

A possible predictive mathematical model for the growth of a periphytic alga

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Abstract. Algae are photosynthetic organisms and have qualities that are very attractive for cultivation and industrial development for commercial purposes. When algal growth is analyzed for the production of biomass usually only the exponential phase of the growth curve is considered and the other phases are ignored. The objective of the work is to present a possible predictive mathematical model that allows a better understanding of the kinetic behavior of a periphytic microalgae by means of the use of the Smoluchowski discrete equation, with special emphasis on the lag phase. More specifically, unknown connection between the discrete Smoluchowski equation and the deterministic Baranyi model is shown in the present study. Analysis of this connection leads to a possible predictive mathematical model about of the kinetic behavior of a periphytic microalgae.

1. Introduction

One of the most efficient approaches for dynamic modelling of coagulation and fragmentation processes in cell biology is through the kinetic (rate) equation, which describes the evolution of interacting clusters distribution with regard to their masses. The first model of this kind, consisting of an infinite system of ordinary differential equations, was derived by Smoluchowski in the physical context [1, 2].

On the other hand, in microbiology, most traditional isothermal microorganism growth models are based on the assumption that bacterial culture growth has three stages: lag, exponential and stationary [3–5]. More precisely, when a bacterium is inoculated into the new environment, it typically needs time to adjust before it can start reproducing. This stage is referred to as the lag phase and it is followed by the exponential growth phase. Later, there is a stationary phase during which the number of cells remains unchanged. Usually, this stages are imposed in the models from the phenomenological point of view, using parameters that sometimes are not easy to measure.

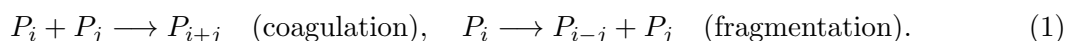
A commonly accepted deterministic growth model is the Baranyi model [6–9]. The aim of this paper is to show an unknown connection between the discrete Smoluchowski equation and the Baranyi model allowing us to characterize this model in terms of the parameters of the Smoluchowski equation, which could potentially be easier to establish in terms of



experimentation. It will also be demonstrated that the lag phase is a consequence of imposed conditions on fragmentation and coagulation rates in the equation.

2. Discrete Smoluchowski equation

For $i \in \mathbb{N}$, let P_i denotes a cell of mass i . As time goes by, cells evolve and, depending on the degree of interaction between them, they can either form cells of larger masses $i + j$ or cells of smaller masses j and $i - j$, which take part in binary reactions. This phenomenon is formally written [10] as Equation (1).



Let $c_t(i)$ denotes the average number of cells of mass i per unit volume, at time t . The expression $ic_t(i)$ represents the part of mass consisting of cells of length i , per unit volume. It is then natural to consider that the coagulation phenomenon ($P_i + P_j \longrightarrow P_{i+j}$), is proportional to $c_t(i)c_t(j)$ with proportionality constant $K_{i,j} = K_{j,i} \geq 0$. In the same way, the fragmentation phenomenon ($P_i \longrightarrow P_{i-j} + P_j$) is considered proportional to $c_t(i)$ with proportionality constant $F_{j,i-j} = F_{i-j,j} \geq 0$. For the discrete case, by (1) and the above, through a mass balance analysis, the Smoluchowski equation is established as Equation (2) [10].

$$\frac{d}{dt}c_t(i) = \frac{1}{2} \sum_{j=1}^{i-1} [K_{j,i-j}c_t(j)c_t(i-j) - F_{j,i-j}c_t(i)] - \sum_{j=0}^{\infty} [K_{i,j}c_t(i)c_t(j) - F_{i,j}c_t(i+j)]. \quad (2)$$

In this paper, we are interested in showing the connection between Equation (2) and a Baranyi model for bacterial growth. We are supposing that the initial data is small [11], this enables us deduce uniqueness for the mass flow equation.

