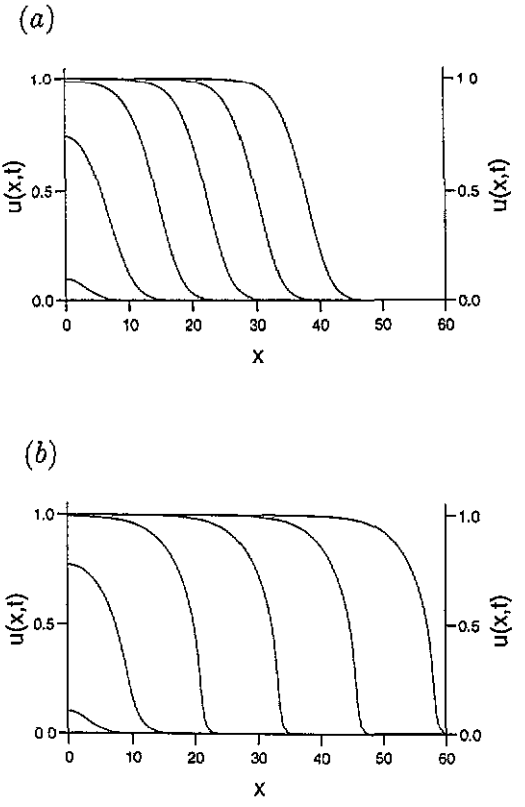

Figure 1. Radial height profile for a Pirt model of bacterial colony growth defined by equation (3.2) at $\lambda t = 0, 4, 8, 12, 16, 20$ for (*a*) $\xi = 1$ and (*b*) $\xi = 100$. Gaussian inoculation with $u(0, 0) = 0.1$ and $(\sigma/h_m) = 2.5$.

First note that in the case of $\xi = 0$, equation (3.2) reduces to Fisher's equation [8] which is known to possess solitary wave solutions with an asymptotic dimensionless radial velocity of two [9]. Figure 1 shows the temporal evolution of the radial height profile of the colony obtained by solving equation (3.2) with zero gradient boundary conditions for two values of the parameter ξ: $\xi = 1$ and $\xi = 100$. The initial condition was a Gaussian inoculation from equation (2.4) with $u(0, 0) = 0.1$ and $(\sigma/h_m) = 2.5$. If we assume $(\lambda h_m^2/\nu) = 1$, these two cases correspond to growth by uniform expansion ($\Lambda = 1$) and a very large lateral growth anistropy ($\Lambda = 100$). In both cases the qualitative features of the solution are the same. After an initial period during which the central colony attains its maximum height, solitary wave behaviour is obtained in the colony height profile. The outer edge of the colony has a shape which is independent of time and moves at a constant radial velocity outwards form the origin. The location of the leading edge of the colony is denoted $x_0(t)$ and here defined by $u(x_0, t) = u(0, 0)/2$. For $\xi \leqslant 10$ the colony height profile and the radial growth velocity (dx_0/dt) are essentially independent of ξ and identical, within numerical accuracy, to those of the Fisher equation with $\xi = 0$. However, for $\xi \gg 10$ significant departures in the shape of the colony around the leading edge from the results for $\xi = 0$ are found and the radial growth velocity increases with ξ. For example at $\xi = 100$ the radial growth velocity is found to be $(dx_0/dt) = 3.08$ and figure 1 shows an increased asymmetry of the colony height

profile at the leading edge with larger ξ. In principle ξ could be used as a free parameter to fit to experiment. But since solutions of the Pirt model are only weakly dependent on the degree of lateral growth anisotropy, this constitutes an ill-defined inverse problem.

The major assumption in Pirt's model of colony growth is that the central region of the colony is flat and its height remains constant. However, experiments by Wimpenny [5] to measure the profile of bacterial colonies grown on solid nutrient agar show that the central height of the colony, like the colony radius, grows linearly with time, albeit at a speed at least an order of magnitude smaller. In addition, the radial height profile of the colonies was seen to be convex in contrast to the flat top of colonies in the Pirt model. Thus a model for the growth of bacterial colonies on a surface must take into account flux limited growth at the centre of the colony.

