

ON A CELL DIVISION EQUATION WITH A LINEAR GROWTH RATE

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Abstract

We consider an initial–boundary value problem that involves a partial differential equation with a functional term. The problem is motivated by a cell division model for size structured cell cohorts in which growth and division occur. Although much is known about the large time asymptotic behaviour of solutions to these problems for constant growth rates, general solution techniques are rare. We analyse the case where the growth rate is linear and the division rate is a monomial, and we develop a method to determine the general solution for a general class of initial data. The large time dynamics of solutions for this case are significantly different from the constant growth rate case. We show that solutions approach a time-dependent attracting solution that is periodic in the time variable.

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1. Introduction

In this paper, we study a special case of a cell division equation that models cell populations structured by size. This model was presented by Hall and Wake [12] in 1989, based on an earlier work by Sinko and Streifer [24]. In these models “size” can be DNA content or mass. The model considers cells that are growing and dividing such that a cell of size x divides into $\alpha > 1$ daughter cells of equal size (in most applications, $\alpha = 2$). Let $n(x, t)$ denote the number density of cell of size x at time t . If cells are growing at a rate $G(x)$ and dividing at a rate $B(x)$, then the cell division equation is

$$n_t(x, t) + (G(x)n(x, t))_x + B(x)n(x, t) = \alpha^2 B(\alpha x)n(\alpha x, t). \quad (1.1)$$

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A solution to this equation must satisfy

$$\lim_{x \rightarrow 0^+} G(x)n(x, t) = 0, \quad \lim_{x \rightarrow \infty} G(x)n(x, t) = 0, \tag{1.2}$$

for $t \geq 0$, and

$$n(x, 0) = n_0(x).$$

The cell division problem is thus a partial differential equation with a functional term, accompanied by conditions of the initial–boundary value type.

Hall and Wake studied a special class of solutions to equation (1.1) for the case where $G(x)$ and $B(x)$ are constant functions [12] and for the case where $G(x) = gx$ and $B(x) = bx^r$, where g, b and r are positive numbers [13]. The solutions they studied were called “steady size distributions” (SSDs). Such solutions correspond to the separable solutions to equation (1.1) that satisfy condition (1.2). Their study was motivated by experimental data on size structured cell populations in certain plant tissues [14]. The observation that motivated the study was that the cell size distribution (number density) evolved to a certain shape that did not depend on the initial distribution n_0 . In other words, for t sufficiently large, the distribution assumed the same shape regardless of the initial distribution. At least for constant growth rates, the SSD solutions matched the data. The long time asymptotic behaviour of solutions to the cell division equation for certain cases was studied prior to the work of Hall and Wake. For instance, Diekmann et al. [8] studied the case where cells were limited to a maximum size and could divide only after a minimum size was reached.

The cell division problem is a special case of the growth-fragmentation problem, namely,

$$n_t(x, t) + (G(x)n(x, t))_x = \int_x^\infty B(\xi)\Delta(x, \xi)n(\xi, t) d\xi - B(x)n(x, t) \int_0^x \frac{\tau}{x} \Delta(\tau, x) d\tau,$$

where the division kernel Δ is given by

$$\Delta(x, \xi) = \alpha \delta\left(\frac{\xi}{\alpha} - x\right).$$

Here, δ denotes the Dirac delta function. The above kernel models division of a cell at size $\xi > x$ into α daughter cells of the same size. Division occurs only when ξ is an α multiple of x and division produces α new cells each of size x .

In the framework of the growth-fragmentation, much progress has been made on the long time asymptotic behaviour of solutions and the existence of SSD-type solutions for a broad class of functions $B(x)$ and constant growth rates [6, 10, 19, 20, 23]. Although much is known about SSD solutions to equation (1.1), there are few techniques for solving initial–boundary value problems that involve a functional argument. Certain general results for the Cauchy problem, such as uniqueness, are given by Borok and Zitomirskii [4] and Derfel and Zitomirskii [7] for a general class of functional partial differential equations, but solution techniques for the initial–boundary value problem are lacking. Recently, Zaidi et al. [27] have developed a

technique whereby the problem can be solved for general initial data when $B(x)$ and $G(x)$ are constant functions.

In this paper, we study the case when $G(x) = gx$ and $B(x) = bx^r$, where g , b and r are positive numbers. We thus consider the equation

$$n_t(x, t) + g(xn(x, t))_x + bx^r n(x, t) = b\alpha^{2+r} x^r n(\alpha x, t), \quad (1.3)$$

which can be put into a simpler form as follows. Let

$$n(x, t) = \frac{e^{gt}}{x^2} \theta(x, t).$$

Then equation (1.3) yields

$$\theta_t(x, t) + gx\theta_x(x, t) + bx^r \theta(x, t) = b\alpha^r x^r \theta(\alpha x, t). \quad (1.4)$$

Let $z = x^r/r$ and $\psi(z, t) = \theta(x, t)$. Then $\theta(\alpha x, t) = \psi(\alpha^r z, t)$, and from equation (1.4)

$$\psi_t(z, t) + \tilde{g}z\psi_z(z, t) + \tilde{b}z\psi(z, t) = \tilde{b}\nu z\psi(\nu z, t), \quad (1.5)$$

where $\tilde{g} = rg$, $\tilde{b} = rb$ and $\nu = \alpha^r > 1$. Equation (1.5) shows that it is sufficient to study the case $r = 1$.

PROBLEM A. We focus on the initial–boundary value problem consisting of the equation

$$m_t(x, t) + gxm_x(x, t) + bxm(x, t) = b\alpha xm(\alpha x, t) \quad (1.6)$$

along with the conditions

$$\lim_{x \rightarrow 0^+} \frac{m(x, t)}{x} = 0, \quad \lim_{x \rightarrow \infty} \frac{m(x, t)}{x} = 0, \quad (1.7)$$

for any $t \geq 0$, and

$$m(x, 0) = m_0(x), \quad (1.8)$$

where $m_0(x) = x^2 n_0(x)$.

The choice $G(x) = gx$ corresponds to the “exponential growth” of a cell. Biologically, this means that the cell size grows at a rate proportional to its size. In contrast, some models assume “linear growth”, which corresponds to the choice $G(x) = \text{constant}$. There are arguments and data that support both choices. Cooper [5] gave an overview of the two growth types and argued in favour of exponential growth; Kubitschek [18], on the other hand, argued that the growth is linear, at least for *Escherichia coli*. Koch [17] provided a review (as of 1993) explaining what led biologists to choose one growth rate over the other. Abner et al. [1] compared and contrasted the two growth rates in the context of the Cooper–Helmstetter (CH) theory for prokaryotic cell cycles.

