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A nonlinear model for crop development as a function of temperature

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Abstract

The Beta function, commonly used as a skewed probability density function in statistics, was introduced to describe the effect of temperature on the rate of crop development. The framework is set by three cardinal temperatures, namely the base (T_b), the optimum (T_o) and the ceiling (T_c) temperature. The model parameters T_b and T_c and three other coefficients μ, α and β can be used to derive the value of T_o and the maximum development rate. Parameter α also characterizes the curvature of the relationship with temperatures between T_b and T_o, and parameter β describes the curvature between T_o and T_c. The model has one parameter less than the Rice Clock Model (RCM); and in contrast to the RCM, it ensures that the maximum development rate occurs exactly at T_o. The model accurately described the response to temperature of several developmental processes, and was superior to two widely used thermal time approaches in predicting rice flowering time.

1. Introduction

Crop development is primarily affected by temperature and can be modified by other factors such as photoperiod (Hodges, 1991). Within a range of temperatures below a

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certain value, crop development rate (DR) often increases proportionally with the temperature (Roberts and Summerfield, 1987). With the global warming due to the greenhouse effect, the effect of high temperatures on DR has also posed particular concern to modelers for predicting crop development (Matthews et al., 1995).

The effect of temperature on DR is often described by using a thermal time concept. One widely used thermal time method (Tollenaar et al., 1979) is the Growing Degree Days (GDD) procedure, which relates DR linearly to temperatures above a crop- or cultivar-specific base temperature (T_b), at or below which the DR remains zero. In some applications of the GDD procedure, an upper limit of temperature is assumed above which the DR remains constant (Hodges, 1991).

Although the GDD system is attractive because of its simplicity and its higher accuracy in predicting phenological events than number of days per se (Kiniry and Keener, 1982), it has been subjected to much criticism over the years. The classical work of Lehenbauer (1914) on the elongation of maize (*Zea mays* L.) seedlings in relation to temperature showed a rapid decline of the elongation rate when the optimum temperature, T_o, was exceeded. The data of Lehenbauer (1914) have been used by many studies (e.g. Gilmore and Rogers, 1958; Coelho and Dale, 1980) to describe DR of crops. For example, based on these data, Gilmore and Rogers (1958) presented a bilinear model (BLM) that included a reversed linear function to account for declining DR at temperatures higher than T_o. Roberts and Summerfield (1987) defined the maximum temperature at which the DR equals zero as a ceiling temperature (T_c). Garcia-Huidobro et al. (1982) and Roberts and Summerfield (1987) described temperatures between T_b and T_o as sub-optimal and those between T_o and T_c as supra-optimal; and T_b, T_o and T_c were referred to as three cardinal temperatures.

Although the BLM describes the data of Lehenbauer (1914) better than the GDD, it does not describe the pattern accurately. The data showed a skew bell-shaped curve: an accelerating increase of the rate at low temperatures, a linear section, an optimum, followed by a rapid fall-off beyond T_o. This type of curve is qualitatively typical for the temperature response of many complex biological processes (Ferguson, 1958; Orchard, 1975; Tyldesley, 1978; Johnson and Thornley, 1985).

Various nonlinear models have been developed to describe the temperature response of developmental processes in plants. Johnson and Thornley (1985) reviewed many nonlinear equations for biological processes based on their underlying theory. A detailed model, which is based on the response of enzymatic reactions to temperature, was found to fit the data of Lehenbauer (1914) very well (Sharpe and DeMichele, 1977). However, when this model was introduced to predict maize development in the field, it did not perform better than the thermal time methods GDD and BLM (Kiniry and Keener, 1982). In addition, its large number of parameters prevented its use under field conditions (Kiniry and Keener, 1982; Hodges, 1991). Most nonlinear approaches use descriptive equations (Robertson, 1968; Coligado and Brown, 1975; Angus et al., 1981; Horie and Nakagawa, 1990; Gao et al., 1992). However, most of these descriptive equations do not account for the frequently observed decline of DR at supra-optimal temperatures (e.g. the power-law function (Coligado and Brown, 1975), the exponential equation (Angus et al., 1981) and the logistic model (Horie and Nakagawa, 1990)). A quadratic equation (e.g. Robertson, 1968) does account for this decline at supra-optimal

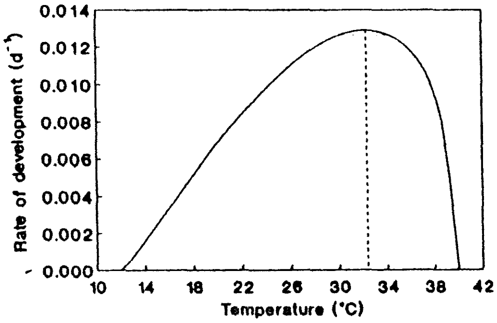

Fig. 1. Relation between temperature and rate of development from emergence to heading in rice cultivar DTWX, based on the basic equation (Eq. 1) of the Rice Clock Model (Gao et al., 1992). The dotted line indicates the discontinuous part given by Eq. 2. Note the discrepancy between the prespecified optimum temperature (30°C) and the temperature at which the rate calculated from Eq. 1 is maximal (shown by the vertical dashed line).

