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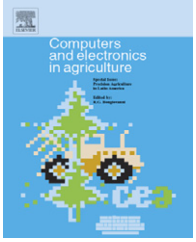

Simulating winter wheat development response to temperature: Modifying Malo's exponential sine equation

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ABSTRACT

Predicting crop developmental events is fundamental to simulation models and crop management decisions. Many approaches to predict developmental events have been developed, however, most only simulate the mean time for reaching a developmental event. An exponential sine equation developed by Malo [Malo, J.E., 2002. Modelling unimodal flowering phenology with exponential sine equation. Funct. Ecol. 16, 413–418] to predict flower number over time was modified to incorporate the response of crop development rate to temperature. The revised model (ExpSine model) uses the base, optimum, and maximum cardinal temperatures specific to a crop or genotype. Most model parameters were estimated from the literature, and four of the five model parameters have physiological significance. Model evaluation for winter wheat (*Triticum aestivum* L.) was based on two controlled environment studies from the literature and two field experiments conducted in the North China Plain (NCP) and the Tibet Plateau (TPC). The r^2 for the modified temperature response function was 0.74 and 0.91 for two different experiments and compared very well (identical mean r^2's) to an existing function (Beta model) [Yin, X., Kropff, M.J., McLaren, G., Visperas, R.M., 1995. A nonlinear model for crop development rate as a function of temperature. Agric. Forest Meteorol. 77, 1–16]. Differences between observed and predicted flowering dates ranged from −2 to 3 days in the NCP and from −7 to 4 days on the TPC, with the mean percent error in both sites less than 1% and no apparent bias observed in the model. This modification of Malo's exponential sine equation expanded the predictive ability of the original equation to simulate phenology across a broader range of environments. The ExpSine model developed can be used as a phenological module in various crop or ecological simulation models.

1. Introduction

Understanding and predicting crop development has a long history of research, spurred in part as a fundamental process of simulation models and increasingly becoming important in improving the efficacy of crop management decisions. Predicting wheat development almost ubiquitously focuses on the dominant role of temperature (McMaster, 2005).

Many temperature response functions, which describe the rate of development with temperature, have been devel-

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oped. These temperature response functions can be linear (McMaster et al., 1992; Russelle et al., 1984), bilinear (e.g., Olsen et al., 1993), multilinear (Coelho and Dale, 1980; Hunt and Pararajasingham, 1995; Jamieson et al., 1998a,b; Porter, 1984, 1993), diverse curvilinear functions such as polynomial function (Streck et al., 2003; Tollenaar et al., 1979; Yan and Wallace, 1996), power-law function (Coligado and Brown, 1975), exponential function (Angus et al., 1981), the logistic model (Horie and Nakagawa, 1990), the Rice Clock Model (RCM, Gao et al., 1992), and the Beta model (Yin et al., 1995; Yan and Hunt, 1999). These models generally are quite accurate in their phenological predictions, but models such as the Beta model most accurately incorporate the observed development rate response to temperature (McMaster, 2005) and the majority of its parameters have physiological significance.

All the above models predict the mean date that main stems, or all shoots or plants, reach a developmental event. Malo (2002) proposed an exponential sine equation to model plant flowering phenology. This equation is of note in that the number of flowers produced over time is predicted. Therefore, more aspects of a developmental event are able to be analyzed than in the above models such as the beginning and ending dates, the date and value of the peak, and the skewness/shape of the curve. However, the equation does not directly consider the response of crop development to temperature, thereby not utilizing the extensive knowledge available and included in the crop models mentioned above. In this paper, Malo's model is modified to include the development response to temperature. Winter wheat was used to evaluate this modification. Controlled environment data were used to evaluate the development rate response to temperature and field data are used to test the date of flowering.

2. Materials and methods

2.1. *Evaluation data sets*

A combination of field and controlled environment data sets were used to evaluate the ExpSine model. Two sets of published controlled experimental data were used to demonstrate the ability of the ExpSine model to describe the response curve of crop development rate to temperature.

