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On Some Classes of Growth Functions and Their Links to Reaction Network Theory

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Abstract. In this work we study some characteristics of sigmoidal growth functions that are solutions to dynamical systems induced by reaction networks. The studied dynamical systems are close to the Gompertzian and logistic type growth models. Apart from the growing species, the considered reaction networks involve additional decaying species interpreted as environmental resource(s). Using reaction network theory approach, we formulate several modifications/generalizations of the classic logistic Verhulst model, borrowing ideas from the reaction network formulation of the Gompertz model. Our study of the monotonicity order-preservation properties of the model solutions is supported by numerical computations and graphical visualizations. We also attempt a classification of the reaction networks inducing growth-decay models based on the types of the elementary reactions incorporated in these networks.

INTRODUCTION

In the present work we study certain characteristics of solutions to dynamical systems induced by (chemical) reaction networks. The studied dynamical systems are close to Gompertzian and logistic type growth models [1, 2]. Apart from the growing species, the considered reaction networks involve (one or more) decaying species interpreted as environmental resource(s) for the growing species [3, 4]. This is the reason to call the models in consideration *"growth-decay models"*.

Growth-decay models are often used in modeling of various processes in biology, ecology, epidemiology, social and economic sciences, demography, etc. Usually the dynamical growth-decay models are formulated in terms of a system of ODE's, or by explicit solutions to an ODE (or a system of ODE's), such as the logistic [5], Gompertz [6] and Richards [7] models. In many situations, in order to choose a suitable model for fitting experimental data, it is important to know the physico-chemical meaning of the model.

A possible approach to achieve a meaningful interpretation of the model's mechanism is to make use of a chemical reaction network presentation [4, 8]. Such an approach can be found in a number of basic dynamical growth-decay models, such as the exponential radioactive decay models, epidemiological SIR/SEIR models, population predator-prey type models, demographic and socio-economic models, *etc.* [8]. The reaction network formulation of a dynamical model contributes to a better understanding of the mechanism of the specific physical process and leads to possible improvements of the existing mathematical models. Often mass action kinetics is assumed, interpreted as homogeneous distribution of the species, see, *e.g.*, [4, 9]. In this way a physico-chemical interpretation of the dynamical model and its ingredients (rate parameters, reacting variables, interaction relations, *etc.*) is obtained. Such reaction networks are known for a number of basic dynamical growth models, such as the exponential decay [10] and the logistic Verhulst model [5]. Several reaction networks that induce dynamical models which are close to the Gompertzian one are proposed in [1]. Reaction network realizations of the Gompertz model, together with some modifications and generalizations, are proposed in [2, 11]. A very useful tool for modeling measurement data for the study of evolutionary growth processes in life sciences are the sigmoidal functions, see [12, 13]. When the time evolution of biological growth processes is studied, often a set of measurement data of the form $(t_i, y_i), i = 1, ..., n$, where y_i is experimentally obtained value at time moment t_i, is available. We have to choose a model function of the form $y = f(t)$ that approximates (fits) the measured data. Usually the function f is chosen from a family of functions depending on some parameters and the fitting process consists in finding a suitable parameter set such that a "good" approximation of f to the data set $(t_i, y_i), i = 1, ..., n$, is achieved.

In this work we introduce some modifications/generalizations of the Gompertz and the Verhulst logistic models, which are studied numerically by varying the parameters using same initial and boundary conditions. The numerical computations are implemented using tools from the scientific Python ecosystem [14, 15, 16].

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PRELIMINARIES: REACTION NETWORKS AND GROWTH-DECAY MODELS

Throughout this work growth-decay models are introduced with their reaction networks presentation. The focus is on the solutions of the induced (systems of) differential equations. The dynamical systems have at least two variables — a monotone increasing function, briefly called *growth function* and a monotone decreasing function, briefly *decay function*. Both the growth and decay functions are defined in some interval $T = [0, \infty)$ with nonnegative values in T. In many situations the dynamical system suggests some "insight" for the "inner mechanism" that controls the behavior of the solutions and for the physical meaning of the parameters involved in the system. The "mechanism" of the process is especially well presented when the dynamical model has a realization in the form of a *reaction network*, [4, 8].

