



Research review paper

The Gompertz model and its applications in microbial growth and bioproduction kinetics: Past, present and future

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ABSTRACT

The Gompertz model, initially proposed for human mortality rates, has found various applications in growth analysis across the biotechnological field. This paper presents a comprehensive review of the Gompertz model's applications in the biotechnological field, examining its past, present, and future. The past of the Gompertz model was examined by tracing its origins to 1825, and then it underwent various modifications throughout the 20th century to increase its applicability in biotechnological fields. The Zwietering-modified version has proven to be a versatile tool for calculating the lag-time and maximum growth rate/quantity in microbial growth. In addition, the present applications of the Gompertz model to microbial growth kinetics and bioproduction (e.g., hydrogen, methane, caproate, butanol, and hexanol production) kinetics have been comprehensively summarized and discussed. We highlighted the importance of standardized citations and guidance on model selection. The Zwietering-modified Gompertz model and the Lay-modified Gompertz model are recommended for describing microbial growth kinetics and bioproduction kinetics, recognized for their widespread use and provision of valuable kinetics information. Finally, in response to the current Gompertz models' focus on internal mortality, the modified Makeham-Gompertz models that consider both internal/external mortality were introduced and validated for microbial growth and bioproduction kinetics with good fitting performance. This paper provides a perspective of the Gompertz model and offers valuable insights that facilitate the diverse applications of this model in microbial growth and bioproduction kinetics.

1. Introduction

The Gompertz model (Gompertz, 1825) was an empirical model originally proposed to represent human mortality rates. Throughout the 20th century, the Gompertz model has undergone modifications and reparameterizations, resulting in the emergence of different forms of the modified Gompertz model (Rietz, 1921; Ludwig, 1929; Winsor, 1932; Laird, 1964; Jefferies et al., 1982; Gibson et al., 1987, 1988; Rogers et al., 1987; Zwietering et al., 1990). Some of the modified Gompertz models have increased the efficiency in analyzing growth phenomena and obtaining valuable parameters, including the maximum growth rate and amount (Winsor, 1932; Zwietering et al., 1990; Lay et al., 1996).

These Gompertz models have subsequently found applications in various biotechnological areas in the 20th and 21st centuries (Tjørve and Tjørve, 2017). These applications include understanding the microbial growth, cell growth, and animal growth kinetics during biological processes (Ribeiro, 2017; Zardin et al., 2019; Chaturvedi et al.,

2023; Czajkowska et al., 2024). Additionally, the Gompertz model has been extensively used in environmental biological processes, contributing significantly to environmental remediation efforts (Wang and Chen, 2006, 2009; Wang and Chu, 2016; Wang and Yin, 2022). At the end of the 20th century, the Gompertz model began to be utilized to analyze the kinetics of bioproduction processes (Lay et al., 1996). Towards the end of the 20th century, the Gompertz model began to be employed for analyzing the kinetics of bioproduction processes (Lay et al., 1996). In the 21st century, the Lay-modified Gompertz model has been widely applied to various bioproduction processes, including biohydrogen, biomethane, and caproate production (Wang and Wan, 2009; Zhang et al., 2022; Yin and Wang, 2022a, 2022b; Yang and Wang, 2019, 2020, 2021).

However, there have been some issues and gaps in the utilization of the Gompertz model. Firstly, the origins of the Gompertz model and how this model, initially designed to describe mortality, can be applied in modeling microbial growth kinetics and further to model bioproduction

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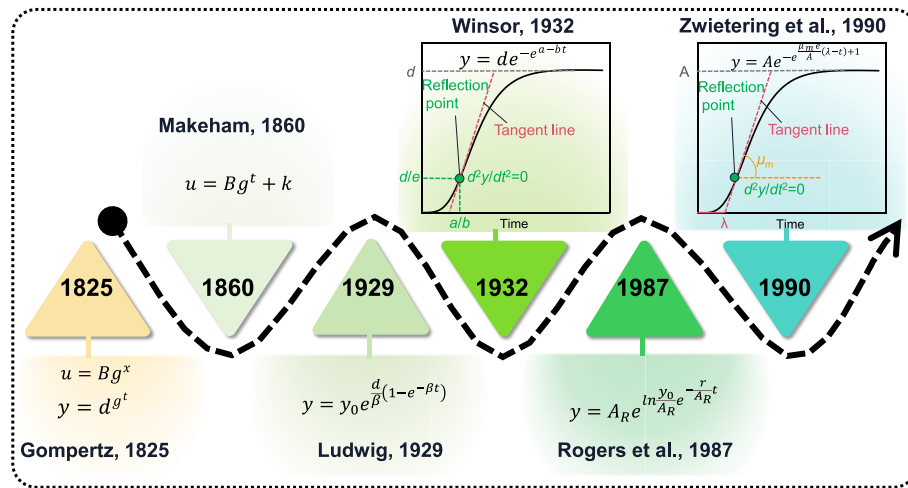


Fig. 1. The development history of the Gompertz model.

kinetics are essential; however, these aspects have rarely been reviewed. Secondly, various modified Gompertz models have been applied to the growth phenomena; the deduction of the modified Gompertz model and the selection of the proper modified Gompertz model should be thoroughly discussed and reviewed. In addition, citing the original research when referencing different forms of the model is essential, but this consistency is not achieved in many published papers. Thus, it is significant to standardize the citations of the models. Thirdly, many frequently used Gompertz models only consider internal mortality (age-dependent mortality). Since external mortality (age-independent random mortality) can also occur in some growth processes (Makeham, 1860, 1867), it is important to modify the Gompertz model to include both internal and external mortality.

Based on the above, we systematically studied the applications of the Gompertz model in biotechnological areas. The objectives of this paper were: (1) to review the original rationale and basic concepts of the Gompertz model; (2) to comprehensively review the modifications/reparameterizations of the Gompertz model; (3) to provide an overview of the applications of this model in growth analysis and bioproduction kinetics; and (4) to identify the limitations of the Gompertz model in current studies and propose prospects for its modification (considering internal and external mortality) and application.

2. The past of Gompertz model

2.1. The origins of Gompertz model

The Gompertz model was first introduced to describe human mortality (Gompertz, 1825). Gompertz calculated the common logarithm (\log_{10}) values of the number of individuals alive (y) at specific ages. He found that the mortality rate exhibits a geometric progression within the specified age range (Gompertz, 1825, 1862, 1872). This phenomenon is referred to as the Gompertz law of mortality. The mortality rate can be described as follows:

$$u = Bg^t \quad (1)$$

Where t (year) is the growth time, u (deaths/year) is the mortality rate at time t , B and g are the model constants.

Under the Gompertz law, the total population at age t can be calculated as follows:

$$y = d^{g^t} \quad (2)$$

Where y is the total population at time t , d and g are the model constants.

2.2. The modification and reparameterization of the Gompertz model

Since its introduction in 1825, the Gompertz model has undergone various modifications and reparameterizations. In the 19th century, Makeham (1860, 1867) suggested that, in contrast to a consistent rate of increase in the logarithms of probabilities in a uniform geometrical progression across all age groups, the logarithms of probabilities of survival exhibited a more rapid pace of increase at higher ages in comparison to younger ages. The mortality results from two co-existing main causes: chance and deterioration (Gompertz, 1825; Makeham, 1860, 1867). Thus, the mortality rate can be better described as follows:

$$u = Bg^t + k \quad (3)$$

Where k (deaths/year) is the age-independent external mortality rate, it is also referred to as the “Makeham term”.