The long time asymptotic behaviour of solutions for the exponential growth case differs markedly from that for the linear growth case. In particular, it can be shown

[22, 23] for a general class of functions B and constant G that there is a unique eigenvalue λ and a corresponding positive eigenfunction y such that, for any initial distribution n_0 ,

$$\|e^{-\lambda t}n(x, t) - y(x)\| \rightarrow 0,$$

as $t \rightarrow \infty$. Here $\|\cdot\|$ is a weighted L^1 norm that depends on B . In contrast, it has been shown for the exponential growth case that there is no dominant eigenvector [8] and that long time asymptotic solutions may include time-dependent oscillations [3]. In fact, there are choices for B (for example, constant division rate) that lead to critical cases where there is no eigenvalue leading to a positive eigenfunction [9].

In the next section, we show that if Problem A has a solution, then it is unique and nonnegative for nonnegative initial data. In Section 3, we derive a general solution to Problem A using the Mellin transform. This solution contains an arbitrary function w_0 that is determined by the initial data m_0 . In Section 4, we obtain an explicit relation defining w_0 in terms of m_0 for $x > 0$, and we show that the behaviour of w_0 as $x \rightarrow 0^+$ is oscillatory. In Section 5, we determine the eigenvalues and eigenfunctions associated with Problem A and show that there is no dominant eigenvalue. We confirm that the solution constructed in Section 3 satisfies the boundary conditions in Section 6 and show that this solution converges in the L^1 norm to a certain “limiting” solution that contains time-dependent oscillatory terms.

2. Some qualitative results

We show that if Problem A has a solution, then it is unique and that any such solution must be nonnegative if the initial function m_0 is nonnegative. Let $\Omega = \{(x, t) \mid 0 \leq x, 0 \leq t\}$ and let \mathcal{N} denote the set of functions $h : \mathcal{N} \rightarrow \mathbb{R}$ with the following assumption.

ASSUMPTION 2.1. *Suppose that:*

- (1) h_x and h_t are continuous on Ω ;
- (2) there is a positive number ℓ such that, for any fixed $T \geq 0$,

$$h(x, T) \sim O(1/x^{1+\ell}) \quad \text{as } x \rightarrow \infty;$$

- (3) for any $\epsilon > 0$ and $T \geq 0$, there is a corresponding $\delta > 0$ and X such that $|xh(x, t)| < \epsilon$, whenever $0 < t - T < \delta$ and $x > X$.

THEOREM 2.2 (UNIQUENESS). *Suppose that $m \in \mathcal{N}$ is a solution to Problem A. Then m is unique among functions in \mathcal{N} .*

PROOF. We first transform equation (1.6). Let

$$m(x, t) = \frac{e^{gt}}{x} \tilde{m}(x, t).$$

Then \tilde{m} satisfies

$$\tilde{m}_t(x, t) + g x \tilde{m}_x(x, t) + b x \tilde{m}(x, t) = b x \tilde{m}(\alpha x, t). \tag{2.1}$$

Suppose that there are two solutions, m_1 and m_2 , in \mathcal{N} . Then there are two corresponding solutions \tilde{m}_1 and \tilde{m}_2 to equation (2.1). Let $u = \tilde{m}_1 - \tilde{m}_2$. The function u satisfies (2.1) along with the conditions

$$u(0, t) = 0, \quad (2.2)$$

$$u(x, 0) = 0. \quad (2.3)$$

Suppose that m_1 and m_2 are distinct. Then there is a point (\hat{x}_0, t_0) at which $u(\hat{x}_0, t_0) \neq 0$. Without loss of generality, we can assume that $u(\hat{x}_0, t_0) > 0$. Since m_1 and m_2 are in \mathcal{N} , we know that u and u_x and u_t are continuous on Ω and that, for any fixed $t \geq 0$, $u(x, t) \rightarrow 0$ as $x \rightarrow \infty$.

Now $u(0, t_0) = 0$, and $u(x, t_0)$ is continuous for all $x \geq 0$. Since m_1 and m_2 are in \mathcal{N} , we know that $m_1(x, t_0) \rightarrow 0$ and $m_2(x, t_0) \rightarrow 0$ as $x \rightarrow \infty$. This means that $u(x, t_0) \rightarrow 0$ as $x \rightarrow \infty$, and therefore $u(x, t_0)$ must have a global maximum, say, $L_0 > 0$ at some $0 < x < \infty$. Let x_0 denote the largest value of x at which $u(x, t_0)$ achieves its global maximum. Thus $u(x_0, t_0) = L_0$, $u_x(x_0, t_0) = 0$ and $u(x_0, t_0) > u(\alpha x_0, t_0)$; hence, equation (2.1) implies that

$$u_t(x_0, t_0) < 0. \quad (2.4)$$

The above inequality indicates that $u(x_0, t) > u(x_0, t_0)$ for some $t < t_0$.

Consider now the compact set $\Omega_0 = \{(x, t) \mid 0 \leq x \leq \alpha x_0, 0 \leq t \leq t_0\}$. The function u must achieve a global maximum in Ω_0 , and it is clear from equations (2.2) and (2.3) that this maximum will not occur on the x - or t -axes. Inequality (2.4) precludes the maximum being achieved on the line $t = t_0$. The maximum either occurs on the line segment $\{(\alpha x_0, t) \mid 0 < t < t_0\}$ or in the interior of Ω_0 . If it occurs on the line segment, then there is a point $(\alpha x_0, t_1)$ with $0 < t_1 < t_0$ at which u achieves a value greater than L_0 .