Reaction Networks

A reaction network is a set of (elementary) reactions. A reaction is defined by a set of *species* that are either *reactants (reagents)* or *products* or both. For instance, let a reaction have three species S, P, X and let species S, X be reactants whereas P and X be products. Then, for example, a possible reaction can be written symbolically in the form:

$$S + X \xrightarrow{k} P + X, \tag{1}$$

where $k > 0$ is a parameter responsible for the rate of the reaction. Applying mass action kinetics, reaction Eq. (1) can be represented by a system of three differential equations, one for the mass (concentration) of each species involved. Usually the differential equations in the dynamical system are called "reaction equations". The reaction network Eq. (1) is "translated" as a dynamical system of three reaction equations for the corresponding masses (concentrations) $s = s(t),\ p = p(t),\ x = x(t)$ of species S, P, X, respectively:

$$s' = -ksx,\ \ p' = ksx,\ \ x' = 0, \tag{2}$$

where $s' = ds/dt,\ p' = dp/dt,\ x' = dx/dt$ denote the derivatives with respect to the time variable t. In Eq. (1) species X appears in both sides of the reaction; such species are called *catalyst*s. We next give three examples of basic reaction networks inducing well-known growth-decay models: the Gompertzian, the logistic (Verhulst) and the exponential radioactive decay reaction chain (Bateman model).

Three Familiar Growth-decay Models as Reaction Networks

The Gompertz Growth-decay Model

The Gompertz growth-decay model is used in numerous applications. Various formulations of the Gompertz model can be found in the literature [17]. The Gompertz growth function is often defined as a solution $x = x(t)$ of the following differential equation:

$$x' = k_G x(c - \ln x), \tag{3}$$

where $k_G > 0$ and c are parameters. Eq. (3) is often considered as an initial value problem involving an initial condition of the form $x(0) = x_0$.

A reaction network inducing Eq. (3) for the masses (concentrations) s, x of species S, X, respectively, is given by [2], [11]:

$$S \xrightarrow{k_1} P, \tag{4a}$$

$$S + X \xrightarrow{k_2} 2X + S. \tag{4b}$$

The second reaction (4b) in model Eq. (4) suggests that species S serves as a catalyst in the growth process $X \xrightarrow{k_2} 2X$. In addition, reaction (4a) shows that species S decays exponentially, being consumed by an "outer" species P. So,

the Gompertz reaction network Eq. (4) can be qualified as a growth-decay model involving a declining species S and a growing species X. The induced dynamical system (via mass action kinetics) for the concentrations s,x of species S,X respectively, reads

$$s' = -k_1 s,\ \ x' - k_2 sx. \tag{5}$$

It can be checked that Eq. (3) is a consequence of dynamical system Eq. (5) [2, 11].

The Verhulst Logistic Growth-decay Model

The Verhulst logistic growth function is usually defined as a solution of the following differential equation [5]:

$$x' = k_L x\left(1 - \frac{x}{K}\right), \tag{6}$$

where k_L and K are positive parameters, respectively called (intrinsic) *reaction rate* and *carrying capacity*.

For our purposes it is more convenient to consider Eq. (6) in the following form:

$$x' = k_L x(c - x), \tag{7}$$

for k_L, c - positive parameters. The solutions of Eq. (6) and Eq. (7) coincide up to an affine transformation of the time variable of the form $t^* = at$, $a = \text{const}$. The two solutions are the same ($a = 1$) whenever $K_L = c = 1$. We can say that the two forms Eq. (6) and Eq. (7) are equivalent in the above sense.

A reaction network inducing a differential equation of the form Eq. (7) is given by [8], [2]:

$$S + X \xrightarrow{k} 2X, \tag{8}$$

where $k > 0$ is the reaction rate parameter and $2X$ is an abbreviation of $X + X$.