The modified forms of the Gompertz model have been raised for modeling the population dynamics in the 20th century (Fig. 1). According to Ludwig (1929), the relative growth rate should exhibit a consistent decrease as growth persists:

$$\frac{1}{y} \frac{dy}{dt} = de^{-\beta t} \quad (4)$$

y can be calculated as follows:

$$y = y_0 e^{\frac{d}{\beta}(1-e^{-\beta t})} \quad (5)$$

Where y_0 is the initial population, d (1/year) and β (1/year) are the model constants.

Winsor (1932) reformulated the Gompertz model into a more convenient expression and discussed the applicability of the Gompertz model to growth analysis.

$$y = de^{-e^{-a-bt}} \quad (6)$$

Where t (h) is the growth time of organisms, a and b (1/h) are the model constants.

Differentiating Eq. (6) yields the rate of change in populations with age:

$$\frac{dy}{dt} = be^{a-bt} de^{-e^{-a-bt}} \quad (7)$$

Further differentiating Eq. (7) yields:

$$\frac{d^2y}{dt^2} = db^2 e^{-e^{-a-bt}} e^{a-bt} (e^{a-bt} - 1) \quad (8)$$

The inflection point corresponds to the point on the growth curve where the rate of change reaches its maximum value. From Eqs. (7) and

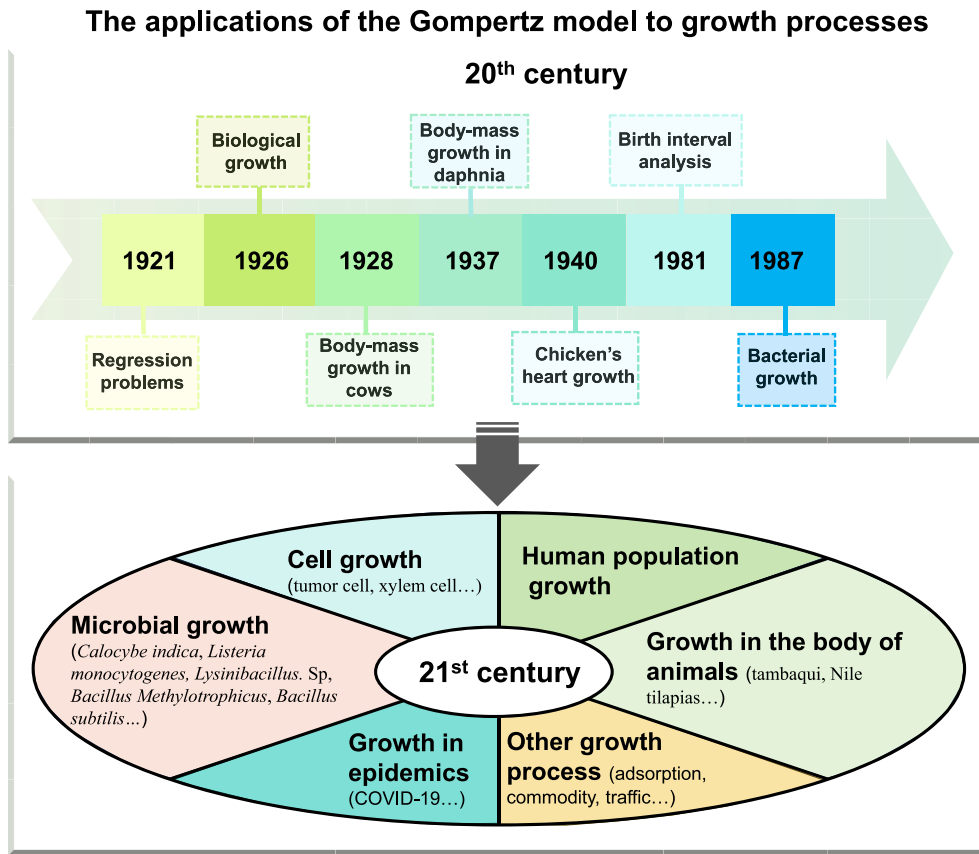


Fig. 2. The applications of the Gompertz model to growth kinetics processes.

(8), the reflection point can be found at $t = a/b$, where $d^2y/dt^2 = 0$. Thus, the reflection point is $(a/b, d/e)$. In other words, the point of reflection is reached when approximately 37% of the growth has occurred.

Rogers et al. (1987) introduced a modified Gompertz model that takes into account the initial populations:

$$y = A_R e^{\ln \frac{y_0}{A_R} e^{-k_R t}} = A_R e^{\ln \frac{y_0}{A_R} e^{-\frac{t}{A_R}}}$$
 (9)

Where A_R , k_R (1/h) and r (1/h) are the model parameters.

In order to make the parameters of the Gompertz model more biologically meaningful, Zwietering et al. (1990) reparametrized the Gompertz model. They have defined the abscissa of the reflection point as $t_i = a/b$ and a parameter $\mu_m = (dy/dt)_{t=t_i} = db/e$. The parameter b in the Gompertz model can be substituted by $(\mu_m e/d)$.

The tangent line through the inflection point can be described as follows:

$$y = \mu_m t + \frac{d}{e} - \mu_m t_i$$
 (10)

The lag-time λ (h) is determined by identifying the t -axis intercept of the tangent line passing through the inflection point (Zwietering et al., 1990):

$$0 = \mu_m \lambda + \frac{d}{e} - \mu_m t_i$$
 (11)

$$\lambda = \frac{(a-1)}{b}$$
 (12)

Then a can be substituted by $(1 + \mu_m e \lambda / d)$. When t approaches infinite, y approaches d . By defining $d = A$, the Gompertz model is transformed into Eq. (13), which is the most frequently used form in describing the growth of organisms.

$$y = A e^{-e^{-\frac{\mu_m}{A} (t-\lambda) + 1}}$$
 (13)

3. The present of the Gompertz model

3.1. The applications of the Gompertz model to growth kinetics

The Gompertz model has undergone modifications and has been harnessed by researchers to address regression-related challenges (Rietz, 1921). Throughout the 20th century, the Gompertz model has played a pivotal role as a predictive tool in demography (Fig. 2). For instance, Ross and Madhavan (1981) used the Gompertz in the birth interval analysis. Mueller et al. (1995) showed the application of the Gompertz equation in predicting the average lifespan and the time at which the n^{th} percentile of mortality occurs. Additionally, Finch and Pike (1996) utilized this model to predict the maximum human life span. The adaptability of the Gompertz model has rendered it a tool for comprehending and forecasting human population dynamics.

In addition to its applications in demography, the Gompertz model has extended its utility to model various macroscopic growth phenomena across the 20th century (Fig. 2). Wright (1926) first suggested using the Gompertz model to describe the biological growth curve. The Gompertz model was subsequently applied to the body-mass growth in cows (Davidson, 1928) and daphnia (Anderson et al., 1937), as well as the growth of chicken's heart (Medawar, 1940) (Fig. 2). The Gompertz model was utilized for the purpose of modeling microorganisms, such as bacterial growth, as demonstrated by previous studies (Gibson et al., 1987; Zwietering et al., 1990). By fitting the growth data to the Gompertz model and analyzing the reflection point of the curve, it can gain a deeper understanding of growth dynamics and make predictions about future trends. These applications illustrate the initial adaptability of the Gompertz model to describe growth curves in different systems.

Table 1
The applications of the Gompertz model in growth analysis.