temperatures. However, it assumes a symmetric response and does not allow for any concave curvature near T_b. These limitations were overcome in the Rice Clock Model (RCM) (Gao et al., 1992), which describes the response of DR to temperature as:

$$DR = \exp(k)\left(\frac{T - T_b}{T_o - T_b}\right)^{\alpha}\left(\frac{T_c - T}{T_c - T_o}\right)^{\beta} \tag{1}$$

where k, α and β are the model parameters, and $\exp(k)$ defines the maximum DR when $T = T_o$ (in the orginal RCM, T_b, T_c, α and β were denoted as T_L, T_U, P and Q, respectively). However, the maximum DR does not always occur at T_o in Eq. 1. For example, using the parameters for an *indica* rice cultivar DTWX as derived by Gao et al. (1992), the temperature for the maximum DR based on Eq. 1 is 2.3°C higher than the prespecified T_o of 30°C (Fig. 1). To make the model have maximum DR at T_o, Gao et al. (1992) added the following restriction:

$$DR = \exp(k) \quad \text{if} \left(\frac{T - T_b}{T_o - T_b}\right)^{\alpha}\left(\frac{T_c - T}{T_c - T_o}\right)^{\beta} > 1 \tag{2}$$

However, this restriction is artificial and can result in a discontinuous nonlinear relationship (Fig. 1).

In this paper, a nonlinear model, which is simpler than the RCM but overcomes the problem of the RCM, is introduced to describe crop development involving the three cardinal temperatures. The model was evaluated using published data sets on several developmental processes, and was compared with the RCM and the two thermal time methods GDD and BLM for predicting the time to flowering of the rice crop.

2. Materials and methods

2.1. The model

A well-known nonsymmetric function, the Beta function (Abramowitz and Stegun, 1965), provides a model for the relationship between DR and temperature which has a form similar to that of the RCM, Eq. 1, but has fewer parameters and allows nonproblematic estimation of T_o. The Beta function is commonly used to give a flexible family of nonsymmetric, unimodal probability density functions with fixed end points (Johnson and Leone, 1964) which allow points of inflexion on either side of the mode. Based on the Beta model, an equation for describing the response of the DR to temperatures between T_b and T_c can be expressed as:

$$\mathrm{DR} = \exp(\mu)(T - T_b)^{\alpha}(T_c - T)^{\beta} \tag{3}$$

where μ, α and β are the model parameters.

In contrast to the RCM, Eq. 3 does not include T_o and the maximum DR as its parameters; however, it can provide estimates of T_o and the maximum DR. T_o is the zero of the first-order derivative DR′ of Eq. 3 which is:

$$\mathrm{DR}' = \exp(\mu)(T - T_b)^{\alpha}(T_c - T)^{\beta}\left(\frac{\alpha}{T - T_b} - \frac{\beta}{T_c - T}\right) \tag{4}$$

Hence

$$T_o = \frac{\alpha T_c + \beta T_b}{\alpha + \beta} \tag{5}$$

Substituting T_o into Eq. 3 results in an estimate of R_o, the maximum DR:

$$R_o = \exp(\mu)\,\alpha^{\alpha}\beta^{\beta}\left(\frac{T_c - T_b}{\alpha + \beta}\right)^{\alpha+\beta} \tag{6}$$

Thus, the Beta model has one parameter less than the RCM; but, unlike the RCM, it can smoothly describe the nonlinear relationship between DR and temperature.

2.2. Experimental data

Three published experimental data sets for different crops were used to illustrate the ability of the Beta model to describe the shape of the temperature response of crop development. The first data set gives the duration between sowing and emergence in two cassava (*Manihot esculenta* Crantz) cultivars MAus10 and MAus7 under a range of diurnally constant temperatures (Keating and Evenson, 1979). The second data set, on meristem temperature effect on the leaf development of maize (cv. 'Erliking' F1 hybrid), was published by Watts (1971). In this experiment, the temperature of the meristematic region was varied between 0 and 40°C, and the temperature of the root zone and the air around the leaves was kept at 25°C. The third data set, on the development from sowing to tassel initiation of maize, was published by Ellis et al.

