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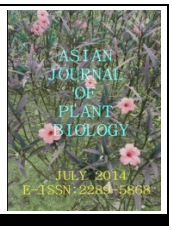

Evaluation of several mathematical models for fitting the growth of the algae *Dunaliella tertiolecta*

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ABSTRACT

Growth curves can be found in a variety of disciplines including fishery, agriculture, biology and biotechnology. Most living matter grows with successive lag, growth, and asymptotic phases and parameters associated with these phase can be used in predictive biology. In this work we studied the growth kinetics of the algae *Dunaliella tertiolecta* based on available published work in the literature using several growth models such as modified logistic, modified Gompertz, modified Richards, modified Schnute, Baranyi-Roberts, Von Bertalanffy, Huang and the Buchanan three-phase linear model. Statistical analysis based on RMSE, adjusted R^2, Bias Factor (BF), Accuracy Factor (AF), Akaike Information Criterion (AIC) and F-test shows mixed results with the best models implied from the statistical analysis were the Baranyi-Roberts and modified Gompertz model. The Baranyi-Roberts model was chosen to fit the growth profile of the algae under various light intensity based on its mechanistically-inclined properties. The results obtained showed that the μ_{max} rose steadily from 0.317 to 1.069 (day^{-1}) whilst the lag time were negative in values at 10 and 20 lux light intensities and steadily increased to 1.189 days at 60 lux light intensity. The results from this work can be used in the further optimization works of this alga in the future.

INTRODUCTION

Algae, similar to microbial growth often shows growth with several phases where the specific growth rate starts at the value of zero. This is followed by acceleration to a maximal value (μ_{max}) for a given period of time, resulting in what is called the lag time (λ). Finally the growth curves exhibit a final phase where the rate decreases and eventually reaches zero or an asymptote (A). The growth phases usually resulted in a sigmoidal curve (Fig. 1). The lag phase just after $t = 0$ is followed by the exponential- and finally a stationary phase. Another valuable parameter of the growth curve asides from the lag period and the asymptotic value is the maximum specific growth rate (μ_{max}). Usually when the logarithm of the bacterial or algal number is used the slope of the line when the organisms grow exponentially is equal to μ_{max}. This value is important for the development of secondary models where the effect of environmental conditions such as temperature, pH and water activity on the growth rate of organism is modelled [1]. In a large number of publications, this parameter is often estimated manually by deciding subjectively
the part of the curve that is nearly linear and then the slope of this curve section is then determined usually by linear regression. A better method is to describe the entire set of data with a nonlinear regression growth model and then estimate μ *max*, λ and A from the model. In addition many published works produced the growth curve but did not attempt any further to fitting the data to available models [1].

The sigmoidal curve can be fitted by different mathematical functions, such as Logistic [1,2], Gompertz [1,3], Richards [1,4], Schnute [1,5], Baranyi-Roberts [6] and Von Bertalanffy [7,8], Buchanan three-phase [9] and more recently Huang models [10]

(Table 1). Apart from demonstrating predictive ability and internal consistency, which is a must, the usefulness of a model should also be judged by its mathematical simplicity, flexibility, the number of its adjustable parameters and, where appropriate, whether they have intuitive meaning. The objective of this work is to evaluate similarities and differences between the models using published available data that lacks modelling and to deal with the question of which model(s) can be used, on the basis of statistical reasoning. This should give new data and results that could spurn further information and improvement in the works already done by researchers.

Table 1. Growth models used in this study.

Model	n	Equation
Modified Logistic	3	$y = \frac{A}{\left\{1+\exp\left[\frac{4\mu_{\max}}{A}(\lambda - t)+2\right]\right\}}$
Modified Gompertz	3	$y = A\exp\left\{-\exp\left[\frac{\mu_{\max} e}{A}(\lambda - t)+1\right]\right\}$
Modified Richards	4	$y = A\left\{1+v\exp(1+v)\exp\left[\frac{\mu_{\max}}{A}(1+v)\left(1+\frac{1}{v}\right)(\lambda - t)\right]\right\}^{\left(\frac{-1}{v}\right)}$
Modified Schnute	4	$y = \left(\mu_{\max}\frac{(1-\beta)}{\alpha}\right)\left[\frac{1-\beta\exp(\alpha\lambda+1-\beta-\alpha t)}{1-\beta}\right]^{\frac{1}{\beta}}$
Baranyi-Roberts	4	$y = A+\mu_{\max}x+\frac{1}{\mu_{\max}}\ln\left(e^{-\mu_{\max}x}+e^{-h_0}-e^{-\mu_{\max}x-h_o}\right) - \ln\left(1+\frac{e^{\mu_{\max}x+\frac{1}{\mu_{\max}}\ln\left(e^{-\mu_{\max}x}+e^{-h_0}-e^{-\mu_{\max}x-h_0}\right)}-1}{e^{(y_{\max}-A)}}\right)$
Von Bertalanffy	3	$y = K\left[1-\left[1-\left(\frac{A}{K}\right)^3\right]\exp^{-\left(rx/3K^{\frac{1}{3}}\right)}\right]^3$
Huang	4	$y = A+y_{\max}-\ln\left(e^{A}+\left(e^{y_{\max}}-e^{A}\right)e^{-\mu_{\max}B(x)}\right)$ $B(x) = x+\frac{1}{\alpha}\ln\frac{1+e^{-\alpha(x-\lambda)}}{1+e^{\alpha\lambda}}$
Buchanan Three-Phase Linear Model	3	Y = A, IF X < LAG Y=A + K(X−λ), IF λ ≤ X ≥ X_{MAX} Y = Y_{MAX}, IF X ≥ X_{MAX}

