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A CELL GROWTH MODEL ADAPTED FOR THE MINIMUM CELL SIZE DIVISION

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Abstract

We study a cell growth model with a division function that models cells which divide only after they have reached a certain minimum size. In contrast to the cases studied in the literature, the determination of the steady size distribution entails an eigenvalue that is not known explicitly, but is defined through a continuity condition. We show that there is a steady size distribution solution to this problem.

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1. Introduction

A simple model for cell division for size-structured cohorts was presented by Hall and Wake [6]. There, 'size' corresponds to mass or DNA content. Their work was based on models developed earlier by Sinko and Streifer [16, 17]. The Hall and Wake model considers cells dividing into $\alpha > 1$ daughter cells of equal size at a division rate $B(x)$. The cells also grow at a rate $G(x)$. Let $n(x, t)$ denote the density of cells of size x at time t. The cell division process is governed by the functional partial differential equation (pde)

$$\frac{\partial}{\partial t}n(x,t) + \frac{\partial}{\partial x}(G(x)n(x,t)) + B(x)n(x,t) = \alpha^2 B(\alpha x)n(\alpha x,t). \tag{1.1}$$

In this equation, the term $B(x)n(x, t)$ represents the loss of cells of size x through division, and the term $\alpha^2 B(\alpha x)n(\alpha x, t)$ represents the gain of cells of size x, as a result of a cell of size αx dividing into α equal cells of size x. The equation is derived in detail by Diekmann et al. [4].

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Equation (1.1) is a special case of the growth–fragmentation equation

$$\frac{\partial}{\partial t}n(x,t) + \frac{\partial}{\partial x}(G(x)n(x,t)) = \int_x^\infty B(\xi)W(x,\xi)n(\xi,t)\,d\xi \\ - \Big(\int_0^x \frac{\tau}{x}W(\tau,x)\,d\tau\Big)B(x)n(x,t),$$

where the fragmentation kernel $W(x,\xi)$ represents the density of cells of size x produced when one cell of size $\xi > x$ divides. The first term on the right-hand side of the equation is the gain of cells of size x from the division of cells of larger size ξ. The second term on the right-hand side represents the loss of cells of size x owing to division to smaller sized cells.

A derivation of equation (1.1) using the above equation for the special case $\alpha = 2$ can be found in [11, 12]. Essentially, the model assumes that when a division occurs a cell of size ξ divides into α daughter cells of equal size x. This means that division to the size x occurs only when $\xi = \alpha x$, and this leads to the kernel

$$W(x,\xi) = \alpha\delta\Big(\frac{\xi}{\alpha} - x\Big),$$

where δ denotes the Dirac delta function. Although we use the language of cell division throughout this paper, equation (1.1) is applicable to growth–fragmentation models where division conserves mass and, when a particle divides, it divides into particles of equal mass.

The cell division problem is of the *initial boundary value* type with the conditions

$$n(0,t) = 0 \quad \text{for all } t \geq 0 \tag{1.2}$$

and

$$n(x,0) = n_0(x) \quad \text{for all } x \geq 0. \tag{1.3}$$

Here, $n_0(x)$ is a given initial cell size distribution, which may be regarded as a probability density function (pdf).

A special class of solutions to equation (1.1) are the so-called steady size distribution (SSD) solutions. These solutions correspond to separable solutions

$$n(x,t) = N(t)y(x), \tag{1.4}$$

which satisfy condition (1.2). Here, $y(x)$ is normalized so that it is a pdf. These solutions are of interest because they represent the long term asymptotic behaviour of the solution to the problem that includes the initial condition (1.3). Roughly speaking, solutions to the problem for any pdf $n_0(x)$ evolve towards the SSD solution. This behaviour was observed experimentally in plant cells [8] and this motivated the study of such solutions by Hall and Wake [6]. In fact, the relationship is generic to a large class of fragmentation-type equations of which the cell division equation is a special case. An account of this for the cell division equation is given by Perthame and Ryzhik [14].