(1) Leaf appearance rates of four soft-white winter wheat cultivars (Nugaines, Stephens, Tres, and Yamhill) were measured under constant day/night temperatures in growth chambers (Cao and Moss, 1989). Temperature treatments ranged from 7.5 to 25 °C with increments of 2.5 °C under a 14 h photoperiod. Extrapolating from their data, base temperature was estimated to be 0.02 °C, which agreed well with other published values of 0 °C (e.g., McMaster and Smika, 1988).
(2) Terminal spikelet initiation of four wheat cultivars (Cappelle Desprez, Condor, Rosella, and Sunset) was measured in phytotrons after a 50-day vernalization pre-treatment (Slafer and Rawson, 1994). Six constant temperatures from 13 to 25 °C by 3 °C increments were maintained throughout the study, and photoperiod (both natural and incandescent lamps) was set to a constant 18 h photoperiod.

Field data were collected at two locations to evaluate the ExpSine model prediction of flowering. Winter wheat phenological data were collected at the Lhasa Agro-Meteorological Station, affiliated with the China Meteorological Administration, from 1992 to 2004 (experiment is denoted as TPC) and Yucheng Integrated Experiment Station of the Chinese Academy of Sciences from 1996 to 2004 (experiment is denoted as NCP). The same wheat cultivar (Gaoyou 503 in the NCP and Bussyd on the TPC) was planted each year for the duration of the experiment. General management practices including fertilizer applications and weed control followed recommended practices and irrigation was applied when soil water content was less than 65% of field capacity.

The Lhasa Agro-meteorological Station (29°41′N, 91°20′E, altitude 3688 m) is located on the Tibet Plateau, and is characterized by low temperatures, and annual mean temperature is 8.0 °C in nearby Lhasa city. On the Tibet Plateau, winter wheat has a long vegetative growth period (from sowing to anthesis), generally 250 days (typical planting date is around 10 October and anthesis date is usually about 20 June). The Yucheng Integrated Experiment Station (36°57′N, 116°36′E, altitude 28 m) is located in the North China Plain. The annual mean temperature is 13.1 °C and the time from sowing (typically about 25 October) to anthesis (typically about 3 May) is normally about 190 days.

At each site, plants were observed three to five times a week for the date that 50% of the plants reached emergence, heading and anthesis. Daily mean air temperature data (average of daily maximum and minimum temperature) in the Lhasa Agro-meteorological Station (located on the experimental site) were provided by the National Meteorological Center of Chinese Meteorology Administration, and the daily mean air temperature data (average of daily maximum and minimum temperature) in the Yucheng Integrated Experiment Station were collected by a weather station located on-site.

2.2. *The model*

Malo (2002) proposed an exponential sine equation for describing plant flowering phenology over time:

$$f(t) = a\left\{\sin\left[\pi\left(\frac{t}{c}\right)^{d}\right]\right\}^{e} \qquad (1)$$

Eq. (1) produces a curve along the *x*-axis (time/date) with the maximum determined by *a*, its length by *c*, asymmetry by *d*, the length of the tails by *e*, and the date of the phenological peak [i.e., when *f*(*t*) is maximized]. Standard errors of the parameters can be calculated, and statistical analysis comparing the parameters for different populations, treatments, etc. can be performed.

Malo's exponential sine equation fits phenological patterns to experimental data and then allows for parameter evaluation. However, it does not consider that the observed phenological patterns likely vary with temperature, which significantly alters development rate. To include the relationship between temperature and development rate, Eq. (1) was modified to:

$$R = R_o\left\{\sin\left[\pi\left(\frac{T-T_b}{T_m-T_b}\right)^{\alpha}\right]\right\}^{\beta} \tag{2}$$

where R is development rate, T is daily average temperature (°C), and T_b and T_m are base and maximum temperature for crop development (°C), respectively. R_o is the crop development rate at optimal temperature (day^{-1}), and α and β are model parameters. Comparing Eqs. (1) and (2), the modified (ExpSine) model replaced the original model's $f(t)$ by R, t by $T - T_b$, and c by $T_m - T_b$.