Note:
a= bacterial lower asymptote;
μ_{max}= maximum specific growth rate;
v= affects near which asymptote maximum growth occurs.
λ=lag time
y_{max}= bacterial upper asymptote;
e = exponent (2.718281828)
t = sampling time
α,β, k = curve fitting parameters
h_0 = a dimensionless parameter quantifying the initial physiological state of the cells. the lag time (day^{-1}) can be calculated as $h_0=\mu_{MAX}$

MATERIALS AND METHODOLOGY

Acquisition of Data

In order to process the data, the graphs were scanned and electronically processed using WebPlotDigitizer 2.5 [11] which helps to digitize scanned plots into table of data with good enough precision [12,13]. Data were acquired from the works of Chen et al. [14] from Figure 4 A which shows the effect of different light intensity on the growth of *Dunaliella tertiolecta* measured optically over several days and then replotted (Fig. 1).

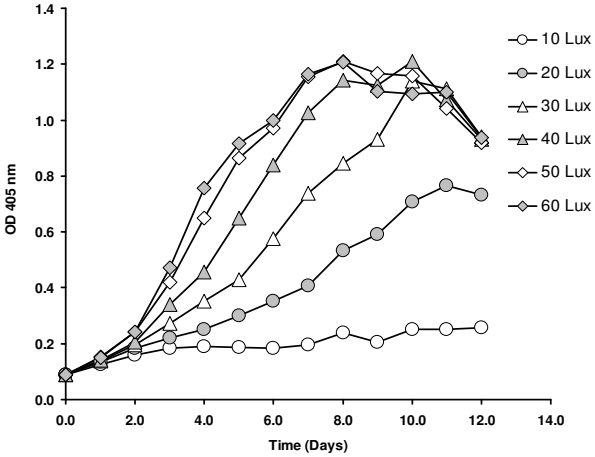

Figure 1: The growth of *Dunaliella tertiolecta* measured as optical density on a microplate under different settings light intensities. Replotted from Chen et al. [14].

Fitting of the data

Growth data will be fitted nonlinearly using nonlinear regression software (CurveExpert Professional software, Version 1.6) that uses the Marquardt algorithm. This algorithm minimizes the sums of square of residuals between the predicted and experimental values. The program can be used in the manual mode or automatic mode where it calculates starting values by searching for the steepest ascent of the curve normally using four datum points to estimate the μ_{max}. The intersection of this line with the x axis is the estimation value of the lag time or λ while the final datum point is the estimation of the asymptote (A). The Huang's model needs to be solved numerically as it is a differential equation. The differential equation was solved numerically using the Runge-Kutta method. A differential equation solver (ode45) in MATLAB (Version 7.10.0499, The MathWorks, Inc., Natick, MA) was used to solve this equation.

Statistical analysis

To decide whether there is a statistically substantial difference between models with different number of parameters, in terms of the quality of fit to the same experimental data was statistically assessed through various methods such as the root-mean-square error (RMSE), adjusted coefficient of determination (R^2), bias factor (BF), accuracy factor (AF), corrected AICc (Akaike Information Criterion) and F-test [15].

The RMSE was calculated according to Eq. (2), where Pd_i are the values predicted by the model and Ob_i are the experimental data, n is the number of experimental data, and p is the number of parameters of the assessed model. It is expected that the model with the smaller number of parameters will give a smaller RMSE values.