Substituting solution form (1.4) into equation (1.1) yields

$$\frac{1}{N(t)}\frac{d}{dt}N(t) = \frac{-1}{y(x)}\Big\{\frac{d}{dx}(G(x)y(x)) + B(x)y(x) - \alpha^2 B(\alpha x)y(\alpha x)\Big\} \\ = \Lambda,$$

where Λ is a constant. Evidently, $N(t) = Ke^{\Lambda t}$ for some constant K, and $y(x)$ must satisfy

$$(G(x)y(x))' + (B(x) + \Lambda)y(x) = \alpha^2 B(\alpha x)y(\alpha x), \tag{1.5}$$

where $'$ denotes d/dx. The function $y(x)$ is required to be a pdf, so that, in particular, $y(x)$ must be nonnegative and

$$\int_0^\infty y(x)\,dx = 1. \tag{1.6}$$

The solution $N(t)y(x)$ is required to be nontrivial, so that $K \neq 0$, and therefore in order to meet condition (1.2),

$$y(0) = 0. \tag{1.7}$$

Under the assumptions that $B(x)y(x)$ is integrable on $[0, \infty)$ and

$$\lim_{x\to 0^+} G(x)y(x) = \lim_{x\to\infty} G(x)y(x) = 0,$$

integrating equation (1.5) from 0 to ∞ yields

$$\Lambda = (\alpha - 1)\int_0^\infty B(x)y(x)\,dx. \tag{1.8}$$

Assuming that y is decaying rapidly enough to have a first moment (that is, $xy(x)$ is integrable), and such that $xB(x)y(x)$ is integrable and $xG(x)y(x) \to 0$ as x goes to ∞ or to 0, an alternative expression for Λ can be obtained by first multiplying equation (1.5) by x and then integrating from 0 to ∞. This gives

$$\Lambda = \frac{\int_0^\infty G(x)y(x)\,dx}{\int_0^\infty xy(x)\,dx}. \tag{1.9}$$

Certainly a crux to finding SSD solutions for specific choices of $B(x)$ and $G(x)$ is the determination of Λ. Hall and Wake [7] studied the case in which these rates are constants. In this case Λ can be readily obtained from equation (1.8). Hall and Wake [7] also examined the case where $G(x)$ is a linear monomial and Λ can be obtained from equation (1.9). The cell division model has been extended to include dispersion (for example [21–23]) and asymmetric cell division [18]. All of these extensions involve (directly or indirectly through a transformation) either B as a constant or G as a linear monomial.

Prima facie it is not clear for general nonnegative functions b and g that there is an eigenvalue Λ such that equation (1.5) yields a pdf. If there is such a value, the corresponding pdf y is called a positive eigenfunction. This problem was studied by

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da Costa et al. [3], who established the existence of a positive eigenvalue under the assumption that the nonnegative functions $B(x)$ and $G(x)$ are such that $B(x)/G(x)$ is integrable on $[0, \infty)$. Although Perthame and Ryzhik [14] did not consider directly the variable growth case, they did establish the existence of a positive eigenfunction for a general class of positive functions $B(x)$ under the assumption that $B(x)$ was uniformly bounded away from 0 and bounded on the interval $[0, \infty)$. In both of these studies, the eigenvalue that produces the positive eigenfunction is unique.

In this paper, we consider the case where the growth rate is constant, but the division rate models cells that divide only when they reach a certain minimum size and after which they divide at a constant rate. We note that Diekmann et al. [4] studied a closely related problem, where division occurred after the minimum size, and there was an upper bound on the maximum cell size. Their analysis established the existence and uniqueness of solutions to the initial boundary value problem. Moreover, they established the existence and uniqueness of an eigenvalue that produces a pdf solution. The model we study is a limiting case where there is no upper bound on the size. For this case, it is possible to determine the SSD solution directly in terms of the eigenvalue.