The optimal temperature for crop development (T_o) can be derived by setting the first-order derivative of Eq. (2) to zero:

$$T_o = T_b + \left(\frac{1}{2}\right)^{1/\alpha}(T_m - T_b) \tag{3}$$

and rearranging for α:

$$\alpha = \log^{2}_{\frac{T_m-T_b}{T_o-T_b}} \tag{4}$$

which can be substituted for α into Eq. (2) resulting in the following form:

$$R = R_o\left\{\sin\left[\pi\left(\frac{T-T_b}{T_m-T_b}\right)^{\log^{2}_{\frac{T_m-T_b}{T_o-T_b}}}\right]\right\}^{\beta} \tag{5}$$

The revised equation (Eq. (5)) only includes one empirical parameter, β; the other four parameters have clear physiological significance and are more readily determined. T_o is one of three cardinal temperatures (along with T_b and T_m) and has been well studied for many crops and cultivars. Usually these cardinal temperatures are considered constant for a specific crop cultivar.

The developmental sequence from emergence to the stage was set to a 0–1 scale, where 0 is emergence stage, and 1.0 is the development stage, such as flowering. This scale setting has also been used in other studies (Penning de Vries et al., 1989; Wang and Engel, 1998). If the development rate (R) is determined (Eq. (5)), development stage (D_{vs}) can be calculated according to the following relationship:

$$D_{vs} = \sum_{i=1}^{n} R \tag{6}$$

where n is the number of days for a crop to complete a specific developmental stage. Since the value of R is not readily measured and the number of development-days is easier to measure, R is usually converted to development-days in Eq. (5). When D_{vs} value reaches 1, the crop will have reached the developmental stage (anthesis), and the number of development-days (n) can be inversely obtained from Eq. (6). The modeled n was used to compare to observed days from emergence to anthesis in field experiments in both NCP and TPC.

2.3. *Determining model parameters*

Most model parameters were derived from the literature. Extensive literature exists for the cardinal temperatures of base, optimal and ceiling temperatures for a wide range of genotypes (e.g., Groot, 1987; McMaster and Smika, 1988; Porter and Gawith, 1999; Van Keulen and Seligman, 1987). Although genotypes may differ slightly in their cardinal temperatures, generally the error in determining these cardinal temperatures and range of optimal temperatures for a genotype suggest that one value can be used for all genotypes as a simplifying assumption. Values in the model can easily be changed if specific knowledge exists. Therefore the values of T_b, T_o and T_m are set to 0, 24 and 35 °C, respectively, for both controlled environment experiments (i.e., Cao and Moss, 1989; Slafer and Rawson, 1994) and both field experiments (i.e., NCP and PTC) in this paper. These values are also typically used in many winter wheat phenological simulation models (e.g., SHOOTGRO, McMaster et al., 1992; CropSim/CERES-Wheat, Hunt and Pararajasingham, 1995; Wang and Engel, 1998).

The maximum development rate (R_o) and β parameters were different for controlled environmental experiments and field experiments because different phenological events were involved in each experiment. For controlled environmental experiments, R_o and β were derived by fitting the controlled environment data using Eq. (5). For field experiments (i.e., NCP and TPC), the value for maximum development rate (R_o) of winter wheat in the vegetative stage (from sowing to anthesis) was set to a mean value of 0.015 day^{-1} (Penning de Vries et al., 1989), and the values for parameter β in each site (NCP or TPC) were determined by fitting the first 4 years of field experiment data for a site (1992–1995 in the NCP and 1996–1999 on the TPC) using OriginPro 7.0 software (OriginLab Corporation, USA, 2002) by least squares estimation. This resulted in values for β in TPC and NCP as 1.218 and 0.897, respectively.

2.4. *Statistical analysis*

The performance of the ExpSine model in the two controlled environment experiments was compared with the Beta model (Yin et al., 1995) by calculating the correlation coefficient (r^2) and standard error of estimated parameters. For the two field experiments, Eq. (5) was evaluated for anthesis (i.e., flowering) by calculating the error (difference of the simulated and observed value) and percent error (absolute value of error/observed day).