Object	Model	Model parameters	Statistical parameters*	References
Microbial growth in Chhana	The Zwietering-modified Gompertz model	$\mu_m = 0.016\text{--}0.038\text{ 1/h}$; $\lambda = 18.6\text{--}38.2\text{ h}$	$R^2 = 0.967\text{--}0.987$	Chaturvedi et al., 2023
Microbial (yeast) growth	The Rogers-modified Gompertz model	$A_R = 1268$; $k_R = 0.1824$	$R^2 = 0.9715$	Ribeiro, 2017
Microbial (<i>B. subtilis</i> , <i>E. coli</i> , and <i>L. monocytogenes</i>) growth	The Zwietering-modified Gompertz model	$A = 7.8\text{--}22.9\text{ CFU}\cdot 10^8/\text{mL}$; $\lambda = 1\text{ h}$ 14 min $\sim 2\text{ h}$ 20 min	–	Czajkowska et al., 2024
Microbial (aerobic mesophilic and yeast mold) growth	The Zwietering-modified Gompertz model	$A = 4.6\text{--}5.26\text{ log CFU/ml}$; $\mu_m = 0.054\text{--}0.06\text{ 1/d}$	$R^2 = 0.92\text{--}0.98$	Panigrahi et al., 2023
Microbial (<i>Salmonella Typhimurium</i>) growth	The Zwietering-modified Gompertz model	$A = 0.6340\text{--}3.4623$; $\mu_m = 0.6340\text{--}3.4623$; $\lambda = 0\text{--}0.8272$	$R^2 = 0.8452\text{--}0.9876$; $RMSE = 0.2357\text{--}0.5303$	Bermudez-Aguirre and Niemira, 2023
Microbial (<i>P. lundensis</i> , <i>P. lundensis</i> , <i>S. putrefaciens</i> , and <i>S. putrefaciens</i>) growth	The Zwietering-modified Gompertz model	$A = 7.69\text{--}10.77\text{ lg CFU/g}$; $\mu_m = 0.0171\text{--}0.1381\text{ 1/h}$; $\lambda = 7.56\text{--}86.72$	$R^2 = 0.984\text{--}0.999$; $MSE = 0.00091\text{--}0.0673$	Coban, 2022
Microbial (<i>Botryococcus Braunii</i> Microalgae) growth	The Zwietering-modified Gompertz model	$A = 10,590\text{ cells/mL}$; $\mu_m = 2907\text{ cells/(mL}\cdot\text{d)}$; $\lambda = 1\text{ d}$	$R^2 = 0.982$	Hanief et al., 2020
Microbial (<i>Lysinibacillus</i> . Sp, <i>Bacillus Methylotrophicus</i> , and <i>Bacillus subtilis</i>) growth	The Zwietering-modified Gompertz model	$A = 9.916\text{--}9.733\text{ cells}$; $\mu_m = 0.238\text{--}0.743\text{ 1/h}$; $\lambda = 4.702\text{--}4.733\text{ h}$	$R^2 = 0.962\text{--}0.993$; $MSE = 0.011\text{--}0.047$	Murunga and Were, 2019
Microbial (psychrotolerant and proteolytic psychrotolerant) growth	The Zwietering-modified Gompertz model	$\mu_m = 1.03\text{--}4.99\text{ ln(CFU/mL)/d}$; $\lambda = 0.5\text{--}7.82\text{ d}$	$R^2\text{ model} = 79.1\text{--}98.4$	Tribst et al., 2019
Microbial (<i>Rhodobacter capsulatus</i>) growth	The Winsor-modified Gompertz model	$d = 2.66\text{--}3.03$; $b = 0.1581\text{--}0.174\text{ 1/h}$; $a = 1.77\text{--}2.18$	$R^2 = 0.9924\text{--}0.9968$	Deseure et al., 2021
Microbial (<i>Listeria monocytogenes</i>) growth	The Zwietering-modified Gompertz model	$A = 0.41\text{--}265$; $\mu_m = 0.011\text{--}0.19$; $\lambda = -8.0\text{--}57$	–	Aalto-Araneda et al., 2020
Milky mushroom (<i>Calocybe indica</i>) growth	The Zwietering-modified Gompertz model	$A = 95.79\text{--}174.06$; $\mu_m = 39.02\text{--}41.95$; $\lambda = 0.1014\text{--}0.1373$	$R^2 = 0.99\text{--}0.9951$	Kumar et al., 2020
Xylem cell growth	The Winsor-modified Gompertz model	$d = 46.21\text{--}54.85$; $a = 5.64\text{--}8.91$; $b = 0.035\text{--}0.045$	$R^2 = 0.6\text{--}0.9$	Rossi et al., 2003
Tumor cell growth	The Ludwig-modified Gompertz model	$d = 0.743$; $\beta = 0.792$	$R^2 = 0.97$; $AICc = -7.62$; $RMSE = 0.41$	Benzekry et al., 2014
Callus (production of <i>Jatropha curcas</i> L.) growth	The Zwietering-modified Gompertz model	$A = 0.38\text{ callus g/25 mL culture}$; $\mu_m = 0.193\text{ 1/h}$; $\lambda = 2.91\text{ d}$	–	Hussein et al., 2016
Growth in the body length of tambaqui (<i>Colossoma macropomum</i>)	The Winsor-modified Gompertz model	$d = 58.4772\text{ cm}$; $b = 0.00592\text{ 1/d}$; $a = 1.669\text{ d}$	–	Mello et al., 2015
Growth in the body weight of tambaqui (<i>Colossoma macropomum</i>)	The Winsor-modified Gompertz model	$d = 4641\text{--}5010\text{ g}$; $b = 0.00507\text{ 1/d}$; $a = 2.407\text{--}2.474\text{ d}$	–	Mello et al., 2015
Growth in the body height of tambaqui (<i>Colossoma macropomum</i>)	The Winsor-modified Gompertz model	$d = 20.7614\text{--}21.2971\text{ cm}$; $b = 0.00941\text{ 1/d}$; $a = 2.795\text{ d}$	–	Mello et al., 2015
Growth in the corporal weight of Nile tilapias	The Winsor-modified Gompertz model	$d = 371\text{--}53,196$; $b = 0.00188$	$SSE = 2,084,806\text{--}13,797,610$	Zardin et al., 2019
Population growth in Sri Lankan	The Rogers-modified Gompertz model	$A_R = 26,107,639.12$; $k_R = 0.0142$	$RMSE = 0.02428$; $MAPD = 0.01062$; $SMAPE = 0.00532$	Welagedara et al., 2019
Growth in the infected populations during epidemics (COVID-19)	The Rogers-modified Gompertz model	$A_R = 6974\text{--}6,834,000$; $r = 0.23\text{--}1.297$	$R^2 = 0.67\text{--}0.92$	Pelinovsky et al., 2022
Growth in the infected populations during epidemics (COVID-19)	The Ludwig-modified Gompertz model	$d = 0.044\text{--}0.075$; $\beta = 0.309\text{--}0.059$	$RMSE = 256.7\text{--}1016.3$; $MAE = 192.6\text{--}832.2$	Bartolomeo et al., 2021
Fixed bed adsorption amount growth	The Winsor-modified Gompertz model	$a = 1.620\text{--}7.562$; $b = 0.0025\text{--}0.027\text{ 1/min}$	$R^2 = 0.9818\text{--}0.9988$; $AICc = -404\sim -118$	Chu, 2020

*: R^2 : coefficient of determination; MAE : mean absolute error; MSE : mean square error; $RMSE$: root mean square error; $AICc$: Akaike information criterion; $MAPD$: mean absolute percentage deviation; $SMAPE$: symmetric mean absolute percentage error.