Suppose that the global maximum is achieved at some point (\hat{x}_1, t_1) in the interior of Ω_0 and not on the line segment. We can always take \hat{x}_1 to be the largest value of x at which $u(x, t_1)$ achieves this maximum and (\hat{x}_1, t_1) is in the interior of Ω_0 . Thus $u(\hat{x}_1, t_1) > L_0$ and $u_x(\hat{x}_1, t_1) = u_t(\hat{x}_1, t_1) = 0$. Equation (2.1) thus implies that $u(\hat{x}_1, t_1) = u(\alpha \hat{x}_1, t_1)$, and we know from the definition of \hat{x}_1 that $\alpha \hat{x}_1 > \alpha x_0$. In any event, there exists a point (\bar{x}_1, t_1) with $\bar{x}_1 \geq \alpha x_0$ and $t_1 < t_0$ at which $u(\bar{x}_1, t_1) > L_0$. Let x_1 be the largest value of x at which the function $u(x, t_1)$ achieves its global maximum $L_1 > L_0$. Then we can repeat the construction above to deduce the existence of a point (\bar{x}_2, t_2) with $\bar{x}_2 \geq \alpha x_1$ and $t_2 < t_1$, where u achieves a value greater than L_1 . Repeating these arguments, it is clear that we can construct sequences $\{x_j\}$, $\{t_j\}$ such that $x_j \rightarrow \infty$ and $t_j \rightarrow T$ as $j \rightarrow \infty$. Here $0 \leq T < t_0$ and $u(x_j, t_j) > L_0 > 0$. Now m_1 and m_2 are in \mathcal{N} , which means that u must satisfy the uniform decay condition (3) in Assumption 2.1. If this condition is applied to the limit T of $\{t_j\}$, then u cannot meet this condition. \square

THEOREM 2.3 (Nonnegative solutions). *Suppose that $m \in \mathcal{N}$ is a solution to Problem A. If $m_0 \geq 0$, then $m(x, t) \geq 0$ for all $(x, t) \in \Omega$.*

PROOF. Suppose that there is a point (\hat{x}, t_0) at which $m(\hat{x}, t_0) < 0$. Then $\tilde{m}(\hat{x}, t_0) < 0$, where \tilde{m} is as defined in the proof of Theorem 2.2. Clearly, the boundary and initial conditions preclude \tilde{m} taking negative values on the x and t axes. We can proceed in a similar way to the proof of uniqueness to first note that the function $\tilde{m}(x, t_0)$ must have a global minimum $l_0 < 0$ and then let x_0 be the largest value at which $\tilde{m}(x, t_0)$ achieves this minimum. It thus follows that $\tilde{m}_t(x_0, t_0) > 0$. We follow the construction in the proof of Theorem 2.2, and we deduce the existence sequences $\{x_j\}, \{t_j\}$ such that $x_j \rightarrow \infty$ as $j \rightarrow \infty$ and $\{t_j\}$ converges to some limit T , where $0 \leq T < t_0$. For each $j \geq 1$, $\tilde{m}(x_j, t_j) < l_0 < 0$, and hence $\tilde{m}(x, T)$ cannot satisfy the uniform decay condition (3). \square

3. A Mellin transform solution

In this section, we derive a solution to equation (1.6) that satisfies condition (1.7). The solution contains an arbitrary function that will be used in the next section to ensure that the solution satisfies the initial condition (1.8).

The Mellin transform of m with respect to x is given by

$$M(s, t) = \int_0^\infty x^{s-1} m(x, t) dx.$$

Assuming that $m \in \mathcal{N}$, we know that $xm(x, t) \rightarrow 0$ as $x \rightarrow \infty$ for all $t \geq 0$, so that equation (1.6) yields the partial differential difference equation

$$M_t(s, t) - gsM(s, t) + b\left(1 - \frac{1}{\alpha^s}\right)M(s + 1, t) = 0. \tag{3.1}$$

Let $M(s, t) = P(s)W(s, t)$, where

$$P(s) = \prod_{k=0}^\infty \left(1 - \frac{1}{\alpha^{k+s}}\right). \tag{3.2}$$

The choice of P is strategic because

$$P(s) = \left(1 - \frac{1}{\alpha^s}\right)P(s + 1).$$

In fact, the partition function P arises in a number of applications with pantograph-type equations [26]. Equation (3.1) implies that

$$W_t(s, t) - gsW(s, t) + bW(s + 1, t) = 0. \tag{3.3}$$

Rather than solving equation (3.3), we solve the corresponding partial differential equation in the original (x, t) space. This equation is not functional in character. Let $w(x, t)$ denote the inverse Mellin transform of $W(s, t)$. Then equation (3.3) corresponds to the partial differential equation

$$w_t(x, t) + gxw_x(x, t) + bxw(x, t) = 0, \tag{3.4}$$

which is equation (1.6) without the functional term.

We now pose the Cauchy problem of solving (3.4) subject to an initial condition of the form $w(x, 0) = w_0(x)$. The characteristic projections are $t = \xi$ and $x = \eta e^{g\xi}$, and hence equation (3.4) has solutions of the form

$$w(x, t) = w_0(xe^{-gt})e^{-\gamma x(1-e^{-gt})},$$

where $\gamma = b/g$.

The infinite product defining P can be converted into an infinite series using the Euler identity [2, p. 17]

$$\prod_{k=0}^{\infty} (1 + zq^k) = 1 + \sum_{k=1}^{\infty} \frac{q^{k(k-1)/2} z^k}{\prod_{j=1}^k (1 - q^j)}, \tag{3.5}$$

which is valid for $|q| < 1$ and $z \in \mathbb{C}$. The Euler identity with $q = 1/\alpha$ and $z = -1/\alpha^s$ indicates that

$$P(s) = 1 + \sum_{k=1}^{\infty} c_k \left(\frac{1}{\alpha^s}\right)^k,$$

where

$$c_k = \frac{(-1)^k \alpha^k}{\prod_{m=1}^k (\alpha^m - 1)} = \frac{(-1)^k q^{k(k-1)/2}}{\prod_{j=1}^k (1 - q^j)}. \tag{3.6}$$

The inverse of $P(s)$ is

$$p(x) = \delta(x - 1) + \sum_{k=1}^{\infty} c_k \delta(\alpha^k x - 1).$$

The inverse transform of $M(s, t) = P(s)W(s, t)$ is given by the Mellin convolution

$$m(x, t) = \int_0^{\infty} w\left(\frac{x}{\xi}, t\right) \frac{p(\xi)}{\xi} d\xi, \tag{3.7}$$

from which we get a solution of the form

$$m(x, t) = w_0(xe^{-gt})e^{-\gamma x(1-e^{-gt})} + \sum_{k=1}^{\infty} c_k w_0(\alpha^k x e^{-gt})e^{-\gamma \alpha^k x(1-e^{-gt})}. \tag{3.8}$$

It is a straightforward (albeit tedious) calculation to show directly that the function defined in equation (3.8) is a solution to equation (1.6) for any choice of differentiable w_0 such that the series can be differentiated term by term.

4. The function w_0

The function w_0 is determined by the initial condition m_0 . Before we determine w_0 , a few conditions are placed on the function m_0 . These conditions ensure that m_0 , regarded as a function on Ω , is in the set \mathcal{N} introduced in Section 2 and that m_0 also satisfies (1.7) for consistency.