4. Reaction zone in a biofilm

The central region of a surface colony can be regarded to a good approximation as a biofilm comprising a layer of bacteria separating the supporting nutrient medium from the atmosphere. Aerobic growth of the bacteria within the biofilm requires diffusion of nutrient (C) and oxygen (A) into the biofilm and results in the addition of biomass (B). A reaction scheme representing aerobic growth can be written in a highly simplified form as [10]

$$A+B+C\rightarrow 2B \qquad \text{rate } \mu. \tag{4.2}$$

In addition there is also a maintenance requirement of the cells within the colony which can be similarly written as

$$A+B+C\rightarrow B \qquad \text{rate } \kappa. \tag{4.2}$$

Let $A(\boldsymbol{r}, t)$, $B(\boldsymbol{r}, t)$ and $C(\boldsymbol{r}, t)$ denote the local concentrations of species A, B and C at position $\boldsymbol{r}$ and time t. The coupled set of reaction-diffusion equations describing the spatio-temproal evolution of an unstirred system incorporating the reaction schemes (4.1) and (4.2) is conventionally given by

$$\partial a/\partial t = D_A \nabla^2 a - (\mu+\kappa)\, abc \tag{4.3}$$

$$\partial b/\partial t = D_B \nabla^2 b + \mu\, abc \tag{4.4}$$

$$\partial c/\partial t = D_C \nabla^2 c - (\mu+\kappa)\, abc \tag{4.5}$$

where $a(\boldsymbol{r}, t) = A(\boldsymbol{r}, t)/A_0$, $b(\boldsymbol{r}, t) = B(\boldsymbol{r}, t)/B_m$ and $c(\boldsymbol{r}, t) = C(\boldsymbol{r}, t)/C_0$ are dimensionless local concentrations. Note that within the framework of such a continuum model, local concentrations must be interpreted as coarse grained averages taken over a local volume which is typically much larger than the characteristic size of the component. A_0 and C_0 denote the uniform bulk concentrations of components A and C in their reservoirs, so that $0 \leqslant a(\boldsymbol{r}, t) \leqslant 1$ and $0 \leqslant c(\boldsymbol{r}, t) \leqslant 1$. B_m denotes the biomass concentration consistent with a close packed configuration of cells in a colony. The Fickian diffusion constants of the three components are denoted D_A, D_B and D_C.

Typically, $D_B \ll D_A \approx D_C$. So for sufficiently small D_B and sufficiently large μ, the local biomass concentration can grow up to, but physically cannot exceed, a value consistent with a close-packed configuration of cells. In such cases the set of equations (4.3)–(4.5) is unable to provide an accurate description of the spatial dependence of

microbial growth kinetics, since equation (4.4) does not constrain the local biomass concentration to the physically acceptable range $0 \leqslant b(\boldsymbol{r}, t) \leqslant 1$. If local biomass growth is restricted by physical constraints, then an additional term must be included in the equation for biomass growth to account for the non-local addition of cells at the surface of a close-packed colony as a result of the growth and reorganization of cells within the colony. This is achieved by replacing equation (4.4) with

$$\partial b/\partial t = D_B \nabla^2 b + \psi(\nabla b)^2 + \mu abcf(b) \tag{4.6}$$

where ψ is the non-local growth coefficient. The local growth limiting function $f(b)$ is a monotonic decreasing function of b on the interval (0, 1) with $f(0) = 1$ and $f(1) = 0$. A convenient form is

$$f(b) = (1 - b^{\alpha}) \tag{4.7}$$

where $\alpha = 1$ corresponds to a logistic form for the local biomass growth rate. However, since physical constraints limiting the local addition of biomass should not be expected to arise until the local biomass concentration approaches the close packing value, typically $\alpha \gg 1$. The non-local growth coefficient ψ is determined from the constraint that the growth rate of the total biomass within the sample, defined by