3. Results

3.1. *Evaluation of development rate and temperature function*

For the purpose of comparison, the Beta model (Yin et al., 1995) was contrasted with the ExpSine model using our data. The base (T_b), optimal (T_o), and maximal (T_m) temperatures of winter wheat were set to 0, 24 and 35 °C in both models. For both models, estimates for crop development rate at T_o (R_o) and parameter β were obtained by fitting to the data. For the ExpSine model, the adjusted correlation coefficient (r^2) for R_o

Table 1 – Comparison between the ExpSine model and Beta (Yin et al., 1995) models in the estimated maximal development rate (R_o) and β parameter values for the data of Cao and Moss (1989)

Wheat genotype	ExpSine model			n_0	Beta model		
	R_o (day^{-1})	β	r^2		R_o (day^{-1})	β	r^2
Yamhill	0.080 (0.007)	0.401 (0.201)	0.55	8	0.080 (0.007)	0.996 (0.474)	0.57
Stephens	0.067 (0.005)	0.406 (0.163)	0.65	8	0.067 (0.005)	0.972 (0.385)	0.66
Nugaines	0.061 (0.003)	0.517 (0.109)	0.87	8	0.060 (0.003)	1.231 (0.264)	0.87
Tres	0.043 (0.001)	0.421 (0.083)	0.88	8	0.043 (0.002)	0.995 (0.206)	0.87
Mean	0.063 (0.004)	0.436 (0.139)	0.74		0.063 (0.004)	1.049 (0.332)	0.74

Standard errors are in parentheses. n_0 is the number of data points.

Table 2 – Comparison between the ExpSine model and Beta (Yin et al., 1995) models in the estimated maximal development rate (R_o) and β parameter values for the data of Slafer and Rawson (1994)

Wheat genotype	ExpSine model			n_0	Beta model		
	R_o (day^{-1})	β	r^2		R_o (day^{-1})	β	r^2
Sunset	0.198 (0.004)	0.204 (0.028)	0.91	6	0.197 (0.003)	0.474 (0.592)	0.92
Cordor	0.198 (0.004)	0.245 (0.030)	0.93	6	0.197 (0.003)	0.570 (0.063)	0.94
Rosella	0.224 (0.003)	0.339 (0.022)	0.98	6	0.223 (0.003)	0.788 (0.044)	0.98
Cappelle Dusprez	0.230 (0.014)	0.462 (0.109)	0.80	6	0.229 (0.014)	1.068 (0.260)	0.79
Mean	0.213 (0.006)	0.313 (0.047)	0.91		0.212 (0.006)	0.725 (0.240)	0.91

Standard errors are in parentheses. n_0 is the number of data points.

ranged from 0.55 to 0.88 for the data of Cao and Moss (1989) (Table 1) and 0.80 to 0.98 for the data of Slafer and Rawson (1994) (Table 2). Similar results were found for the Beta model, with r^2 ranging from 0.57 to 0.87 for Cao and Moss (1989) (Table 1) and 0.79 to 0.98 for Slafer and Rawson (1994) (Table 2). The mean values of r^2 were identical between the ExpSine and Beta models: 0.91 and 0.74 for the data of Slafer and Rawson (1994) and Cao and Moss (1989), respectively. Estimated genotype values of R_o for the ExpSine model differed considerably between the two experiments and ranged from 0.043 to 0.080 for the data of Cao and Moss (1989) (Table 1) and from 0.198 to 0.230 for the data of Slafer and Rawson (1994) (Table 2). Nearly