ASSUMPTION 4.1. *We make the following assumptions on the function m_0 .*

- (1) $m_0(x) \geq 0$ for all $x \geq 0$ and m_0 is not identically zero on $[0, \infty)$.
- (2) $m_0''(x)$ is continuous for all $x \geq 0$.
- (3) There exists a positive number ℓ such that:
 - (a) $m_0(x) \sim O(1/x^{1+\ell})$ as $x \rightarrow \infty$;
 - (b) $m_0(x) \sim O(x^{1+\ell})$ as $x \rightarrow 0^+$;
 - (c) $m_0'(x) \sim O(1/x^{1+\ell})$ as $x \rightarrow \infty$.

We use the Mellin transform to deduce a relationship for w_0 . Conditions 3(a) and 3(b) in Assumption 4.1 ensure that the Mellin transform of m_0 is holomorphic in a strip that includes $\{s \in \mathbb{C} \mid -1 \leq \Re(s) \leq 1\}$.

Equation (3.7) implies that

$$m_0(x) = \int_0^\infty w_0\left(\frac{x}{\xi}\right) \frac{P(\xi)}{\xi} d\xi, \tag{4.1}$$

and taking the Mellin transform of both sides of equation (4.1), noting that the integral is a Mellin convolution, yields

$$W_0(s) = \frac{M_0(s)}{P(s)}, \tag{4.2}$$

where W_0 and M_0 are the Mellin transforms of w_0 and m_0 , respectively, and P is given by (3.2). The function $1/P$ is a well-known partition function studied by Morgan [21]. We can use another partition identity [2, p. 17] to show that

$$\frac{1}{P(s)} = \sum_{k=0}^\infty R_k(\alpha) \frac{1}{\alpha^{ks}},$$

where $R_0(\alpha) = 1$, and, for $k \geq 1$,

$$R_k(\alpha) = \prod_{j=1}^k \left(1 - \frac{1}{\alpha^j}\right)^{-1}.$$

Equation (4.2) thus gives

$$W_0(s) = M_0(s) \sum_{k=0}^\infty R_k(\alpha) \frac{1}{\alpha^{ks}}$$

for $\Re(s) > 0$ and, since the above series is uniformly convergent in $\{s \in \mathbb{C} \mid \Re(s) \geq \sigma\}$ for any $\sigma > 0$, the transform can be inverted term by term to get the inverse transform

$$w_0(x) = \sum_{k=0}^\infty R_k(\alpha) m_0(\alpha^k x). \tag{4.3}$$

Let

$$R(\alpha) = \prod_{k=1}^\infty \left(1 - \frac{1}{\alpha^k}\right)^{-1}.$$

The value of R can be expressed in terms of elliptic integrals, theta functions, the Dedekind eta function or Euler’s pentagonal number series [12, 21, 26]. The sequence $\{R_k(\alpha)\}$ is monotonically increasing and bounded above by $R(\alpha)$. In Assumption 4.1, the decay condition 3(a) on m_0 ensures that the series in equation (4.3) is uniformly convergent in $[x_0, \infty)$ for any $x_0 > 0$. However, the behaviour of $w_0(x)$ as $x \rightarrow 0^+$ is not clear. (Note that the series $\sum_{k=0}^{\infty} R_k(\alpha)$ diverges.)

The behaviour of $w_0(x)$ near zero can be gleaned directly from the Mellin transform using a well-known asymptotic relation [11, Theorem 4]. Specifically, suppose that F is the Mellin transform of a function f , that the strip of holomorphy for F is $a < \Re(s) < c$ and that F is meromorphic for $a \leq \Re(s) \leq c$. The leading order terms for f as $x \rightarrow 0^+$ are determined by the singularities on the line $\Re(s) = a$. In particular, suppose that F has the poles a_1, \dots, a_j on this line. Then

$$f(x) = \sum_{k=1}^j \text{Res}(F(s)x^{-s}, a_k) + O(x^{-A})$$

as $x \rightarrow 0^+$, where A is some number less than a that depends on the position of the singularities of F with real part less than a . The formula can be refined to include more singularities (producing lower-order terms), and it can be extended to the case where there are an infinite number of singularities on the line $\Re(s) = a$, provided the infinite series is convergent.

Now $M_0(s)$ is holomorphic for $-1 \leq \Re(s) \leq 1$, and $P(s)$ is an entire function with first-order zeros at $s = -\ell + i\tau_j$, where $\ell = 0, 1, 2, \dots$ and $\tau_j = 2\pi j / \log \alpha$ for any integer j . The function $W_0(s)$ is thus holomorphic in a strip that includes $\Re(s) = 1$ and has simple poles along the imaginary axis at $i\tau_j$. These poles will determine the behaviour of w_0 near 0.

$$\begin{aligned} \text{Res}(W_0(s)x^{-s}, i\tau_j) &= \text{Res}\left(\frac{M_0(s)}{P(s)}x^{-s}, i\tau_j\right) \\ &= \frac{R(\alpha)}{\log \alpha} M_0(i\tau_j)x^{-i\tau_j} \\ &= \frac{R(\alpha)}{\log \alpha} M_0(i\tau_j)\{\cos(\tau_j \log x) - i \sin(\tau_j \log x)\}, \end{aligned}$$

and hence, as $x \rightarrow 0^+$,

$$w_0(x) = \frac{R(\alpha)}{\log \alpha} \sum_{-\infty}^{\infty} M_0(i\tau_j)\{\cos(\tau_j \log x) - i \sin(\tau_j \log x)\} + O(x^{\sigma_0}). \tag{4.4}$$

Here $0 < \sigma_0 < 1$, since the “next” poles of W_0 in the left half-plane are on the line $\Re(s) = -1$. We have made the strong assumption that m_0 is twice continuously differentiable. Under this assumption, we can appeal to the Riemann Lebesgue lemma [25] to assert that

$$|M_0(i\tau_j)| \sim O(|\tau_j|^{-2}),$$

as $j \rightarrow \pm\infty$, and this ensures the convergence of the series $\sum_{-\infty}^{\infty} |M_0(i\tau_j)|$. Clearly, this condition can be relaxed, but we will not pursue this. The Riemann Lebesgue lemma can also be used to refine the $O(x^{\sigma_0})$ term in (4.4). In particular, this term arises from the contour integral of the inverse transform along the line $\Re(s) = -\sigma_0$. Now

$$\left| \int_{-\sigma_0-i\infty}^{-\sigma_0+i\infty} W_0(-\sigma_0 + i\eta)x^{-(\sigma_0+i\eta)} d\eta \right| \leq x^{\sigma_0} \int_{-\sigma_0-i\infty}^{-\sigma_0+i\infty} \left| \frac{M_0(-\sigma_0 + i\eta)}{P(-\sigma_0 + i\eta)} \right| d\eta \leq \rho_0 x^{\sigma_0},$$

where

$$\rho_0 = \frac{1}{|P(-\sigma_0)|} \int_{-\sigma_0-i\infty}^{-\sigma_0+i\infty} |M_0(-\sigma_0 + i\eta)| d\eta.$$

