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Plastic temperature response function accurately simulates crop flowering or heading date

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Abstract

Although crop phenology is responsive and adaptable to cultural and climatic conditions, many phenology models are too sensitive to variable climatic conditions. We developed a plastic temperature response function by assuming that development rate was linearly related to temperature and that the linearity was linearly responsive to day of year (DOY_V) of the starting date of the vegetative growth period (VGP). Phenology observations and weather data were acquired for winter wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), maize (*Zea mays* L.), and soybean [*Glycine max* (L.) Merr.] at 12 locations over 15–26 yr. Additional data were observed for maize grown in an interval planting experiment. For 78.6% of the sites, the crop development rate during the VGP was positively affected by DOY_V. Partial correlation analysis (controlling for temperature) indicated that DOY_V was independent of temperature. When averaged over all crops and sites, the RMSE for a plastic phenology model based on both response and adaptation mechanisms was lower (RMSE = 2.81 d) than models (RMSE = 3.39) based only on response mechanism ($p < .01$). Furthermore, simulations produced by the plastic model showed less bias to DOY_V, temperature, and year. The plastic function provided a simple and effective method for achieving better phenology simulation accuracy. According to the plastic function, growing season under warming conditions will not be reduced by as much as simulated by models based only on response mechanism, so yield loss due to warming is likely to be overestimated.

1 | INTRODUCTION

Accurate crop phenology predictions are required to accurately assess the effects of climate variability on crop yields (Estrella, Sparks, & Menzel, 2007; Kumudini et al., 2014; Lollato, Edwards, & Ochsner, 2017; Olesen et al., 2012; Siebert & Ewert, 2012; Tao, Zhang, & Zhang, 2012). For most crops, temperature is the most important factor affecting phenology (Porter & Gawith, 1999; Sanchez, Rasmussen, & Porter, 2014). Many response functions have been developed to describe how crop development rate responds to temperature (Parent, Millet, & Tardieu, 2019). The response function is nonlinear in nature, but, for ease of application, it has often been simplified as a linear,

Abbreviations: CMA, Chinese Meteorology Administration; DOY, day of year; DOY_V, day of year of the starting date of vegetative phase; RGP, reproductive growth period; VGP, vegetative growth period.

bilinear, multilinear, or curvilinear function (McMaster, Wilhelm, & Morgan, 1992; Olsen, McMahon, & Hammer, 1993; Porter, 1993; Wang et al., 2017). Three cardinal temperatures are often used to describe the shape of these response functions (Bonhomme, 2000). Cardinal temperatures (i.e., base, optimum, and maximum temperatures) can vary with different developmental stages (Porter & Gawith, 1999; Sanchez et al., 2014). However, for easy application, cardinal temperatures are generally assumed to remain unchanged over a long period of the growing season (Wang & Engel, 2000; Wu, Feng, Zhang, Gao, & Wang, 2017; Zhang, Tao, & Zhang, 2017).

It is widely accepted that many crop phenotypes are plastic with environment (Grogan et al., 2016; Hodge, 2004; Nicotra et al., 2010; Peltonen-Sainio, Jauhiainen, & Sadras, 2011; Rozendaal, Hurtado, & Poorter, 2006; Sadras, Mahadevan, & Zwer, 2017; Sadras, Reynolds, De la Vega, Petrie, & Robinson, 2009). Phenotype plasticity is thought to be evidence of crop adaption to the environment (Sandras & Richards, 2014). For example, in some crop models, specific leaf area is considered a parameter that is independent of environmental factors (Supit, Hooijer, & van Diepen, 1994). However, it has been reported that specific leaf area varies with irradiance in order to maximize growth under different light conditions (Rozendaal et al., 2006). Also, roots often proliferate within nutrient-rich zones (Hodge, 2004). The plastic response of roots has been considered as the major adaptive mechanism by which crops can make full use of available nutrients. For a given region, the climate resources appear regularly in an annual cycle, and as such a crop may have the ability to adjust its phenological progression in order to make full use of climate resources. This indicates that crops may be less sensitive to temperature in warmer than cooler years. Wu et al. (2019a) developed a plastic function that accounts for this adaptability. Their plastic function assumed that the relationship between temperature and growth rate was affected by the day of year (DOY) at the starting date of the examined phase. However, most phenology models do not account for this adaptability.