Without loss of generality, we can always scale the size variable and use the constant function $G(x) = 1$. The division rate can be modelled by

$$B(x) = bH(x - c),$$

where b is some positive constant, c represents the minimum size at which a cell will divide, and H is the Heaviside function. We thus seek a pdf solution to

$$y'(x) + (bH(x - c) + \Lambda)y(x) = b\alpha^2 H(\alpha x - c)y(\alpha x) \tag{1.10}$$

that satisfies conditions (1.6) and (1.7). For this problem, Λ cannot be found by (1.8) or (1.9), and the division rate does not fall directly into the class considered by [3] or [14]. Nonetheless, it is sufficiently simple that a solution can be constructed.

Equation (1.10) can be regarded as three equations for the pdf y in three size intervals. In particular,

$$y_1'(x) + \Lambda y_1(x) = 0, \quad 0 \le x < c/\alpha, \tag{1.11}$$

$$y_2'(x) + \Lambda y_2(x) = b\alpha^2 y_3(\alpha x), \quad c/\alpha \le x < c, \tag{1.12}$$

$$y_3'(x) + (b + \Lambda)y_3(x) = b\alpha^2 y_3(\alpha x), \quad c \le x. \tag{1.13}$$

Equation (1.11) is simply an ordinary differential equation (ode), which with the initial value (1.7) gives the unique solution $y_1(x) = 0$ for all $x \in [0, c/\alpha)$. If y_3 is known, then equation (1.12) is an ode for y_2 that can be readily solved. Equation (1.13) is the only equation that is functional in character; it contains the nonlocal term $y(\alpha x)$. This equation is an example of the well-known pantograph equation, which has been studied extensively by several researchers. Detailed analytical accounts can be found in the literature [9, 10]. Aside from the intrinsic analytical interest of this functional equation, some substantial studies reflect the fact that it appears in many applications.

For instance, aside from cell division models, the pantograph equation appears in a simple model for the absorption of light in the Milky Way [1], a problem in ruin theory [5], and a model for the collection of current from an electric train [13].

We seek a continuous nonnegative solution to (1.10); thus, equations (1.11)–(1.13) are supplemented with the continuity conditions

$$y_1(c/\alpha) = y_2(c/\alpha) = 0, \tag{1.14}$$

$$y_2(c) = y_3(c). \tag{1.15}$$

Note that, in general, the derivative of $y(x)$ is not continuous at c/α or c.

Although Λ cannot be determined directly, it is possible to get upper and lower bounds on the eigenvalue. Specifically, equation (1.8) implies

$$\Lambda = b(\alpha - 1)\int_c^\infty y(x)\,dx.$$

Given that y is a pdf solution, we know that the value of the above integral lies between 0 and 1. If $\Lambda = 0$, then the integral would have to be zero and, since y is nonnegative, this means that the solution to equation (1.13) would have to be the trivial solution. Equation (1.12) and continuity conditions then force y_2 to also be trivial. Since the only solution to (1.11) is the trivial solution, we conclude that $y(x) = 0$ for all $x \geq 0$. But y is a pdf, so this cannot be the case; hence,

$$0 < \Lambda \leq b(\alpha - 1). \tag{1.16}$$

We establish the existence of an eigenvalue in Section 3, where we construct a solution. It is well known that a class of rapidly decaying solutions to pantograph equations such as (1.13) can be expressed as Dirichlet series. In the next section, we turn to the Dirichlet series and study certain properties that are needed to establish the eigenvalue. In particular, we will see in Section 3 that the continuity condition (1.14) determines any eigenvalues Λ as the zeros of a function involving a Dirichlet series and its integral. It is not obvious that there is a zero that satisfies inequality (1.16) and, if there is such a zero, it is not clear that the resulting solution is nonnegative. In order to resolve these problems, a closer study of the Dirichlet series as a function of both x and the eigenvalue parameter is required.