Equation (4.4) can thus be written as

$$w_0(x) = h_0(x) + x^{\sigma_0} r_0(x), \quad (4.5)$$

where

$$h_0(x) = \frac{R(\alpha)}{\log \alpha} \sum_{-\infty}^{\infty} M_0(i\tau_j) \{\cos(\tau_j \log x) - i \sin(\tau_j \log x)\}, \quad \text{and} \quad |r_0(x)| \leq \rho_0.$$

The asymptotic behaviour of w_0 as $x \rightarrow 0^+$ can be further refined by using a contour that also encloses the poles along the line $\Re(s) = -1$. We know that M_0 is holomorphic along the line $\Re(s) = -1$ so that there is a σ_1 , $1 < \sigma_1 < 2$, such that W_0 is holomorphic along the line $\Re(s) = -\sigma_1$. If we incorporate the poles on $\Re(s) = -1$, following the above approach, w_0 can be expressed in the form

$$w_0(x) = h_0(x) + x h_1(x) + x^{\sigma_1} r_1(x), \quad (4.6)$$

where

$$h_1(x) = \frac{R(\alpha)}{(1-\alpha)\log \alpha} \sum_{-\infty}^{\infty} M_0(-1 + i\tau_j) \{\cos(\tau_j \log x) - i \sin(\tau_j \log x)\},$$

and there is a constant ρ_1 such that $|r_1(x)| \leq \rho_1$. This form will be used later to show that m meets the boundary condition (1.7).

The next lemma summarises some of the important properties of w_0 that will be needed in Section 6.

LEMMA 4.2. *Let w_0 be defined by equation (4.3). Under conditions (1)–(3) on m_0 in Assumption 4.1:*

- (1) w_0 is bounded on $(0, \infty)$;
- (2) $w'_0 \in C^1(0, \infty)$; and
- (3) w'_0 is bounded on $[x_0, \infty)$ for any $x_0 > 0$.

PROOF. The Mellin transform can also be used to examine the decay rate of $w_0(x)$ as $x \rightarrow \infty$. Briefly, $1/P$ is holomorphic in the right half-plane and M_0 is holomorphic in the strip $-1 \leq \Re(s) \leq 1$. This means that the strip of holomorphy for the Mellin transform W_0 must include a strip of the form $0 < \Re(s) < c$, for some $c > 1$, and this implies that

$$w_0(x) \sim O(x^{-c}) \quad (4.7)$$

as $x \rightarrow \infty$. Condition 3(c) in Assumption 4.1 yields a similar result for w'_0 .

The decay conditions on m_0 as $x \rightarrow \infty$ show that in any interval of the form $[x_0, \infty)$, where $x_0 > 0$, the series in (4.3) is uniformly convergent, and the continuity of m_0 implies that w_0 is also continuous in that interval. Relation (4.7) implies that w_0 must be bounded on $[x_0, \infty)$ and relation (4.4) shows that w_0 is bounded on the interval $(0, \infty)$.

To show that $w_0 \in C^1(0, \infty)$, we note that $m_0 \in C^1(0, \infty)$, and condition 3(c) ensures that the series $\sum_{k=0}^{\infty} R_k(\alpha) \alpha^k m'_0(\alpha^k x)$ is uniformly convergent in $[x_0, \infty)$ for any $x_0 > 0$. The boundedness of w'_0 in $[x_0, \infty)$ can be established in the same manner as for w_0 . \square

5. Dominant eigenvalues and eigenfunctions

The eigenvalues and eigenfunctions associated with Problem A can be derived by studying the class of nontrivial solutions of the form $\bar{m}(x, t) = A(t)y(x)$. Substituting this solution form into equation (1.6) yields

$$\frac{A_t(t)}{A(t)} = \frac{1}{y(x)} (-xy_x(x) - \gamma xy(x) + \gamma \alpha xy(\alpha x)) = \lambda,$$

where λ is a constant. The above expression implies that

$$A(t) = \kappa e^{\lambda t},$$

where κ is a constant, and y satisfies the equation

$$xy'(x) + (\gamma x + \lambda)y(x) = \gamma \alpha xy(\alpha x), \quad (5.1)$$

where $'$ denotes the first derivative. There is precisely one *real* eigenvalue $\lambda_{0,0}$ such that $\bar{m} \in \mathcal{N}$ is nonnegative in Ω and satisfies condition (1.7). Since $\bar{m} \in \mathcal{N}$, y is integrable on $[0, \infty)$. Moreover, condition (1.7) indicates that

$$\lim_{x \rightarrow 0^+} \frac{y(x)}{x} = 0,$$

so that $y(0) = 0$, and $y(x)/x$ is also integrable on $[0, \infty)$. Since $\bar{m}(x, t) \geq 0$ and $\bar{m}(x, t)$ is nontrivial, $\int_0^\infty y(x) dx \neq 0$ and $\int_0^\infty y(x)/x dx \neq 0$. These observations allow us to glean a value for $\lambda_{0,0}$. Specifically, if we divide both sides of equation (5.1) by x and integrate from 0 to ∞ , we find that $\lambda_{0,0} = 0$, and hence equation (5.1) yields the pantograph equation

$$y'(x) + \gamma y(x) = \gamma \alpha y(\alpha x). \quad (5.2)$$

A detailed analysis of this equation can be found in [15, 16]. The probability density function (pdf) solution to this equation was derived by Hall and Wake in [12], where they showed that there is a unique pdf solution y . In fact, they studied the exponential growth case [13], and they used their solution to the pantograph equation to construct what they called an SSD solution to Problem A. Briefly, the solutions to equation (5.2) are of the form

$$y(x) = CD(x, \gamma),$$

where C is a positive constant and

$$D(x, \gamma) = e^{-\gamma x} + \sum_{k=1}^{\infty} c_k e^{-\gamma \alpha^k x},$$

where c_k is given by equation (3.6). The constant C is generally chosen to normalize the corresponding separable solution to the original equation (1.3) to be a pdf at $t = 0$. For the original partial differential equation, however, the normalization comes from the initial data.