Theorem 1. With the above notations, if $K_{i,j} = \beta ij$ (where $\beta > 0$ is a given constant), $\sum_{i=0}^{\infty} i^2 c_0(i) < \infty$, and $\sum_{i=0}^{\infty} i c_0(i) = 1$, then Equation (2) admits a unique solution c_t on $[0, T_0)$ with $T_0 = \left(\beta \sum_{i=0}^{\infty} i^2 c_0(i) \right)^{-1}$. Moreover, $\sum_{j=0}^{\infty} j c_t(j) = 1$ for all $t \in [0, T_0)$, and for each i , $s \mapsto \sum_{j=0}^{\infty} \frac{i}{i+j} F_{i,j} i c_s(i+j)$ is integrable on $(0, T_0)$. This sentence is a consequence of Theorem 2.6 and Corollary 3.2 in [12].

Remark. Let $S_m(t) := \sum_{k=1}^m k c_t(k)$ for all $t \in [0, T_0)$. Given that $(S_m)_{m \in \mathbb{N}}$ is a monotone sequence of continuous functions that converges pointwise on the compact space $[0, T]$ (with $T < T_0$) to $\sum_{k=0}^{\infty} k c_t(k) = 1$ (Theorem 1), where the limit function is also continuous, then $(S_m)_{m \in \mathbb{N}}$ is uniformly convergent on $[0, T]$ (with $T < T_0$), i.e., $(S_m)_{m \in \mathbb{N}}$ is uniformly Cauchy on $[0, T]$ (with $T < T_0$). In addition, letting $f_m(t) := \sum_{k=1}^m c_t(k)$ and noting that in Equation (3) it is given by,

$$|f_{n+k}(t) - f_n(t)| = \sum_{k=n+1}^{n+k} c_t(k) < \sum_{k=n+1}^{n+k} k c_t(k) = |S_{n+k}(t) - S_n(t)|, \quad (3)$$

the sequence $(f_m)_{m \in \mathbb{N}}$ is, by Equation (3), uniformly Cauchy on $[0, T]$ (with $T < T_0$), hence $(f_m)_{m \in \mathbb{N}}$ uniformly convergent on $[0, T]$ (with $T < T_0$) to a function $X(t) := \sum_{i=1}^{\infty} c_t(i)$. Here, $X(t) = \sum_{i=1}^{\infty} c_t(i)$ is understood as the total average number of cells per unit volume.

Theorem 2. If $K_{i,j} = \beta ij$, where $\beta > 0$ is a given constant, $\sum_{i=0}^{\infty} i^2 c_0(i) < \infty$, $\sum_{i=0}^{\infty} i c_0(i) = 1$, $F_{1,j} = 0$ for all $j \geq 1$, and exists a constant α that is defined by Equation (4).

$$\frac{1}{2} \sum_{j=2}^{i-1} F_{j,i-j} - \frac{\beta}{2} i = \alpha \quad \text{for all } i \geq 4, \quad (4)$$

then, we obtain the Equation (5).

$$\frac{d}{dt} \sum_{i=4}^{\infty} c_t(i) = \sum_{i=4}^{\infty} \frac{d}{dt} c_t(i) \quad \text{for all } t \in [0, T_0) \text{ with } T_0 = \left(\beta \sum_{i=0}^{\infty} i^2 c_0(i) \right)^{-1}. \quad (5)$$

Proof. By Equation (2), we obtain the Equation (6).