2. A class of Dirichlet series

The Dirichlet series D is defined as

$$D(x,\lambda) = e^{-\lambda x} + \sum_{k=1}^{\infty} \frac{(-1)^k (b\alpha^2)^k}{\lambda^k \prod_{m=1}^{k}(\alpha^m - 1)} e^{-\lambda\alpha^k x} \tag{2.1}$$

for $x \geq 0$ and $\lambda > 0$. It can be verified directly that this series is a solution to the pantograph equation

$$D_x(x,\lambda) + \lambda D(x,\lambda) = b\alpha^2 D(\alpha x,\lambda), \tag{2.2}$$

where $D_x = \partial D/\partial x$. This series has been studied in detail for the special value $\lambda = b\alpha$ by Hall and Wake [6]. Suitably normalized, the function $D(x, b\alpha)$ is the pdf solution to their cell division model. The series also appears in the analysis of the pantograph equation by Kato and McLeod [10] and Iserles [9] among others. Dirichlet series for second order versions of the pantograph equation have been studied in [23], and a double series version of D can be found in [18] in connection with an asymmetric cell division model. The focus in most of these studies was on particular values of λ. The interpretation of λ as an eigenvalue parameter, aside from its rôle in cell division models as the value that produces a pdf solution, was made for a related problem in [19, 20]. We also note that an eigenvalue problem for a second order version was studied in [22].

The pantograph equation (1.13) has a solution of the form (2.1) with $\lambda = b + \Lambda$. Inequality (1.16) shows that for any pdf solution

$$b < \lambda \leq b\alpha, \tag{2.3}$$

and it is in this interval that we wish to study D. In order to do this, however, we need to study D for larger values of λ. A key property of the Dirichlet series that links D for different eigenvalues is

$$D_x(x, \lambda) = -\lambda D(\alpha x, \lambda/\alpha). \tag{2.4}$$

THEOREM 2.1. *If $\lambda \geq b\alpha^2$, then $D(x, \lambda) > 0$ for all $x \geq 0$. Moreover, $D(x, \lambda)$ is monotonic and strictly decreasing with respect to x on the interval* $(0, \infty)$.

PROOF. For any $\lambda > 0$,

$$\begin{aligned} D(0, \lambda) &= 1 + \sum_{k=1}^{\infty} \frac{(-1)^k (b\alpha^2)^k}{\lambda^k \prod_{m=1}^{k}(\alpha^m - 1)} \\ &= 1 + \sum_{k=1}^{\infty} \frac{(-1)^k (b\alpha/\lambda)^k}{\alpha^{k(k-1)/2} \prod_{m=1}^{k}(1 - \alpha^{-m})}. \end{aligned}$$

The above series can be recast as an infinite product using the Euler identity [2]

$$\prod_{k=0}^{\infty}(1 + zq^k) = 1 + \sum_{k=1}^{\infty} \frac{q^{k(k-1)/2} z^k}{\prod_{m=1}^{k}(1 - q^m)}$$

with $z = -b\alpha/\lambda$ and $q = 1/\alpha$ to get

$$D(0, \lambda) = \prod_{k=0}^{\infty}\Big(1 - \frac{b\alpha}{\lambda\alpha^k}\Big), \tag{2.5}$$

which immediately gives all the zeros of $D(0, \lambda)$, namely, $\lambda_n = b\alpha^{1-n}$ for $n = 0, 1, 2 \ldots$. These values correspond to the eigenvalues determined by van Brunt and Vlieg-Hulstman [19]. Here, we simply note that $D(0, \lambda) > 0$ for all $\lambda > b\alpha$.

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We now show that $D(x, \lambda)$ cannot have any local extrema if $\lambda \geq b\alpha^2$. First note that for any λ,

$$\lim_{x\to\infty} D(x, \lambda) = 0. \tag{2.6}$$

Suppose that D has a positive local maximum at $x = m_1$. Then equation (2.2) implies that

$$\lambda D(m_1, \lambda) = b\alpha^2 D(\alpha m_1, \lambda)$$

and, since $\lambda \geq b\alpha^2$, the above equation along with equation (2.6) imply the existence of another positive local maximum at some point $m_2 \geq \alpha m_1$, at which $D(m_2, \lambda) \geq D(m_1, \lambda)$. We can continue this argument, and thereby construct a sequence $\{m_k\}$ of local positive maxima such that $m_k \to \infty$ as $k \to \infty$, and $D(m_k, \lambda) \geq D(m_1, \lambda) > 0$ for all $k \geq 1$. This contradicts equation (2.6) and we thus conclude that D cannot have a positive local maximum. The same argument can be applied to $-D$ to preclude the possibility of a negative local minimum. Evidently, D cannot have a positive local minimum or a negative local maximum and satisfy (2.6) as well.