Note that the value of $D(0, \gamma)$ can be determined from the Euler identity (3.5) with $z = -1$. This gives

$$D(0, \gamma) = 1 + \sum_{k=1}^{\infty} c_k = \prod_{k=0}^{\infty} (1 - \alpha^{-k}) = 0.$$

Since D is a solution to equation (5.2), it follows that all the derivatives of D with respect to x also vanish at $x = 0$. This can also be deduced directly from the Euler identity because

$$1 + \sum_{k=1}^{\infty} c_k \alpha^{jk} = \prod_{k=0}^{\infty} (1 - \alpha^{j-k}) = 0$$

for any positive integer j . The next lemma gives a summary of some important properties of the Dirichlet series. The proof of these properties can be found in [12].

LEMMA 5.1. *For any positive constant β , the Dirichlet series*

$$D(x, \beta) = e^{-\beta x} + \sum_{k=1}^{\infty} c_k e^{-\beta \alpha^k x}$$

is a solution to

$$D_x(x, \beta) + \beta D(x, \beta) = \beta \alpha D(\alpha x, \beta).$$

The function D has the following properties.

- (1) D has derivatives of all orders with respect to x .
- (2) D and all the derivatives of D with respect to x vanish at $x = 0$ and as $x \rightarrow \infty$.
- (3) $D(x, \beta) > 0$ for all $x > 0$.

Returning to equation (5.1), it is a straightforward calculation to show that, for any integer j , $\lambda_{(0,j)} = i\tau_j$ is also an eigenvalue with a corresponding eigenfunction $y_j(x) = x^{i\tau_j}y(x)$. (In fact, all the zeros of P are eigenvalues.) The dominant real eigenvalue is 0, but $\Re(\lambda_{(0,j)}) = 0$ for all integers j , so there is no dominant eigenvalue, and this is the source of oscillatory terms in the long time asymptotic behaviour of the solutions to Problem A.

6. The solution and long time dynamics

We first establish that equation (3.8) provides the solution to Problem A.

THEOREM 6.1. *Let m_0 satisfy conditions (1)–(3) of Assumption 4.1. Then the function m defined by (3.8), where w_0 is given by equation (4.3), is the solution to Problem A.*

PROOF. The uniqueness and positivity of the solution was established in Section 2. Lemma 4.2 shows that the series in (3.8) is uniformly convergent in the quadrant $\{(x, t) \mid (x, t) \in [x_0, \infty) \times (0, \infty)\}$ for any $x_0 > 0$ and is differentiable. By construction, the series satisfies the partial differential equation (1.6) and the initial condition (1.8). It remains, however, to show that the boundary conditions (1.7) are satisfied for $t > 0$.

Let

$$\Phi_0(x, t) = h_0(xe^{-gt}), \quad \frac{R(\alpha)}{\log \alpha} \sum_{-\infty}^{\infty} |M_0(i\tau_j)| = \Upsilon_0,$$

$$\Phi_1(x, t) = h_1(xe^{-gt}), \quad \frac{R(\alpha)}{(\alpha - 1)\log \alpha} \sum_{-\infty}^{\infty} |M_0(-1 + i\tau_j)| = \Upsilon_1,$$

and note that $\Phi_k(x, t) = \Phi_k(\alpha x, t)$ for $k = 0, 1$. Equation (4.5) implies that

$$m(x, t) = \Phi_0(x, t)D(x, \beta(t)) + x^{\sigma_0}e^{-\sigma_0gt}R_0(x, t), \tag{6.1}$$

where $\beta(t) = \gamma(1 - e^{-gt})$, $0 < \sigma_0 < 1$, and

$$R_0(x, t) = r_0(x)e^{-\beta(t)x} + \sum_{k=1}^{\infty} c_k \alpha^{\sigma_0 k} r_0(\alpha^k x) e^{-\beta(t)\alpha^k x}.$$

Now

$$|R(x, t)| \leq \rho_0 \left(1 + \sum_{k=1}^{\infty} |c_k| \alpha^{\sigma_0 k} \right),$$

and since the above series converges, there is thus a number κ_0 such that $|R(x, t)| \leq \kappa_0$. Hence, for any $t > 0$,

$$\left| \frac{m(x, t)}{x} \right| \leq \frac{\Upsilon_0}{x} D(x, \beta(t)) + \frac{\kappa_0}{x^{1-\sigma_0}}.$$

We know from Lemma 5.1 that $D(x, \beta(t)) \rightarrow 0$ as $x \rightarrow \infty$, and since $\sigma_0 < 1$, the above inequality indicates that

$$\lim_{x \rightarrow \infty} \frac{m(x, t)}{x} = 0 \quad \text{for any } t > 0.$$

Equation (4.6) shows that, for $t > 0$,

$$m(x, t) = \Phi_0(x, t)D(x, \beta(t)) + \frac{xe^{-gt}}{-\beta(t)}\Phi_1(x, t)D_x(x, \beta(t)) + x^{\sigma_1}e^{-\sigma_1gt}R_1(x, t),$$

where $1 < \sigma_1 < 2$, and

$$R_1(x, t) = r_1(x)e^{-\beta(t)x} + \sum_{k=1}^{\infty} c_k a^{\sigma_0 k} r_1(a^k x) e^{-\beta(t)a^k x}.$$

A bound for the term $|R_1|$ can be obtained in a manner similar to that for $|R_0|$, so that there is a number κ_1 such that $|R_1(x, t)| \leq \kappa_1$. Hence,

$$\left| \frac{m(x, t)}{x} \right| \leq \frac{\Upsilon_0}{x} D(x, \beta(t)) + \frac{\Upsilon_1}{\beta(t)} |D_x(x, \beta(t))| + x^{\sigma_1-1} \kappa_1.$$

Lemma 5.1 shows that $D_x(x, \beta) \rightarrow 0$ as $x \rightarrow 0^+$; consequently, $D(x, \beta(t))/x \rightarrow 0$ (l'Hôpital's rule) and $|D_x(x, \beta(t))| \rightarrow 0$ as $x \rightarrow 0^+$. Since $\sigma_1 > 1$, x^{σ_1-1} also vanishes in this limit, and thus, for any $t > 0$

$$\lim_{x \rightarrow 0^+} \frac{m(x, t)}{x} = 0. \quad \square$$

We now consider the behaviour of m for large time. The main result is the following theorem.

