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The "general" ontogenetic growth model is inapplicable to crop growth

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ABSTRACT

West et al. (2001) provided a model to describe the ontogenetic growth in organisms. They claimed that this model is general for many species. They also developed other ontogenetic growth models based on this model. However, there are many questions regarding the theory of this model. It lacks the raw data from different organisms which were used to test this model. We have grown 11 different species of most common crops in northern China. Dry and wet weights were recorded 15 times during the growth season of these crops. The dry weights of these crops were used to test the ontogenetic growth model. We used the optimization method to fit the dry weight data for estimating the parameters of the ontogenetic model. We found that the ontogenetic growth model failed to explain the growth patterns of all the species used in this study. The asymptotic maximum dry weights predicted by the ontogenetic growth model were also unreliable. However, the logistic model had a good fit to the growth data, and the predicted asymptotic maximum dry weights were also reliable. The ontogenetic growth model proposed by West et al. (2001) does not have the characteristic of "generality" for crop growth. It failed to explain the growth pattern of all the crops, and it also had problems in explaining the animal growth pattern. In contrast, the logistic model showed the better fit to most of the data from animal and plant growth patterns. Therefore, the ontogenetic growth models provided by West et al. (2001) should be further checked carefully for the problems in its basic formulations.

1. Introduction

West et al. (2001) provided an ontogenetic growth model (OGM) for describing the growth pattern of all the species. They used some data of animal growth to show the practicability of this model. Guiot et al. (2003) found that the OGM was also applicable to tumor growth. However, many researchers (e.g. Banavar et al., 2002; Ricklefs, 2003; Makarieva et al., 2004; van der Meer, 2006; Makarieva et al., 2009) questioned the OGM for its reliability and universal applicability. Regarding these questions, the advocators of the OGM did some theoretical debates only, without providing convincing experimental evidence to further support the OGM (e.g. West et al., 2004; Moses et al., 2008). However, the theoretical debates of the advocators could not answer the questions raised by Makarieva et al. (2004) which further weakens the reliability of OGM. Makarieva et al. (2004) reported that the basis on which the OGM was derived (West et al., 2001, Eq. (1)), itself violated the energy conservation law. Facing with a barrage of questions, the advocators of the OGM are still insisting on developing new models based on the OGM without thoroughly answering those questions (e.g. Hou et al., 2008, 2011). These new models were also questioned by some investigators of insight (e.g. Makarieva et al., 2009; Sousa et al., 2009).

The reliability of OGM for describing the growth patterns of animals and plants depends on the experimental evidence. If the model does not fit the corresponding data well, it is not reliable. West et al. (2001) stated that the applicability of OGM can also be extended to plants without any data analyses on plants. Authors may be emphasizing the "generality" of the OGM by making such a

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Table 1
Experimental crops and the correlation between their individual wet and dry weights.

Code	English name	Latin name	Family	R
1	Sunflower	*Helianthus annuus* L.	Asteraceae	0.968
2	Peanut	*Arachis hypogaea* L.	Fabaceae	0.968
3	Black soybean	*Glycine max* (L.) Merr.	Fabaceae	0.992
4	Soybean	*Glycine max* (L.) Merr.	Fabaceae	0.994
5	Kidney bean	*Phaseolus vulgaris* L.	Fabaceae	0.974
6	Garden pea	*Pisum sativum* L.	Fabaceae	0.996
7	Adzuki bean	*Vigna angularis* (Willd.) Ohwi et Ohashi	Fabaceae	0.940
8	Mungbeans	*Vigna radiata* (L.) R. Wilczek	Fabaceae	0.979
9	Cotton	*Gossypium* spp.	Malvaceae	0.997
10	Sweet sorghum	*Sorghum bicolor* (L.) Moench	Poaceae	0.904
11	Corn	*Zea mays* L.	Poaceae	0.939
12	Mexican corn	*Zea mexicana* (Schrad.) Kuntze	Poaceae	0.973

Here, r represents the correlation coefficient between wet and dry weights. The Latin name of Black soybean is the same as Soybean.

statement. In his comments on the OGM and the related metabolic theory of ecology, van der Meer (2006) stressed that a new theory or model should be in agreement with empirical observations. Several researchers (e.g. Reed and Holland, 1919; Ricklefs, 1968, 1975; Natsukari et al., 1988; Alford and Jackson, 1993) reported that the logistic model had a good fit to the ontogenetic growth data from many species.