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(Pd_i - Ob_i)^2}{n-p}} \quad (1)$$

In linear regression models the coefficient of determination or R^2 is used to assess the quality of fit of a model. However, in nonlinear regression where difference in the number of parameters between one models to another is normal, the adoption of the method does not readily provides comparable analysis. Hence an adjusted R^2 is used to calculate the quality of nonlinear models according to the formula where RMS is Residual Mean Square and s_y^2 is the total variance of the y-variable.

$$Adjusted\ (R^2) = 1 - \frac{RMS}{s_Y^2} \quad (2)$$

$$Adjusted\ (R^2) = 1 - \frac{(1-R^2)(n-1)}{(n-p-1)} \quad (3)$$

The Akaike information criterion (AIC) provides a means for model selection through measuring the relative quality of a given statistical model for a given set of experimental data [16]. The equation incorporates number of parameters penalty, the more the parameters, the less preferred the output or the higher the AIC value. Hence, AIC not merely rewards goodness of fit, but in addition does not encourage using more complicated model (overfitting) for fitting experimental data. Since the data in this work is small compared to the number of parameter used a corrected version of AIC, the Akaike information criterion (AIC) with correction or AICc is used instead. The AICc is calculated for each data set for each model according to the following equation;

$$AICc = 2p + n\ln\left(\frac{RSS}{n}\right) + 2(p+1) + \frac{2(p+1)(p+2)}{n-p-2} \quad (4)$$

Where n is the number of data points and p is the number of parameters of the model. The method takes into account the change in goodness-of-fit and the difference in number of parameters between two models. For each data set, the model with the smallest AICc value is highly likely correct.

The F-test is a statistic test used to find the most significant model between available predicted curve-fitting models. The analysis procedure includes selecting the model with the smallest RSS among all the models with the same or different number of fitting parameters followed by comparing the relative value of the F-ratio. In the event the F-ratio of the two models surpasses the upper quartile, the better complicated model is accepted as statistically significant [15]. Equation 5 is for models with same number of parameters while Equation 6 is for models with different number of parameters;

$$F = \frac{SS_1}{SS_2} \quad (5)$$

$$F = \frac{(SS_1 - SS_2)/(df_2 - df_1)}{SS_2 / df_2} \quad (6)$$

Accuracy Factor (AF) and Bias Factor (BF) to test for the goodness-of-fit of the models as suggested by Ross [17] were also used. The Bias Factor equal to1 indicate a perfect match between predicted and observed values. For microbial growth curves or degradation studies, a bias factor with values < 1 indicates a fail-dangerous model while a bias factor with values > 1indicates a fail-safe model. The Accuracy Factor is always ≥ 1, and higher AF values indicate less precise prediction.

$$\text{Bias factor} = 10^{\left(\sum_{i=1}^{n}\log\frac{(Pd_i/Ob_i)}{n}\right)} \quad (7)$$

$$\text{Accuracy factor} = 10^{\left(\sum_{i=1}^{n}\log\frac{|(Pd_i/Ob_i)|}{n}\right)} \quad (8)$$

RESULTS AND DISCUSSION

One of the most important results from curve fitting in growth curve model is the ability to use a growth model that have a strong underlying mechanistic function based on sound theoretical knowledge of the system. One of the best of such model is the Michaelis-Menten kinetics that models the effect substrate on the initial enzyme activity of the enzyme. In order to find the best model, eight different growth models were used in this study to match the experimental data. The resultant fitting shows visually acceptable fitting (Fig. 2). The statistical analysis results (Table 2) indicated mixed results.

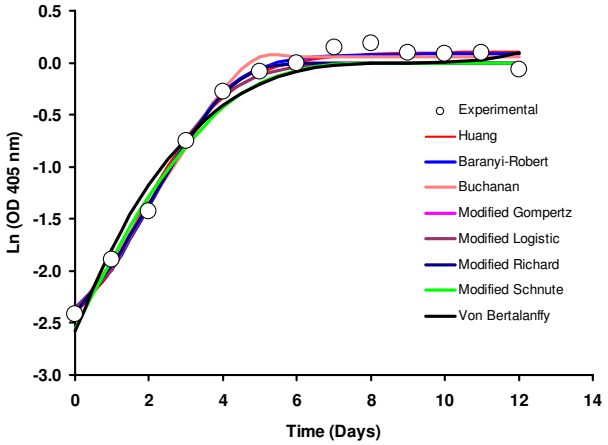

Figure 2: Growth curves of *Dunaliella tertiolecta* fitted by various growth models available in the literature. The optical density was transformed into natural logarithm.

Table 2. Statistical analysis of the various fitting models.