We know that $D(0, \lambda) > 0$. Suppose that D has a zero at $\xi \in (0, \infty)$. Then D must be identically zero on the interval $[\xi, \infty)$, because otherwise it would require a nonzero local extremum to satisfy (2.6). For any $\lambda > 0$, however, $D(z, \lambda)$, regarded as a function of the complex variable z, is holomorphic in the right half plane. Since D is not identically zero in the half plane, the identity theorem [15] rules out the possibility of this function being zero on any such interval. We thus see that D must be positive for all $x \geq 0$ whenever $\lambda \geq b\alpha^2$. Finally, we note that $D_x(x, \lambda) < 0$ for all $x > 0$, since $D_x(x, \lambda) = 0$ would induce a local positive maximum. □

Corollary 2.2. *If* $b\alpha \leq \lambda < b\alpha^2$, *then* $D(x, \lambda) > 0$ *for all* $x > 0$ *and it has precisely one local maximum in* $(0, \infty)$.

Proof. Equation (2.4) can be recast as

$$D_x(x, \alpha\lambda) = -\alpha\lambda D(\alpha x, \lambda)$$

and, because $\alpha\lambda \geq b\alpha^2$, the positivity of D follows immediately from Theorem 2.1.

Concerning the existence of the maximum, the result has already been established for the case $\lambda = b\alpha$ (see [3]). Suppose that $b\alpha < \lambda < b\alpha^2$. Equation (2.2) implies that

$$D_x(0, \lambda) = (b\alpha^2 - \lambda) D(0, \lambda).$$

We know that $D(0, \lambda) > 0$ by equation (2.5); hence, $D_x(0, \lambda) > 0$. Condition (2.6) indicates that D must have at least one local positive maximum. In fact, the positivity of the derivative at $x = 0$ precludes the possibility that the global maximum occurs at $x = 0$. Now,

$$D_x(x, \lambda) = -\lambda e^{-\lambda x} + O(e^{-\lambda\alpha x})$$

as $x \to \infty$, so there cannot be a sequence $\{x_k\}$ such that $x_k \to \infty$ as $k \to \infty$ with $D_x(x_k, \lambda) = 0$. The function D can thus have only a finite number of local maxima. Suppose that D has more than one local maximum, and let M denote the largest value of x at which D has a local maximum. Since D has more than one maximum, there must be at least one local minimum. Let m denote the largest value of x at which D has a local minimum. The positivity of D implies that $m < M$. Equation (2.2) implies that $\lambda D(m,\lambda) = b\alpha^2 D(\alpha m,\lambda)$, so that in particular $D(\alpha m,\lambda) < D(m,\lambda)$ and hence $M < \alpha m$. Moreover, differentiating equation (2.2) and noting that $D_{xx}(m,\lambda) \geq 0$, we see that D_x must be nonnegative at $x = \alpha m$. The derivative cannot be positive, since the last local maximum occurred at M; hence, the derivative must be zero at αm and this means that D_{xx} must also be zero there because there are no more local extrema beyond M. We can now apply the same argument at the point αm to assert that D_x and D_{xx} must both vanish at $x = \alpha^2 m$. It is clear in this manner that we could construct a sequence $\{x_k\}$ such that with $D_x(x_k,\lambda) = 0$, $x_k \to \infty$ as $k \to \infty$. This contradiction shows that D can have only one local maximum. □

We finally reach the interval with which we are most concerned. Equation (2.5) shows that $D(0,\lambda) < 0$ for all $\lambda \in (b, b\alpha)$. Although the Dirichlet series starts out negative, it is clear that it is positive for a sufficiently large x. Since this Dirichlet series will form part of a pdf solution, it is important to identify the zeros of the function, and where it is positive.