Table 1
Treatments, observed days to flowering in the controlled-temperature experiment of IRRI (1977) on rice cultivar IR8, and predicted days by each of the four models: the Growing Degree Days procedure (GDD), the bilinear model (BLM), the Rice Clock Model (RCM) and the Beta model (Beta), using the parameters (presented in Fig. 5) derived from an independent experiment with five diurnally constant temperatures

Treatment No.	Temperature (°C) [a]			Observed (d)	Predicted (d)			
	Day	Night	Mean		GDD	BLM	RCM	Beta
a	24	24	24.0	98	100	100	99	99
b	26	23	24.0	84	100	100	99	99
c	28	22	24.0	112	100	100	102	102
d	30	21	24.0	118	106	100	108	108
e	32	20	24.0	130	112	112	117	117
f	36	18	24.0	> 155	125	161	162	162
g	32	18	22.7	148	125	127	137	137
h	28	18	21.3	153	125	125	138	138
i	24	18	20.0	145	143	143	157	157
j	20	18	18.7	> 155	167	167	195	195
k	24	22	22.7	106	112	112	112	112
l	24	20	21.3	129	125	125	131	131

[a] In the experiment of IRRI (1977), durations of day and night temperatures were 8 h and 16 h per day, respectively.

(1992). In this experiment, plants of five cultivars (Tuxpeno Crema I C 18, Cravinhos 8445, B73 × Mo17, H-32, and Across 8201) were grown in growth chambers with 10 diurnally constant temperatures ranging from 12 to 37°C at a photoperiod of 12 h d^{-1}.

A fourth data set was used to compare the predictive capacity of the Beta model with the RCM and two widely-used thermal time methods GDD and BLM. This data set was obtained from a phytotron experiment on the effect of temperature on days from sowing to flowering in rice (*Oryza sativa* L.) cultivar IR8 (IRRI, 1977). Treatments in the experiment included one diurnally constant temperature (24°C) and 11 diurnally alternating regimes with different day and night temperatures (Table 1). In all alternating temperature treatments, the day temperature was applied for 8 h d^{-1} and the night temperature for 16 h d^{-1}. The four models were parameterized using independent data for IR8 from an experiment conducted in 1993 with five diurnally constant temperatures 22, 24, 26, 28 and 32°C at a photoperiod of 12 h d^{-1} (Yin and Kropff, unpublished data, 1993). Days to flowering at the common constant temperature treatment of 24°C were 98 d in the IRRI (1977) experiment and 97 d in the 1993 data set, indicating that the effective photoperiod was compatible between these two experiments.

2.3. Analytical approaches

When values of T_b and T_c were given, the parameter values were determined by least squares regression after log-transforming Eq. 3 into its linear form:

$$\ln DR = \mu + \alpha \ln(T - T_b) + \beta \ln(T_c - T)$$

Otherwise the nonlinear optimization package PROC NLIN of the Statistical Analysis Systems Institute (SAS, 1988) was used to estimate parameter values when T_b and T_c were not given. The SAS procedure was also used to parameterize Eq. 1 of the RCM.

However, observations at only five temperatures in the 1993 data set for cv. IR8 of rice were not enough to estimate the six parameters in Eq. 1. Because the models were evaluated using data from phytotron experiments of IRRI (1977) where the temperatures were not close to the extremes of T_b and T_c, the model performance might not be very sensitive to the values for T_b and T_c. To reduce the number of parameters to be estimated, values for T_b and T_c were predefined for the RCM and the Beta model based on sensitivity analysis by varying T_b and T_c within an adequate range.

To compare the performance of the models in predicting rice flowering, the mean absolute deviation (MD) was used to indicate the accuracy of the predictions. All models were run with an 8-h time step to account for the difference in the duration of day and night temperatures in the data set of IRRI (1977).

3. Results

3.1. Illustration of the descriptive ability of the Beta model

Keating and Evenson (1979) showed that cassava plants of MAus10 did not emerge below 14.8°C or above 36.6°C, whereas MAus7 did not emerge below 12.5°C or above 39.8°C. From these observations, values of T_b and T_c for the two cultivars were determined. Values for the other parameters of the Beta model were estimated by least squares regression of log-transformed data (Table 2). The model described the shape of the response quite accurately, although the DR of MAus7 around T_o was somewhat underestimated (Fig. 2). The results indicate that the nonlinear response is not symmetric.

In the data of Watts (1971) on meristem temperature effect on maize leaf development, no distinct value for either T_b or T_c was determined. All five parameters of the Beta model were then obtained from the nonlinear optimization package of SAS. The model adequately described the data (Table 2 and Fig. 3). The relatively low value for T_b can be explained by the fact that the temperature of air and root-zone was kept at 25°C which may have been high enough to trigger maize leaf extension even though the meristem temperature was below 0°C. However, this estimation for T_b was based on extrapolation far beyond the range of temperatures used in the experiment, resulting in a high standard error (Table 2). Watts (1971) fitted the data between 0 and 30°C with an exponential curve using a Q_{10} of 2.0, a factor by which the rate is increased as temperature rises 10°C. That approach does not account for the rapid decline of the rate above T_o (Fig. 3).