Different from the reproductive growth period (RGP), development rate during the vegetative growth period (VGP) is additionally affected by photoperiod (Sinclair, Kitani, Hinson, Bruniard, & Horie, 1991). Depending on the effect of day length on development rate, crops can be divided into long-day species (e.g., winter wheat [*Triticum aestivum* L.]) and short-day species (e.g., single rice [*Oryza sativa* L.], maize [*Zea mays* L.], and spring soybean [*Glycine max* (L.) Merr.]) (Blanchard & Runkle, 2010; Yano, Kojima, Takahashi, Lin, & Sasaki, 2001). For long-day crops, flowering date is advanced with longer day length, whereas shorter day lengths advance flowering date for short-day crops (King, Moritz, Evans, Junttila, & Herlt, 2001). For long-day crops that are primarily harvested in the summer, advanced development stage leaves subsequent growth phases in a shorter day length period, thus reducing the effects of temperature on the development growth rate (Hodges & Ritchie, 1991; Mccown, Hammer, Hargreaves, Holzworth, & Freebairn, 1996), which in turn leads to a delayed flowering date. As for short-day crops that are harvested primarily in the autumn, advanced development stage leaves subsequent growth phases in a longer day length period, resulting in reduced effects of temperature on the crop development rate (Bouman et al., 2001; Jones & Kiniry, 1986; Jones et al., 2010), which delays the flowering date. Therefore, long-day and short-day crops have one common feature (i.e., if the starting date of VGP is advanced, the effect of temperature on development rate will be reduced, and vice versa). As a result, the plastic function developed by Wu et al. (2019a) may be applied to describe the common features of long-day and short-day crops. However, this hypothesis has not been confirmed or tested. Therefore, the objectives of this research were to investigate the independence of emergence date or jointing date regarding temperature impacts on heading date or flowering date and to evaluate the plastic function through comparisons of simulations from phenology modules that are used in several typical traditional crop models.

Core Ideas

- A plastic phenology model was applied to simulate crop vegetative phase.
- Wheat, rice, maize, and soybean phenology observations under long-term natural cultivation and an interval planting experiment were used.
- Plastic model assumes development rate is linearly related to temperature and that the linear relationship is affected by day of year of the starting date of vegetative phase.
- Plastic model accurately predicts flowering/heading date similar to other models in a simple and effective way.

2 | MATERIALS AND METHODS

2.1 | Sites and observations

Two data sets were assembled in which phenology was observed under varying temperature conditions to evaluate model performance under varying climate

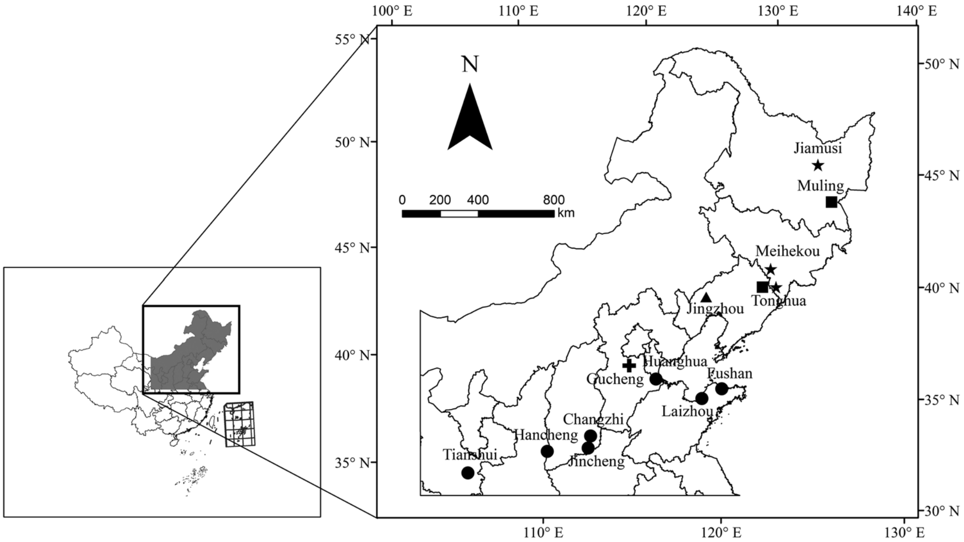

FIGURE 1 Locations of 11 agro-meteorological observation sites and one experimental site in China. Plus sign denotes the site where the interval planting experiment was carried out, circles are winter wheat observation sites, squares are rice sites, stars are maize sites, triangle is the soybean site. Tonghua station had both rice and maize observations, with the star above the Tonghua label indicating the actual position for the observations. To show the two crops at the same location, we show the rice site to the left of the actual position.