$$\begin{aligned} \frac{d}{dt} \sum_{i=4}^m c_t(i) &= \sum_{i=4}^m \left[\frac{1}{2} \sum_{j=1}^{i-1} (\beta j(i-j) c_t(j) c_t(i-j) - F_{j,i-j} c_t(i)) \right] \\ &\quad - \sum_{i=4}^m \sum_{j=0}^{\infty} [\beta i j c_t(i) c_t(j) - F_{i,j} c_t(i+j)] \\ &= \frac{\beta}{2} \sum_{j=1}^3 \sum_{i=4}^m j(i-j) c_t(j) c_t(i-j) + \frac{\beta}{2} \sum_{j=4}^{m-1} \sum_{i=j+1}^m j(i-j) c_t(j) c_t(i-j) \\ &\quad - \sum_{i=4}^m \left(\alpha + \frac{\beta i}{2} \right) c_t(i) - \beta \sum_{i=4}^m i c_t(i) \sum_{j=0}^{\infty} j c_t(j) + \sum_{i=4}^m \sum_{j=i}^{\infty} F_{i,j-i} c_t(j) \\ &= \frac{\beta}{2} \sum_{j=1}^3 j c_t(j) \sum_{i=4-j}^{m-j} i c_t(i) + \frac{\beta}{2} \sum_{j=4}^{m-1} j c_t(j) \sum_{i=1}^{m-j} i c_t(i) - \alpha \sum_{i=4}^m c_t(i) \\ &\quad - \frac{\beta}{2} \sum_{i=4}^m i c_t(i) - \beta \sum_{i=4}^m i c_t(i) \sum_{j=1}^{\infty} j c_t(j) + \sum_{i=4}^m \sum_{j=i}^{\infty} F_{i,j-i} c_t(j) \\ &= \frac{\beta}{2} \sum_{j=1}^3 j c_t(j) (S_{m-j}(t) - S_{4-j-1}(t)) - \alpha (f_m(t) - f_3(t)) \\ &\quad - \frac{\beta}{2} (S_m(t) - S_3(t)) + \frac{\beta}{2} (S_{m-1}(t) - S_3(t)) - \frac{\beta}{2} \sum_{j=4}^{m-1} j c_t(j) \sum_{i=m-j+1}^{\infty} i c_t(i) \\ &\quad - \beta (S_m(t) - S_3(t)) + \sum_{j=4}^m c_t(j) \sum_{i=4}^{j-2} F_{i,j-i} + \sum_{j=m+1}^{\infty} c_t(j) \sum_{i=4}^m F_{i,j-i}. \end{aligned} \quad (6)$$

Then by Equation (6), we obtain the Equation (7).

$$\begin{aligned}
\frac{d}{dt} \sum_{i=4}^m c_t(i) &= \frac{\beta}{2} \sum_{j=1}^3 j c_t(j) (S_{m-j}(t) - S_{4-j-1}(t)) - \frac{3\beta}{2} (S_m(t) - S_3(t)) \\
&+ \frac{\beta}{2} (S_{m-1}(t) - S_3(t)) - \frac{\beta}{2} \sum_{j=4}^{m-1} j c_t(j) \sum_{i=m-j+1}^{\infty} i c_t(i) \\
&- \alpha (f_m(t) - f_3(t)) + \sum_{j=4}^m c_t(j) \sum_{i=4}^{j-2} F_{i,j-i} + \sum_{j=m+1}^{\infty} c_t(j) \sum_{i=4}^m F_{i,j-i}.
\end{aligned} \tag{7}$$

This way, using Equation (7) and the last remark, we conclude that the sequence given by $g'_m(t) := \frac{d}{dt} \sum_{i=4}^m c_t(i)$ is uniformly convergent on $[0, T]$ ($T < T_0$), and given that (g_m) is uniformly convergent on $[0, T]$ ($T < T_0$), $(g_m = f_m - f_3)$, and then $\frac{d}{dt} \sum_{i=4}^{\infty} c_t(i) = \sum_{i=4}^{\infty} \frac{d}{dt} c_t(i)$ for all $t \in [0, T_0)$. Using Theorem 1, Theorem 2, and Equation (2), the Corollary 1 can be easily obtained.

Corollary 1. If proportionality constants $K_{i,j}$, $F_{i,j}$ in Equation (2) satisfy the same hypothesis of the previous theorem then is defined Equation (8).

$$\frac{dX}{dt} = -\beta e^{-\beta t} c_0(1) + \sum_{i=2}^{\infty} \frac{d}{dt} c_t(i) \quad \text{for all } t \in [0, T_0) \quad \text{with } T_0 = \left(\beta \sum_{i=0}^{\infty} i^2 c_0(i) \right)^{-1}. \tag{8}$$

Proof. Using Equation (2) with $i = 1$ and $K_{1,j} = \beta j$, we obtain Equation (9).

