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ORIGINAL ARTICLE

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Simulation of rice biomass accumulation by an extended logistic model including influence of meteorological factors

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Abstract The biomass (X) of a biological population, described by growth models, depends only on time (t), i.e., $X = f(t)$. Some parameters in these models are frequently taken as constants, but they may vary with growth processes under different ecological conditions. An extended logistic model including changes in the influence of meteorological factors is developed to simulate biomass accumulation processes of rice sown on different dates. The model may be generally described as $X = f(p, t)$, in which p stands for meteorological factors. The model can be used to generalize population growth processes in experiments carried out under different environments. It is shown that the model may account for 96.6% of the variance of rice biomass on the basis of sowing dates, developmental stage, solar radiation and temperature in the Yangtze River valley in China.

Keywords Rice · Biomass · Logistic model · Solar radiation · Temperature

Introduction

Population growth models have a long history (Lotka 1925; Pearl 1925; Ginzburg and Golenberg 1985; Kingsland 1985; Caswell 1989; Thompson 1992; Murray 1993; Huxley 1993). The logistic, Gompertz, Richards and Chanter models all express plant biomass as function of time (t). The logistic model is a classical one:

$$\frac{dX}{X\,dt} = \mu\left(1 - \frac{X}{X_m}\right) \tag{1}$$

in which X is population density, X_m is the maximum population, and μ is the maximum relative growth rate. The model is based on the hypothesis that there is a linear relation between relative growth rate (dX/Xdt) and nutrient availability ($1 - X/X_m$). The model was first used to describe the growth of microorganisms, and then widely applied to many ecological problems. This linear relation is a first-order approximation to non-linear relations. Generally, nutrient limitation is not obvious in the beginning but it may become significant when the population increases and then more and more pronounced with population growth. This relation may not be a linear one; therefore, Cui and Lawson (1982) proposed that

$$\frac{dX}{X\,dt} = \mu\left(1 - \frac{X}{X_m}\right)\left(1 - \frac{X}{X'_m}\right) \tag{2}$$

in which X'_m is a parameter reflecting the non-linear relation between relative growth rate and population. Hereafter, the model is referred to as a logistic model of the C-L type.

It is widely accepted that these growth models can simulate population growth processes with high precision, but their weakness is that they can describe only one process of growth. The value of the parameters will differ with the growth processes under different ecological conditions. For example, bacterial growth under different temperatures follows different growth curves. Although the processes can be simulated by a growth model, they cannot be generalized into one comprehensive model, because temperature influences growth rate. If the influence of temperature is incorporated into the model, the model will not only describe characteristics of population growth, but also express the limiting effect of the environment. For example, Overman et al. (1994), Overman (1995), Overman and Wilkinson (1995) extended the logistic model by taking account of the dependence of the increment in biomass upon the length of time before harvest and water availability (year-to-year). In the extended model, the parameters were taken to be functions of nutrient and water content.

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The objective of this study is to merge several models describing S-shaped curves into a general one, and then to introduce ecological factors into the growth model to simulate the growth processes of a crop in different environments. The work can be taken as an extension of the growth models to cover biomass growth under different ecological conditions.

As there are many sound reviews discussing growth models (e.g., Charles-Edwards et al. 1986; France and Thornley 1984; Hunt 1982), especially the one by Banks (1994), here we focus on extending the logistic model, trying to incorporate ecological factors and then forming a generalized model including the influence of the environment.

Materials and methods

The experimental site was located in Nanjing, the capital of Jiangsu Province, which lies in the Yangtze River valley. The meteorological Station of Nanjing (32°00′N, 118°48′E, and 36 m above sea level) is one of the national meteorological stations, and is representative for the area, since topographical variation and regional differences in climatic variables are small. The soil type is sandy loam and the experimental site is 4 km away from the station. The experiment was conducted in 1980 as part of a national study on the meteorological conditions suitable for hybrid rice.

Experimental conditions

Variety. The hybrid rice Shanyou 6 was chosen.

