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On the chemical meaning of some growth models possessing Gompertzian-type property†

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Growth models are often used when modelling various processes in life sciences, ecology, demography, social sciences, etc. Dynamical growth models are usually formulated in terms of an ODE (system of ODS's) or by an explicit solution to an ODE, such as the logistic, Gompertz, and Richardson growth models. To choose a suitable growth model it is useful to know the physics-chemical meaning of the model. In many situations this meaning is best expressed by means of a reaction network that possibly induces the dynamical growth model via mass action kinetics. Such reaction networks are well known for a number of growth models, such as the saturation-decay and the logistic Verhulst models. However, no such reaction networks exist for the Gompertz growth model. In this work we propose some reaction networks using mass action kinetics that induce growth models that are (in certain sense) close to the Gompertz model. The discussion of these reaction networks aims to a better understanding of the chemical properties of the Gompertz model and "Gompertzian-type" growth models. Our method can be considered as an extension of the work of previous authors who "recasted" the Gompertz differential equation into a dynamical system of two differential equations that, apart of the basic species variable, involve an additional variable that can be interpreted as a "resource." Two new growth models based on mass action kinetics are introduced and studied in comparison with the Gompertz model. Numerical computations are presented using some specialized software tools.

KEYWORDS

fitting biological measurement data, Gompertzian growth model, logistic growth model, mass action kinetics, nonlinear ODE's, Sigmoidal growth functions

1 | INTRODUCTION

When studying the time evolution of various growth processes from the fields of life sciences, ecology, demography, social sciences, etc, we often have a set of measurement data of the form (t_i, y_i), where y_i is an experimental measurement (or a vector of such measurements) value obtained at the time moment $t_i, i = 1, \dots, n$. We then have to choose a model (vector) function $y = f(t)$ that fits the measurement data. In some cases the function f is chosen from a class of explicitly defined functions, eg, the class of linear functions of the form $f = at + b$, in other situations the function f is determined

†Dedicated to the memory of Prof. Rene Alt

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as a solution to a class of dynamical systems. The dynamical system involves the rates of certain characteristics of the process, which allows for a better interpretation of the intrinsic properties of the process. It is still more useful to be able to find, if possible, a reaction network that induces (precisely) the dynamical model via reaction kinetics.[1,2]

In this way we obtain a physics-chemical interpretation of the dynamical model and its ingredients (rate constants, reacting variables, interaction relations, etc). Such reaction networks are known for a number of basic dynamical growth models, such as the saturation delay and the logistic Verhulst models. However, no reaction network exists that induces the Gompertzian growth model, which is often used in modeling various dynamical processes (in demography, cancer research, etc). In this work we focus attention to Gompertzian-type growth models, proposing several reaction networks that induces dynamical models that are close to the Gopmertzian one. Our method can be considered as an extension of the work of previous authors who "recast" the Gompertz differential equation into a dynamical system of two differential equations that, apart of the species variable, involve an additional variable that can be interpreted as "resource." Let us mention that vast literature has been devoted to such a "recasting" procedure.[3-11] Numerical computations are presented using specialized software tools.

Growth models and their interpretation. We shall be interested in growth models that can be formulated solutions of differential equations. For simplicity we shall consider growth functions defined in $[0, \infty)$ with values ranging in the interval [0, 1]. In many situations the dynamical system provides some insight of the behavior of the solutions. In this work we shall demonstrate two powerful methods that, if possible to apply, provide more information for the nature of the growth proves (1) the method of "recasting" the dynamical model into a system having additional species and (2) the method of finding realization of the system in the form of a reaction network possibly satisfying mass action kinetics. For some references on related areas the order may consult.[12-29] The next section is of preliminary character and may be ignored by expert readers.

2 | PRELIMINARIES: MASS ACTION KINETICS REACTION NETWORKS, EXAMPLES

Recall the mass action kinetic (MAK) on the simple reaction network:

$$A + B \xrightarrow{k} C \qquad (*)$$

Applying the MAK principle, reaction $(*)$ is "translated" into the dynamical system:

$$c' = kab, \ a' = b' = -kab \qquad (P)$$

where k is a rate constant. System (P) possesses the conservation relations:

$$c + a = C_1 = \text{const}, \quad c + b = C_2 = \text{const} \qquad (CL)$$

which allows to reduce (P) to a differential equation for a single variable, say $c' = k(C_1 - c)(C_2 - c)$.