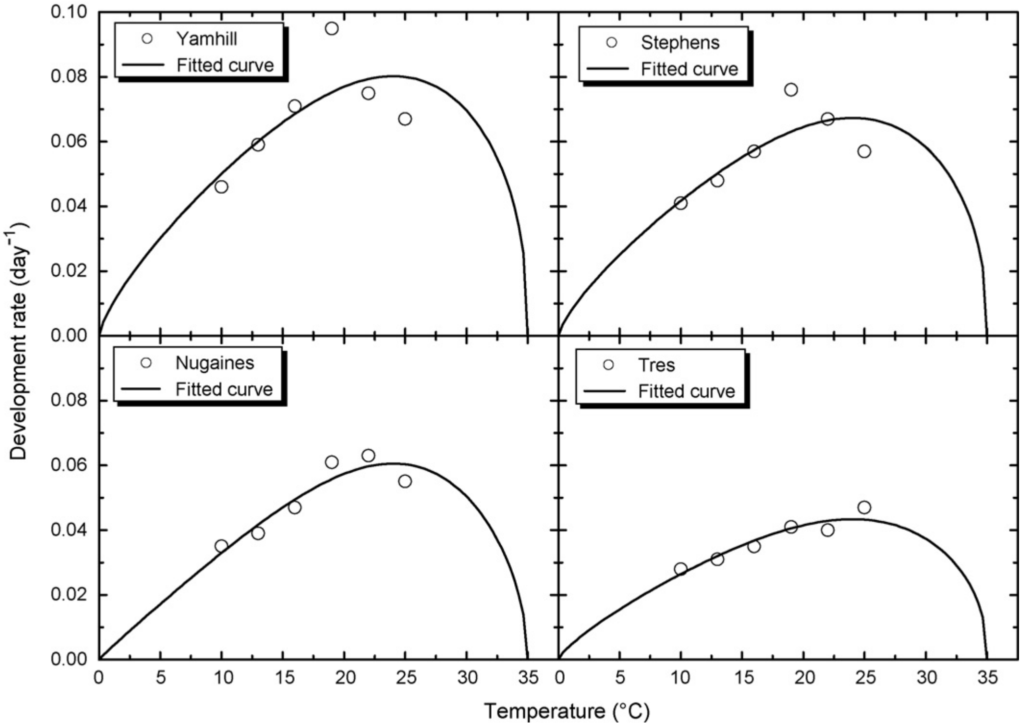

Fig. 1 – Relationship between temperature and the rate of development (*R*) towards terminal spikelet initiation (data of Cao and Moss, 1989). Fitted curves were derived from Eq. (5) with parameter values presented in Table 1.

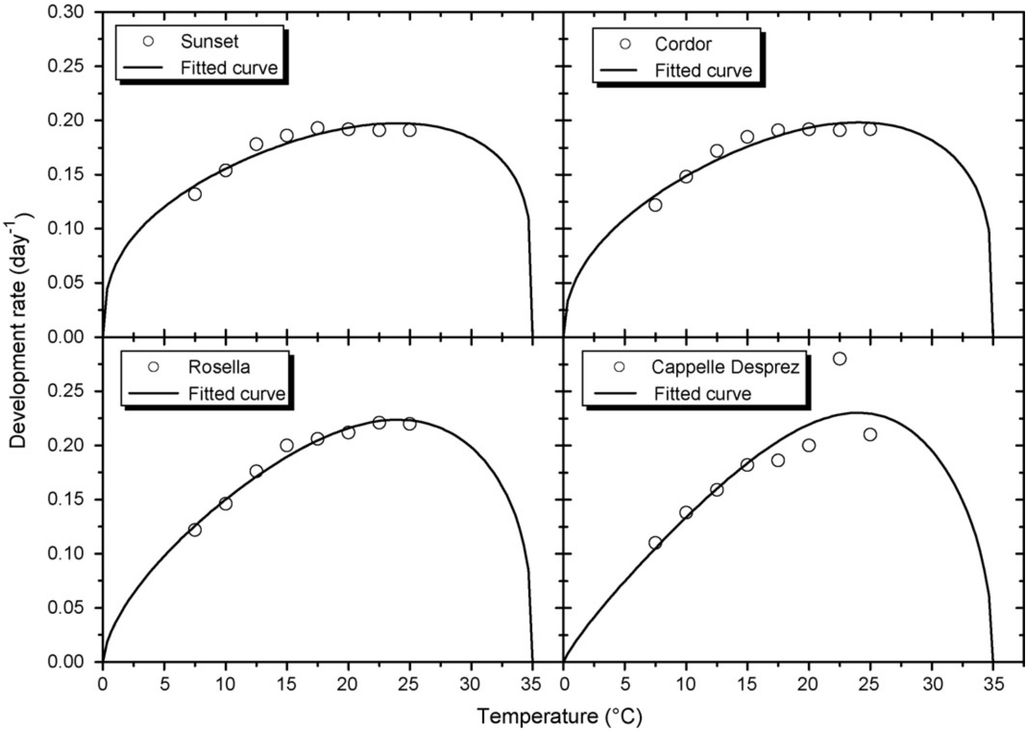

Fig. 2 – Relationship between temperature and the rate of development (*R*) towards terminal spikelet initiation (data of Slafer and Rawson, 1994). Fitted curves were derived from Eq. (5) with parameter values presented in Table 2.

identical genotype values of R_o and r^2 were observed for the Beta model.