Sowing date. Seeds were sown six times at intervals of 10 or 20 days in the main growth period, i.e., 25 April, 15 May, 25 May, 5 June, 15 June, and 5 July.

Experimental area. A plot of 20 m^2 was used for each treatment with three repeats; the plots were randomly distributed.

Growth conditions. The quantity of seed sown, the number of basic seedlings, and the times and amount of fertilization were uniform. Pests and diseases were controlled.

Sampling. The biomass was weighed at ten stages of growth: when the shoots were turning green, at the appearance of the 9th, 11th, 13th and 15th leaves, at earlier booting, at the beginning of heading, and on the 10th, 20th and 30th days after heading. The samples were collected at four points for each investigation, and the biomass in an area of 0.5 m^2 was harvested for each point.

The meteorological observations were made according to the national standard. The sunshine hours are observed regularly in meteorological stations in China, but solar radiation is observed in some of the stations. As there is a close relation between solar radiation and sunshine hours, these were used to derive the values for solar radiation. The solar radiation (Q) can be expressed by the global solar radiation (Q_0) and the percentage of sunshine (S, the ratio between sunshine hours and its maximum value), i.e., $Q = Q_0(0.160 + 0.612S)$ (Zuo et al. 1991). The unit of solar radiation in this equation is MJ m^{-2}. Sunshine hours were measured by radiometry. The meteorological data were rearranged as required for model fitting.

The model

The length of the crop growth period from seedling to maturity varies with climate, so the time scale must first be normalized, i.e. $t = 0$ at the beginning of growth, and 1 at fall ripening. If the duration of each growth period is n_0 days and the time from the start to an observation time is n, the normalized time scale should be:

$$t = n/n_0 \tag{3}$$

An extended logistic model may be expressed as

$$\frac{dX}{X\,dt} = \mu \frac{X_m - X}{X_m + \nu X} \quad \text{for } \mu > 0,\ X_m > 0,\ \nu \geq -1,\ X > 0 \tag{4}$$

Equation 4 becomes the exponential model if $\nu = -1$, the logistic model if $\nu = 0$, the logistic model of the C-L type if $-1 < \nu < 0$; and the Smith (1963) model if $\nu > 0$.

Although in many studies the growth rate (μ) and carrying capacity (X_m) are assumed to be constant, they can also be taken as functions of time, such as the linear variable growth rate, the hyperbolically variable growth rate, the exponentially variable growth rate and the sinusoidally variable growth rate (Banks 1994). The carrying capacity also has these types of function. Here we consider the relation between growth rate and the meteorological factors, and X_m is assumed to be the potential productivity under suitable soil and climate conditions, a constant determined by the genetic character of the crops. The influence of meteorological factors is introduced into the extended logistic model through the relationship

$$\mu = \mu_0 f(p) \tag{5}$$

in which p represents meteorological factors and $f(p)$ is a function representing the impact of p on μ. For different relations, the function $f(p)$ takes different forms, which reflects the limitation of the meteorological factors under consideration. μ_0 is the growth rate when meteorological factors are most favorable for the population growth. Therefore, the following relation holds:

$$0 \leq f(p) \leq 1 \tag{6}$$

in which meteorological factors are most suitable for population growth when $f(p) = 1$, and population growth stops under the constraint of meteorological factors when $f(p) = 0$; for example, the crop suffers from low-temperature stress and stops growing.

As X is the biomass accumulated from the start to the time under consideration, t, the growth rate, μ, will represent the cumulative effect within this period; also $f(p)$ will represent integration with respect to time, which may vary and should not be taken as an average value. Generally, the ratios between meteorological factors or their functions will satisfy Eq. 6, and the function $f(p)$ can be parameterized accordingly.