Ellis et al. (1992) indicated that the value of T_c for maize cvs. H-32 and Across 8201 was about 37°C based on their experimental results that plants of these two cultivars grown at the constant temperature 37°C died before reaching tassel initiation whereas 37°C was not lethal to plants of other three cultivars. Based on these, the value of DR at 37°C for each of H-32 and Across 8201 was determined. The Beta model closely described the nonsymmetric temperature response for rate of development between sowing and tassel initiation in the five cultivars (Fig. 4). A clear varietal difference in

Table 2
Values of the five parameters (with standard errors in parentheses) in the Beta model (Eq. 3) estimated from different data sets, and the resultant estimates of the optimum temperature (T_o) and the maximum development rate (R_o)

Cultivar	Model Parameters					n [a]	r^2 [b]	T_o	R_o
	μ	α	β	T_b	T_c				
(a) *Cassava (sowing – emergence)* [d]									
MAus10 [c]	−6.484	1.071	0.469	14.8	36.6	7	0.997	30.0	0.0683
	(0.301)	(0.066)	(0.070)						
MAus7 [c]	−11.035	2.077	1.268	12.5	39.8	9	0.975	29.5	0.1118
	(0.813)	(0.179)	(0.159)						
(b) *Maize leaf extension* [d]									
Erliking	−9.683	2.563	0.132	−12.8	40.1	7	0.998	37.5	1.6118
	(7.100)	(1.570)	(0.163)	(14.8)	(0.01)				
(c) *Maize (sowing – tassel initiation)* [d]									
Tuxpeno Crema I C 18	−4.876	0.504	0.207	11.0	37.1	10	0.994	29.5	0.0504
	(0.288)	(0.070)	(0.043)	(0.4)	(0.07)				
Cravinhos 8445	−5.743	0.754	0.308	9.7	37.2	10	0.990	29.2	0.0573
	(0.768)	(0.189)	(0.085)	(1.4)	(0.21)				
B73×Mo17	−5.313	0.651	0.233	10.1	37.2	10	0.990	30.0	0.0546
	(0.598)	(0.148)	(0.070)	(1.1)	(0.16)				
H-32	−4.941	0.290	0.482	11.8	37.0	10	0.990	21.2	0.0518
	(0.286)	(0.058)	(0.064)	(0.2)	(0.01)				
Across 8201	−5.366	0.398	0.530	11.3	37.0	10	0.965	22.3	0.0505
	(0.726)	(0.160)	(0.137)	(0.9)	(0.02)				

[a] n is the number of environments fitted.
[b] r^2 is for least squares regression in cassava, and for the simple linear regression between values of observed and calculated by the model in maize (see text).
[c] T_b and T_c were determined as temperatures at which the cassava plants did not emerge.
[d] Data source: (a) Keating and Evenson (1979); (b) Watts (1971); (c) Ellis et al. (1992).

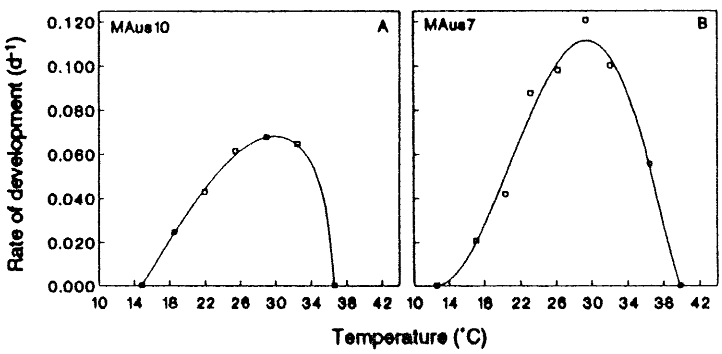

Fig. 2. Rate of development from sowing to emergence in two cassava cultivars as a function of temperature (data of Keating and Evenson, 1979). Fitted curves were derived from Eq. 3 with parameter values as in Table 2.

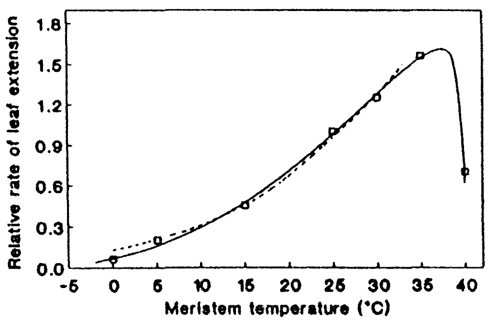

Fig. 3. Relative leaf extension rate in maize as affected by temperature at the meristem region (data of Watts, 1971). The solid curve was based on Eq. 3 with parameter values in Table 2, while the dashed one was drawn from the concept of Q_{10} of 2.0 used by Watts (1971).

the T_o was found to range from 21.2 to 30.0°C, whereas the varietal difference in either T_b or T_c was quite small (Table 2). Ellis et al. (1992) fitted the data of each cultivar by the equation $DR = a + bT + cT^2 + dT^3$ (where a, b, c and d are constants), for the sub-optimal and supra-optimal ranges separately. They indicated the problem of determining a value for T_o by visual examination of the data, as the observed T_o often did not represent a specific value or even a narrow range (e.g. Fig. 4(C)). Eq. 3 can be used to explicitly estimate T_o for each cultivar.