conditions. The first data set was comprised of phenology observations of four crop species (winter wheat, rice, maize, and soybean) at 12 sites (Figure 1). At these sites, crop variety remained unchanged for at least 15 yr and for up to 26 yr. On average, these sites had 20 yr of observations. Wu et al. (2019b) presented a detailed description of the data collected for winter wheat, rice, and maize. The soybean cultivar TF29 was planted at the Jinzhou Agricultural Ecosystem Experiment Station (41°49′10″ N, 121°12′4″ E) from 1999 to 2015. In total, 13 crop varieties were planted at these sites. Seven, two, three, and one sites were available for the four crops, respectively. Both rice and maize were planted at the Tonghua station (41°24′0″ N, 125°26′24″ E). Phenological observations were conducted by the Chinese Meteorology Administration (CMA) by trained agricultural technicians following standardized methods (CMA, 1993).

Different from the other three crops, winter wheat has a dormancy phase (from the start of overwintering to spring dormancy break). During this phase, the temperature response is different from other phases, and this response cannot be reflected by the plastic model. The spring dormancy break stage is not a true development stage. The next true stage observed by CMA is jointing. As a result, the start of VGP for winter wheat was set as jointing, and the start of VGP for the other three crops was set as emergence. The dates of heading and flowering for rice are very close (generally within 2–3 d), so CMA only recorded the heading date. Therefore, the end of VGP for rice was set as heading, whereas for the other three crops the end of VGP was set as flowering. The corresponding BBCH codes for the above-mentioned emergence, jointing, heading, and flowering stages are BBCH10, BBCH31, BBCH55, and BBCH64, respectively. Management practices included irrigation, fertilizer applications, and weed control and were generally the same as or better than local traditional practices (Tao et al., 2013). All phenology observation data were obtained from the National Meteorological Information Center. Historical weather data at agro-meteorological observation sites, including mean temperatures and precipitation during the same years as the phenology observations, were also collected from the National Meteorological Information Center. Table 1 shows the site information and summary meteorological information for these sites. This data set represents the historical response of heading and flowering date to climate change under normal field planting conditions.

Because these observations occurred over at least 15 yr, the temperature response may be confounded by the improved field management practices during those years (e.g., better fertilization and irrigation management). Therefore, an interval planting experiment for summer maize under controlled conditions was conducted. This experiment was carried out at Gucheng Ecometeorological Observation Experiment Station (39°08′2″ N, 115°48′14″ E) (Figure 1) in 2018. The sandy loam soil at this site has a pH value of 8.19, with total nitrogen and total phosphorus of 0.98 and 1.02 g kg^{-1}, respectively. The maize cultivar was ZD958 (Hou et al., 2014; Liu et al., 2013). Planting occurred every 5 d from DOY 130 to DOY 170, for a total of nine planting dates. The planting date treatments were not replicated. After planting, the

TABLE 1 Summary information for sites in which the planted variety remained unchanged for at least 15 yr

Site name	Number of observations	Variety[a]	Date of emergence or jointing	Date of heading or flowering	Vegetative growing season[b] Duration	Average temperature	Rainfall
			DOY		d	°C	mm
Winter wheat							
Changzhi	17	CZ648	111 ± 6[c]	136 ± 4	26 ± 4	15.3 ± 1.3	40 ± 22
Hancheng	15	XY6	92 ± 8	119 ± 6	28 ± 6	16.0 ± 1.3	24 ± 16
Jincheng	21	5819	103 ± 7	130 ± 4	29 ± 4	15.5 ± 1.0	38 ± 28
Huanghua	23	71321	108 ± 5	130 ± 4	22 ± 3	17.3 ± 1.1	25 ± 21
Laizhou	21	YN15(LZ)	94 ± 6	127 ± 4	35 ± 5	14.9 ± 0.9	36 ± 19
Fushan	26	YN15(FS)	96 ± 5	134 ± 4	38 ± 5	14.4 ± 0.7	56 ± 34
Tianshui	19	7464	96 ± 5	132 ± 5	37 ± 5	14.8 ± 1.0	46 ± 23
Rice							
Muling	16	SY397	130 ± 3	213 ± 5	84 ± 5	19.3 ± 0.7	225 ± 55
Tonghua	26	QG	119 ± 5	220 ± 2	102 ± 4	18.4 ± 0.7	513 ± 153
Maize							
Jiamusi	18	DN248	150 ± 6	209 ± 6	60 ± 4	21.3 ± 1.1	187 ± 94
Meihekou	15	TD4	137 ± 4	211 ± 5	75 ± 5	20.4 ± 0.8	299 ± 112
Tonghua	20	JD101	134 ± 4	205 ± 3	72 ± 4	18.9 ± 1.0	316 ± 92
Soybean							
Jingzhou	17	TF29	137 ± 5	198 ± 4	62 ± 4	22.5 ± 0.8	201 ± 99

[a]Laizhou and Fushan planted the same winter wheat variety ('YN15'). To distinguish between the two, the variety names are marked as 'YN15(LZ)' and 'YN15(FS)', respectively.
[b]The definition of vegetative growing season for winter wheat is from jointing to flowering, for rice is from emergence to heading, and for maize and soybean is from emergence to flowering.
[c]The date of emergence and jointing, date of heading and flowering, vegetative growing season duration, vegetative growing season average temperature, and vegetative growing season rainfall are presented as mean values ±1SD.