In our experiment, the supplies of water and fertilizers were adequate for rice growth. The main factors affecting biomass production are solar radiation (Q) and temperature (T), of which solar radiation is the main limiting factor because the solar radiation density varies from 0 to values that exceed the saturation point of photosynthesis nearly every day, and temperature exerts its influence to a lesser degree (Yu et al. 2001). The growth rate can be written as

$$\mu = \mu_0 f(Q,T) \tag{7}$$

For the convenience of application, the relation between variables is represented as multiplication:

$$\mu = \mu_0 f(Q) f(T) \tag{8}$$

The growth rate of a crop is closely related to solar radiation and temperature. The higher the solar radiation within certain limits, the more rapidly the crop grows.

The basic unit of time is 1 day. Q is the daily solar radiation, and T the daily mean temperature. The daily light-thermal index is defined as

$$F(Q,T) = F(Q)F(T) \tag{9}$$

For the simplest type of $F(Q)$,

$$F(Q) = Q \tag{10}$$

This relation implies that biomass increases with solar radiation.

The temperature regime for crop growth can be described in terms of three cardinal temperatures, i.e. the optimal temperature under which the crop grows most rapidly, and the maximum and minimum temperatures under which the crop stops growing.

$$F(T) = \mathrm{e}^{[-a(T-T_{\mathrm{op}})^2/(T-T_{\mathrm{min}})(T_{\mathrm{max}}-T)]} \tag{11}$$

in which $F(T)$ is a bell-shaped curve that is similar to the 'rice clock' model (Gao et al. 1992) and the beta function (Yin et al. 1995). T_{op}, T_{max} and T_{min} are respectively the optimal, maximum and minimum temperatures. The parameter, a, represents the convexity of the response curve. It can be found from Eq. 11 that

$$0 \le F(T) \le 1 \tag{12}$$

$F(T) = 1$, when $T = T_{\mathrm{op}}$; $F(T) = 0$, when $T = T_{\mathrm{min}}$ or $T = T_{\mathrm{max}}$.

So $F(T)$ is a correction function for the influence of temperature.

Types of $f(p)$ are discussed as follows and shown in Table 1.

μ is a constant

There are two methods. Method 1 assumes that μ is unchanged for the whole growth period, which is a traditional assumption. Method 2 assumes that μ is constant for a specific growth period and variable for a different growth period. The condition is applicable to cases where meteorological factors are steady or vary only slightly, such as bacterial growth under constant temperature. The light-thermal index at all development stages (K) for the jth sowing period of rice growth is accumulated as:

$$K(j) = \int_0^1 F(Q)F(T)\mathrm{d}t = \sum_{i=1}^{n_0(j)} F(Q_i)F(T_i) \tag{13}$$

the light-thermal index is the sum of the daily index in the growth period. The maximum of the index is

$$K_{\mathrm{max}} = \max\{K(j)\} \tag{14}$$

making

$$f(p_j) = \frac{K(j)}{K_{\mathrm{max}}} \tag{15}$$

in which $f(p_j)$ is the $f(p)$ for the jth sowing period. Therefore, the growth rate in the jth sowing or growth period is

$$\mu(j) = \mu_0 \frac{K(j)}{K_{\mathrm{max}}} \tag{16}$$

The expression satisfies the condition set by Eq. 6.

The function $f(p)$ will assume a more complex form when the relation between growth and environmental factors is taken into consideration. Photosynthesis responses to solar radiation can be expressed by a Michaelis-Menten function:

$$f(p_j) = \frac{mK(j)/K_{\mathrm{max}}}{1 + qK(j)/K_{\mathrm{max}}} \tag{17}$$

in which m and q are parameters. From Eq. 6, $f(p_j) = 1$, if $K(j) = K_{\mathrm{max}}$. So $m = 1 + q$

$$f(p_j) = \frac{(1+q)K(j)/K_{\mathrm{max}}}{1 + qK(j)/K_{\mathrm{max}}} \tag{18}$$

It can be seen that the equation is equivalent to Eq. 15 when $q = 0$. If $q \to \infty$, $f(p_j) = 1$, $\mu = \mu_0$. It means that the differences in meteorological factors do not cause significant difference in the form of the function, and the many processes can be generalized into one model.