In the 21st century, the Gompertz model continues to be highly versatile and relevant (Fig. 2). It has been applied in various fields to model growth curves and analyze growth processes. Fig. 2 provides an overview of different applications of the Gompertz model in the 21st century, especially in microbial growth and cell growth. Table 1 shows how the Gompertz model continues to be relevant and applicable in present growth analysis. The model parameters and statistical parameters (such as the coefficient of determination (R^2), mean absolute error (MAE), mean square error (MSE), root mean square error ($RMSE$), and Akaike information criterion ($AICc$)) are summarized in Table 1. As shown in Table 1, the Gompertz model has found applications in various fields, including microbial growth, cell growth, and the growth of

animals. Most studies used the values of R^2 to evaluate the fitting results of the Gompertz model. The high values of R^2 in these studies suggest that the Gompertz model effectively captures and represents growth patterns across these diverse fields. The Winsor-modified Gompertz model (Winsor, 1932) has found application in several growth analyses in Table 1. Specifically, it can be employed in the analysis of microbial growth (e.g., *Rhodobacter capsulatus*), xylem cell growth, and growth analysis of tambaqui in terms of body length, weight, and height. The y_0 form Gompertz (Rogers-modified and Ludwig-modified Gompertz models) also has found several applications in modeling population growth. This form of the Gompertz model considers the initial amount of the population size, denoted as “ y_0 ” in the equations. As shown in

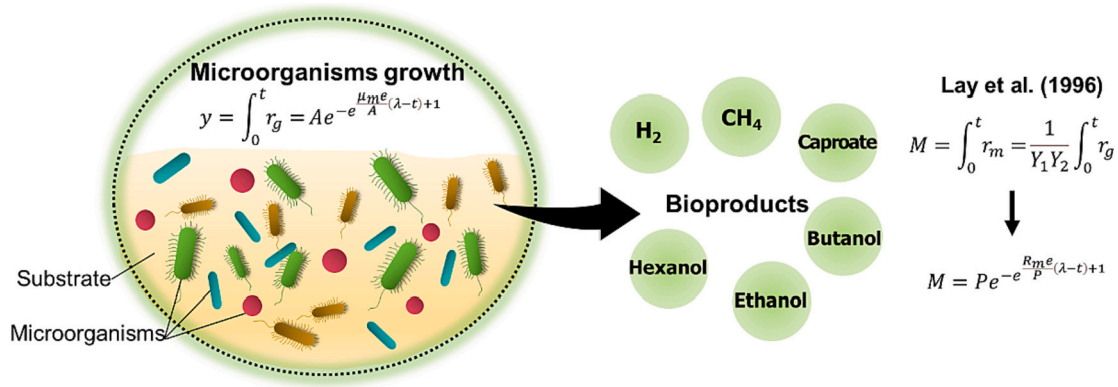


Fig. 3. The bioproduction processes and the extension of the Gompertz model to the bioproduction kinetics.

Table 1, the most widely used form of the Gompertz model is the Ziwietering-modified Gompertz model.

In analyzing organisms' growth, the Gompertz model reparameterized by Ziwietering et al. (1990) allows for the direct calculation of critical parameters, including the maximum growth rate, maximum growth amount, and lag-time. These parameters are essential for comprehending and predicting organism growth dynamics. Moreover, the Ziwietering-modified Gompertz model is the most frequently used in the growth analysis (Table 1). Applying this form of the Gompertz model facilitates the comparison of the model parameters with previous studies. Therefore, we recommend using the Ziwietering-modified Gompertz model for growth analysis. When dealing with growth that involves the initial population, we recommend using the modified Gompertz models by Rogers et al. (1987) or Ludwig (1929). These models incorporate the initial populations (y_0) and have found widespread use in the analysis of cell growth (Benzekry et al., 2014) and human population growth (Welagedara et al., 2019; Pelinovsky et al., 2022; Bartolomeo et al., 2021).

The adaptability, precision, and versatility of the Gompertz model have allowed it to evolve from a model for human mortality to an analytical tool in growth analysis biological field. Its enduring relevance in diverse areas highlights its effectiveness in understanding and predicting complex growth dynamics.

Other models, such as the Logistic model (Verhulst, 1838, 1845) and first-order model (Ørskov and McDonald, 1979) can also be applied to model microbial growth kinetics. The Logistic model assumes that the growth rate is rapid when the growth amount is well below the maximum growth amount (K_m). As the population approached K_m , the growth rate gradually slowed down. The Logistic model can be expressed as follows:

$$\frac{dy}{dt} = r_1 y \left(1 - \frac{y}{K_m} \right) \quad (14)$$

Where r_1 (1/h) is the growth rate constant, K_m is the maximum growth amount.

The Logistic model offers valuable insights into the kinetics of microbial growth, such as *E. aerogenes* and *S. cerevisiae* (Lakshmidhevi and Muthukumar, 2010; Germec et al., 2019). It provides essential parameters including the growth rate and maximum growth amount.

The first-order model is also frequently employed to describe microbial growth kinetics (e.g. *E. aerogenes* (Boshagh and Rostami, 2021)).

$$y = k_1 (1 - e^{-c_1 t}) \quad (15)$$

Where k_1 is the maximum growth amount, c_1 (1/h) is the rate constant.

3.2. The application of the Gompertz model to bioproduction kinetics

Bioproduction technology can be employed to generate a wide array of biological products, including biohydrogen, biomethane, fatty acids, ethanol, etc. (Fig. 3). This technology utilizes living organisms such as bacteria, yeast, or other microorganisms to produce these bio-based products (Ribeiro, 2017; Yin and Wang, 2021a, 2021b; Lou et al., 2023). In previous sections, we have concluded that the Gompertz model successfully predicts the growth curves of living organisms. As bioproduction processes heavily rely on the cultivation of living organisms to generate bio-based products, the application of the Gompertz model can provide valuable insights into understanding and forecasting the growth and production dynamics of various biological products.

Lay et al. (1996, 1997, 1998a, 1998b) appear to be the first to apply the Gompertz model to methane fermentation by municipal solid wastes. They rewritten the Gompertz model proposed by Ziwietering et al. (1990) as follows:

$$y = \int_0^t r_g = A e^{-e^{-\frac{\mu_m}{A}(\lambda-t)+1}} \quad (16)$$

Where r_g is the growth rate of microorganisms.

Then the growth rate of microorganisms can be represented by Eq. (17):

$$r_g = Y_1 (1 - r_{su}) \quad (17)$$

Where Y_1 is the maximum yield coefficient, r_{su} (1/h) is the substrate utilization rate.

The methane production is described as follows:

$$-r_{su} = Y_2 r_m \quad (18)$$

Where Y_2 (1/mL) is the maximum yield coefficient, r_m (mL/h) is the methane production rate.

The cumulative methane production (M (mL)) at time t is:

$$M = \int_0^t r_m = \int_0^t \frac{r_g}{Y_1 Y_2} = \frac{1}{Y_1 Y_2} \int_0^t r_g \quad (19)$$

Then Lay et al. (1996) proposed the methane production model:

$$M = P e^{-e^{-\frac{R_m}{P}(\lambda-t)+1}} \quad (20)$$

Where P (mL) is defined as $A/Y_1 Y_2$, R_m (mL/h) is defined as $\mu_m/Y_1 Y_2$.