We can then formulate a mathematical problem, eg, an initial value (IV) ODE problem and find an algebraic or numerical solution to it. For example, an initial value (IV) problem related to (P): $c(0) = 0$, $a(0) = b(0) = 1$ yields solutions for $a = b$ and c as function of time t. The solutions can be expressed analytically or computed numerically and visualized as shown on Figure 1. Note that the solutions are symmetric relative to the line $y = (C_1 + C_2)/2$, as can be expected from relation (CL).

2.1 | The saturation-decay model

The above approach will be demonstrated in the examples to follow in the sequel.

The saturation-decay model (SD model) is induced by the following reaction network:

$$X \xrightarrow{k} Y \tag{1}$$

Using MAK, we obtain the following dynamical system:

$$x' = -kx, \quad y' = kx \tag{2}$$

The reactant x decays whereas the reactant y grows. We have $x' + y'' = 0$, leading thus to the conservation law:

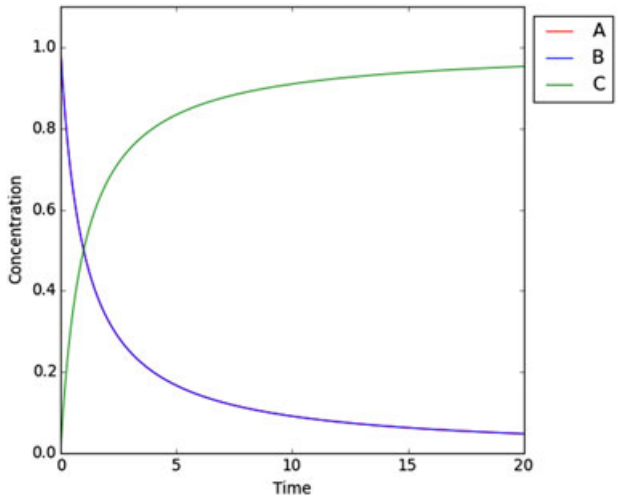

FIGURE 1 Solutions to reaction $A + B \xrightarrow{k} C$; $k = 1.0$, $A(0) = B(0) = 1$, $C(0) = 0$ [Colour figure can be viewed at wileyonlinelibrary.com]

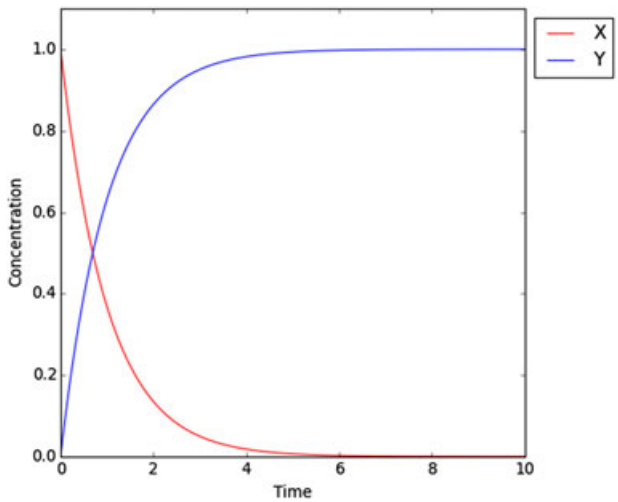

FIGURE 2 Solutions to SD model $X \xrightarrow{k} Y$; $k = 1.0$, $X(0) = 1$, $Y(0) = 0$ [Colour figure can be viewed at wileyonlinelibrary.com]

$$x + y = \text{const} = a, \qquad (SDCL)$$

hence y is a solution to the differential equation

$$y' = k(a - y), \tag{3}$$

known as saturation growth model. The solution of model 3 can be explicitly written as

$$y(t) = y(0)(a - e^{-t}). \tag{4}$$

The solutions to model (1) and (2) are visualized in Figure 2.

2.2 | The iterated saturation-decay model

Reaction 3 can be iterated meaning that the product of each SD reaction becomes the substrate of another SD reaction:

$$S_1 \xrightarrow{k_1} S_2 \xrightarrow{k_2} S_3 \xrightarrow{k_3} \cdots \xrightarrow{k_{n-1}} S_n \quad \text{(ISD)}$$

As can be seen in Figure 3 the graph of concentration S_n is a sigmoidal function.

