



## Comparison of two ontogenetic growth equations for animals and plants



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### ABSTRACT

Ontogenetic growth reflects the changes of biomass, height (or body length) of a biological organism as a function of time. Many growth equations have been built but few can accurately predict the ending time of growth. Here we are attempting to provide two growth equations for predicting the time when growth terminates. Meanwhile, these models are also expected to apply to different growth patterns of biological organisms. Two time-dependent growth equations with four parameters each were obtained by replacing temperature with time in two non-linear mathematical models that describe the temperature-dependent developmental and growth rates of poikilotherms. Both models can generate a skewed or symmetrical bell-shaped curve. We obtained the growth equations by integrating these two temperature-dependent developmental rate models with temperature replaced by time. The dry weight data of six species of agricultural crops, the height data of four bamboo species, the tree-ring width data of two coniferous species, and the fresh weight data of 16 animals were used to fit these growth equations. Both growth equations agree well with the actual growth data of animals and plants. Additionally, one equation exhibits wide applicability and is better than the other in describing the tree-ring width. The time of reaching the maximal biomass or height can be predicted by these two models. The growth equations are valuable for predicting the time when the maximal biomass and height (or body length) are reached. Parameters of these equations can directly reflect the growth rate: the conceptual starting time of growth, the ending time of growth, the maximal growth, and the time associated with the maximal growth rate that is actually the inflection point of the growth equation. We show that these two equations apply to many diverse species. It is worthwhile to explore and compare the growth patterns of biological organisms. In addition, the prediction of tree-ring width of conifers will be helpful to accurately predict the carbon storage in forest ecosystems.

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### 1. Introduction

Ontogenetic growth of animals and plants is always a hot subject in ecological research, and many growth models have been built and compared (von Bertalanffy, 1957; Richards, 1959; Zweifel and

Lasker, 1976; Sharpe et al., 1985; Birch, 1999; Heinen, 1999; West et al., 2001, 2004; Yin et al., 2003; Makarieva et al., 2004; Thornley et al., 2007; Paine et al., 2012; Shi et al., 2014, 2016a). Many growth equations such as the logistic, Gompertz, von Bertalanffy equations provide an asymptotic value for predicting the maximal biomass, height (or body length), or superficial area. Yin et al. (2003) proposed a sigmoid growth equation based on the beta function, which predicts the time when the biomass of plants reaches its maximum. We refer to it as the beta sigmoid equation (BSE) below. Shi et al. (2016a) further demonstrated that the BSE can be applied to the growth of many plants. The beta function was first proposed

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by Yin et al. (1995) to describe the effect of temperature on the developmental rates of crops. There are other mathematical models that have similar curve shapes that describe the temperature-dependent developmental rates of insects (Régnière et al., 2012; Shi et al., 2016b and references therein). Shi et al. (2016b), using ten datasets on insects, found that the model proposed by Ratkowsky et al. (1983) exhibits greater fitting flexibility than the beta function. However, Ratkowsky and Reddy (2017), using the same ten datasets, demonstrated that the model proposed by Lobry et al. (1991) is even better than the one proposed by Ratkowsky et al. (1983). Even when the sample size is relatively small, the estimators of the parameters of the former model are relatively unbiased with respect to the latter, and are close to being normally distributed and are close to the minimum variance bound (Ratkowsky, 1990). In fact, at an earlier date Rosso et al. (1993) compared their model with that proposed by Ratkowsky et al. (1983), and showed that the former has advantages over the latter in terms of the biological interpretability of their parameters. We refer to the model proposed by Rosso et al. (1993) as the LRF function below.

Interestingly, the LRF function and the beta function have the same four parameters: a) a conceptual lower temperature threshold where development starts, b) a conceptual upper temperature threshold where development terminates, c) the maximal developmental rate, and d) an 'optimal' temperature associated with the maximal developmental rate. In the ontogenetic growth equation, the conceptual lower and upper temperature thresholds are replaced by the starting time and ending time of growth; the maximal developmental rate represents the maximal (absolute) growth rate; and the temperature associated with the maximal developmental rate is replaced by the time when growth reaches its maximum. The BSE was obtained by integrating the beta function; by the same token we could obtain a new growth equation by integrating the LRF function. Although the number and mean-

ings of model parameters in both growth equations of interest are the same, the model structures are different.