$$\frac{d}{dt} c_t(1) = - \sum_{j=0}^{\infty} \beta j c_t(1) c_t(j) + \sum_{j=0}^{\infty} F_{1,j} c_t(1+j). \tag{9}$$

Since $F_{1,j} = 0$ for all $j \geq 1$ then, due to Equation (9), $\frac{d}{dt} c_t(1) = - \left(\sum_{j=0}^{\infty} \beta j c_t(j) \right) c_t(1)$. From Theorem 1, we get $\frac{d}{dt} c_t(1) = -\beta c_t(1)$, and then $c_t(1) = e^{-\beta t} c_0(1)$. Now, by Equation (5), we obtained Equation (10).

$$\begin{aligned}
\frac{dX}{dt} &= \sum_{i=1}^{\infty} \frac{d}{dt} c_t(i) = \frac{d}{dt} c_t(1) + \sum_{i=2}^{\infty} \frac{d}{dt} c_t(i) \\
&= -\beta c_t(1) + \sum_{i=2}^{\infty} \frac{d}{dt} c_t(i) = -\beta e^{-\beta t} c_0(1) + \sum_{i=2}^{\infty} \frac{d}{dt} c_t(i),
\end{aligned} \tag{10}$$

for all $t \in [0, T_0)$. The result follows observing that Equation (10) is equivalent to Equation (8).

3. A deterministic Baranyi model for bacterial growth

When a bacterium is inoculated into a new environment, it typically needs time to adjust before it can start reproducing. This time is referred to as the lag phase and it is followed by the exponential growth phase (or log phase). Hereunder we show a deterministic model for bacterial growth proposed by Baranyi [8]. Let the cell population be divided in two parts: cells which are still in the lag phase, $Y_{Lag}(t)$, and cells which are in the exponential phase, $Y_{Exp}(t)$. We assume that cells are transforming from lag to exponential phase at a constant rate called ω . Supposing that all cells are in the lag phase at time zero, our compartment model can be described by a system of two linear differential equations with two initial values, Equation (11).

$$\frac{d}{dt}Y_{Lag} = -\omega Y_{Lag}, \quad \frac{d}{dt}Y_{Exp} = \mu Y_{Exp} + \omega Y_{Lag}, \quad Y_{Lag}(0) = Y_0, \quad Y_{Exp}(0) = 0. \quad (11)$$

The solution of Equation (11) is Equation (12).

$$Y(t) := Y_{Lag} + Y_{Exp} = Y_0 \left(\frac{\omega}{\omega + \mu} e^{\mu t} + \frac{\mu}{\omega + \mu} e^{-\omega t} \right), \quad (12)$$

where $Y_{Lag}(t) = Y_0 e^{-\omega t}$; $Y_{Exp}(t) = Y_0 \frac{\omega}{\omega + \mu} (e^{\mu t} - e^{-\omega t})$; likewise, Equation (13) is equivalent to the Equation (12).

$$\ln Y(t) = \ln Y_0 + \mu \left[t - \frac{-\ln \left(\frac{\omega}{\omega + \mu} + \frac{\mu}{\omega + \mu} e^{-(\omega + \mu)t} \right)}{\mu} \right]. \quad (13)$$

Moreover, by Equation (13), $\ln Y(t)$ converges asymptotically to the linear function, Equation (14).

$$t \rightarrow \ln Y_0 + \mu(t - L) \quad \text{where} \quad L = \frac{\ln \left(1 + \frac{\mu}{\omega} \right)}{\mu}, \quad (14)$$

L defined in Equation (14) is the value which Baranyi defined as the population lag time. The result obtained in Equation(12) can also be related with the discrete Smoluchowski equation using the Theorem 3.