Throughout the 21st century, the Lay-modified Gompertz model has been widely applied in various bioproduction processes, as summarized in Table 2. All the studies listed in Table 2 utilized Eq. (20) to describe various bioproduction processes. The consistently high R^2 values observed in these studies underscore the Gompertz model's effectiveness in characterizing bioproduction kinetics. As shown in Table 2, this model has proved valuable in understanding and predicting the dynamics of processes such as hydrogen production, methane production,

Table 2

The applications of the Gompertz model in bioproduction processes.

Bioproduction processes	Inoculum	Model equation	Model parameters	Statistical parameters*	References
Hydrogen production	Heat-pretreated sludge	The Lay modified Gompertz model	$P = 0.23\text{--}0.94 \text{ mmol/L}$; $R_m = 0.007\text{--}0.12 \text{ mmol/h}$; $\lambda = 4.03\text{--}42.81 \text{ h}$	–	Nemestóthy et al., 2018
Hydrogen production	Photosynthetic bacteria	The Lay modified Gompertz model	$P = 357.64\text{--}547.99 \text{ mL}$; $R_m = 21.5\text{--}27.11 \text{ mL/h}$; $\lambda = 11.74\text{--}18 \text{ h}$	$R^2 = 0.9977\text{--}1$	Xiang et al., 2023
Hydrogen production	Photosynthetic bacteria	The Lay modified Gompertz model	$P = 38.63\text{--}291.65 \text{ mL}$; $R_m = 0.836\text{--}6.038 \text{ mL/h}$; $\lambda = 14.58\text{--}28.39 \text{ h}$	$R^2 = 0.9658\text{--}0.9992$	Liu et al., 2021
Hydrogen production	Mixed photosynthetic bacteria	The Lay modified Gompertz model	$P = 366.64\text{--}633.14 \text{ mL}$; $R_m = 9.06\text{--}12.18 \text{ mL/h}$; $\lambda = 3.30\text{--}6.2 \text{ h}$	$R^2 = 0.9901\text{--}0.9988$	Li et al., 2022
Hydrogen production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 18.07\text{--}34.00 \text{ mL}$; $R_m = 3.883\text{--}6.003 \text{ mL/h}$; $\lambda = 0\text{--}1.347 \text{ h}$	$R^2 = 0.9711\text{--}0.9976$	Chen et al., 2022
Hydrogen production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 6.01\text{--}187.57 \text{ mL}$; $R_m = 2.05\text{--}24.51 \text{ mL/h}$; $\lambda = 9.24\text{--}21.03 \text{ h}$	$R^2 = 0.99\text{--}0.999$	Cao et al., 2023
Hydrogen production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 12.56\text{--}55.79 \text{ mL}$; $R_m = 1.65\text{--}6.44 \text{ mL/h}$; $\lambda = 6.90\text{--}8.93 \text{ h}$	$R^2 = 0.996\text{--}0.999$	Yang and Wang, 2021
Hydrogen production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 5.52\text{--}19.99 \text{ mL/gVS}$; $R_m = 1.34\text{--}5.48 \text{ mL/(hgVS)}$; $\lambda = 4.58\text{--}7.61 \text{ h}$	$R^2 = 0.99\text{--}0.999$	Yang and Wang, 2020
Hydrogen production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 31.84\text{--}60.49 \text{ mL}$; $R_m = 2.9\text{--}6.4 \text{ mL/h}$; $\lambda = 5.9\text{--}6.8 \text{ h}$	$R^2 = 0.99\text{--}0.996$	Yang and Wang, 2019
Methane production	Primary sludge	The Lay modified Gompertz model	$P = 1692.5\text{--}8069.2 \text{ mL}$; $R_m = 174.4\text{--}610.5 \text{ mL}$; $\lambda = 14.58\text{--}28.39 \text{ h}$	$R^2 = 0.998\text{--}1$	Amoochadi et al., 2023
Methane production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 49\text{--}102 \text{ mL/gVS}$; $R_m = 3.1\text{--}7.2 \text{ mL/(gVS-d)}$; $\lambda = 6.6\text{--}15.8 \text{ d}$	$R^2 = 0.988\text{--}0.996$; $MBE = -0.24 \sim -0.1$; $MAE = 1.2\text{--}4.6$; $RMSE = 1.7\text{--}6$; $AICc = 34.9\text{--}159.5$	Pardilhó et al., 2022
Methane production	Effluent collected from digestion processes of date palm fruit wastes	The Lay modified Gompertz model	$P = 90.5\text{--}186.7 \text{ L/kgVS}$; $R_m = 7.9\text{--}25.28 \text{ L/(kgVS-d)}$; $\lambda = 1.188\text{--}22.79 \text{ d}$	$R^2 = 0.9916\text{--}0.9985$	Khedher et al., 2022
Methane production	Mesophilic inoculum obtained from the mesophilic reactor of a plant	The Lay modified Gompertz model	$P = 266.9\text{--}436.8 \text{ mL/gVS}$; $R_m = 32.85\text{--}62.68 \text{ L/(gVS-d)}$; $\lambda = 4.023\text{--}5.837 \text{ d}$	$R^2 = 0.995\text{--}0.999$; $\%Dev = 0.2\text{--}1.4$	Üveges et al., 2023
Methane production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 171\text{--}207 \text{ mL/gVS}$; $R_m = 0.07\text{--}0.12 \text{ 1/d}$; $\lambda = 1.37\text{--}4.44 \text{ d}$	$R^2 = 0.99\text{--}0.995$; $AICc = -190 \sim -106$	Hu et al., 2020
Caproate production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 39.40\text{--}97.33 \text{ mmol-C/L}$; $R_m = 6.09\text{--}55.66 \text{ mmol-C/L/d}$; $\lambda = 1.54\text{--}6.4 \text{ d}$	$R^2 = 0.9572\text{--}0.9882$	Yin and Wang, 2022a
Butanol production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 9.81\text{--}17.98 \text{ mmol-C/L}$; $R_m = 1.75\text{--}14.46 \text{ mmol-C/L/d}$; $\lambda = 0.81\text{--}5.62 \text{ d}$	$R^2 = 0.9901\text{--}0.9999$	Yin and Wang, 2022a
Hexanol production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 1.96\text{--}4.12 \text{ mmol-C/L}$; $R_m = 0.12\text{--}0.69 \text{ mmol-C/L/d}$; $\lambda = 1\text{--}4.14 \text{ d}$	$R^2 = 0.9840\text{--}0.9913$	Yin and Wang, 2022a
Butyrate production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 44.13\text{--}120.68 \text{ mmol-C/L}$; $R_m = 10.30\text{--}37.11 \text{ mmol-C/L/d}$; $\lambda = 0\text{--}5.47 \text{ d}$	$R^2 = 0.9840\text{--}0.9913$	Yin and Wang, 2022b
Caproate production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 47.63\text{--}118.62 \text{ mmol-C/L}$; $R_m = 4.05\text{--}76.68 \text{ mmol-C/L/d}$; $\lambda = 0\text{--}7.84 \text{ d}$	$R^2 = 0.9553\text{--}0.9967$	Yin and Wang, 2022b
Heptylate production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 2.31\text{--}10.3 \text{ mmol-C/L}$; $R_m = 0.08\text{--}5.15 \text{ mmol-C/L/d}$; $\lambda = 0\text{--}4.89 \text{ d}$	$R^2 = 0.8735\text{--}0.9719$	Yin and Wang, 2022b
Caprylate production	Anaerobically digested sludge	The Lay modified Gompertz model	$P = 3.27\text{--}11.54 \text{ mmol-C/L}$; $R_m = 0.18\text{--}0.44 \text{ mmol-C/L/d}$; $\lambda = 0 \text{ d}$	$R^2 = 0.08222\text{--}0.8567$	Yin and Wang, 2022b
Ethanol production	<i>S. cerevisiae</i>	The Lay modified Gompertz model	$P = 10.8 \text{ g/L}$; $R_m = 0.88 \text{ g/L/h}$; $\lambda = 22.41 \text{ h}$	–	Bhuyar et al., 2022

*: R^2 : coefficient of determination; MBE : mean bias error; MAE : mean absolute error; $RMSE$: root mean square error; $AICc$: Akaike information criterion; $\%Dev$: percentage deviation.

caproate production, butanol production, hexanol production, butyrate production, etc. Its adaptability makes it a useful tool for analyzing growth and production in biotechnology throughout the 21st century.