μ is a variable in the growth period

This takes into account the meteorological factors affecting crop growth markedly. For instance, the growth rate of rice changes with seasonal changes in solar radiation and temperature. This condition is unlike those of ordinary growth models, in which μ is constant, and two methods are developed. Method 3 assumes μ is variable for each growth, only depending on solar radiation; method 4 assumes that μ depends not only on solar radiation but also on temperature.

The function $f(p)$ is determined in the same way as in the previous study by introducing the light/thermal index from the start to any growth stage.

Suppose that accumulated light/thermal index up to the mth developmental stage in the jth sowing period is:

$$K_j^m = \sum_{j=1}^{m(j)} F(Q_j)F(T_j) \tag{19}$$

and

$$K_{\max}^m = \max\{K_j^m\} \tag{20}$$

As in Eq. 16

$$\mu_j^m = \mu_0 \frac{K_j^m}{K_{\max}^m} \tag{21}$$

This can be written in the form of Eq. 18. So Eq. 21 indicates that the growth rate μ_j^m at any stage (m) correlates with the ecological factors operating from the start of growth ($t = 0$) to the stage under consideration ($t = m$).

A popular method used to fit the growth model to experimental data transforms the logistic model into a linear relationship between the population function and that of time by rearrangement, and then constructs the model by a statistical method. This is the method adopted here.

The integration of Eq. 4 from X_0 to X, and from t_0 to t yields

$$\int_{X_0}^{X} \frac{X_m + \nu X}{X(X_m - X)} \mathrm{d}X = \int_{t_0}^{t} \mu \,\mathrm{d}t \tag{22}$$

The left-hand side of Eq. 22 can be resolved to two terms in the following way:

$$\begin{aligned} \int_{X_0}^{X} \frac{X_m + \nu X}{X(X_m - X)} \mathrm{d}X &= \int_{X_0}^{X} \left(\frac{1}{X} + \frac{1+\nu}{X_m - X} \right) \mathrm{d}X \\ &= [\ln X - (1+\nu)\ln(X_m - X)]_{X_0}^{X} \\ &= \ln \frac{X}{X_0} - (1+\nu) \ln \frac{X_m - X}{X_m - X_0} \\ &= \ln \left[\frac{X}{X_0} \left(\frac{X_m - X}{X_m - X_0} \right)^{-(1+\nu)} \right] \end{aligned} \tag{23}$$

So we have

$$\ln \left[\frac{X}{X_0} \left(\frac{X_m - X}{X_m - X_0} \right)^{-(1+\nu)} \right] = \mu(t - t_0) \tag{24}$$

$$\frac{X}{X_0} \left(\frac{X_m - X}{X_m - X_0} \right)^{-(1+\nu)} = \exp[\mu(t - t_0)] \tag{25}$$

If $t_0 = 0$, $\alpha = 1 + \nu$, and $\beta = \ln[(X_m - X_0)^{1+\nu}]/X_0$, then

$$\mu t = \beta + \ln X - \alpha \ln(X_m - X) \tag{26}$$

$$\frac{(X_m - X)^{\alpha}}{X} = \exp(\beta - \mu t) \tag{27}$$

Substituting Eq. 5 into the above equation,

$$f(p)t = \frac{\beta}{\mu_0} + \frac{1}{\mu_0} \ln X - \frac{\alpha}{\mu_0} \ln(X_m - X) \tag{28}$$

This equation is a linear relation between $f(p)t$ and ln X and ln(X_m – X), which can be obtained by multiple regression. A presumed value of X_m is the initial one to fit the model by regression. The goodness is judged by the criterion that the coefficient of determination or correlation coefficient (r^2) reaches its maximum value with a particular value of X_m. The coefficient represents the goodness of regression for certain samples. The closer the r^2 approaches 1, the better the fit. A satisfactory result may be eventually obtained by revising X_m and repeating the regression process.