Estimates for the β parameter differed significantly between the ExpSine and Beta models. The ExpSine model estimated β values ranging from 0.401 to 0.507, and standard errors ranging from 0.109 to 0.201 for the data of Cao and Moss (1989), and estimated β values ranging from 0.204 to 0.462, and standard errors ranging from 0.022 to 0.109 for the data of Slafer and Rawson (1994). However, the Beta model estimated much higher β values ranging from 0.972 to 1.231, and standard errors ranging from 0.206 to 0.474 for the data of Cao and Moss (1989), and estimated β values ranging from 0.474 to 1.068, and standard errors ranging from 0.260 to 0.592 for the data of Slafer and Rawson (1994). The results also indicate that the β values in both the ExpSine and the Beta models varied among wheat cultivars. However, the ExpSine model gave smaller standard errors than the Beta model (mean values of 0.139 vs. 0.332 for the data of Cao and Moss, 0.047 vs. 0.240 for the data of Slafer and Rawson, Tables 1 and 2).

Figs. 1 and 2 show the developmental rate calculated by the ExpSine model with temperature for the data of Cao and Moss (1989) and Slafer and Rawson (1994), respectively. When T_b and T_m were set to 0 and 35 °C, respectively, this determined the minimum and maximum temperatures when the development rate dropped to zero. The optimal temperature (T_o, set to 25 °C) corresponds to the maximum developmental rate (R_o) that varied with cultivar (Tables 1 and 2). Differences in R_o and β for different cultivars resulted in different fitted curves to the data shown in Figs. 1 and 2. The asymmetry of the fitted development rate-temperature curve is determined by the value of α (a logarithmic function of T_b, T_o, and T_m, Eq. (4)). The same asymmetry for all cultivars was due to using the same values of T_b, T_o, and T_m for all cultivars. Values of β determine the length of the tails of the fitted curves. Therefore, cultivars with larger values of β (Tables 1 and 2) showed longer tails.

3.2. *Evaluation of predicting flowering dates*

Field data measuring flowering at two locations were used to evaluate the ExpSine model in predicting flowering phenology. The relative development rate (R/R_o, Eq. (5)) is the relationship between the development rate at a temperature and the maximum development rate at the optimal temperature (T_o). The relative development rate at a given temperature was determined for both the North China Plain (NCP) and Tibet Plateau (TPC) using first 4 years of data for each site (Fig. 3). The relative development rate for the TPC site was lower than the NCP site, except for the three cardinal temperatures (T_b, T_o, T_m) which is expected since the cardinal temperatures were the same for both sites.

The observed and predicted days from emergence to anthesis were used to evaluate the ExpSine model predictions of flowering date (Eq. (5)). The error of predicted dates from the observed varied from −2 to 3 days (mean = 0 days) in the NCP site and from −7 to 4 days (mean = 1.0 days) in the TPC site (Tables 3 and 4). This corresponded to an absolute percent error ranging from 0.5 to 1.6% (mean = 0.0%) in the NCP and 0.4 to 3.1% (mean = 0.4%) in the TPC. While the prediction error was slightly greater for the TPC site, the prediction of flowering dates using the ExpSine model was quite low (3.1% was the maximum absolute percent error for 12 years) and little bias in prediction was observed.

Table 3 – Simulated and observed days from emergence to anthesis for winter wheat in the North China Plain (NCP experiment)

Year	Observed (day)	Simulated (day)	Error[a] (day)	Percent error[b] (%)
2000–2001	193	191	−2	1.0
2001–2002	190	191	+1	0.5
2002–2003	197	195	−2	1.0
2003–2004	182	185	+3	1.6
Mean	190.5	190.5	0	0

[a] Error = simulated days − observed days.
[b] Percent error = (absolute value of error)/observed days.