The iterated saturation-decay model is a special case of the general linear reaction network considered in the work of Kyurkchiev and Markov.[14]

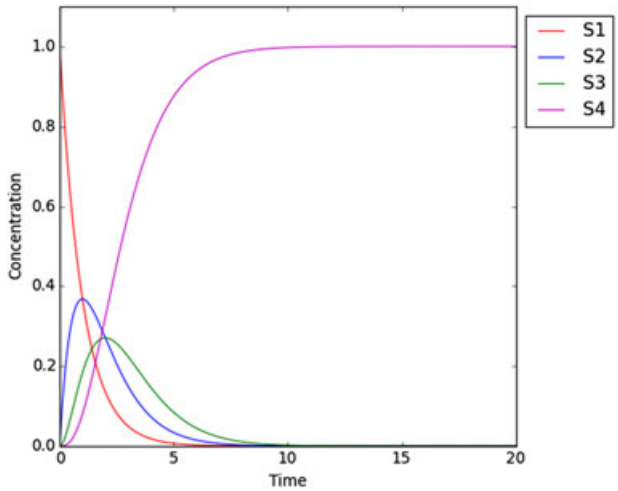

FIGURE 3 Solutions to ISD model $S_1 \xrightarrow{k_1} S_2 \xrightarrow{k_2} S_3 \xrightarrow{k_3} \cdots \xrightarrow{k_{n-1}} S_n$; $n = 4, k_i = 1.0, S_1(0) = 1, S_2(0) = S_3(0) = S_4(0) = 0$ [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Catalyzed growth models

We shall next focus on so-called catalytic reaction networks that are characterized by having a reactant simultaneously in both sides of the reaction.

The SD model 1 describing the transformation of a substrate S into a product P ($S \to P$) can be catalyzed via a catalyst X according to the reaction network:

$$S + X \xrightarrow{k} P + X. \qquad \text{(CSD)}$$

If X does not participate in other reactions that change its concentration, then x is constant and plays the role of a coefficient that multiplies the rate constant in the induced dynamical system. Hence, if $x < 1$, then X acts as inhibitor of the reaction, and if $x > 1$, then X is an accelerator of the reaction.

Analogously to ISD, the CSD model can be repeatedly iterated in the sense that the product of any single CSD model becomes the substrate for another CSD model:

$$\begin{array}{ccc} S_0 + X & \xrightarrow{k_1} & S_1 + X \\ S_1 + X & \xrightarrow{k_2} & S_2 + X \\ & \cdots & \\ S_{n-1} + X & \xrightarrow{k_n} & S_n + X \end{array} \qquad \text{(ICSD)}$$

Remark 1. The catalyst X in the above reaction network may be different species (having different rate constants). If the catalyst X in the reaction network varies in time, say by adding some reaction like $X \to P$, then the behavior of the reaction network may totally change.

3 | AUTOCATALYTIC REACTION NETWORKS AND GROWTH MODELS

In autocatalytic reaction networks a catalyst is also a product. Such is the case with the logistic (Verhulst) reaction network. Vethust model is probably the most important catalytic reaction. Its solution is S shaped (sigmoidal). This model is widely applicable in practice.

3.1 | The logistic (Verhulst) growth model

The logistic (Verhulst) growth (V model) is presented by the following differential equation[30]:

$$x' = kx(a - x) \qquad \text{(V)}$$

We shall be interested in solutions of (V) ranging in the interval [0, 1]; hence, we shall set $a = 1$ in (V) and consider initial conditions $x(0) = x_0$, such that $0 < x_0 < 1$. An explicit solution has the form

$$V(t) = \frac{1}{1+e^{-kt}}. \qquad (VE)$$

Consider the dynamical system

$$s' = -ksx,\ x' = ksx \qquad \text{(DV)}$$

We have $s' + x' = 0$, hence the following conservation relation

$$s + x = \text{const} = a \qquad \text{(CR)}$$

holds true.

Proposition 1. *(1) Assume that x is a solution to model (V) with initial condition $x(0) = x_0$ and let $s(0) = a - x_0$. Then the functions $x, s = a - x$ satisfy the differential system (DV) with initial conditions $x(0) = x_0, s(0) = a - x_0$. (2) Conversely, assume that the functions $x, s = a - x$ satisfy the differential system (DV) with initial conditions $x(0) = x_0, s(0) = a - x_0$. Then x is a solution to model (V) with initial condition $x(0) = x_0$.*

Proof. Substituting $s = a - x$ in (VD): $x' = ksx$ leads to (V). □

Remark 2. The procedure of passing from the dynamical model (V) to model (DV) is called "recasting" in the work of Savageau.[6] Such a procedure gains to a better understanding of the physical meaning of the model. Indeed, the introduction of the additional variable s suggests that the growth of species x happens for the expenses of another species s that can be interpreted as a (nutritional) resource for the species x. On the basis of this suggestion, we arrive to the following proposition that throws further light on the interaction between the species x and s.