3.2. Comparison of the Beta model with GDD, BLM, and RCM in predictive capability

Parameters of the models

From sensitivity analysis by varying T_b from 5 to 15°C and T_c from 35 to 45°C in 1°C steps, it was established that the values of T_b and T_c had little impact on goodness of fit of both the RCM and the Beta model to the 1993 data set on the development to flowering in rice cultivar IR8. The R^2 value varied from 0.98 when $T_b = 5$ and $T_c = 35$°C to 0.97 when $T_b = 15$ and $T_c = 45$°C for both models. For each set of T_b and T_c values, the two models had the same R^2 value, indicating that one extra parameter in the RCM compared to the Beta model did not result in a higher descriptive ability. Since the R^2 value of both models hardly changed within a wide range of values for T_b and T_c, we selected 8 and 42°C as values for T_b and T_c. These values are commonly used in rice crop growth simulation models (Alocilja and Ritchie, 1991; Kropff et al., 1994).

Based on visual inspection of the data, 28°C was assumed as the upper temperature (T_u) for the GDD model above which the DR remains constant, and 32°C was assumed to be supra-optimal for the BLM model. Parameters for the range with the increasing DR in both GDD and BLM were then estimated by linear regression on the observations at 22, 24, 26 and 28°C. For the supra-optimal range of the BLM, parameter values were estimated assuming that $T_c = 42$°C.

The parameter values for the four models, including the maximum DR (R_o) estimated by each model, are given in Fig. 5. All models described the data quite

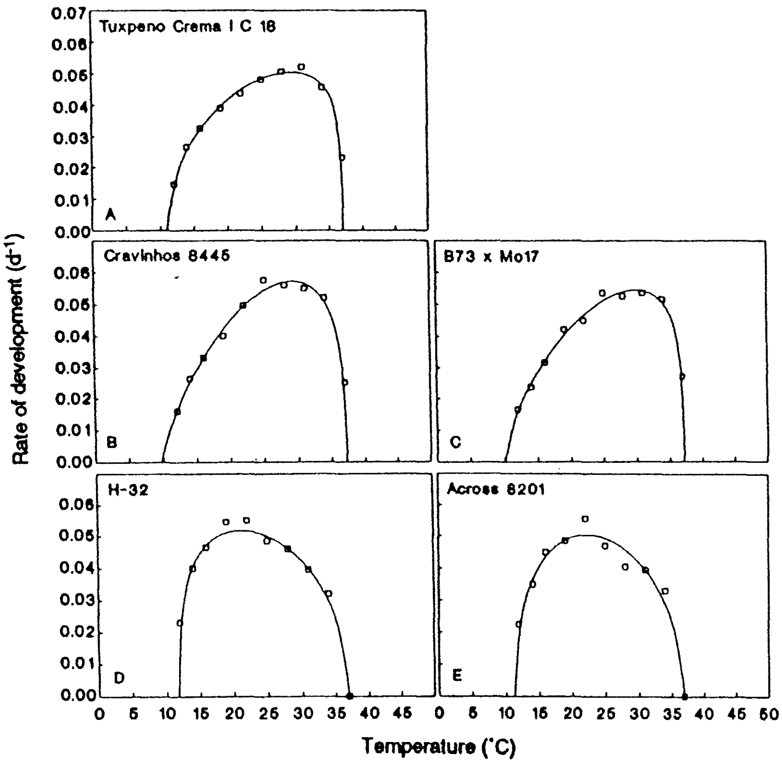

Fig. 4. Relations between temperature and the rate of development from sowing to tassel initiation in five maize cultivars at a photoperiod of 12 h d^{-1} (data of Ellis et al., 1992). The curves represent the relations of Eq. 3 with parameters shown in Table 2.

accurately. The estimated maximum DR was highest in the BLM and lowest in the GDD model. The temperature for the maximum DR calculated from Eq. 1 of the RCM was 30.2°C, only 0.8°C higher than the generated value of T_0; so the discontinuous part of the RCM given by Eq. 2 is not obvious in Fig. 5(C).

Performance of the models

Observed and predicted days to flowering are given in Table 1. The predicted days to flowering were exactly the same for the RCM and the Beta model. The comparisons between observed and predicted days to flowering for the four models are shown in Fig. 6. This figure does not include results of the regimes 36/18 and 20/18°C, at which observed days to flowering were recorded as > 155 d. The nonlinear models performed better than the linear ones. The MD values were 12.3 d for the GDD, 12.7 d for the BLM and 9.4 d for the two nonlinear models (Fig. 6).