Corollary 2.3. *If $b \leq \lambda < b\alpha$, then $D(x,\lambda)$ has only one zero $z \in (0,\infty)$; moreover,*

$$z \leq \frac{\alpha}{b(\alpha-1)}.$$

Proof. The existence and uniqueness of z follow immediately from Corollary 2.2 and relation (2.4). Here, z/α corresponds to the maximum for $D(x,\alpha\lambda)$. Equation (2.2) and the positivity of $D(x,\alpha\lambda)$ for $\lambda \geq b$ imply that

$$\begin{aligned} D(z/\alpha,\alpha\lambda) &= \alpha\lambda \int_{z/\alpha}^{z} D(\xi,\alpha\lambda)\,d\xi + (\alpha\lambda - b\alpha)\int_{z/\alpha}^{\infty} D(\xi,\alpha\lambda)\,d\xi \\ &\geq \alpha\lambda \int_{z/\alpha}^{z} D(\xi,\alpha\lambda)\,d\xi \\ &\geq \alpha\lambda z(1-1/\alpha)D(z,\alpha\lambda), \end{aligned}$$

where we have used the fact that $D(x,\alpha\lambda)$ is monotonically decreasing after the local maximum at z/α. Equation (2.2) also shows that

$$\alpha\lambda D(z/\alpha,\alpha\lambda) = b\alpha^2 D(z,\alpha\lambda);$$

hence,

$$z \leq \frac{b\alpha}{\lambda^2(\alpha-1)} \leq \frac{\alpha}{b(\alpha-1)}.$$ □

Note that equation (2.5) shows that $D(0,\lambda) < 0$, and it is clear for x large that $D(x,\lambda) > 0$. We thus see that $D(x,\lambda)$ changes sign from negative to positive as x increases. The function $D(x,\lambda)$ is graphed for different values of λ in Figure 1.

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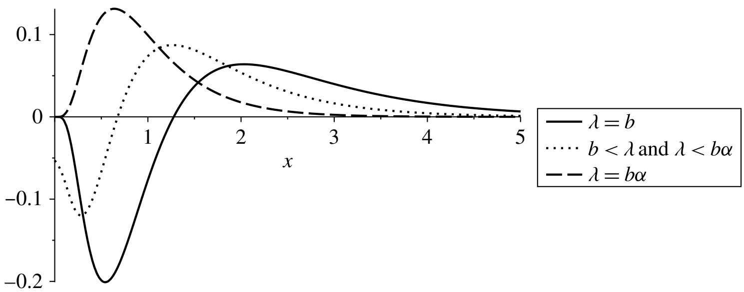

FIGURE 1. $D(x, \lambda)$ for different values of λ with $\alpha = 2$, $b = 1$.

3. A pdf solution

In this section, we construct a pdf solution to equation (1.10) that satisfies conditions (1.7), (1.14), and (1.15). We know from Section 2 that equation (1.13) has a solution of the form

$$y_3(x) = kD(x, \lambda), \tag{3.1}$$

where k is a constant and

$$\lambda = \Lambda + b.$$

It is straightforward to determine the solution of (1.12), namely,

$$y_2(x) = kb\alpha^2 e^{-(\lambda-b)x} \int_{c/\alpha}^{x} e^{(\lambda-b)\xi} D(\alpha\xi, \lambda)\, d\xi, \tag{3.2}$$

where we have used equation (1.14). The constant k can be used eventually to normalize y to make it a pdf. The main problem now is to show that there is an eigenvalue that produces a positive eigenfunction. The continuity condition (1.15) places a restriction on λ. In particular, equations (3.1), (3.2), and (1.15) imply that

$$F(\lambda) = 0, \tag{3.3}$$

where

$$F(\lambda) = b\alpha^2 \int_{c/\alpha}^{c} e^{(\lambda-b)\xi} D(\alpha\xi, \lambda)\, d\xi - e^{(\lambda-b)c} D(c, \lambda).$$