Proposition 2. (Kyurkchiev and Markov[31])
The V model is induced by the autocatalytic reaction network:

$$S + X \xrightarrow{k} X + X \qquad (\text{V}^*)$$

Proof. Applying MAK to reaction network $(V*)$ yields the dynamical system (DV). According to proposition 1 system (DV) induces Verhulst model (V).

The V model can be repeatedly iterated in the manner applied to the SD model, that is, the product of a V model becomes the substrate for another V model. □

3.2 | A modified Verhulst growth model (VM model)

The VM model is presented by the following dynamical system:

$$x' = kx(a-x)^n \qquad \text{(VM)}$$

Remark 3. The V model is a special case of the VM model for $n = 1$.

Proposition 3. *The VM model is induced by the following autocatalytic reaction network:*

$$nS + X \xrightarrow{k} X + nX \qquad (VM^*)$$

The biochemical interpretation of the VM model is as follows: the VM model takes into account the interaction between various species (and resources), such as various types of foods and other environmental resources (water, air, light, etc).

According to Lente,[1] it is unlikely in reality that more than 3 species react simultaneously. Therefore, we shall focus our attention to the restriction $n = 2$.

The solutions for $n = 2$ are graphically presented in Figure 4.

3.3 | Another modified Verhulst growth model (VSM model)

The VSM model is presented by the following dynamical system:

$$x' = kx(a-x)(b-x) \quad \text{(VSM*)}$$

Proposition 4. *The VSM model is induced via MAK from the following autocatalytic reaction network:*

$$S_1 + S_2 + X \xrightarrow{k} X + X + X \quad \text{(VSM)}$$

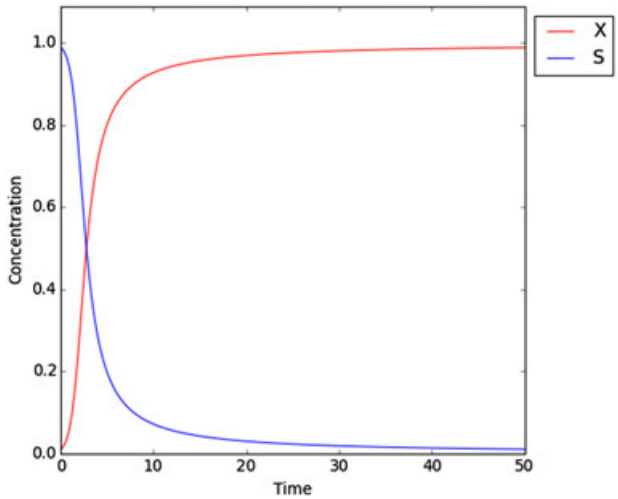

FIGURE 4 Solutions to $2S + X \xrightarrow{k} 3X$; $k = 1.0$; $S(0) = 0.99, X(0) = 0.01$ [Colour figure can be viewed at wileyonlinelibrary.com]

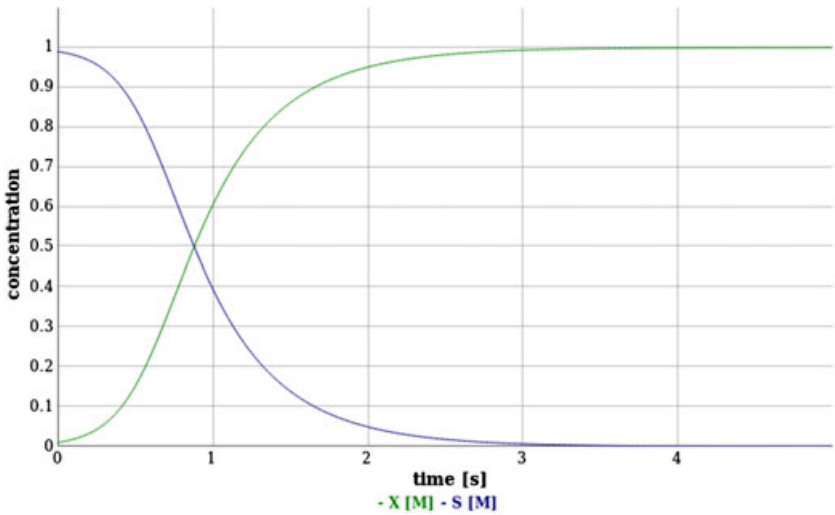

FIGURE 5 Solutions to $S_1 + S_2 + X \xrightarrow{k} X + X + X$; $k = 1.0$; $X(0) = 0.01, S(0) = 0.99, a = 2, b = 3$ [Colour figure can be viewed at wileyonlinelibrary.com]

The solutions to model (VSM) for $a = 2, b = 3$ are visualized in Figure 5.