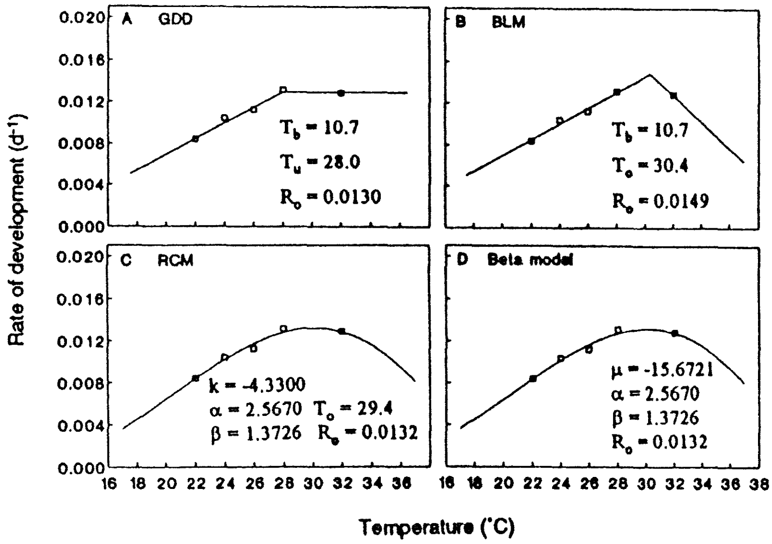

Fig. 5. Rate of development from sowing to flowering of rice (cv. IR8) at five diurnally constant temperatures (Yin and Kropff, unpublished data, 1993), fitted respectively by the Growing Degree Days procedure (GDD), the bilinear model (BLM), the Rice Clock Model (RCM), and the Beta model. Values for T_b and T_c used in both RCM and the Beta model were 8 and 42°C, respectively.

All models correctly predicted no flowering at 155 days for the regime of 20/18°C. However, the GDD model, which does not allow for the detrimental effect of high temperatures, overestimated the development rate at 36/18°C (Table 1). Because the

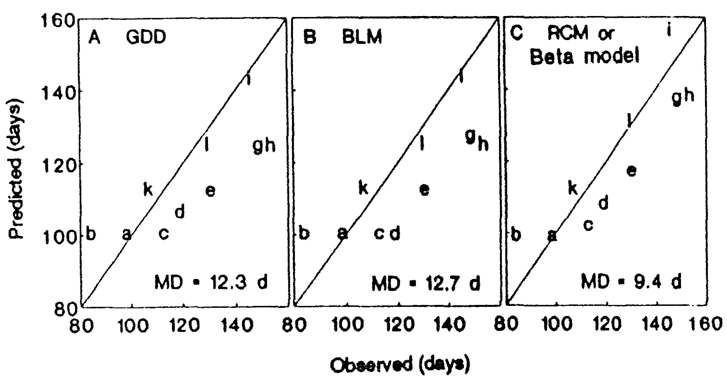

Fig. 6. Observed vs. predicted days from sowing to flowering of rice (cv. IR8) (data of IRRI, 1977) for the four models. The predicted values were based on the parameters derived from an independent experiment with five diurnally constant temperatures (presented in Fig. 5). The letters correspond to the treatment numbers specified in Table 1. The solid line represents the 1:1 ratio. MD is the mean absolute derivation of predictions from the observed days.

DR was assumed to be constant for $T > T_u$, the GDD model also failed to predict the actual difference in the flowering date among 28/18, 32/18 and 36/18°C treatments. However, the MD value for the GDD model was somewhat lower than that for the BLM (Fig. 6). This was because the BLM tended to overestimate the DR at temperatures close to T_o (Fig. 5), so the BLM underestimated days to flowering at 30/21°C (Table 1).

The superiority of the nonlinear models was particularly obvious for the 28/22, 30/21, 32/20, 32/18 and 28/18°C treatments, where the night temperature was relatively low. For these regimes, days to flowering were considerably underestimated by the linear models. This can be attributed to the fact that development rates at temperatures < 22°C were somewhat higher for the linear models than the nonlinear ones (Fig. 5).

A clear problem with the linear models is their inability to predict the observed difference in the flowering date between the treatments with the same average daily temperature of 24°C but with different diurnal amplitudes. The GDD model had the same prediction for these treatments where the day temperature was lower than T_u, while the BLM had the same prediction for those where the day temperature was sub-optimal (Table 1). Actual difference in the flowering date among these treatments was predicted by the two nonlinear models to some extent. A similar result also occurred for the comparison between 28/18 and 24/20°C, which had the same mean daily value as 21.3°C.