Theorem 3. If proportionality constants $K_{i,j}$, $F_{i,j}$ in Equation (2) satisfy: $K_{i,j} = \beta i j$, where $\beta > 0$ is a given constant, $\sum_{i=0}^{\infty} i^2 c_0(i) < \infty$, $\sum_{i=0}^{\infty} i c_0(i) = 1$, $F_{1,j} = 0$ for all $j \geq 1$, and exists $\alpha > 0$ according to Equation (15).

$$\frac{1}{2} \sum_{j=1}^{i-1} F_{j,i-j} - \frac{\beta i}{2} = \alpha \quad \text{for all } i \geq 4, \quad (15)$$

then the Smoluchowski equation, Equation (2), implies that exist $M \geq 0$ according to Equation (16).

$$\alpha \left[X - \frac{\alpha + \frac{1}{2}\beta}{\alpha} c_0(1) e^{-\beta t} \right] - M \leq \frac{dX}{dt} \leq \alpha \left[X - \frac{\alpha + \frac{1}{2}\beta}{\alpha} c_0(1) e^{-\beta t} \right], \quad (16)$$

for all $t \in [0, T]$ with $T < T_0$.

Proof. From Corollary 1 and Equation (2), we obtain Equation (17).

$$\begin{aligned}
\frac{dX}{dt} &= -\beta e^{-\beta t} c_0(1) + \sum_{i=2}^{\infty} \frac{d}{dt} c_t(i) \\
&= -\beta e^{-\beta t} c_0(1) + \sum_{i=2}^{\infty} \left[\frac{1}{2} \sum_{j=1}^{i-1} (\beta j(i-j) c_t(j) c_t(i-j) - F_{j,i-j} c_t(i)) \right] \\
&\quad - \sum_{i=2}^{\infty} \sum_{j=0}^{\infty} [\beta i j c_t(i) c_t(j) - F_{i,j} c_t(i+j)] \\
&= -\beta e^{-\beta t} c_0(1) + \sum_{i=2}^{\infty} \left[\frac{1}{2} \sum_{j=1}^{i-1} (\beta j(i-j) c_t(j) c_t(i-j) - F_{j,i-j} c_t(i)) \right] \\
&\quad - \sum_{u=2}^{\infty} \sum_{i=2}^u [\beta i(u-i) c_t(i) c_t(u-i) - F_{i,u-i} c_t(u)] \\
&= -\beta e^{-\beta t} c_0(1) + \sum_{i=2}^{\infty} \left[\frac{1}{2} \sum_{j=1}^{i-1} (\beta j(i-j) c_t(j) c_t(i-j) - F_{j,i-j} c_t(i)) \right] \\
&\quad - \sum_{i=2}^{\infty} \sum_{j=2}^i [\beta j(i-j) c_t(j) c_t(i-j) - F_{j,i-j} c_t(i)] \\
&= -\beta e^{-\beta t} c_0(1) + \frac{1}{2} \sum_{i=2}^{\infty} \sum_{j=1}^{i-1} F_{j,i-j} c_t(i) \\
&\quad + \frac{1}{2} \sum_{i=2}^{\infty} \beta(i-1) c_t(1) c_t(i-1) - \frac{1}{2} \sum_{i=3}^{\infty} \sum_{j=2}^{i-1} \beta j(i-j) c_t(j) c_t(i-j).
\end{aligned} \tag{17}$$

Using Theorem 1, it is possible to see that Equation (17) is equivalent to Equation (18).

$$\begin{aligned}
\frac{dX}{dt} &= -\frac{\beta}{2} \beta e^{-\beta t} c_0(1) + \sum_{i=2}^{\infty} \left[\frac{1}{2} \sum_{j=1}^{i-1} F_{j,(i-j)} \right] c_t(i) - \frac{1}{2} \sum_{i=3}^{\infty} \sum_{j=2}^{i-1} \beta j(i-j) c_t(j) c_t(i-j) \\
&= -\frac{1}{2} \beta e^{-\beta t} c_0(1) + \sum_{i=2}^{\infty} \left[\frac{1}{2} \sum_{j=1}^{i-1} F_{j,(i-j)} \right] c_t(i) - \frac{1}{2} \sum_{j=2}^{\infty} \sum_{i=j+1}^{\infty} \beta j(i-j) c_t(j) c_t(i-j) \\
&= -\frac{1}{2} \beta e^{-\beta t} c_0(1) + \sum_{i=2}^{\infty} \left[\frac{1}{2} \sum_{j=1}^{i-1} F_{j,(i-j)} \right] c_t(i) - \frac{1}{2} \sum_{j=2}^{\infty} \beta j c_t(j) \\
&= -\frac{1}{2} \beta e^{-\beta t} c_0(1) + \sum_{i=2}^{\infty} \left[\frac{1}{2} \sum_{j=1}^{i-1} F_{j,(i-j)} - \frac{1}{2} \beta i \right] c_t(i).
\end{aligned} \tag{18}$$