Results

Early and late rice are the dominating crops cultivated in the Yangtze River valley. Rice can be sown after the daily average temperature stabilizes above 10 °C. In autumn, when the temperature falls below 20 °C at flowering, fertilization will be harmed and thereby kernel formation of the rice (Sharma and Singh 1999). The sowing date for late rice should set in such a way that the temperature at the heading stage will not fall below 20 °C.

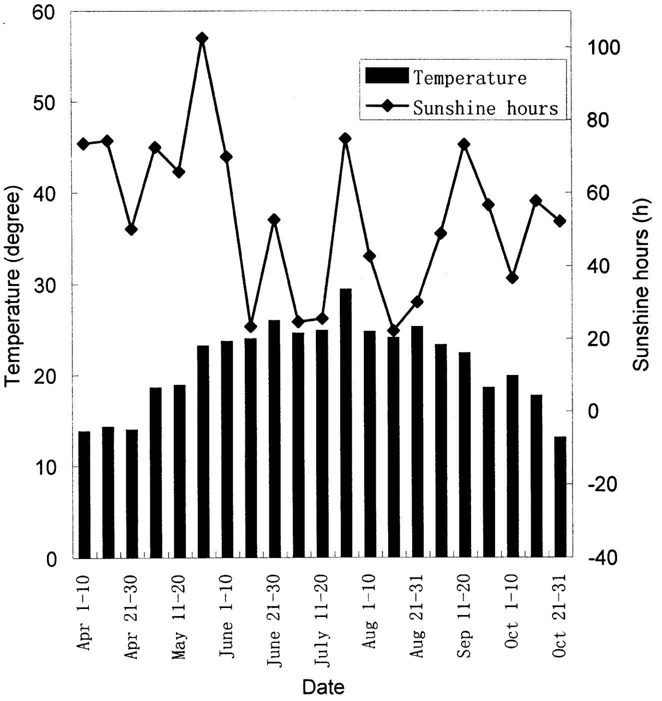

Fig. 1 Daily temperature and sunshine hours in Nanjing, Yangtze River Valley, over the rice growth period in 1980

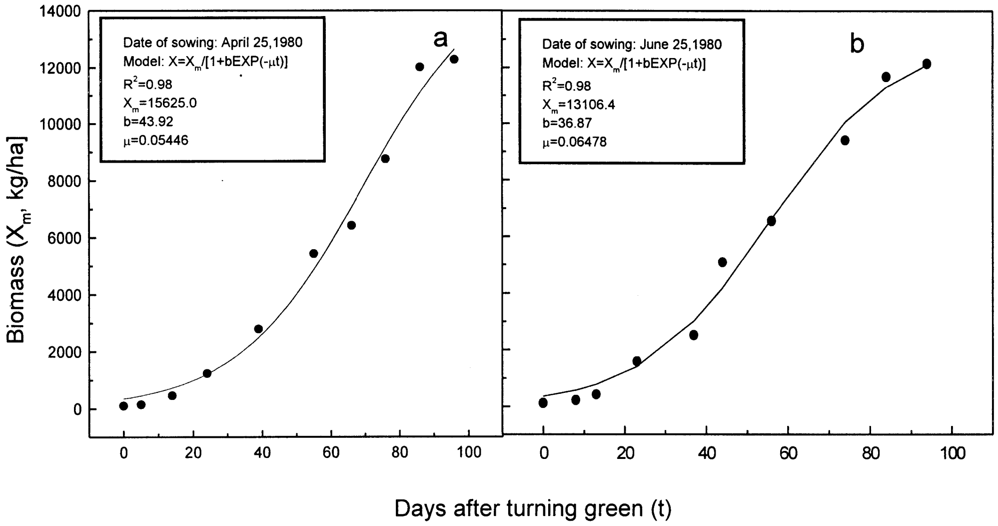

Fig. 2a, b Simulation, by the classic logistic model, of biomass accumulation of rice sown on different dates in Nanjing in 1980

Table 1 Results of fitting the extended logistic model to rice biomass accumulation in Nanjing, Yangtze River Basin, China (1980)