4. Discussion

4.1. Model performance

The thermal time approaches are often used to describe the effect of temperature on crop development, because the relationship between development and temperature becomes linear over a wide range of temperatures once the rate (inverse of the duration) is used (Roberts and Summerfield, 1987). However, evidence from several experiments showed that the rate also responds to temperature in a nonlinear way (e.g. Fig. 4). The two widely used thermal time methods GDD and BLM did not predict rice flowering dates as accurately as the two nonlinear models (Table 1 and Fig. 6). Hodges (1991) emphasized that a linear equation has to be reparameterized for applications outside the range of conditions for which the parameters were derived. However, this may result in different estimates of T_b for the same cultivar. For example, based on a linear function, Summerfield et al. (1992) reported that T_b for the development to panicle emergence in rice cultivar IR36 was 10.9°C, whereas Ellis et al. (1993) reported a T_b of 8.6°C for this cultivar. This is most probably due to the fact that temperatures used by Summerfield et al. (1992) included lower regimes than those used by Ellis et al. (1993).

4.2. Relationships between the Beta model and the RCM

Several nonlinear models have been developed to quantify the response of crop development to temperature (Robertson, 1968; Coligado and Brown, 1975; Angus et al., 1981; Horie and Nakagawa, 1990; Gao et al., 1992). The RCM (Gao et al., 1992) shows some advantages over others, since it is flexible enough to handle nonsymmetric responses. However, the basic equation of the RCM, Eq. 1, does not necessarily predict a maximum DR at the predetermined T_o (Fig. 1). Gao et al. (1992) attempted to overcome this problem by adding the restriction of Eq. 2, which, however, can make the RCM take a discontinuous form. By setting the first-order derivative of Eq. 1 equal to zero:

$$\mathrm{DR}' = \exp(k)\left(\frac{T-T_b}{T_o-T_b}\right)^{\alpha}\left(\frac{T_c-T}{T_c-T_o}\right)^{\beta}\left(\frac{\alpha}{T-T_b}-\frac{\beta}{T_c-T}\right)=0 \qquad (7)$$

an expression for calculating T_o in the unconstrained RCM is derived; and this expression is the same as Eq. 5. Substituting this expression for T_o into Eq. 1 leads to a form of the Beta model similar to Eq. 1, but equivalent to Eq. 3:

$$\mathrm{DR} = \exp(k^*)\left(\frac{T-T_b}{T_c-T_b}\right)^{\alpha}\left(\frac{T_c-T}{T_c-T_b}\right)^{\beta} \qquad (8a)$$

where $k^* = k + \alpha\ln((\alpha+\beta)/\alpha) + \beta\ln((\alpha+\beta)/\beta)$. The form of the Beta model given in Eq. 3 results from placing the terms in $(T_c - T_b)$ of Eq. 8 in the constant, μ, so that $\mu = k^* - (\alpha+\beta)\ln(T_c - T_b)$. On the other hand, substituting expressions for α or β from Eq. 5 into Eq. 1 produces the Beta model in two other forms [1]:

$$\mathrm{DR} = \exp(k)\left[\left(\frac{T-T_b}{T_o-T_b}\right)^{\frac{T_o-T_b}{T_c-T_o}}\left(\frac{T_c-T}{T_c-T_o}\right)\right]^{\beta} \qquad (8b)$$

and

$$\mathrm{DR} = \exp(k)\left[\left(\frac{T-T_b}{T_o-T_b}\right)\left(\frac{T_c-T}{T_c-T_o}\right)^{\frac{T_c-T_o}{T_o-T_b}}\right]^{\alpha} \qquad (8c)$$

Clearly, T_o, or α, or β in Eq. 1 of the RCM is superfluous; dropping one of them results in the Beta model. The RCM gives similar or identical estimates of DR to the Beta model when the difference between predetermined T_o and the calculated T_o from the constraint of Eq. 7 is small Table 1). However, this difference can be large in which case the Beta model will give a more reliable description than the RCM.

4.3. Flexibility of the Beta model

Although the Beta model has one parameter less than Eq. 1 of the RCM, it has the same property as Eq. 1, that is, both low and high temperature effects have been

[1] **Note added in proof.** The equations for development rate presented here assume a unit for development rate. To make the unit explicit it is better to replace the factor exp(k) in Eq. 8b or Eq. 8c by the factor R_0, which stands for the rate at optimum temperature, T_0. This rate is not dimensionless and could be expressed as development units per day, or in another case as mm per day. Future users should be aware of this implied unit.