In addition to the Lay-modified Gompertz model, other models, such as the Logistic model and first-order model, have found applications in describing bioproduction kinetics, such as biohydrogen (Ramprakash and Muthukumar, 2018; Hu et al., 2020) and biomethane (Membere and Sallis, 2018) production kinetics.

These models (Logistic, first-order, and Gompertz models) are all applicable in modeling microbial growth kinetics and bioproduction

kinetics. However, the basic assumptions of these models are distinct. The Gompertz model is rooted in the assumption that the mortality rate of organisms increases exponentially with time. The first-order model posits that the growth rate is directly proportional to the growth amount. In contrast, the Logistic model assumes that the growth rate slows down as the growth amount approaches its maximum, reflecting resource limitations or other factors influencing the growth phenomenon. Furthermore, the obtained kinetics parameters from these models exhibit differences. The Gompertz model yields insights into both the maximum growth amount/rate and lag-time, whereas the first-order

Table 3

The references for various forms of the Gompertz model.

Gompertz model equation	Model parameters	References
$y = d g^x$	d and g	Gompertz, 1825
$u = B g^x$	B and g	Gompertz, 1825
$u = B g^x + k$	B , g , and k	Makeham, 1860
$y = y_0 e^{\frac{d}{\beta} (1 - e^{-\beta t})}$	y_0 , d , and β	Ludwig, 1929
$y = d e^{-e^{-bt}}$	d , a , and b	Winsor, 1932
$y = A e^{\frac{y_0}{bt} e^{-\frac{r}{A} t}}$	y_0 , A , R , and r	Rogers et al., 1987
$y = A e^{-\frac{\mu_m e}{A} (\lambda - t) + 1}$	A , λ , and μ_m	Zwietering et al., 1990
$M = P e^{-\frac{R_m e}{P} (\lambda - t) + 1}$	P , λ , and R_m	Lay et al., 1996

model only provides information about the maximum growth amount.

4. The future of the Gompertz model

4.1. The future prospect in the application of the Gompertz model for describing the growth kinetics

In previous sections, we conducted an in-depth review of the origins and development of the Gompertz model, thoroughly examining its diverse applications in growth analysis. However, there are some issues that need clarification to enhance the future applications of the Gompertz model.

The first issue pertains to the citation of different forms of the

Gompertz model. In many published papers, such as Mello et al. (2015), Zardin et al. (2019), Welagedara et al. (2019), Pelinovsky et al. (2022), Bartolomeo et al. (2021), Jaimes-Estévez et al. (2023), Yang et al. (2023), Chan et al. (2023), and Delavar and Wang (2023), the specific form of the Gompertz model was cited from sources other than the original paper that proposed the model. In Table 3, we have compiled references for various forms of the Gompertz model, providing researchers with a guide for proper citation.

Secondly, the prevailing Gompertz model (such as the Gompertz models modified by Ludwig (1929), Zwietering et al., (1990), and Lay et al. (1996)) is primarily developed based on Eq. (1). This equation assumes that mortality is a consequence of an increased inability of the individual to withstand destruction (internal mortality). It does not account for mortality that occurs unexpectedly and randomly (external mortality). As a result, this model exhibits limitations in its ability to accurately predict mortality when external mortality factors cannot be disregarded. For a more comprehensive description of mortality rates, both internal and external mortality factors are better captured by Eq. (3) (Makeham, 1860, 1867). We have developed a general form of the Makeham-Gompertz model by introducing the extrinsic mortality rate and parametrizing it to represent better the growth curve incorporating both internal and external mortality.

The total population y can be described as follows:

$$-\frac{1}{y} \frac{dy}{dt} = B g^t + k \quad (21)$$

Eq. (21) can be transformed into Eq. (22) by substitution of g into e^a :

$$-\frac{1}{y} \frac{dy}{dt} = B e^{at} + k \quad (22)$$

Thus, the total population y can be calculated as follows:

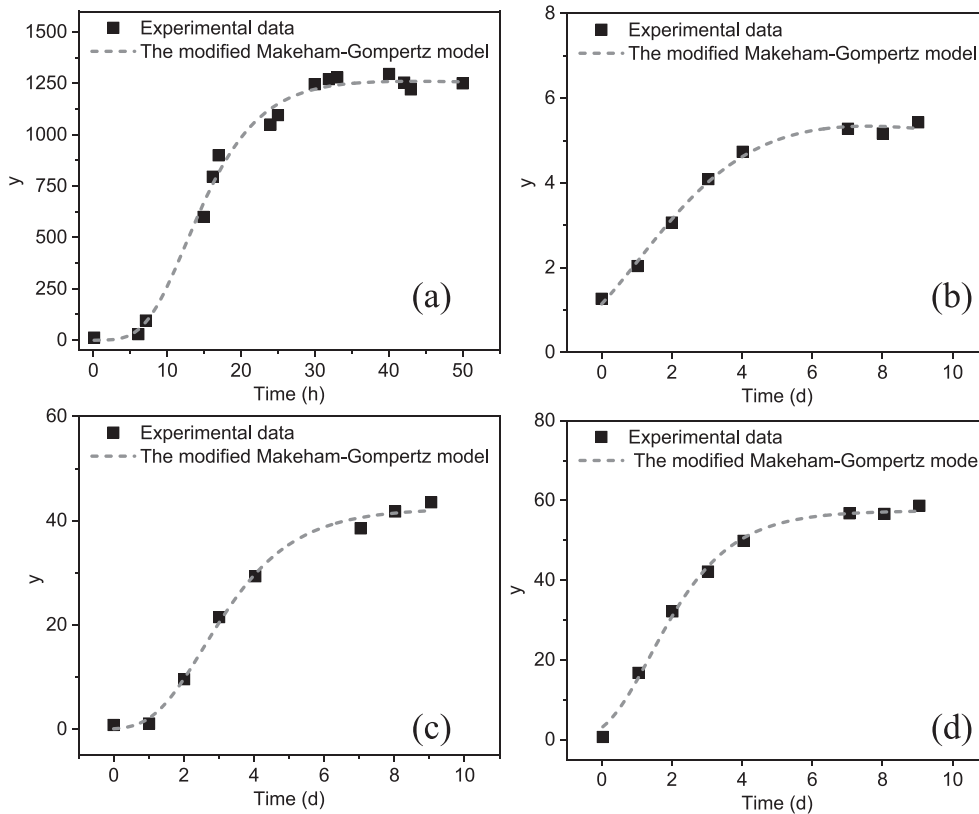


Fig. 4. The fitting results of the modified Makeham-Gompertz model to the growth data: (a) yeast growth; (b) Microbial (*C. vulgaris*) growth (Media/Conditions = Synthetic wastewaters SWW2); (c) Microbial (*C. vulgaris*) growth (Media/Conditions = Synthetic wastewaters SWW1-T15); and (d) Microbial (*C. vulgaris*) growth (Media/Conditions = Synthetic wastewaters SWW1-T35).