We know from inequality (2.3) that for any pdf solution λ must be in the interval $(b, b\alpha]$, but it is not clear that equation (3.3) has a solution in this interval. Certainly, one complication is that $D(x, \lambda)$ changes sign once along the positive x-axis. Theorem 2.1 and Corollary 2.2 show, in contrast, that $D(x, \alpha\lambda) > 0$ for all $x > 0$ when $\lambda \in (b, b\alpha]$. We can recast F using equations (2.2) and (2.4) along with integration by parts to get

$$F(\lambda) = D(c/\alpha, \alpha\lambda)\Big(\frac{b\alpha}{\lambda} e^{(\lambda-b)c/\alpha} - e^{(\lambda-b)c}\Big) + \frac{b\alpha}{\lambda}(\lambda - b) \int_{c/\alpha}^{c} e^{(\lambda-b)\xi} D(\xi, \alpha\lambda)\, d\xi. \tag{3.4}$$

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Lemma 3.1. *For any $c > 0$, there exists a solution to equation (3.3) in the interval $(b, b\alpha)$.*

Proof. The function F is continuous on the interval $[b, b\alpha]$. Now, using equation (3.4),

$$F(b) = (\alpha - 1)D(c/\alpha, \alpha\lambda) > 0$$

and

$$F(b\alpha) = D(c/\alpha, b\alpha^2)(e^{b(\alpha-1)c/\alpha} - e^{b(\alpha-1)c}) + b(\alpha - 1)\int_{c/\alpha}^{c} e^{b(\alpha-1)\xi} D(\xi, b\alpha^2)\, d\xi.$$

Theorem 2.1 shows that $D(x, \alpha\lambda)$ is monotonically decreasing on $[0, \infty)$; hence,

$$\begin{aligned} F(b\alpha) &< D(c/\alpha, b\alpha^2)(e^{b(\alpha-1)c/\alpha} - e^{b(\alpha-1)c}) + b(\alpha - 1)D(c/\alpha, b\alpha^2)\int_{c/\alpha}^{c} e^{b(\alpha-1)\xi}\, d\xi \\ &= D(c/\alpha, b\alpha^2)(e^{b(\alpha-1)c/\alpha} - e^{b(\alpha-1)c}) + D(c/\alpha, b\alpha^2)(e^{b(\alpha-1)c} - e^{b(\alpha-1)c/\alpha}) \\ &= 0. \end{aligned}$$

We thus see that F changes sign in the interval and, therefore, must have a zero in this interval. □

Although there is a solution to equation (3.3) in the interval $(b, b\alpha)$, it is not clear that the resulting solution to equation (1.10) is nonnegative. For instance, it may be, for some choice of $c > 0$, that $D(c, \lambda) < 0$. For each $\lambda \in (b, b\alpha)$, the function $D(x, \lambda)$ has precisely one zero $z(\lambda)$ in $[0, \infty)$ and hence the question is whether equation (3.3) precludes the case $c < z(\lambda)$. Corollary 2.3 shows that for c sufficiently large, $D(c, \lambda) > 0$ for any $\lambda \in (b, b\alpha)$. The next lemma shows that this is true for all $c > 0$.

Lemma 3.2. *Let $c > 0$ and suppose that $\lambda \in (b, b\alpha)$ is a solution to equation (3.3). Then $D(c, \lambda) > 0$.*

Proof. Recall from the proof of Corollary 2.3 that if $m(\lambda)$ is the maximum for $D(x, \alpha\lambda)$, then $\alpha m(\lambda)$ is the zero for $D(x, \lambda)$. The lemma will be established if it can be shown that $m(\lambda) < c/\alpha$.