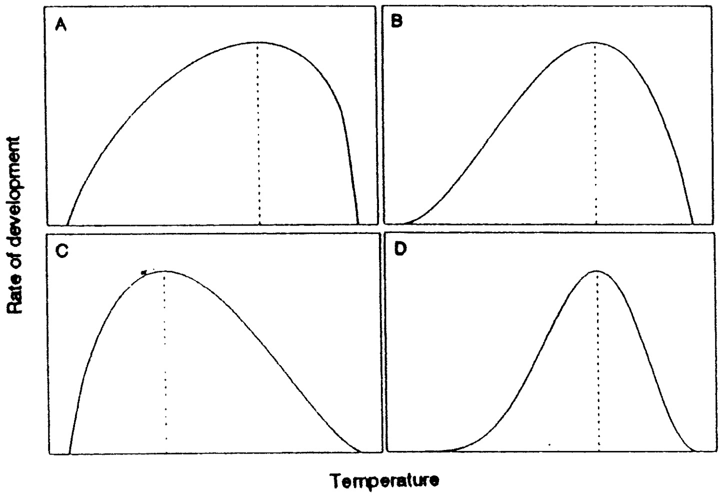

Fig. 7. Four theoretical nonsymmetric forms of the nonlinear curve for the temperature response of development rate as determined by parameters α and β in the Beta model: (A) $\alpha < 1$ and $\beta < 1$, no inflexion within both sub-optimal and supra-optimal ranges; (B) $\alpha > 1$ but $\beta < 1$, an inflexion with the sub-optimal range but no inflexion within the supra-optimal range; (C) $\alpha < 1$ but $\beta > 1$, no inflexion with the sub-optimal range but an inflexion within the supra-optimal range; (D) $\alpha > 1$ and $b > 1$, an inflexion within each of sub-optimal and supra-optimal ranges.

considered in a single equation, and the nonsymmetric response can be flexibly handled (Figs. 2-4). The flexibility of the Beta model is illustrated by the fact that the model can describe any inflexion of response in the sub-optimal or supra-optimal range. The temperatures at which the inflexion occurs can be calculated as the values at which the second-order derivative equals zero. These values can be derived as:

$$T_{f1} = \frac{\alpha T_c + \beta T_b}{\alpha + \beta} - \frac{T_c - T_b}{\alpha + \beta}\sqrt{\frac{\alpha\beta}{\alpha + \beta - 1}} \quad (9a)$$

$$T_{f2} = \frac{\alpha T_c + \beta T_b}{\alpha + \beta} + \frac{T_c - T_b}{\alpha + \beta}\sqrt{\frac{\alpha\beta}{\alpha + \beta - 1}} \quad (9b)$$

where T_{f1} and T_{f2} represent the temperatures of the inflexion points located respectively at the sub-optimal and supra-optimal range. Eq. 9 showed that $T_{f1} = T_b$ if $\alpha = 1$, whereas Eq. 9 shows that $T_{f2} = T_c$ if $\beta = 1$. It can be further analyzed that an inflexion occurs in the sub-optimal range only if $\alpha > 1$ (Fig. 2(B), Fig. 3), and an inflexion occurs in the supra-optimal range only if $\beta > 1$ (Fig. 2(B)). Parameter α, therefore, determines the curvature of the relationship over the sub-optimal range, whereas parameter β determines the curvature in the DR at supra-optimal temperatures. Different combinations of values for parameters α and β make the model flexible to fit four possible nonsymmetric forms of the relationship between the DR and temperature (Fig. 7).

In addition, some of the existing models can be generated from the Beta model. For example, the Beta model becomes a simple linear thermal time model if $\alpha = 1$ and $\beta = 0$, a power-law model if $\beta = 0$, a quadratic model if $\alpha = \beta = 1$, or a general symmetric model if $\alpha = \beta$.

4.4. Application of the Beta model and the need for further studies

Although the Beta model was introduced to describe the temperature response of crop development, it may apply to other biological processes. For example, according to the data of Tanaka (1976), effects of temperature on rice photosynthesis rate can be described by it. Many thermal response patterns, as presented by Ferguson (1958), Orchard (1975), Tyldesley (1978), and Johnson and Thornley (1985), coincide with the different forms of the model shown by Fig. 7. The model can be easily parameterized since it can be linearized if values of T_b and T_c are predetermined from the data or external sources.

For application to crop development processes, this study indicates that the model describes the response to constant temperatures quite well (Figs. 2–4). For the response to alternating temperatures, however, the mean deviation between observed and predicted days to flowering in rice was about 9 d (Fig. 6). In the present study, no difference in the effect of day and night temperature on crop development was assumed. With the data on IR8 rice (Table 1), however, IRRI (1977) indicated independent effects of day and night temperatures and a relatively more important role of night temperature than the day value. But this conclusion was made based on a linear model which did not realistically describe DR-temperature relationship. The greater influence of night temperature can be due to the fact that in the experiment of IRRI (1977), night temperature was in the range where DR increases proportionally with the temperature whereas day temperature was often supra-optimal (Table 1). Nevertheless, Coligado and Brown (1975) indicated an effect of diurnal temperature range on the development in maize. As the Beta model tends to have a larger discrepancy for the treatments with a higher diurnal amplitude (Table 1), the approach might be improved by accounting for the effect of the diurnal temperature range. This gives an element that needs further study.

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