Unlike the catalytic reaction Eq. (4b), in Eq. (8) species S is no more a catalyst, but serves the role of a "food" resource for the growing species X. It is instructive to note that a reaction network for the logistic model can be formally constructed on the basis of the Gompertzian reaction Eq. (4b) as follows

$$S + X \xrightarrow{k} P + X, \tag{9a}$$

$$S + X \xrightarrow{k} 2X + S. \tag{9b}$$

The roles of S in reaction network Eq. (9) are two-fold: S is a food resource for P in Eq. (9a) and S is a catalyst in Eq. (9b). Such a separation of the roles of species S (food or catalyst) suggests certain modifications of the logistic model as proposed below.

Both reaction networks Eq. (8) and Eq. (9) induce the following dynamical system for the concentrations s,x of species S,X respectively via mass action kinetics:

$$s' = -k_1 sx,\ \ x' - k_2 sx. \tag{10}$$

It can be checked that Eq. (7) is a consequence of dynamical system Eq. (10).

The Bateman Exponential Growth-decay Model

The n-step Bateman exponential (radioactive) growth-decay chain is given by a reaction network of the following form:

$$S \xrightarrow{k_1} P \xrightarrow{k_2} Q \xrightarrow{k_3} \ldots \xrightarrow{k_n} X. \tag{11}$$

For applications in biology the n-step Bateman chain (11) is usually used in the special cases $n = 1$ (one-step):

$$S \xrightarrow{k_1} X, \tag{12}$$

and $n = 2$ (two-step Bateman chain):

$$S \xrightarrow{k_1} P \xrightarrow{k_2} X. \tag{13}$$

The one-step Bateman exponential growth-decay model (12) is used in marine ecology under the name "von Bertalanffy model." For the detailed characteristics of the 2-step Bateman model and its application in epidemiology see [3].

General Characteristics of the Growth-decay Reaction Networks

We next present an attempt for a classification of the growth-decay reaction networks relative to the "elementary reactions" incorporated in them. Such a classification may be useful for the formulation of new growth-decay reaction networks used for modeling and simulation of biological data.

The growth-decay GD-property. The Gompertz reaction network Eq. (4) clearly distinguishes the roles of the declining species S and the growing species X. All models studied in this paper are induced by reaction networks involving at least one growing species and at least one decaying species. We underline the presence of this property by using the name "growth-decay models" in contrast to just "growth models" as usually done in the scientific literature [12], [13], [9].

In the simplest cases, a reaction network has a GD-property if it includes a one-step Bateman reaction of the form $S \xrightarrow{k} X$ or in the catalysed form $S + X \xrightarrow{k} P + X$. Note that the logistic reaction network is a GD-model due to the (auto-)catalytic reaction $S + X \xrightarrow{k} X + X$, which can be considered as a one-step reaction $S \xrightarrow{k} X$, (auto-)catalysed by species X.

The auto-catalytic growth ACG-property. The autocatalytic growth (ACG) reaction $S + X \xrightarrow{k} X + X$, or just $X \xrightarrow{k} X + X$, possibly inducing exponential growth, is a component of both the logistic and the Gompertz reaction networks (4), (8).

The reaction network theory view-point suggests that the Gompertz model has certain characteristic properties especially related to the declining species in the model.

The competitive utiliser CU-property. The first reaction Eq. (4a) in Gompertzian model suggests that the catalyst species S decays, being utilised/consumed not only by the growing species X but by another competitive species P distinct from species X. The CU-property is typical for the Gompertz model, the other two basic models (logistic and Bateman models) do not possess the CU-property.

The catalyst substrate CS-property. The growth reaction (4b) in the Gompertz reaction network (4) indicates that "substrate" species S serves as a catalyst in the growth process. The CS-property is typical again for the Gompertz model, the other two basic models (logistic and Bateman models) do not possess the CS-property.