THEOREM 6.2. *Under the conditions of Theorem 6.1,*

$$\int_0^{\infty} |m(x, t) - \Phi_0(x, t)D(x, \gamma)| dx \rightarrow 0 \tag{6.2}$$

as $t \rightarrow \infty$.

PROOF. Using equation (6.1),

$$m(x, t) - \Phi_0(x, t)D(x, \gamma) = \Phi_0(x, t)(D(x, \beta(t)) - D(x, \gamma)) + x^{\sigma_0}e^{-\sigma_0gt}R_0(x, t).$$

Consequently,

$$|m(x, t) - \Phi_0(x, t)D(x, \gamma)| \leq \Upsilon_0 |D(x, \beta(t)) - D(x, \gamma)| + x^{\sigma_0}e^{-\sigma_0gt}|R_0(x, t)|. \tag{6.3}$$

Now $\beta(t) = \gamma(1 - e^{-gt}) < \gamma$; therefore,

$$\begin{aligned} |D(x, \beta(t)) - D(x, \gamma)| &= \left| (e^{-\beta(t)x} - e^{-\gamma x}) + \sum_{k=1}^{\infty} c_k (e^{-\beta(t)a^k x} - e^{-\gamma a^k x}) \right| \\ &\leq (e^{-\beta(t)x} - e^{-\gamma x}) + \sum_{k=1}^{\infty} |c_k| (e^{-\beta(t)a^k x} - e^{-\gamma a^k x}), \end{aligned}$$

so that, by integrating,

$$\begin{aligned} \int_0^\infty |D(x, \beta(t)) - D(x, \gamma)| dx &\leq \Upsilon_0 \left(\frac{e^{-gt}}{\beta(t)} + \sum_{k=1}^\infty |c_k| \frac{e^{-gt}}{\alpha^k \beta(t)} \right) \\ &\leq \frac{\Upsilon_0 e^{-gt}}{\beta(t)} \left(1 + \sum_{k=1}^\infty |c_k| \right). \end{aligned} \tag{6.4}$$

We know that $\beta(t) \rightarrow 1$ as $t \rightarrow \infty$, so that, for (say) $t > (\log 2)/g$, $\beta(t) > 1/2$. The series in (6.4) converges so that, for $t > (\log 2)/g$,

$$\int_0^\infty |\Phi_0(x, t)| |D(x, \beta(t)) - D(x, \gamma)| dx \leq \tilde{\Upsilon}_0 e^{-gt}, \tag{6.5}$$

where

$$\tilde{\Upsilon}_0 = 2\Upsilon_0 \left(1 + \sum_{k=1}^\infty |c_k| \right).$$

Also, for $t > (\log 2)/g$,

$$\begin{aligned} |R_0(x, t)| &\leq |r_0(xe^{-gt})| e^{-\beta(t)x} + \sum_{k=1}^\infty |c_k| \alpha^{\sigma_0 k} |r_0(\alpha^k xe^{-gt})| e^{-\beta(t)\alpha^k x} \\ &\leq \rho_0 e^{-\gamma x/2} \left(1 + \sum_{k=1}^\infty |c_k| \alpha^{\sigma_0 k} \right). \end{aligned} \tag{6.6}$$

The series in (6.6) converges and $x^{\sigma_0} e^{-\gamma x/2} \in L^1[0, \infty)$, and hence there is a number $\tilde{\rho}_0$ such that

$$\int_0^\infty x^{\sigma_0} |R_0(x, t)| dx \leq \tilde{\rho}_0. \tag{6.7}$$

Equations (6.3), (6.5) and (6.7) imply that

$$\int_0^\infty |m(x, t) - \Phi_0(x, t)D(x, \gamma)| dx \sim O(e^{-g\sigma_0 t}) \quad \text{as } t \rightarrow \infty. \quad \square$$

7. Discussion

In this paper, we developed a method for solving an initial–boundary value problem that involves a partial differential equation with a functional term. The problem was originally presented as a model for cell division by Hall and Wake [13], who studied the separable solution. Although the results were tailored to Problem A, it is clear from the transformations leading to equation (1.6) that the method can be used for solving the differential equation (1.3), provided $r > 0$. The results can be refined for a broader class of initial data. However, it is not clear that the approach used in Section 3 can be adapted to division rates that are not monomials. A key step in deriving the solution form (3.8) is the identification of a ‘‘partition function’’, P , that yields a Mellin

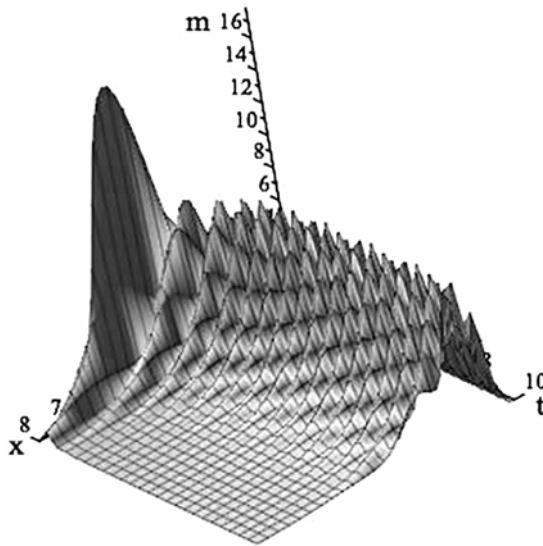


FIGURE 1. Solution for $m_0(x) = x^2 e^{-(x-4)^2/2}$.

transform equation corresponding to a partial differential equation without a functional term (equation (3.4)). A number of pantograph-type ordinary differential equations have this structure. For example, the basic model with constant growth and division rates leads to the same partition function P [26], but the general solution for the partial differential equation reflects this structure only in the long time asymptotic behaviour of solutions [27].

Theorem 6.2 shows that the solution m converges (exponentially) in the L^1 norm to the function $\Phi_0 D$ as $t \rightarrow \infty$. What is remarkable is that Φ_0 depends on t and the initial condition m_0 . For constant growth rates, the limiting solution is purely a function of x and depends weakly on the initial data through a normalization constant [22, 23]. Another feature of Φ_0 is that it is periodic in the time variable, that is,

$$\Phi_0(x, t) = \Phi_0(x, t + g^{-1} \log \alpha),$$

and this gives the limiting solution its oscillatory character. The amplitude of the oscillations depend on the initial data through the Mellin transform and the value of D . It was shown by Bernard et al. [3] that exponential growth gives rise to oscillating solutions for a class of coagulation-fragmentation equations that includes the present cell division equation. The extra structure of this cell division model, however, allows one to not only solve the general problem explicitly, but also to determine the limiting solution in detail.