Model	n	AIC	RMSE	MSE	R^2	Adjusted R^2	Bias Factor	Accuracy Factor
Huang	4	-48.1	0.093	0.009	0.992	0.988	0.995	1.005
Baranyi-Robert	4	-52.0	0.082	0.007	0.993	0.990	0.988	1.012
Modified Gompertz	3	-50.7	0.099	0.010	0.989	0.985	0.980	1.021
Buchanan	3	-53.5	0.088	0.008	0.991	0.989	0.951	1.052
Modified Logistic	3	-48.2	0.108	0.012	0.986	0.981	0.957	1.045
Modified Richard	4	-45.1	0.104	0.011	0.989	0.983	0.951	1.052
Modified Schnute	4	-37.3	0.140	0.020	0.979	0.969	0.974	1.026
Von Bertalanffy	3	-38.4	0.158	0.025	0.970	0.960	0.975	1.025

Statistical analysis based on the AIC, RMSE and adjusted R2 values show that the Baranyi-Roberts was the better model whilst the Bias Factor (BF) and Accuracy Factor (AF) results indicate that the Huang model was a better fit. The Von Bertalanffy model was the least acceptable model according to the AIC, RMSE and adjusted R^2 values whilst the least acceptable model according to the AF and BF values were the modified Richard and Buchanan models. The F-test ratio showed mixed results with the Baranyi Robert model was as good as the modified Gompertz model in fitting the growth results.

However, the Baranyi-Roberts model was reputed to be more mechanistic in properties than the modified Gompertz model, with its parameters can be given a more biological meaning than the modified Gompertz model. The Baranyi-Roberts model was chosen to fit the growth profile of the algae under various light intensity based on its mechanistically-inclined properties compared to the modified Gompertz model despite having 4 parameters to be fitted (Table 2). A three-parameter model is recommended over a four-parameter model because of the simplicity of the model, it is easier to use and solution is more stable since less correlated parameters are involved. In addition, it is imperative that parameters do have biological meanings, and this is often not the case in models with more than 3 parameters with the extra parameters functions as curve fitting parameters and can be extremely large under certain circumstances. Future models could impose a penalty on these huge extra curve fitting parameters where numbers larger than 10,000 are often reported. Furthermore, model with a lower number of parameters have more degrees of freedom and can give more reliability in statistical tests such as RMSE and AICc especially when smaller number of experimental data is available. One suggested way to increase the statistical significant of a mechanistic model with four parameter over a non-mechanistic three-parameter model is to increase the number of sets of data [1].

In the model proposed by Baranyi et al. [18] the variation of the cell population (x) with time is described by a first-order differential equation [19].

$$\frac{dx}{dt} = \alpha(t)\mu(x)x \tag{9}$$

The following relationship for the growth rate is assumed

$$\mu = \mu_{\max}\left(1 - \frac{x}{x_{\max}}\right) \tag{10}$$

This model can be rewritten in its generic form [6]

$$\mu(t) = \frac{1}{x(t)}\frac{dx}{dt} = \mu_{\max}\alpha(t)f(t) \tag{11}$$

The $\alpha(t)$ function of Baranyi and Roberts [6] is based on the Michaelis–Menten 'Bottle-Neck' kinetic assumption; namely that the growth is inhibited by an intracellular substance $p(t)$ during the lag phase. The physiological state of the inoculums is represented by the quotient q_0. The model assumes that the ratio between $p(t)$ and its Michaelis–Menten constant grows exponentially from an initial value q_0, at a constant vs specific rate. The $\alpha(t)$ increases monotonously with the limits $0 \le \alpha \le 1$ and $\lim_{t\to\infty}\ \alpha(t)=1$ as follows;

$$\alpha(t) = \frac{P(t)}{P(t)+K_p} = \frac{q(t)}{1+q(t)} = \frac{q_0}{q_0 + e^{-\mu_{\max}t}} \tag{12}$$

The end-of-growth inhibition is represented as the $f(t)$ function in Eq. (13). It decreases monotonically with $f(0) = 1$ and $\lim_{t\to\infty} f(t) = 0$. Most dynamics models describe $f(t)$ by a logistic inhibition function as shown below;

$$f(t) = 1 - \left(\frac{x}{x_{\max}}\right) \tag{13}$$

Baranyi and his co-workers were able to derive solutions to this differential equation under certain conditions, e.g. fixed temperatures (isothermal). Initially this was done using six parameters;

$$y = A + \mu_{\max}x + \frac{1}{\mu_{\max}}\ln\left(e^{-vx} + e^{-h_0} - e^{-vx-h_o}\right) - \frac{1}{m}\ln\left(1 + \frac{e^{m\mu_{\max}x + \frac{1}{\mu_{\max}}\ln\left(e^{-vx}+e^{-h_0}-e^{-vx-h_0}\right)} - 1}{e^{m(y_{\max}-A)}}\right) \tag{14}$$

where;