$$\mathrm{d}b(t)/\mathrm{d}t = \int \mathrm{d}\boldsymbol{r}\, \partial b(\boldsymbol{r}, t)/\partial t \tag{4.8}$$

must be the same from both equations (4.4) and (4.6). Thus

$$\mu \int \mathrm{d}\boldsymbol{r}\, abc = \int \mathrm{d}\boldsymbol{r}[\psi(\nabla b)^2 + \mu abcf(b)]. \tag{4.9}$$

Consider the particular case of growth of a biofilm of aerobic bacteria on the flat surface of a nutrient-rich growth medium under an oxygen-rich atmosphere from a uniform inoculation covering the surface. Neglecting edge effects and in the absence of fluctuations, concentration variations in the system will be unidimensional and normal to the surface. The equations describing the evolution of the system reduce to

$$\partial a/\partial t = D_A\, \partial^2 a/\partial z^2 - (\mu + \kappa) abc \tag{4.10}$$

$$\partial b/\partial t = D_B\, \partial^2 b/\partial z^2 + \psi(\partial b/\partial z)^2 + \mu abcf(b) \tag{4.11}$$

$$\partial c/\partial t = D_C\, \partial^2 c/\partial z^2 - (\mu + \kappa) abc \tag{4.12}$$

where $a(z, t)$, $b(z, t)$ and $c(z, t)$ are the dimensionless concentrations per unit area of biofilm. Components A and C are intially separted with

$$a(z, 0) = 1 - c(z, 0) = \theta(z) \tag{4.13}$$

where $\theta(z)$ is the Heaviside theta function ($\theta(z) = 0$ if $z < 0$ and $\theta(z) = 1$ if $z > 0$) and the inoculum is assumed to have a Gaussian form with

$$b(z, 0) = b(0, 0) I(z, \sigma). \tag{4.14}$$

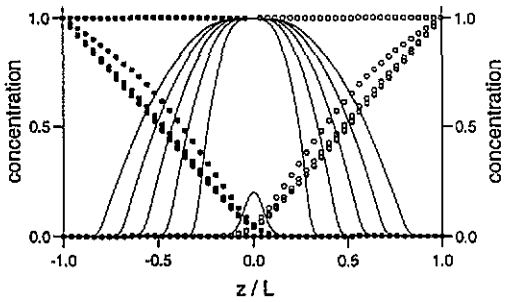

Figure 2. Spatio-temporal evolution of the component concentration profiles through a biofilm from equations (4.10)–(4.15) with fixed boundary conditions, $\kappa = 0$, $D_C = D_A$, $(D_B/D_A) = 10^{-2}$ and $(\mu/D_A)^{1/2}L = 50$. Components A and C are initially separated and there is a Guassian inoculation for B with $b(0, 0) = 0.2$ and $(\sigma/L) = 0.05$. The reduced biomass concentration profile $b(z, t)$ is denoted by a solid line, while for clarity the continuous curves for the reduced oxygen and nutrient concentrations are represented by symbols: (○) for $c(z, t)$ and (●) for $a(z, t)$. Results are shown at times $\mu t = 0, 40, 80, 120, 160, 200$.

Equations (4.10)–(4.14) are solved numerically on the interval $-L \leqslant z \leqslant L$ for $L \gg \sigma$ with fixed boundary conditions at $z = \pm L$. The nonlinear growth coefficient is given from equation (4.9) by

$$\psi \int_{-L}^{L} \mathrm{d}z\, (\partial b/\partial z)^2 = \mu \int_{-L}^{L} \mathrm{d}z\, abc[1-f(b)]. \tag{4.15}$$