The continuous function $D(x, \alpha\lambda)$ has one local maximum and no local minimum. Consequently, on any compact interval of $[0, \infty)$, the global minimum of the function over this interval must occur at an end point of the interval. Specifically, for any $c > 0$, the global minimum of $D(x, \alpha\lambda)$ on the interval $[c/\alpha, c]$ must occur at either c/α or c. Suppose that this minimum occurs at c/α. Then the second term in (3.4) can be bounded as follows:

$$\begin{aligned} \frac{b\alpha}{\lambda}(\lambda - b)\int_{c/\alpha}^{c} e^{(\lambda-b)\xi} D(\xi, \alpha\lambda)\, d\xi &> \frac{b\alpha}{\lambda}(\lambda - b)D(c/\alpha, \alpha\lambda)\int_{c/\alpha}^{c} e^{(\lambda-b)\xi}\, d\xi \\ &= \frac{b\alpha}{\lambda} D(c/\alpha, \alpha\lambda)(e^{(\lambda-b)c} - e^{(\lambda-b)c/\alpha}). \end{aligned}$$

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Hence,

$$F(\lambda) > D(c/\alpha, \alpha\lambda)\Big(\frac{b\alpha}{\lambda} - 1\Big)e^{(\lambda-b)c} > 0,$$

so that λ cannot be a solution to equation (3.3). We thus conclude that the minimum cannot be achieved at c/α and must, therefore, be at c. This leads to the inequality

$$\begin{aligned} F(\lambda) &> D(c/\alpha, \alpha\lambda)\Big\{\frac{b\alpha}{\lambda}e^{(\lambda-b)c/\alpha} - e^{(\lambda-b)c}\Big\} + D(c, \alpha\lambda)\frac{b\alpha}{\lambda}\{e^{(\lambda-b)c} - e^{(\lambda-b)c/\alpha}\} \\ &= e^{(\lambda-b)c}\Big\{\frac{b\alpha}{\lambda}D(c, \alpha\lambda) - D(c/\alpha, \alpha\lambda)\Big\} + e^{(\lambda-b)c/\alpha}\{D(c/\alpha, \alpha\lambda) - D(c, \alpha\lambda)\} \end{aligned}$$

and, using equation (2.2), this yields

$$F(\lambda) > \frac{e^{(\lambda-b)c}}{\lambda}D_x(c/\alpha, \alpha\lambda) + e^{(\lambda-b)c/\alpha}\{D(c/\alpha, \alpha\lambda) - D(c, \alpha\lambda)\}.$$

The last term in the above expression is clearly positive, since the minimum is at c. If $c/\alpha < m(\lambda)$, then $D_x(c/\alpha, \alpha\lambda) > 0$, which leads to the contradiction that $F(\lambda) > 0$. We thus conclude that $m(\lambda) < c/\alpha$. □

The above lemma indicates that $D(x, \lambda) > 0$ for all $x \geq c$, which ensures that a positive solution y_3 exists. It is clear from equation (3.2) that the positivity of y_3 implies that of y_2, and that a suitable positive constant k can be obtained to normalize the solution to satisfy (1.6). In summary, we have the following result.

THEOREM 3.3. *For any $c > 0$, there exist an eigenvalue $\Lambda \in (0, b(\alpha - 1))$ and a positive eigenfunction y that satisfy equation* (1.10).

4. Conclusions

In this paper, we studied the cell growth model of Hall and Wake for a cell division function that models cells which divide only after they reach a minimum size. Unlike the earlier models of Hall and Wake, the determination of the SSD solution involves an eigenvalue that could not be found explicitly. This problem brings to the fore a class of Dirichlet series that solves a pantograph equation. It is shown directly that there are an eigenvalue and a corresponding SSD solution to this cell growth model. Under a rapid decay condition on the pdf (that is, assuming the pdf has moments of all orders), it is possible to show that the eigenvalue is simple. This, however, is of limited value until it is known whether the eigenvalue itself is unique. Certainly, numerical evidence indicates that equation (3.3) has a unique solution in $(b, \alpha b)$, but there may be non-Dirichlet series solutions for y_3 if the rapid decay condition is relaxed.

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