A solution m can be plotted directly from equations (3.8) and (4.3) for a given initial condition m_0 . We provide three examples that illustrate the influence of the initial data and the oscillatory character of the limiting solution. In all of these examples, we use $\alpha = 2$, $\gamma = 1$ and $g = 1$. For the first example, let $m_0 = x^2 e^{-(x-4)^2/2}$. Figure 1 depicts

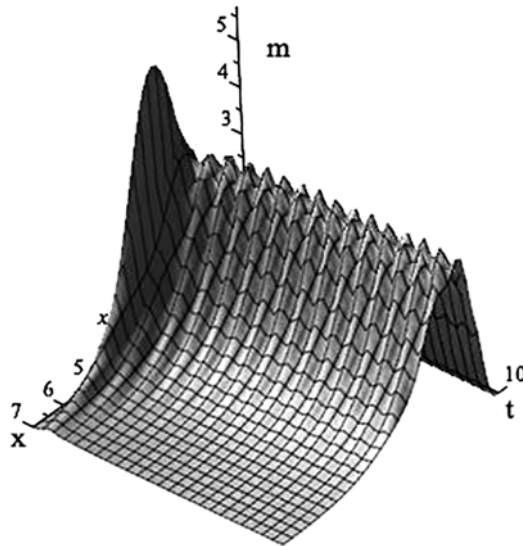


FIGURE 2. Solution for $m_0(x) = x^2 e^{-x^2/2}$.

a graph of the solution, which clearly shows the oscillatory nature of the solution. If we change the initial data to $m_0 = x^2 e^{-x^2/2}$, then the character of the solution changes noticeably for larger time (Figure 2).

The oscillations are still there, but the effect of the term Φ_0 is less striking. As an “extreme” case, let $m_0(x) = H(x - 1) - H(x - 2)$, where H denotes the Heaviside function. In this case, $M_0(s) = (2^s - 1)/s$, so that the zeros of M_0 coincide with those of $P(s)$ leaving the simple pole at $s = 0$. Although m_0 does not satisfy the differentiability conditions, we have that $M(i\tau_j) = 0$ for all $j = \pm 1, \pm 2, \dots$, so there is no question about the series defining Φ_0 converging. As predicted by the analysis, the solution does not have any oscillations (Figure 3).

In terms of the original number density n with $r = 1$, equation (6.2) translates to

$$\int_0^\infty x^2 |e^{-gt} n(x, t) - \Phi_0(x, t) D(x, \gamma)| dx \rightarrow 0,$$

so that convergence to the limiting solution is in a weighted L^1 norm. For general $r > 0$, the solution to (1.3) can be recovered by calculating m as before and then substituting $z(x) = x^r/r$ for x , α^r for α and gr for g in m . This gives a solution of the form $n(x, t) = e^{-gt} m(z(x), t)/x^2$. Making the same substitutions in the limiting function $\Phi_0 D$,

$$\int_0^\infty x^{r+1} |e^{-gt} n(x, t) - \Phi_0(z(x), t) D(z(x), \gamma)| dx \rightarrow 0.$$

The parameter r thus determines the weighting of the norm. Note that it does not change the period of Φ_0 .

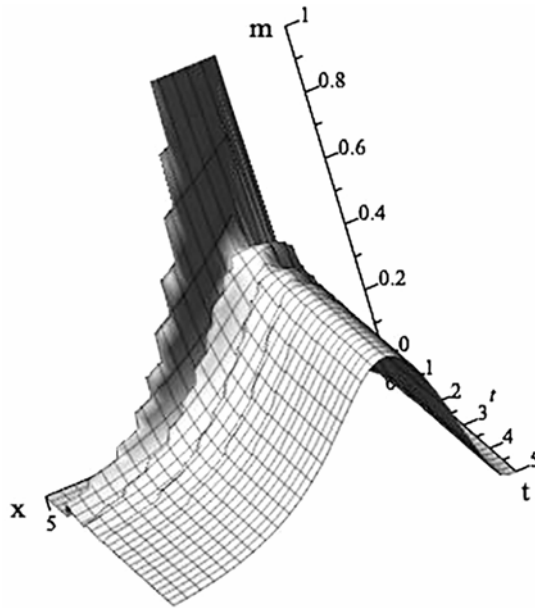


FIGURE 3. Solution for $m_0(x) = H(x - 1) - H(x - 2)$.

Finally, the transformations used to construct the solution rely crucially on $r > 0$. If $r \leq 0$, then the construction breaks down. Of special interest is the “critical case” when $r = 0$. The large time asymptotic behaviour for this case was studied by Doumic and Escobedo [9], who showed that the long time dynamics of solutions for this case are very different.

The first signs of trouble occur when one looks for a solution of the form $n(x, t) = A(t)y(x)$, where y is a pdf. Substituting this solution form into equation (1.3) with $r = 0$ leads to the equation

$$g(xy(x))' + (b + \lambda)y(x) = b\alpha^2y(\alpha x), \quad (7.1)$$

where λ is a constant of separation. The problem is that there are two ways of finding λ . Integrating both sides of equation (7.1) from 0 to ∞ gives $\lambda = b(\alpha - 1)$. On the other hand, assuming that y has a first moment, then multiplying both sides of equation (7.1) by x and integrating from 0 to ∞ yields $\lambda = g$. Thus for any solution y that decays fast enough to have a first moment, we must have $g = b(\alpha - 1)$, which, in general, is not true.

Doumic and Escobedo [9] show, more generally, that there are no solutions of the form $A(t)y(xf(t))$, where A and f are continuously differentiable functions on $[0, \infty)$. They also derive an explicit solution form in terms of an inverse Mellin transform. In fact, the problem can be solved directly if the initial condition n_0 is smooth and bounded. Note that the uniqueness and nonnegativity results of Section 2 can be

adapted for the case $r = 0$. The solution in this case is

$$n(x, t) = e^{-(b+g)t} \sum_{k=0}^{\infty} n_0 (\alpha^k x e^{-gt}) \frac{(b\alpha^2 t)^k}{k!}.$$

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