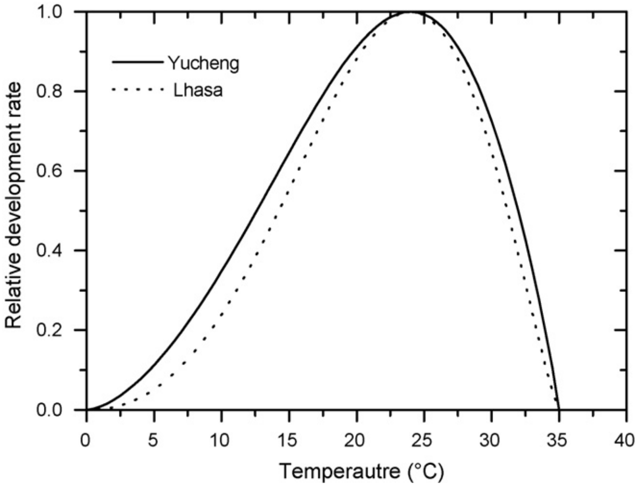

Fig. 3 – Response curves of relative development rate (R/R_o) to temperature in the NCP and TPC field experiments. Values of T_b, T_o, T_c were fixed at 0, 24 and 35 °C, respectively. Values of β in the NCP and TPC experiments were 0.897 and 1.218, respectively. Fitted curves were based on the first 4 years of observed.

4. Discussion

The exponential sine function proposed by Malo (2002) was modified to characterize the relationship between the development rate of a plant and temperature. We found that the ExpSine model well characterized the relationship between the development rate of a plant and temperature under both controlled environments and field grown conditions.

The ExpSine model is based on three cardinal temperatures (base, optimum, and maximum) to describe the response of crop development rate to temperature, yet retains all advantages of the exponential sine function explored by Malo (2002). Modifying the development rate of the plant by the temperature has marked and direct advantages. For example, the curvature of the plant development rate to temperature response function is determined by the value of the α and T_o parameters, and the sensitivity of the development rate to temperature is indicated by the value of the β parameter. Other parameters, T_b, T_c and R_o (i.e., maximum development rate at optimum temperature) have obvious physiological significance. The ExpSine model prediction errors range from −2 to 3 days in the NCP and from −7 to 4 days on the TPC, with the mean percent error in both sites less than 1% and no apparent bias observed in the model. This predictive accuracy compares extremely well to existing models (e.g., AFRCWHEAT2, Ewert et al., 1996; Sirius, Jamieson et al., 1998b; SHOOTGRO, Zalud et al., 2003; CropSim/CERES-Wheat, unpublished data of McMaster, 2008).

Although the ExpSine model is robust and flexible in simulating crop development, it did not consider the effects of other factors that can influence some winter wheat phenological events such as photoperiod, vernalization, and water deficits. In addition, while the three cardinal temperatures were the same for all genotypes in this paper and derived from the liter-

Table 4 – Simulated and observed days from emergence to anthesis for winter wheat on the Tibet Plateau (TPC experiment)

Year	Observed (day)	Simulated (day)	Error[a] (day)	Percent error[b] (%)
1996–1997	243	242	−1	0.4
1997–1998	234	235	+1	0.4
1998–1999	226	219	−7	3.1
1999–2000	231	235	+4	1.7
2000–2001	231	232	+1	0.4
2001–2002	238	233	−5	2.1
2002–2003	239	236	−3	1.3
2003–2004	230	232	+2	0.8
Mean	234.0	233.0	−1	0.4

[a] Error = simulated days − observed days.
[b] Percent error = (absolute value of error)/observed days.

ature to demonstrate the validity of the modification to Malo's equation, there likely are some differences among genotypes and possibly within the life cycle of the plant (McMaster et al., 2008). The ExpSine model could be improved by distinguishing among genotypes in the cardinal temperatures used. The cardinal temperatures for a genotype can be derived by fitting a curve to experimental data. However, when fitting models to data, caution is needed. Sufficient data points (at least 4–5) are required to fit an exponential sine model, and the experimental data should cover a wide temperature range both below and above the optimum temperature.

In conclusion, the modification to the exponential sine function developed by Malo (2002) to predict flowering to include the differential effects of temperature on development rate resulted in accurate estimation of flowering phenology in diverse environmental conditions. This modification of the exponential sine equation developed by Malo expanded the predictive ability of the equation to simulate phenology across a broader range of environments. The ExpSine model developed can be used as a phenological module in various crop or ecological simulation models.

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