For simplicity consider a symmetric system with no cell maintenance requirement such that $D_A = D_C$ and $\kappa = 0$. Figure 2 shows the evolution of the concentration profiles for $D_B/D_A = 10^{-2}$, $\alpha = 4$ and $(\mu/D_A)^{1/2}L = 50$ with $b(0, 0) = 0.2$ and $(\sigma/L) = 0.05$. Initially the total biomass in the biofilm can increase as a result of the local addition of biomass alone. However, once the biomass concentration at the centre of the biofilm approaches close packing, biomass is added to the biofilm by both local and non-local growth mechanisms. The central region of the biofilm where $abc \neq 0$ constitutes the reaction zone of the biofilm and controls the magnitude of both local and non-local contibutions to the growth of biomass within the biofilm. For $\mu t > 100$ $a(z, t)$ and $c(z, t)$ achieve steady-state forms which are characterized by a linear decrease in concentration from the boundary reservoir to the reaction zone at the centre of the biofilm. The reaction zone also assumes a steady-state form for $\mu t > 100$ since the size of the reaction zone is smaller than the close-packed core of the biofilm. Thus in the steady-state regime biofilm growth occurs soley by the non-local growth mechanism. The two surfaces of the biofilm are located at $z_+(t)$ and $z_-(t)$ by a height condition, such as $b(z_+, t) = b(0, 0)/2$ for $z > 0$ and $b(z_-, t) = b(0, 0)/2$ for $z < 0$. In the steady-state regime both of the biofilm surfaces propagate at constant velocity away from the plane of inoculation and thus the thickness of the biofilm, defined as $h(t) = (z_+(t) - z_-(t))$, will increase linearly with time. The exponent α acts as a weak control on the shape of the biomass concentration profile through the biofilm which becomes more rounded with decreasing α for $\alpha < 4$. This is a result of retardation of the local growth contribution well before the biomass concentration approaches close packing for such small values of α. Note that the linear time dependence of the biofilm thickness is not a result of the symmetry assumptions employed here, but also occurs for $D_A \neq D_C$.

Thus for colonies of aerobic bacteria growing on the surface of a solid growth medium, the flux limited growth of the thick biofilm found at the centre of the colony can be expected. This will result in a linear increase in time of the central colony height due to the existence of a steady state, finite sized reaction zone within the colony.

5. Flux limited growth of colonies

A more general colony growth model than that due to Pirt can thus be defined within the framework of equation (2.2) by writing the normal growth velocity as

$$v(h(r, t)) = \lambda \min(h(r, t), h_m) \tag{5.1}$$

where h_m is now the maximum size of the growth zone of the colony. We have assumed this form for v, since it represents the simplest function that encompasses the required physical constraints. Thus substituting equation (5.1) into equation (2.3) we have

$$\partial u/\partial t^* = (1/x)\partial/\partial x(x\partial u/\partial x) + \min(u, 1)[1 + (\xi/2)(\partial u/\partial x)^2]. \tag{5.2}$$

This equation must be supplemented by the initial condition that $u(r=0, t=0) > 0$ and the boundary condition $(\partial u/\partial r)_{r=0} = 0$.

Figure 3 shows the temporal evolution of the radial height profile obtained by solving equation (5.2) with zero gradient boundary conditions at two values of the