4 | THE GOMPERTZ MODEL

The Gompertz growth function is a solution $y = y(t)$ to the dynamical equation[32]:

$$dy/dt = ky(c - \ln y) \qquad \text{(G)}$$

4.1 | Some properties of the Gompertz model

The following propositions hold true.

Proposition 5. *The solution y to (G) is the exponent of the solution to the SD model.*

Proof. Let $z(t) = \ln y(t)$. Then $dz/dt = (dy/dt)/y$. Substituting in (G) written as

$$y'/y = k(c - \ln y) \qquad (\text{G}^*)$$

we obtain the ODE to the SD model:

$$dz/dt = k(c - z). \qquad (\text{G}^{**})$$

□

Lemma 1. *The solutions s, y to the dynamical system*

$$ds/dt = -ks,\ dy/dt = ksy \qquad \text{(SG)}$$

satisfy the "conservation" relation

$$s + \ln y = c = \text{const} \qquad \text{(gg)}$$

Proof. From (SG) we have

$$ds/dt + dy/dt/y = 0$$

hence (gg). □

Proposition 6. *The functions y, s, such that y is a solution to (G) and $s = c - lny$ satisfy the dynamical system (SG). Conversely, if y, s are solutions to system (SG), then y is a solution to (G).*

Proof. According to the Lemma from (SG) we have the relation (gg); thus, $s = c - \ln\ y$. Substituting s in the equation: $dy/dt = ksy$ we obtain equation (G). □

Remark 4. System (SG) is discussed in the works of Laird[4] and Bajzer and Vuk-Pavlovic[5] as belonging to the class of "synergistic and saturable systems" considered in the work of Savageau.[6] System (SG) is considered as "recasted" variant of equation (G) in the terminology of the previous work.[6]

Remark 5. If $c = 0$ in (gg), then $\ln y \to 0$ with $t \to \infty$ (as $s \to 0$), resp. $y \to 1$. The G model then has the form

$$dy/dt = ky(-\ln y) \quad \text{(G0)}$$

or

$$y'/y = -k \ln y = e^{-kt}$$

known as *Gompertz law of mortality*.

Remark 6. System (SG) shows that the Gompertz model cannot be realized as an MAK network in the sense of the work of Chellaboina et al.[33] Indeed, the first equation of system (SG) tells us that the species S does not interact with the other species X, whereas the second equation tells the opposite. Knowing this important fact, we shall look for MAK networks that possibly possess the G property.

4.2 | The G property

Definition 1. G property (Gompertz property). A (sigmoidal) growth function $y = f(t)$ defined in $[0, \infty)$, such that $f(t) > 0, \lim_{t\to\infty} f(t) = 1$, has the G property, if it grows slower than the logistic curve v, that is, for every logistic curve $v \in (0, 1)$ there exists f, such that $f(t) \leqslant v(t)$ for all $t \geqslant 0$.

Remark 7. As mentioned, the Gompertz model possesses no realization in the sense of previous work,[33] that is, in terms of mass action reaction network. However, there are sigmoidal curves induced by MAK that possess Gompertzian property. To this end we shall need the following Lemma.

Lemma 2. *Let $x_0 \in (0, 1)$. For all $x \in [x_0, 1)$ the inequality*

$$\frac{-\ln x}{-\ln x_0} \leqslant \frac{1-x}{1-x_0}$$

holds true.