Table 4

The parameters of the Gompertz models for microbial growth.

Object	Model equation	Model parameters	Statistical parameters	References
Microbial (yeast) growth	The Rogers-modified Gompertz model	$A = 1268; k_R = 0.1824$	$R^2 = 0.9715$, $adjR^2 = 0.9668$	Ribeiro, 2017
Microbial (<i>C. vulgaris</i>) growth (Media/Conditions = Synthetic wastewaters SWW2)	The modified Makeham-Gompertz model	$k_n = 1305$, $\gamma = 2.26$; $a_n = 0.179$, $k = 0.000723$	$R^2 = 0.991$, $adjR^2 = 0.989$	Sousa et al., 2021
Microbial (<i>C. vulgaris</i>) growth (Media/Conditions = Synthetic wastewaters SWW1-T15)	The modified Makeham-Gompertz model	$A = 3.44$; $\mu_m = 0.54$; $\lambda = 2.31 \times 10^{-10}$	$R^2 = 0.774$, $adjR^2 = 0.6045$	
Microbial (<i>C. vulgaris</i>) growth (Media/Conditions = Synthetic wastewaters SWW1-T15)	The modified Makeham-Gompertz model	$k_n = 7.049$, $\gamma = 0.598$; $a_n = 0.442$; $k = 0.02823$	$R^2 = 0.99416$, $adjR^2 = 0.98977$	
Microbial (<i>C. vulgaris</i>) growth (Media/Conditions = Synthetic wastewaters SWW1-T35)	The modified Makeham-Gompertz model	$A = 42.33$; $\mu_m = 11.01$; $\lambda = 1.14$	$R^2 = 0.9955$, $adjR^2 = 0.9937$	
Microbial (<i>C. vulgaris</i>) growth (Media/Conditions = Synthetic wastewaters SWW1-T15)	The modified Makeham-Gompertz model	$k_n = 42.33$, $\gamma = 1.81$; $a_n = 0.707$; $k = 0$	$R^2 = 0.9955$, $adjR^2 = 0.9921$	
Microbial (<i>C. vulgaris</i>) growth (Media/Conditions = Synthetic wastewaters SWW1-T35)	The modified Makeham-Gompertz model	$A = 57.4$; $\mu_m = 16.44$; $\lambda = 0.105$	$R^2 = 0.9957$, $adjR^2 = 0.994$	
Microbial (<i>C. vulgaris</i>) growth (Media/Conditions = Synthetic wastewaters SWW1-T35)	The modified Makeham-Gompertz model	$k_n = 57.4$, $\gamma = 1.08$; $a_n = 0.778$; $k = 0$	$R^2 = 0.9957$, $adjR^2 = 0.9925$	

$$y = y_0 e^{\frac{B}{\alpha} - \left(\frac{B}{\alpha} e^{-\alpha t} + kt \right)} = y_0 e^{\left(\frac{B}{\alpha} (1 - e^{-\alpha t}) + kt \right)} \quad (23)$$

By the definition B/α of e^Y , α of $-\alpha_n$, $y_0 e^{e^Y}$ of k_n , Eq. (23) is transferred into:

$$y = k_n e^{-(e^Y e^{-\alpha_n t} + kt)} = k_n e^{-(e^Y - \alpha_n t + kt)} \quad (24)$$

Where α_n (1/h) is a positive constant (Winsor, 1932).

This model provides a more comprehensive representation of population growth, accounting for both internal and external mortality factors. To validate this modified Makeham-Gompertz model, we collected growth data from published papers (Ribeiro, 2017; Sousa et al., 2021) and fitted the data to our model. The R^2 and adjusted R^2 ($adjR^2$) were calculated to evaluate the fitting results:

$$R^2 = 1 - \frac{SSE}{SST} \quad (25)$$

$$adjR^2 = 1 - (1 - R^2) \frac{(N_{exp} - 1)}{(N_{exp} - N_{para} - 1)} \quad (26)$$

Where SST is the total sum of squares, SSE is the residual sum of squares, N_{exp} is the number of experimental data, and N_{para} is the number of model parameters.

The modeling results are presented in Fig. 4, and the statistical parameters are summarized in Table 4. As depicted in Fig. 4 and Table 4, the modified Makeham-Gompertz model can adequately describe the kinetics data of microbial growth data, with R^2 and $adjR^2$ values exceeding 0.98. Notably, the modified Makeham-Gompertz model outperforms or equals the originally applied Gompertz model (Rogers-modified and Lay-modified Gompertz models) in these studies. In the growth of yeast and *C. vulgaris* (SWW2), the values of k (the external

mortality rate) are higher than zero. This observation suggests that external mortality (mortality by chance) occurs during growth. Conversely, the values of k are equal to zero in the growth of *C. vulgaris* under SWW1-T15 and SWW1-T35 conditions. Thus, the modified Makeham-Gompertz model can be reduced to the Gompertz model as rewritten by Winsor (1932), where internal mortality dominates in these growth processes.

4.2. The future prospect in the application of the Gompertz model for describing the bioproduction kinetics

Similar to the Gompertz model used to describe the growth kinetics discussed in the previous section, the Gompertz model employed in the bioproduction process does not consider deaths that occur randomly. As a result, the model is restricted in its ability to describe the external mortality among organisms. To better predict bioproduction in cases where external mortality factors cannot be disregarded, we therefore proposed a general form of the Makeham-Gompertz model that incorporates both internal and external mortality rates (Makeham (1860, 1867).

The quantity of organisms can be described as follows:

$$y = k_n e^{-(e^Y - \alpha_n t + kt)} \quad (27)$$

Considering a delay time (t_b , (h)) between the growth of organisms and the actual production of the bioproduct, the total bioproduction amount M (mL) can be calculated as follows:

$$M = \int_0^{t-t_b} r_m = \frac{1}{k_b} k_n e^{-(e^Y - \alpha_n (t-t_b) + k(t-t_b))} \quad (28)$$

By the substitution of k_n/k_b into A_{bn} , Eq. (28) is transferred into:

$$M = A_{nb} e^{-(e^Y - \alpha_n (t-t_b) + k(t-t_b))} \quad (29)$$

The modified Makeham-Gompertz model has the potential to improve the accuracy of growth curve predictions in bioproduction by accounting for both internal and external mortality factors affecting microorganisms. Next, we collected several sets of bioproduction data (Kovalev et al., 2023; Gökçek and Erdoğan, 2024; Ketsub et al., 2021) to evaluate the modified Makeham-Gompertz model. The modeling results are shown in Fig. 5 and Table 5. The bioproduction data of hydrogen and methane have been effectively fitted to the modified Makeham-Gompertz model, as demonstrated in Fig. 5 and Table 5. The adequacy of the model fit is demonstrated by the R^2 values exceeding 0.96 and the $adjR^2$ values surpassing 0.91. This result demonstrates the good performance of the modified Makeham-Gompertz model for describing bioproduction kinetics data. Furthermore, the utility of the model extends to extracting valuable insights, such as the determination of delay time (t_b) between the growth of microorganisms and the production of hydrogen and methane, as shown in Table 5.