A is the initial cell concentration and y_{max} is the asymptomatic cell concentration in ln (c.f.u./ml), m is the curvature parameter to characterize the transition from the exponential phase, v is the curvature parameter to characterize the transition to the exponential phase and h_o is a dimensionless parameter quantifying the initial physiological state of the cells. The lag time $\lambda(h)$ can be calculated as h_o/μ_{max}. μ_{max} is the maximum specific growth rate ($1/h$). For the curvature parameters, Baranyi [20] suggests $v = \mu_{max}$ and $m=1$, values that are also adopted in this paper. This decreases the number of parameters by two, so the model has four parameters: μ_{max}; h_0; a and y_{max} (eqn. 15).

$$y = A + \mu_{\max}x + \frac{1}{\mu_{\max}}\ln\left(e^{-\mu_{\max}x} + e^{-h_0} - e^{-\mu_{\max}x-h_o}\right) - \ln\left(1 + \frac{e^{\mu_{\max}x + \frac{1}{\mu_{\max}}\ln\left(e^{-\mu_{\max}x}+e^{-h_0}-e^{-\mu_{\max}x-h_0}\right)} - 1}{e^{(y_{\max}-A)}}\right) \tag{15}$$

Baranyi and Roberts [6] noted that h_0 can be thought of as a suitability indicator of the micro-organism population to the actual environment. If the experimental procedure is standardized, this suitability indicator will be more or less constant which is equivalent to the assumption that the lag time λ and μ_{max} are inversely proportional.

Using the Baranyi-Robert model as a basis, the effect of light intensities to the growth of the algae was then fitted (Fig. 3). The resultant μ_{max} for each light intensities rose steadily from 0.317 to 1.069 (day^{-1}) whilst the lag time were negative in values at 10 and 20 lux light intensities and steadily increased to 1.189 days at 60 lux (Table 3).

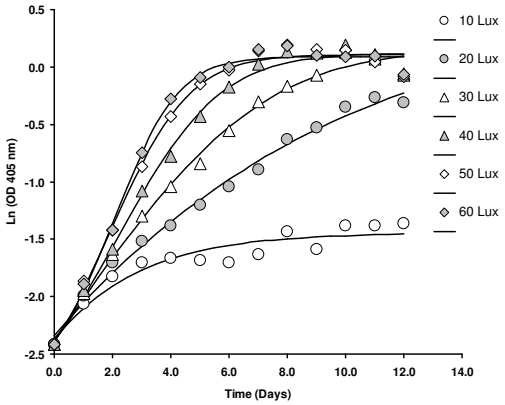

Figure 3. Growth curves of *Dunaliella tertiolecta* under various light intensities measured over time fitted with the Baranyi-Roberts model.

Table 3. Fitted growth parameters according to the Baranyi-Roberts model.

Parameters	Light Intensity (Lux)					
	10	20	30	40	50	60
A or Y_0 (ln Od)	-2.299	-2.347	-2.342	-2.349	-2.352	-2.357
μ_{max} (day^{-1})	0.317	0.383	0.414	0.678	0.866	1.069
h_0	-0.057	-0.037	0.010	0.400	0.629	1.271
Lag time (λ) (day)	-0.179	-0.096	0.024	0.590	0.726	1.189
Y_{max} (ln Od)	-1.456	-0.233	-0.234	-0.116	-0.077	0.145

The Baranyi and Roberts model is capable of producing a good fit for microbial growth curves, i.e. *Bacillus* spp., *Brochothrix thermosphacta*, *Clostridium* spp., *Escherichia coli* O157:H7, *Listeria monocytogenes*, *Salmonella* Typhimurium, *Staphylococcus* spp. and *Yersinia enterocolitica* [22–26]. The model is popular due to several reasons: first, it shows a good fitting capacity; secondly, it is applicable under dynamic environmental conditions, and thirdly, most of the model parameters are biologically interpretable [26–28]. The Baranyi-Roberts model has been successfully used to model algae growth as shown in several works on algae [29–31].

In conclusion, the various models used to fit the growth of the algae have shown that almost all of them could be used to fit the growth profile with the Baranyi-Roberts and the modified Gompertz model becoming two good candidates as assessed statistically. The mechanistically-inclined Baranyi-Roberts model was chosen to model the growth of the algae showing an increasing maximum specific growth rate and lag times as the light intensity was increased from 10 to 60 lux units. The results from this work can be used in the further optimization works of the algae.

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