TABLE 2 Dates of planting, emergence, and flowering, length of vegetative growing period (VGP, from emergence to flowering), average temperature, and accumulated temperature for maize in the interval planting experiment at Gucheng, China, in 2018

Planting date	Emergence date	Flowering date	VGP length	Average temperature in VGP	Accumulated temperature in VGP[b]
	DOY[a]		d	°C	°C d^{-1}
130	135	189	55	25.3	953.5
135	141	194	54	25.7	955.1
140	146	199	54	26.3	987.5
145	150	203	54	26.8	1014.0
150	154	205	52	27.0	988.0
155	159	209	51	27.1	976.6
160	165	215	51	28.2	1029.4
165	169	217	49	28.5	1005.1
170	175	219	45	28.5	921.9

[a]Day of year.
[b]The effective accumulated temperature above 8 °C.

developmental stages (including emergence, heading, and flowering) were recorded daily. Each planting date plot had dimensions of 5.5 by 15 m, with a row spacing of 0.33 m and a within-row plant spacing of 0.50 m. At planting, 80 mm of irrigation water and 150, 75, and 75 kg ha^{-1} of N, P, and K fertilizer, respectively, were applied. Management practices were used to minimize yield reductions due to nutrients, weeds, and pests. A weather station located 10 m north of the experimental field provided daily average temperature. Table 2 provides detailed information for each planting, including planting, emergence, and flowering dates and daily average temperature data. This data set characterized the response of maize flowering date to the various combinations of temperature and day length without the effects of changing field management practices.

2.2 | Introduction to the plastic temperature response function

The plastic phenology model proposed by Wu et al. (2019a) was used in this paper. The model assumes development rate is linearly related to temperature and that the linear relationship is affected by day of year of vegetative emergence and jointing date (DOY_v). Three kinds of regression relationships were designed to investigate how R^2 was improved by coupling DOY_v with a linear temperature response function.

The response of development rate to temperature is essentially nonlinear, but it is approximately linear over a wide temperature range. In this study, all sites were located in northern China, and their latitudes were higher than 34°. The probability of daily average temperature exceeding the optimum temperature is very small. For simplicity, we assumed a linear response function:

$$\text{Rate} = a_1 + b_1 \times T \quad (1)$$

where Rate is the development rate over a specified growth period (d^{-1} or $°C^{-1}\ d^{-1}$), a_1 and b_1 are regression coefficients, and T is growth period average temperature (°C). Depending on the value of b_1, the thermal/photothermal time requirement may respond positively or negatively with increased temperature. Therefore, Equation 1 is an extension of traditional models that are based on a constant thermal/photothermal time requirement. We further assumed that the linear slope (b_1 in Equation 1) was affected by DOY_v. Thus, the mathematical equation for the plastic model was:

$$\text{Rate} = a_2 + (b_2 + c_2 \times DOY_v) \times T \quad (2)$$

where Rate and T mean the same as in Equation 1, and a_2, b_2, and c_2 are regression coefficients. If DOY_v does affect temperature sensitivity, the R^2 of this relationship is expected to be much greater than for the linear temperature response function. Because Equation 2 is an extension of Equation 1, Equation 2 is also an extension of traditional models.

However, R^2 of Equation 2 can be partially explained by the linear relationship between DOY_v and T. Thus, we replaced DOY_v in Equation 2 with the linear relationship between DOY_v and T and obtained the quadratic polynomial relationship:

$$\text{Rate} = a_3 + b_3 \times T + c_3 \times T^2 \quad (3)$$

where Rater and T mean the same as in Equation 1, and a_3, b_3, and c are regression coefficients. If the effect of DOY_v on development rate is not primarily caused by the linear relationship between DOY_v and T, R^2 in Equation 2 is expected to be much greater than that for the quadratic polynomial relationship.