5. Concluding remarks

This paper provides a comprehensive review of the past, present, and future of the Gompertz model, exploring its applications in microbial growth and bioproduction kinetics. The origins of the Gompertz model can be traced back to 1825, marked by the identification of a systematic geometric trend in the correlation between mortality rate and age (within specific age groups). The mortality encompasses both internal mortality, which is age-related, and external mortality, which is random and unrelated to age. Throughout the 20th century, the Gompertz model that considered internal mortality has undergone various modifications and reparameterizations to enhance its effectiveness in analyzing growth phenomena. Diverse variations proposed by Makeham, Ludwig, Winsor, and others have contributed to the model's adaptability. Notably, the Winsor-modified Gompertz model can capture the maximum growth rate and quantity, thus establishing it as a valuable

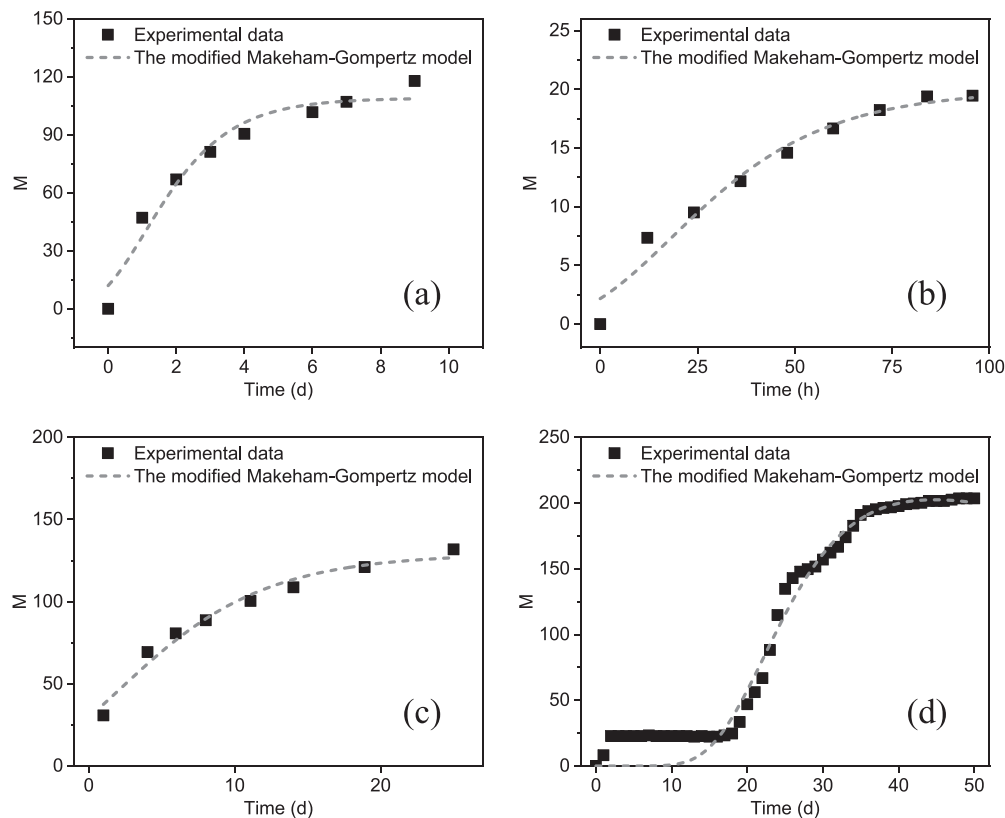


Fig. 5. The fitting results of the modified Makeham-Gompertz model to the bioproduction kinetics data: (a) hydrogen production (inoculum: *Thermoanaerobacterium thermosaccharolyticum*); (b) hydrogen production (inoculum: sludge collected from an advanced biological wastewater treatment plant, Turkey); (c) methane production (inoculum: sludge collected from a sewage wastewater treatment plant, Queensland); and (d) methane production (inoculum: anaerobic sludge from the Beijing Donghuashan Biogas Plant).

Table 5
The parameters of the Gompertz models for bioproduction processes.

Bioproduction processes	Inoculum	Model equation	Model parameters	Statistical parameters	References
Hydrogen production	<i>Thermoanaerobacterium thermosaccharolyticum</i>	Lay-modified Gompertz model The modified Makeham-Gompertz model	$P = 107.4; R_m = 1.427; \lambda = 0$ $k_n = 109; \gamma = 0.454; a_n = 0.72; k = 0; t_b = 0.467$	$R^2 = 0.957; adjR^2 = 0.925$ $R^2 = 0.962; adjR^2 = 0.911$	Kovalev et al., 2023
Hydrogen production	Sludge collected from Kayseri Advanced Biological Wastewater Treatment Plant, Turkey	Lay-modified Gompertz model The modified Makeham-Gompertz model	$P = 133.071; R_m = 11.07; \lambda = 3.538$ $k_n = 19.95; \gamma = 0.459; a_n = 0.0438; k = 0; t_b = 7.75$	$R^2 = 0.956; adjR^2 = 0.930$ $R^2 = 0.972; adjR^2 = 0.944$	Gökçek and Erdoğan, 2024
Methane production	Sludge collected from a sewage wastewater treatment plant, Queensland	Lay-modified Gompertz model The modified Makeham-Gompertz model	$P = 119.7; R_m = 14.1; \lambda = 0$ $k_n = 129.2; \gamma = -0.0627; a_n = 0.173; k = 0; t_b = 2.59$	$R^2 = 0.894; adjR^2 = 0.815$ $R^2 = 0.9751; adjR^2 = 0.9564$	Ketsub et al., 2021
Methane production	Anaerobic sludge from the Beijing Donghuashan Biogas Plant	Lay-modified Gompertz model The modified Makeham-Gompertz model	$P = 204.2; R_m = 13; \lambda = 15.8$ $k_n = 294; \gamma = 3.03; a_n = 0.135; k = 0.0072; t_b = 0.469$	$R^2 = 0.975; adjR^2 = 0.973$ $R^2 = 0.975; adjR^2 = 0.973$	Li et al., 2018

and versatile tool for understanding growth kinetics. The applications of the Gompertz model have extended beyond human mortality to encompass a wide array of growth phenomena in the 20th and 21st centuries. The Gompertz model continues to prove effective in bioproduction processes, which include the growth of organisms and the production of bioproducts. Lay (1996) first explored the model’s adaptations to biomethane production data. Later in the 21st century, the Gompertz model further extended its capabilities to various

bioproduction processes, including hydrogen, methane, caproate, butanol, and hexanol. Some prospects in the applications of the Gompertz model have been proposed. A significant recommendation for future research involves standardizing citations across various formulations of the Gompertz model. We provided the original sources of the frequently used Gompertz models. It is essential to prioritize referencing the original research when citing different forms of the model. Additionally, given the diverse

applications of various forms of the Gompertz model, it is crucial to offer guidance on selecting the appropriate model for specific applications. The Zwietering-modified Gompertz model is recommended for analyzing growth kinetics.

Considering that many current Gompertz models primarily focus on internal mortality, we have developed modified Makeham-Gompertz models to describe both growth and bioproduction processes. These models are validated using growth kinetics and bioproduction kinetics data, demonstrating good fitting performance. The efficacy of the modified Makeham-Gompertz models positions them as valuable tools for describing organisms' growth and bioproduction systems when external mortality cannot be ignored.

Overall, this paper offers a historical perspective and a comprehensive understanding of the Gompertz model and contributes to the ongoing development of versatile models for describing complex growth and bioproduction processes. The insights provided lay the foundation for future applications of the Gompertz model.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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