The Bateman growth-decay B_n-property. A reaction network incorporating the Bateman radioactive (spontaneous) decay reaction (11) will be said to have a B_n-property (the B_1-property being written briefly as B-property).

The catalysed one-step Bateman growth-decay B_{cat}-property. When a B-reaction is catalysed, we shall call the respective reaction network a B_{cat}-reaction network or a B_{cat}-model. Such is reaction network (1).

The multiple substrate MS-property. In certain situations the growing species X may consume/utilize two or more distinct species as food substrates or catalysts. Such a property will be denoted as multiple substrate property, briefly MS-property.

When a reaction network possesses properties of a certain type, we shall say that the reaction network itself and the induced model (dynamical system) are of that type. For instance the Gompertz reaction network is of types GD, ACG, B_{cat}, B, CU, CS and MS. The logistic reaction network is of the first three types: GD, AG and B_{cat}.

MODIFIED/GENERALISED MODELS USING BASIC REACTION NETWORKS

Based on the above mentioned three classical models (Gompertz, Verhulst and Bateman models) and their characteristics, it is possible to propose combinations of their reaction networks inducing innovative dynamical systems leading to useful sigmoidal growth-decay functions/models.

The Modified Verhulst Model (Type 1)

The formulations of the Gompertz and the Verhulst logistic models in terms of reaction networks reveals significant links between these two growth-decay models [2]. As mentioned above, both their reaction networks possess same properties, namely: GD, ACG, B_{cat}. In order to pass from the Verhulst logistic model Eq. (7) to Gompertz model Eq. (4), we need to perform two steps in the modification process: i) to add a new B-type reaction $S \xrightarrow{k_1} P$, showing that the resource S is no more utilised by the single species X but there is one more competitive utiliser (P), and ii) to turn species S into a catalyst by adding S as product in the right-hand side of Eq. (8), obtaining this the second reaction ($S+X \xrightarrow{k_2} 2X+S$) of the Gompertz reaction network Eq. (4).

This observation suggests to consider the following reaction network following only the first part of the above mentioned modification process:

$$S \xrightarrow{k_1} P, \tag{14a}$$

$$S+X \xrightarrow{k_2} 2X. \tag{14b}$$

Similarly to reaction Eq. (9a), reaction (14a) involves an additional "outer" species P.

Proposition 1. Reaction network (14) induces the following dynamical system for the concentrations (masses) s,p,x of species S,P,X :

$$s' = -k_1 s - k_2 xs, \qquad p' = k_1 s, \qquad x' = k_2 sx, \tag{15}$$

where k_1, k_2 are positive rate parameters. Dynamical system (15) satisfies the conservation law: $s+p+x = c =$const. System (15) together with initial conditions

$$s(0) = s_0 > 0, \qquad p(0) = 0, \qquad x(0) = x_0 > 0, \tag{16}$$

generates the following differential equation for the growth function x:

$$x' = k_M x(c - x - \ln x^{\rho}), \qquad \rho = k_1/k_2, \tag{17}$$

where $c = s(0) + x(0) + \ln x(0)^{\rho}$.

Proof. By using mass action principle and noting that $s' + p' + x' = 0$ and $p' = \rho(X'/X)$.

We shall refer to model (14)-(15) as M-Verhulst type 1, briefly MV1 model ("M" for modified/mixed model).

Numerical Comparison between the Gompertz, Logistic Verhulst and MV1 Growth Models

Figure 1 provides a graphical comparison between the Gompertz, the M-Verhulst type 1 (MV1) and the Logistic Verhulst models for selected values of the model parameters. In the simulations that follow the standard Gompertz model is taken as reference, with Eq. (3) parameterized as

$$x' = k_G x(-\ln x). \tag{18}$$

The parameter K_G is set equal respectively to 1.0 and 3.5 in the simulations.