Since the LRF function is better than the beta function in terms of its estimation properties in non-linear regression (Ratkowsky and Reddy, 2017), we expect the integral of the former to also be better than the BSE in fitting biomass, height (or body size) of animals and plants. Hence, we have attempted to compare these two growth equations by using different datasets. In addition, there are two more reasons that we have compared them: (i) both equations can predict the time when biomass or body size reaches its maximum, and (ii) the growth rate curve can be symmetrical or not. The traditional three-parameter logistic model only produces

$$\frac{dw}{dt} = r(t) = \begin{cases} r_{\text{opt}} \left[ \left( \frac{t_{\text{max}} - t}{t_{\text{max}} - t_{\text{opt}}} \right) \left( \frac{t - t_{\text{min}}}{t_{\text{opt}} - t_{\text{min}}} \right) \frac{t_{\text{opt}} - t_{\text{min}}}{t_{\text{max}} - t_{\text{opt}}} \right]^{\delta} & \text{if } t \in (t_{\text{min}}, t_{\text{max}}) \\ 0 & \text{if } t \notin (t_{\text{min}}, t_{\text{max}}) \end{cases} \quad (2)$$

a symmetrical growth rate curve, which to a large extent reduces the fitting flexibility.

## 2. Material and methods

### 2.1. Data

We used the dry weight data of six species of agricultural crops: kidney bean (*Phaseolus vulgaris*), adzuki bean (*Vigna angularis*), mungbean (*Vigna radiata*), cotton (*Gossypium* spp.), sweet sorghum (*Sorghum bicolor*), and corn (*Zea mays*). For each species, the mean dry weight (aboveground + underground) was calculated by using 20 random samples at a specific time (see Shi et al. (2013) for details).

In the spring of 2016 (from April to June), we investigated the height growth of four species of bamboos (*Phyllostachys iridescens*, *Phyllostachys mannii*, *Sinobambusa tootsik*, and *Pleiolobatus maculatus*) that are cultivated in the Nanjing Forestry University campus. For each bamboo species, we chose the height data of an individual at different times for parameter fitting.

We also used tree-ring width data record from two species of conifers: Qilian juniper (*Sabina przewalskii*) and white spruce (*Picea glauca*). The tree-ring width record of Qilian juniper is from 1059 A.D. to 1975 A.D., which contains 917 data in total (Zhuo, 1981). The tree-ring width data of white spruce is from 1880 A.D. to 2011 A.D., for a total of 132 data points (Huang et al., 2013).

To further check whether the models can be applied to animals, we used the published weight data of 12 species of animals in West et al. (2001). In addition, we also used the mean weight data of two species of nestling birds: Florida scrub jay (*Aphelocoma c. coerulescens*; Woolfenden, 1978) and California scrub jay (*Aphelocoma c. superciliosa*; Ritter, 1984).

### 2.2. Beta function and the derived growth equation

Yin et al. (1995) proposed a beta function for describing the temperature-dependent developmental rates (or growth rates) of crops:

$$r(T) = \begin{cases} r_{\text{opt}} \left[ \left( \frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}} \right) \left( \frac{T - T_{\text{min}}}{T_{\text{opt}} - T_{\text{min}}} \right) \frac{T_{\text{opt}} - T_{\text{min}}}{T_{\text{max}} - T_{\text{opt}}} \right]^{\delta} & \text{if } T \in (T_{\text{min}}, T_{\text{max}}) \\ 0 & \text{if } T \notin (T_{\text{min}}, T_{\text{max}}) \end{cases} \quad (1)$$

where  $r$  represents the developmental rate (or growth rate) at temperature  $T$ ;  $T_{\text{min}}$  represents the conceptual lower temperature threshold below which the developmental rate diminishes to zero;  $T_{\text{max}}$  is the conceptual upper temperature threshold beyond which the developmental rate also equals 0;  $T_{\text{opt}}$  is the optimal temperature at which the developmental rate is a maximum ( $=r_{\text{opt}}$ ); and  $\delta$  is a scaling constant, which controls the concavity and convexity of the curve. We term  $T_{\text{min}}$  and  $T_{\text{max}}$  'conceptual' lower and upper temperature thresholds as these two parameters are usually not their actual thresholds. Development might terminate even though temperature is slightly higher than  $T_{\text{min}}$  or slightly lower than  $T_{\text{max}}$ . Yin et al. (2003) built a growth equation based on the above beta function by replacing all occurrences of a temperature ( $T, T_{\text{min}}, T_{\text{opt}}, T_{\text{max}}$ ) by a time ( $t, t_{\text{min}}, t_{\text{opt}}, t_{\text{max}}$ ):

Here,  $w$  represents the biomass or body size of a biological organism at time  $t$ ;  $r$  represents the growth rate at time  $t$ ;  $t_{\text{min}}$  and  $t_{\text{max}}$  represent the conceptual starting and ending times of growth;  $r_{\text{opt}}$  represents the maximal growth rate at time  $t_{\text{opt}}$ ;  $\delta$

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