Proof. Notice that for $0 < x \leqslant 1$, we have $1 - x \leqslant -\ln x$. Because function $-\ln x$ is convex (has positive second derivative), $1 - x \leqslant l(x)$, where $l(x)$ is the line passing through the points $(x_0, -\ln x_0)$ and $(0, 1)$ lying on $-\ln x$. We have

$$l(x) = (-\ln x_0)((1-x)/(1-x_0)).$$

Let us divide the lime by the value $l(0) = (-\ln x_0)/(1-x_0)$, then the line $l/l(0)$ coincides with the line $1 - x$ (both lines pass through the points $(0, 1)$ and $(1, 0)$). Hence, $(-\ln x)/l(0) \leqslant 1 - x$, which proves the lemma. □

Proposition 7. *The Gompertz model (G) possesses the G property.*

Proof. We shall prove that for each logistic curve $v(t), t \in [0, \infty)$ there is a Gompertz curve $g(t), t \in [0, \infty)$ that lies below the logistic one in the interval $t \in [0, \infty)$. Consider model (V) with $a = 1$: $x' = kx(1 - x)$, and fix an arbitrary initial condition $x(0) = x_0$ and a rate constant $k > 0$. Consider the Gompertzian model (G) with $c = 0$. Choose initial condition $y(0) = x_0$, and determine the Gompertzian rate constant h so that $y'(0) = x'(0)$. Under these conditions the chosen Gompertzian curve satisfies the initial value ODE problem:

$$dy/dt = hy(-\ln y), y_0 = x_0, \qquad (G_0)$$

wherein h is determined from the conditions $y_0 = x_0, y'(0) = x'(0)$, that is, $hy_0(-\ln y_0) = kx_0(a - x_0)$, hence $h(-\ln x_0) = k(1 - x_0)$, $h = k\frac{1-x_0}{-\ln x_0}$.

We shall show that for all points in the phase plane (t, u), $t \geqslant 0, 0 < u < 1$, the slope of the Gompertz curve at (t, u) is less than the slope of the logistic curve at the sane phase point (t, u), that is,

$$y'|_{(t,u)} \leqslant x'|_{(t,u)},$$

hence

$$hu(-\ln u) \leqslant ku(1 - u),$$

that is

$$k\frac{1 - x_0}{-\ln x_0}u(-\ln u) \leqslant ku(1 - u).$$

Dividing the above inequality by $ku > 0$, we obtain

$$\frac{1 - x_0}{-\ln x_0}(-\ln u) \leqslant (1 - u),$$

or

$$(-\ln u)/(-\ln x_0) \leqslant (1 - u)/(1 - x_0),$$

which is true according to Lemma 2.

We thus obtain the proof of the proposition. □

Remark 8. The solutions to the logistic and Gompertzian model as defined in the proposition are visualized in Figure 6. Figure 6 presents the logistic function $x = x(t)$ and the Gompertz function $y = y(t)$ in the interval $t \in [0, \infty)$, as solutions to the following two ODE initial value problems

$$x' = kx(1 - x), k = 1, x_0 = 0.01;$$

$$dy/dt = hy(-\ln y), y_0 = x_0 h = k\frac{(1 - x_0)}{(-\ln x_0)}.$$

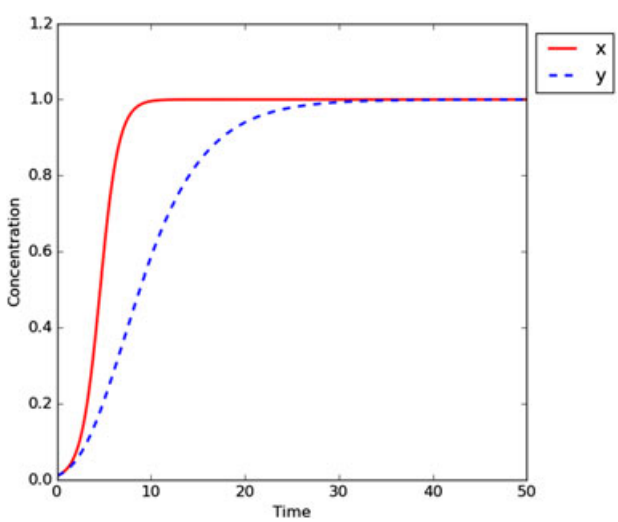

FIGURE 6 The logistic (red) and Gompertz (blue dash) curves starting from same point with same slopes [Colour figure can be viewed at wileyonlinelibrary.com]