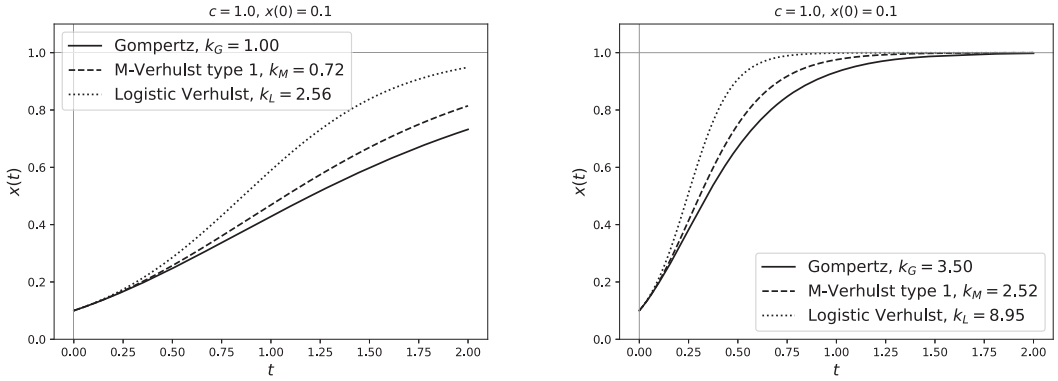

FIGURE 1. Comparison between the Gompertz, M-Verhulst type 1 and the Logistic Verhulst models

The M-Verhulst type 1 and Logistic Verhulst models are parameterized through the K_M and K_L constants to have slope equal to the slope of the Gompertz curve at $t = 0$. The constant c is taken to equal 1.0, ensuring that the three models share the same stationary point. In this numerical research we take $\rho = 1$.

Our numerical experiments suggest that the solutions to the three models are globally ordered when the constraints of having a common initial value and equal slopes at the initial time are imposed. As the figure illustrates, the Logistic Verhulst model entails the fastest convergence to the equilibrium, while the Gompertz model is the slowest to converge. The M-Verhulst type 1 model takes an intermediate position, suggesting that it can be used in empirical work where the properties of the other two models are deemed too extreme for the particular application.

Modified Verhulst Model Tpe 2

Borrowing an idea from [11], we can consider species S in reaction network (8) as a food resource that arrives in the environment of the growing species as a chain-link of a two-step Bateman exponential growth-decay model (13) $S \xrightarrow{k_1} P \xrightarrow{k_2} Q$.

The familiar logistic model makes use of the first species of such a chain. However, it is more realistic for the food species to be some of the next species in the food chain. Assuming the simpler case when the food species is the second one in the exponential chain, we obtain the following model:

$$S \xrightarrow{k_1} P \tag{19a}$$
$$P + X \xrightarrow{k_2} 2X \tag{19b}$$

Proposition 2. Reaction network (19) induces the following "Modified Verhulst" dynamical system for the concentrations (masses) s, p, x :

$$s' = -k_1 s, \qquad p' = k_1 s - k_2 p x, \qquad x' = k_2 p x, \tag{20}$$

where k_1, k_2 are positive parameters. Dynamical system (20) satisfies the conservation law: $s + p + x = c$.

Proof. By using mass action principle and noting that $s' + p' + x' = 0$.

Model (19)–(20) will be referred to as the Modified Verhulst model type 2 (M-Verhulst model type 2, MV2).

A Generalization of the Verhulst Model

The Verhulst growth model can be generalized by the following autocatalytic reaction network ([11], Proposition 1):

$$X + \sum_{i=1}^{n} S_i \xrightarrow{k} X + mX, \tag{21}$$

with $n, m \geq 1$ integer.

Proposition 3. Reaction network (21) induces the following "Generalized Verhulst" dynamical system for the concentrations (masses) x, s_i:

$$\begin{aligned} x' &= kmx \prod_{j=1}^{n} s_j, \\ s_i' &= -kx \prod_{j=1}^{n} s_j, \; i = 1, \ldots, n. \end{aligned} \tag{22}$$

The growth function x in (22) satisfies the differential equation:

$$x' = kmx \prod_{i=1}^{n} \left(c_i - \frac{x}{m} \right), \tag{23}$$

where $c_i > 0$ are appropriate constants.