Model	Capacity (X_m) ($\times 10^3$ kg/ha)	Initial growth rate (μ_0)	ν	Multi-correlation coefficient (r^2)
1. μ_j is constant for all growth	12.1	16.35	25.33	0.885*
2. μ_j is constant for each growth depending on radiation and temperature: $f(p) = F(Q)F(T)$	12.1	16.42	24.66	0.950*
3. μ_j is variable for each growth depending on radiation: $f(p) = F(Q)$	12.1	16.17	25.63	0.960*
4. μ_j is variable for each growth depending on radiation and temperature: $f(p) = F(Q)F(T)$	12.1	16.22	25.03	0.966*

*Significance level <0.01, $n = 49$

Therefore, the growth period is defined by the annual course of temperature changes in this region. Temperature and solar radiation are the growth-defining factors for rice yield in the region (Yu et al. 2001). Figure 1 shows the changes in temperature and sunshine hours in the rice growth period in 1980. The temperature changed from 13.7 °C in spring to 29.3 °C in summer, and sunshine hours also changed greatly with the rainy season.

The progress of the accumulation of biomass in rice may be interpreted by a logistic model except that the dry matter of rice decreases in the late period of growth as the leaves fall off. Biomass accumulation in rice is simulated by a logistic model in Fig. 2, which shows that such a model can be used to fit biomass accumulation closely. However, because of variation in the growth environment caused by different sowing dates, the curves of the accumulation processes are quite different. Model parameters may therefore need be changed to take account of such an effect.

In fitting the model, parameters, a, q, T_{op}, T_{min}, T_{max} and X_m are used to characterize the particular crop under consideration. Generally, T_{op} ranges from 25 °C to 27 °C, and T_{min} from 35 °C to 38 °C (Wang 1989). Assigning values to the parameters, fitting the model by progressive regression, and adjusting the parameters means carrying-out many tests to achieve the best fit. The results of fitting are shown in Table 1, and the appropriate values of the parameters are $a = 1.1$, $q = 0.23$, $T_{op} = 27$ °C, $T_{min} = 11$ °C and $T_{max} = 36$ °C.

The coefficient of determination (r^2) is an indication of the correspondence between the regression curve and observational data. Table 1 shows that the growth model is of the Smith type because $\nu > 0$. Method 1, which takes μ to be constant in each growth process, has a relatively poor fit, but is convenient and useful. Method 2, which supposes that μ is changing in each growth process but considers only the influence of changes in solar radiation, results in a relatively good fit. Method 3, which is the same as method 2 except that the effect of temperature is also taken into account, gives the fit of the three methods, but it is also the most complex.

The function expressing the influence of temperature on biomass accumulation is a one-peaked curve. It is similar to the temperature-response curves of many other

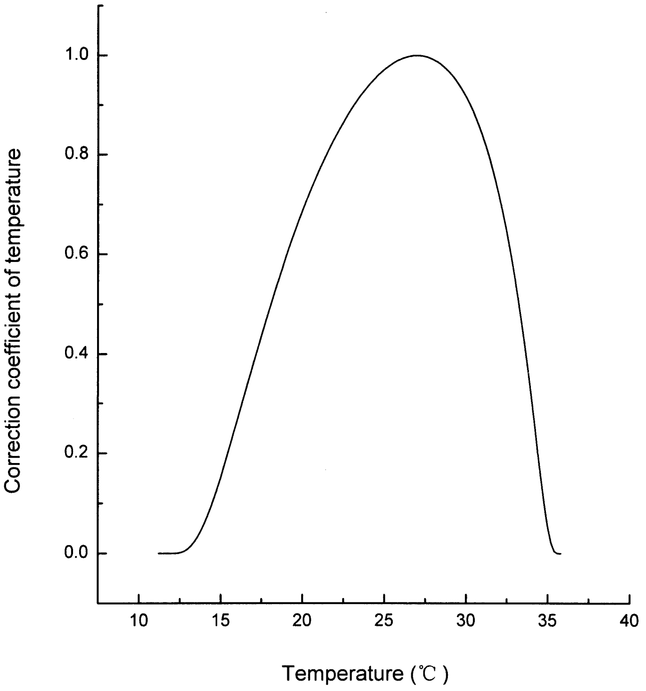

Fig. 3 Correction coefficient of temperature for biomass accumulation. The curve is based on Eq. 11 with parameter values obtained by fitting the equation to the data