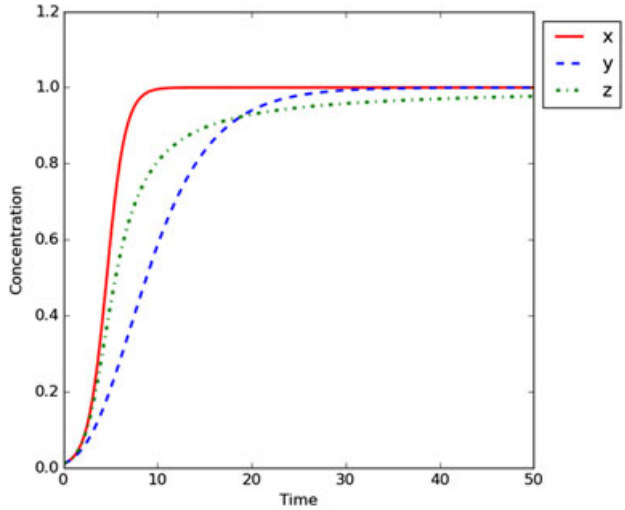

FIGURE 7 Same as Figure 6 plus the solution of the VM model (green dash) [Colour figure can be viewed at wileyonlinelibrary.com]

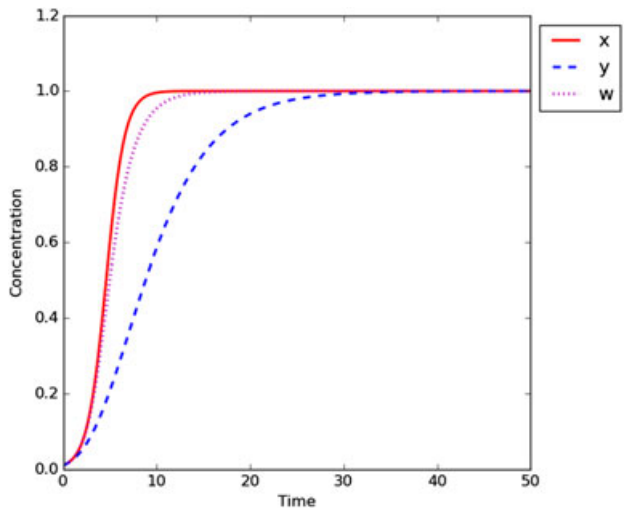

FIGURE 8 Same as Figure 6 plus the solution of the VSM model [Colour figure can be viewed at wileyonlinelibrary.com]

Proposition 8. *The modified Verhulst models (VM) and (VSM) possess the G property.*

Remark 9. The proof is similar to the proof of the G property of the Gompertz model (Proposition 7). Proposition 8 is graphically visualized in Figures 7 to 9.

Solutions of the logistic and Gompertz models as well as the two modified Verhulst models are graphically presented in Figures 7 and 8.

Figure 9. Solutions to the logistic model (blue), Gompertz model (purple), and the two modified Verhulst models.

5 | COMPUTATIONAL EXPERIMENTS

For numerical simulations we used SmoWeb – an open source web computational platform (developed in Python) that provides an infrastructure for rapid development of scientific applications with graphical user interface. The applications are in the fields of thermodynamics, heat and fluid flow, and bioprocess modeling. All computations are performed in Web Cloud.[34]

A software tool has been developed in CAS Mathematica for testing the closeness between growth functions is visualized, a screenshot, in Figure 10. Figures 11 and 12 present graphically computer experiments for testing the closeness between the Gompertz model and the modified Verhulst models.

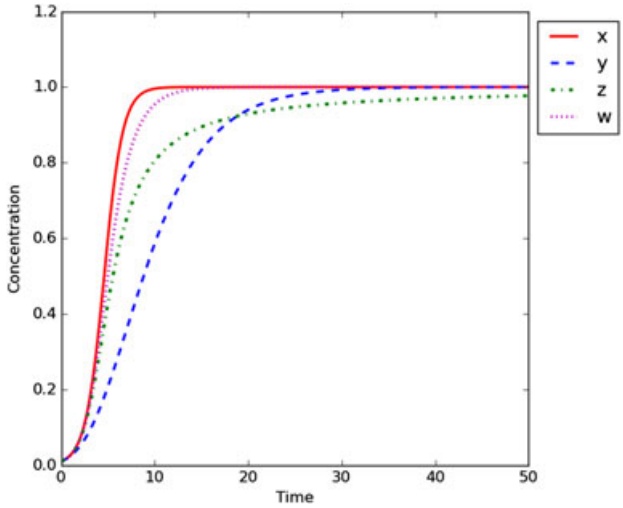

FIGURE 9 Solutions to the logistic model (blue), Gompertz model (purple), and the two modified Verhulst models [Colour figure can be viewed at wileyonlinelibrary.com]