In the special case when $n = m = 2$, the reaction network (21) takes the form

$$X + S_1 + S_2 \xrightarrow{k} X + 2X. \tag{24}$$

When $n = m$ and $S_i = S$, $i = 1, \ldots, n$, the reaction network (21) reduces to

$$X + nS \xrightarrow{k} X + nX. \tag{25}$$

In the numerical experiments reported below we consider the case $n = 2$.

Numerical Analysis of Reaction Networks (19), (24) and (25)

In this subsection we use numerical simulations to investigate the properties of the reaction networks (19), (24) and (25) ($n = 2$), compared to the Gompertz and Logistic Verhulst models. The simulations were set up according to the principles outlined above, namely, common initial conditions and common slopes at $t = 0$ calibrated to match the Gompertz model, as well as stationary point at $x(\infty) = 1$.

Figure 2 shows the behavior of the MV2 model (19) compared to the Gompertz and Logistic Verhulst models. The initial conditions for s and p are taken to be $s(0) = 0.6$ and $p(0) = 0.3$, respectively. The results suggest the conjecture that the global ordering property may be valid for some values of the parameter k_1 and violated for others.

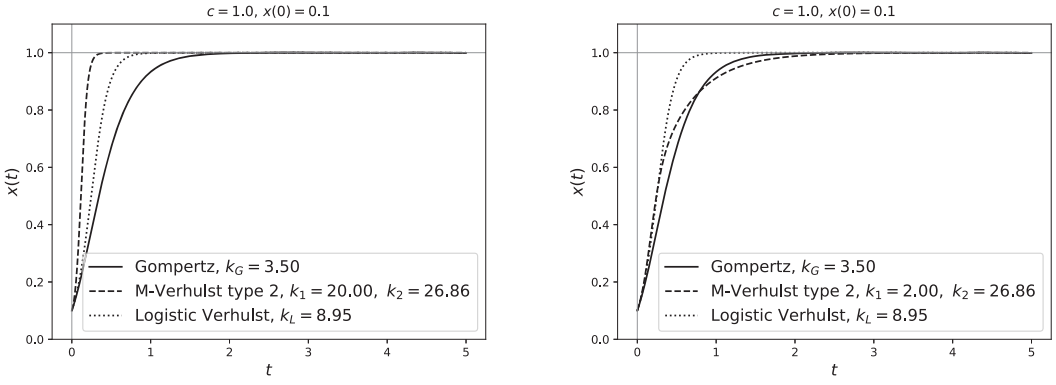

FIGURE 2. Comparison between reaction network (19), the Gompertz and the Logistic Verhulst models

Figure 3 presents the solutions to the Gompertz and Logistic Verhulst models, and reaction network (24) for different values of the parameters. The network (24) was parameterized as

$$\frac{dx}{dt} = K_M x \left(c_1 - \frac{x}{2} \right) \left(c_2 - \frac{x}{2} \right),$$

with K_M corresponding to km in Eq. (23). This simulation setup leaves one free parameter (in this case c_2) that allows us to vary the solution of Eq. (24).