From hypothesis Equation (15), exists $\alpha \neq 0$ such that $\frac{1}{2} \sum_{j=1}^{i-1} F_{j,i-j} - \frac{1}{2} \beta i = \alpha$ for all $i \geq 4$, and consequently Equation (18) can be written as Equation (19).

$$\begin{aligned}
\frac{dX}{dt} &= -\frac{1}{2}\beta e^{-\beta t} c_0(1) + \alpha \sum_{i=4}^{\infty} c_t(i) - \beta c_t(2) - \frac{3\beta}{2} c_t(3) \\
&= -\frac{1}{2}\beta e^{-\beta t} c_0(1) - \alpha(c_t(1) + c_t(2) + c_t(3)) + \alpha X - \beta c_t(2) - \frac{3\beta}{2} c_t(3) \\
&= \alpha X + \left(-\frac{1}{2}\beta - \alpha\right) e^{-\beta t} c_0(1) - (\alpha + \beta)c_t(2) - \left(\alpha + \frac{3}{2}\beta\right) c_t(3).
\end{aligned} \tag{19}$$

Taking $M := \max_{t \in [0, T]} [(\alpha + \beta)c_t(2) + (\alpha + \frac{3}{2}\beta)c_t(3)]$, $T < T_0$, and Equation (19), we obtain Equation (16).

Remark. Checking that $Y(t)$ defined in Equation (12) is the unique solution of the initial value problem $\frac{dX}{dt} = \alpha \left[X - \frac{\alpha + \frac{1}{2}\beta}{\alpha} c_0(1) e^{-\beta t} \right]$, $X(0) = \left(1 + \frac{\beta}{2\alpha} c_0(1) \right)$ with $\mu := \alpha > 0$, $\omega := \beta > 0$, letting $f(t) = \ln X(t)$ and using Equation (16) and Equation (12), there is $c > 0$ which let us obtain the Equation (20).

$$\begin{aligned}
f(t) &\leq \ln Y_0 + \mu \left(t - \frac{-\ln \left(\frac{\omega}{\omega + \mu} + \frac{\mu}{\omega + \mu} e^{-(\omega + \mu)t} \right)}{\mu} \right) \\
f(t) &\geq \ln Y_0 + \mu \left(t - \frac{-\ln \left(\frac{\omega}{\omega + \mu} + \frac{\mu}{\omega + \mu} e^{-(\omega + \mu)t} - ct e^{-\mu t} \right)}{\mu} \right)
\end{aligned} \tag{20}$$

for all $t \in [0, T]$ with $T < T_0$. Taking $\sum_{i=0}^{\infty} i^2 c_0(i) < \frac{\alpha}{\beta \ln \left(1 + \frac{\alpha}{\beta} \right)}$ we obtain $T_0 > \frac{\ln \left(1 + \frac{\mu}{\omega} \right)}{\mu}$ and if t is near to $\frac{\ln \left(1 + \frac{\mu}{\omega} \right)}{\mu}$ and it is large enough then $f(t)$ is near to $f_{\infty}(t) = \ln Y_0 + \mu(t - L)$ with L the value of the population lag time defined in [8] by Baranyi (see Equation (14) and Equation (20)).

4. Conclusions

The connection shown in this article between the Smoluchowski equation and the Baranyi model suggests a potential path of experimental and theoretical study of models for bacterial growth; by establishing a comparison between Baranyi Robert model and our model we can assert that the fundamental difference is that in our model the population lag time surges as a physical consequence of the growth of the particles and is not imposed in the equation as occurs in the Baranyi model. Besides, in our model the population lag time can be calculated using parameters which could be experimentally measured in a clear form, while in the other model it is not clear the way how estimate this lag time.

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