The objectives of this study were to test the generality of the OGM on different crop species in northern China, and to compare the goodness-of-fits between the OGM and other non-linear models that are often used to describe the ontogenetic growth.

2. Experiment

We have grown 11 species of common crops in northern China (Table 1) in an experimental field (117°04′E, 36°42′N) in Jinan on June 27, 2011. We randomly chose 20 samples (i.e., 20 whole plants) from a species to measure their wet and dry weights. The same procedure was repeated 15 times from July 11 to September 20, 2011. The samples were collected between 7:00 am and 8:00 am during each sampling. The roots with soil were washed by fresh water and aired between 8:00 am and 10:00 am. We measured the wet weights between 10:00 am and 11:30 am. To measure the dry weights, the samples were dried in drying ovens. During first 10 sampling dates, all the samples were dried at 60 °C for 1–2 days. In the last five sampling dates, the samples of sunflower, sweet sorghum, corn and Mexican corn were dried at 80 °C for 3 days because of larger body sizes and biomass, and all others were dried at 60 °C for 2 days.

3. Data fitting

Due to high correlation between wet and dry weights each crop (Table 1), we used only dry weight to represent the body mass. In fact, dry weight has always been considered as the better estimation of body mass (e.g. Ricklefs, 1975; de Jong, 2010). Four models were tried to fit the dry weight data against time.

(I) Logistic model (Verhulst, 1845; Pearl and Reed, 1920; Davidson, 1944; Ricklefs, 1968; Thornley and France, 2005; Wu et al., 2009):

$$m = \frac{M}{1 + \exp(a - b \cdot t)} \quad (1)$$

Here, m represents the body mass at time t; M represents the asymptotic maximum body mass, which is constant; a and b are also constant.

(II) Gompertz model (Gompertz, 1825; Ricklefs, 1968; Martin and Huey, 2008):

$$m = M \cdot \exp[-a \cdot \exp(-b \cdot t)] \quad (2)$$

Here, m, t and M are the same as in Eq. (1); a and b are constant.

(III) von Bertalanffy model (von Bertalanffy, 1957; Banavar et al., 2002)

$$m = M \cdot \left\{ 1 - \left[1 - \left(\frac{m_0}{M} \right)^{1-\alpha} \right] \cdot \exp(-\gamma \cdot t) \right\}^{1/(1-\alpha)} \quad (3.1)$$

$$\gamma = \frac{a \cdot (1-\alpha)}{M^{1-\alpha}} \quad (3.2)$$

Here, m represents the body mass at time t; M represents the asymptotic maximum body mass, which is constant; m_0 represents the body mass at $t = 0$, which is constant; a and α are constant. In the original reference of von Bertalanffy (1957), α was presented as $2/3 \leq \alpha \leq 1$. He proposed three types of α: $\alpha = 2/3$, $\alpha = 1$, and $2/3 < \alpha < 1$ at that time.

(IV) Ontogenetic growth model (OGM) (West et al., 2001, 2004; Moses et al., 2008):

$$m = M \cdot \left\{ 1 - \left[1 - \left(\frac{m_0}{M} \right)^{1/4} \right] \cdot \exp\left(-\frac{a}{4M^{1/4}} \cdot t \right) \right\}^4 \quad (4)$$

The parameters are the same as in Eq. (3). Although West et al. (2001, 2004) emphasized again and again that the OGM is entirely different from the special case of von Bertalanffy model with $\alpha = 3/4$ due to the detailed biological meanings of its parameters. However, the OGM base (i.e., West et al., 2001, Eq. (1)) violated the energy conservation law (Makarieva et al., 2004). Thus, the parameters in the OGM do not have true biological meanings, and they are only common fitted parameters (van der Meer, 2006). In this situation, the superiority of OGM over the other models will only rely on its relatively better fitness to the experimental data.

We used the optimization algorithm proposed by Nelder and Mead (1965) to estimate all the parameters of Eqs. (1)–(4). The parameters of non-linear models were chosen based on least χ^2 values (Ikemoto et al., 2013). A general program based on *R* statistical software for estimating the parameters of the logistic model is provided (Appendix).

4. Results

All the aforementioned four models can fit the data very well (Tables 2–5) based on the coefficient of determination (r^2) values. However, the predicted values of M by the last three models (i.e., Gompertz model, von Bertalanffy model, OGM) are too high. The