biological variables (France and Thornley 1984; Yin et al. 1995). Figure 3 is the result of fitting in this work. It shows that the temperature curve changes between 11 °C and 39 °C within the limits of the maximum and minimum temperatures. The curve is not symmetrical and the optimum temperature is 26 °C, which is slightly closer to $T_{\max}$ than to $T_{\min}$.

Discussion

As there has been some development of software for the statistical analysis of specific growth processes, this paper demonstrates a need for nonlinear regression software to fit the parameters of the generalized model. Similarly, Heinen (1999) proposed generalized expressions for the growth models, including exponential, monomolecular, logistic, Gompertz, Richards, and second-order exponential polynomial models. The extended logistic model described here is characterized by the inclusion of meteorological factors.

The S-shaped growth curve correlates with environmental variables, such as solar radiation and soil nutrition, and competition among plants. Reck and Overman (1996) demonstrated that there was a linear dependence of model parameter X_m on the seasonal water supply for maize. But the growth rate (μ) of crops is more sensitive to environmental changes than the capacity (X_m) for the specific variety of rice grown in the area, according to our statistical analysis. Changes in X_m, within certain limits, have little influence on the goodness of fit. Although it is important to seek goodness of fit, it is essential to choose parameters with biological or physiological meanings. In Fig. 2, the simulated accumulation curves show that the parameters vary over a large range. For example, the value of X_m is largely determined by an envelope of points in the later period of growth; if there is still any increase at maturity, for a good statistical result, X_m will be much higher than it usually is. X_m is assumed to be the potential productivity in this example of statistics based on biological principles. But the determination of the value of X_m needs further study.

An extended logistic model to describe population growth is proposed in this work, and a statistical method is applied to fit model parameters that change with meteorological variables. The significance of the extended model depends on differences in the environment at each stage of growth and development. Although some of the periods of growth and development with different sowing dates overlap each other, the statistical result is that it is still reasonable to attribute the difference of growth to the effects of changing climate conditions (Table 1). This extended logistic model and the statistical method used for its fitting are expected to apply to the population growth of other species or to other environments.

The type of $f(p)$ depends on the type of relationship between population growth and environment. This correction factor is not only applicable to the generalized model proposed here, but also to classic logistic models. The condition where $f(p) = 1$ means that the meteorological factors are the most suitable ones for all of the growth processes.

The effects of radiation and temperature on crop growth vary with the stage of growth and development. At the initial stage of growth, when the leaf area index is small, the influence of the environment on biomass accumulation may be small, and at maturity, when consenescence of leaves is evident, the influence is also small. These elements are also included in the growth models. Three methods of fitting the model with variable parameters were considered, and it was found that there is a great difference between fixed and variable growth rates. It is therefore suggested that μ should be changed only for different growth processes and be fixed for each growth stage for the convenience of statistical analysis. On the other hand, method 2 is preferable to method 1. Methods 3 and 4 are inadequate for changing μ in one growth period, as Eq. 28 is derived for constant μ. It is supposed that μ changes within certain limits when methods 3 and 4 are used. In this study, we are exploring the possible application of this method and comparing it with the method using fixed μ. The result shows that methods 3 and 4 could be abandoned, as the improvement of significance is limited but the complexity increases greatly.

A method to calculate biomass accumulation from meteorological variables has been presented. Given the values of the parameters for different varieties in the model, we can analyze the influence of climate on their growth and yield formation, and it is possible to find suitable varieties and their sowing dates to avoid disadvantageous climatic conditions in key periods of rice growth. Although precipitation also influences rice yield in this region, solar radiation and temperature have a more significant influence under conditions where there is an ample supply of water (Yu et al. 2001).

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