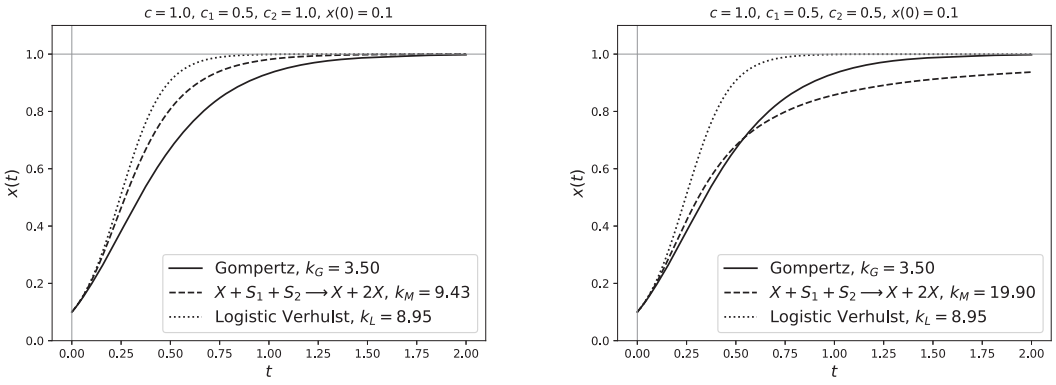

FIGURE 3. Comparison between reaction network (24), the Gompertz and the Logistic Verhulst models

On the basis of Figure 3 we can conjecture that there are parameter combinations for which the solutions to the three models are globally ordered. As the right panel of the figure illustrates, for other parameter combinations the curves intersect, violating the global ordering property. Overall, these numerical results suggest that further analytical work is required to establish more precisely the properties of reaction network (24).

Figure 4 presents a visual comparison of the solutions of reaction network (25), the Gompertz and Logistic Verhulst models. The network (25) was parameterized as

$$\frac{dx}{dt} = K_M x \left(c_1 - \frac{x}{2}\right)^2$$

and the simulation was constructed as outlined above. Compared to reaction network Eq. (24), there is no free parameter in this case, so the different simulations are obtained through the K_G parameter of the Gompertz model. In our experiments we were unable to obtain a globally-ordered configuration for this setup.

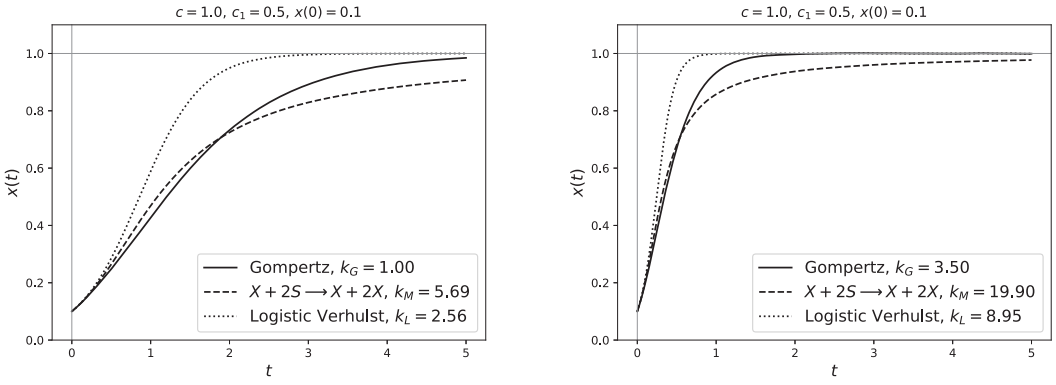

FIGURE 4. Comparison between reaction network (25), the Gompertz and the Logistic Verhulst models

CONCLUSION

We propose three reaction networks that are modifications/generalizations of the logistic and Gompertz reaction networks. The induced dynamical systems generate growth-decay functions of sigmoidal form that are possibly suitable

for fitting measurement data from biological processes. We study some characteristics of the growth functions that are solutions to dynamical systems and compare them to the Gompertzian and logistic type growth functions. Apart from the growing species, the proposed reaction networks involve additional decaying species interpreted as an environmental food resource. Our study is focused on the monotonicity order-preserving properties of the model solutions and is supported by numerical computations and graphical visualizations. The results obtained suggest that the global ordering properties for the models studied in this work are generally dependent on the specific model parameterization. The graphical visualizations indicate that further analytical work needs to be undertaken to better understand the properties and characteristics of the growth-decay reaction networks considered in this work. As a first step in this direction we attempt a classification of the reaction networks inducing growth-decay models based on the types of the elementary reactions incorporated in these networks.

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