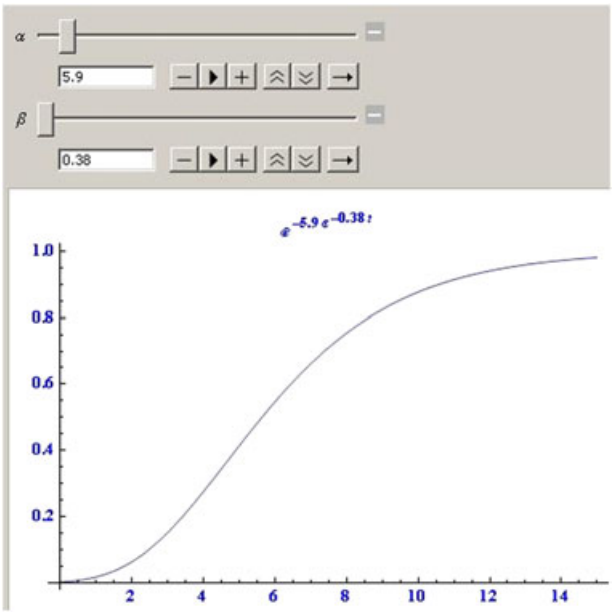

FIGURE 10 Software tools for animation and visualization in *CAS Mathematica* [Colour figure can be viewed at wileyonlinelibrary.com]

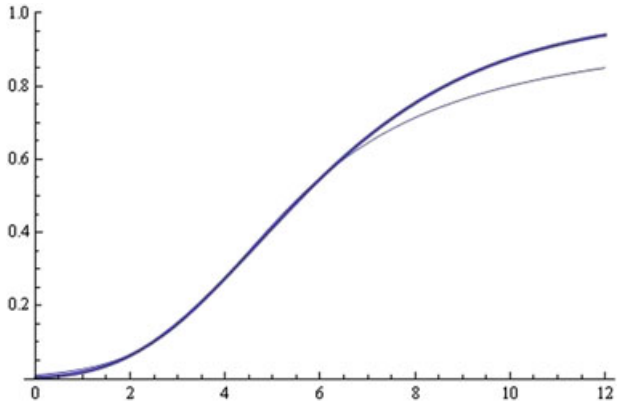

FIGURE 11 Comparison between $x(t)$ from (VM) for $n = 2$ (blue) and $G(t)$ (thick) for $\alpha = 5.9$ and $\beta = 0.38$ [Colour figure can be viewed at wileyonlinelibrary.com]

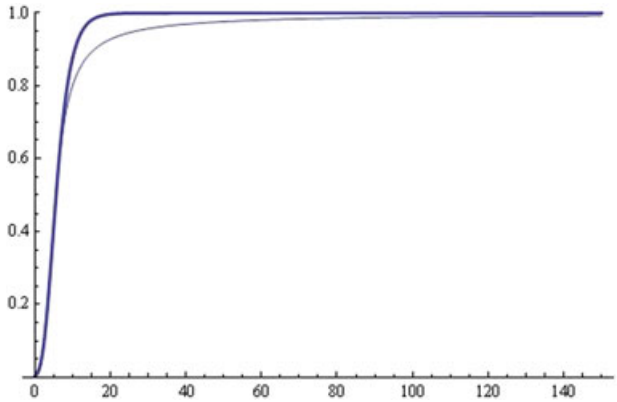

FIGURE 12 Comparison between $x(t)$ from (VM) for $n = 2$ (blue) and $G(t)$ (thick) for $\alpha = 5.9$ and $\beta = 0.38$ for large values of t [Colour figure can be viewed at wileyonlinelibrary.com]

6 | CONCLUDING REMARKS

A possible approach to achieve a G property of a growth logistic-type model curve using MAK is to introduce additional resources and reactions in the logistic reaction network influencing the growth process. A general interpretation of this result is that a more involved reproduction mechanism leads to the Gompertzian property.

Biological growth functions are usually presented in the literature by means of their explicit form or as solutions of a dynamical system. In a situation when the growth model possesses a realization in terms of a chemical reaction network, the modeler has an additional possibility of a (bio)chemical interpretation of the model. We have demonstrated this in the case of the Gompertz model that cannot be realized in terms of a reaction network; however, there are reaction networks that induce a model close to the Gompertzian one. In the process of constructing reaction network to a specific growth model the approach of introducing additional species (recasting) may be useful.

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