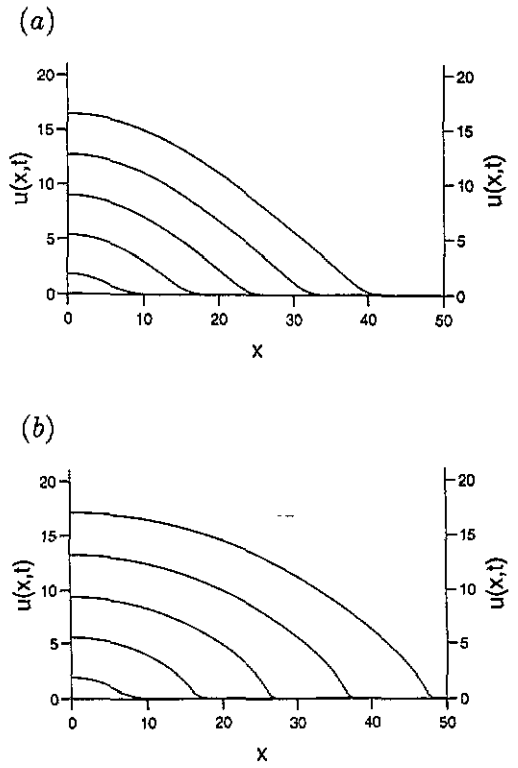

Figure 3. Radial height profile for the model of bacterial colony growth defined by equation (5.2) at times $\lambda t = 4, 8, 12, 16, 20$, for (*a*) $\xi = 1$ and (*b*) $\xi = 4$. Gaussian inoculation with $u(0, 0) = 0.1$ and $(\sigma/h_m) = 2.5$. The curve denoting the colony profile at inoculation would not be visible on the scale of this figure.

parameter ξ: $\xi = 1$ and $\xi = 4$. A Gaussian inoculation from equation (2.4) with $u(0, 0) = 0.1$ and $(\sigma/h_m) = 2.5$ was used as the initial condition. If we assume $(\lambda h_m^2/\nu) = 1$, these two cases correspond to uniform expansion growth ($\Lambda = 1$) and a significant, but not large, lateral growth anisotropy ($\Lambda = 4$). After an initial period in which the colony attains a time-independent convex shape, both the height and radius of the colony propagate outward at constant velocity. The overall shape of the colony profile is markedly different from that found for the Pirt model and increasing values of ξ lead to more rounded colony shapes. An important quantity characterizing the solutions of equation (5.2) is $\zeta = [(dx_0/dt)/(du(0, t)/dt)]$, which is a ratio of the radial to the vertical growth velocity. Numerical results for $\xi = 1$ show $\zeta = 2.10$, while for $\xi = 4$ we find $\zeta = 2.75$. Increasing ξ to much larger values leads to a dramatic increase in this velocity ratio. However, the central height velocity is only weakly dependent on ξ with $(du(0,t)/dt) = 0.93$ at $\xi = 1$ and $(du(0, t)/dt) = 0.96$ at $\xi = 4$. For $\xi \geqslant 8$ the central height velocity obtains an asymptotic value of $(du(0. t)/dt) = 0.98$. Thus rapid increases ζ with increasing ξ for $\xi \geqslant 8$ are solely due to the radial growth velocity. Note that since the form of the normal growth velocity in equation (5.1) contains a discontinuity in gradient for $h = h_m$, there is a corresponding discontinuity in gradient in the radial height profile of the colony although this is not marked for $\xi < 8$. Comparison with experiment [5, 6] suggests that solutions of equation (5.2) display the characteristic features of surface colony growth.

6. Discussion

We have introduced a continuum model for the spatio-temporal growth of bacterial colonies on the surface of a solid substrate which utilizes a reaction-diffusion equation for growth. The key element in the model is the functional form of normal growth velocity v which is determined by the microscopic mechanism controlling growth within the colony. Fluctuations could be included within this model by replacing v with $(v + \eta)$ where η is an appropriate noise term. Then, for constant v the resulting stochastic differential equation for surface growth would be of the type studied in the small noise amplitude and small gradient limit by Vicsek *et al* [11] with quenched randomness and by Kardar *et al* [7] for time-dependent noise. For colony growth from equation (2.2) in the flux-limited regime with $v[\min(h(r, t), h_m) + \eta]$ such an approach could only be valid on the top surface of a bacterial colony where $h(r, t) > h_m$. Kinetic roughening observed near the leading edge of the colony where $h(r, t) < h_m$ will not, in general, display the same class of roughening behaviour as the top surface of the colony. Discrete particle effects are of key importance in determining the roughening at the leading edge of the colony and this problem is considered elsewhere within the context of a generalized Eden model [12].

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