Regressions for the above three models were performed for each crop and cultivar by the ordinary least squares method. Significance levels were determined by two-tailed t tests. Because both reciprocal of number of days and reciprocal of thermal time accumulation have been widely used to express the development rate, regressions were performed twice on each of the three models.

2.3 | Testing the driving effect of DOY_v on temperature sensitivity

Linear regression analyses between DOY_v and development rate were conducted for each crop and cultivar to determine whether DOY_v affects the development rate. The significance level of coefficients of determination was determined by two-tailed t test.

Readers should be aware that DOY_v and average temperature are not totally independent. The relative influence of DOY_v on development rate was tested for each crop and cultivar by using partial correlation analysis (controlling for temperature). The significance level of the partial correlation coefficient was determined by two-tailed t test. Differences in R^2 values between Equations 2 and 3 were tested by paired t test to determine to what extent the improvement of R^2 in Equation 2 was caused by the dependency between DOY_v and temperature. Values of Akaike's information criteria were used to select the best equations among Equations 1, 2, and 3 (Akaike, 1974; Ren, Qin, Ren, Sui, & Zhang, 2019):

$$\text{AICc} = n \times \ln\left(1 - R^2\right) + 2k + \frac{2k \times (k+1)}{n-k-1} \quad (4)$$

where n represents the number of observations, and k is the number of parameters needed to be fitted. For Equations 1, 2, and 3, k equals 2, 3, and 3, respectively.

Because both reciprocal of number of days and reciprocal of thermal time accumulation are widely used to represent development rate, the linear regression analysis and partial correlation analysis were performed twice to find

TABLE 3 Descriptions and optimization ranges and loop steps for parameters in phenology modules used in WOFOST, ORYZA2000, CERES-Maize, and DSSAT-Soybean models

Model name	Parameter	Range of value	Loop step	Explanation
WOFOST	Tsum1	300–600	1	Temperature sum from jointing to flowering
ORYZA2000	DVRJ	0.0001–0.0025	0.0001	Development rate in basic vegetative phase
	DVRI	0.0001–0.0025	0.0001	Development rate from end of basic vegetative phase to panicle initiation
	DVRP	0.0001–0.0025	0.0001	Development rate from panicle initiation to heading
	SHCKD	0.0–0.1	0.01	Transplanting shock
	PPSE	0.0–0.6	0.01	Photoperiod sensitivity
CERES-Maize	P1	50–200	1	Thermal time from emergence to the end of the juvenile period
	P2	0–2	0.01	Photoperiod sensitivity measured in days of tassel initiation delay per hour of photoperiod increase
	PHINT	30–70	1	Phyllochron interval
DSSAT-Soybean	CSDVAR	10.5–15.0	0.1	Day length threshold below which developmental progress is a maximum f
	CLDVAR	15.1–21.0	0.1	Day length at which developmental progress is a minimum
	PHTHRS(2) + PHTHRS(3)	121–160	1	Photothermal sum from emergence to end of juvenile phase
	PHTHRS(4) + PHTHRS(6)	450–800	1	Photothermal sum from end of juvenile to flowering

out if different expressions affect the results. For simplicity, the first one was named Method 1 (using reciprocal of number of days for development rate), and the second one was named Method 2 (using reciprocal of thermal time accumulation).

2.4 | Model comparison

For each crop, a phenology module used in a widely applied traditional crop model was selected to simulate the phenology. For winter wheat, rice, maize, and soybean, the selected phenology submodels were taken from WOFOST (Supit et al., 1994), ORYZA2000 (Bouman et al., 2001), CERES-Maize (Jones & Kiniry, 1986), and DSSAT-Soybean (Jones et al., 2010), respectively. For the four traditional models, all parameters were optimized except for the three cardinal temperatures. The values of the three cardinal temperatures were the default values set by the models. The number of parameters affecting development rate were one, five, three, and four, respectively. Parameters for each model were optimized over a wide range with a small loop step (Table 3). Ranges of values for parameter optimizations were wider than values shown in published reports (Porter & Gawith, 1999; Sanchez et al., 2014; Setiyono et al., 2007).

At each site, all observations were used to calibrate the traditional and plastic models. All coefficients were calibrated simultaneously to search for a global rather than a local optimum. The principle of optimization was RMSE minimization. Parameter values that produced the minimum RMSE were considered as the best values.

Simulation errors of heading or flowering dates and corresponding RMSE produced by the traditional and plastic models were calculated. Differences in RMSE values between the traditional and plastic models were tested by paired two-tailed *t* test to determine whether they were significant. Trends of simulation errors over average temperature, DOY_V, and year were calculated to evaluate model performance and compared for both the traditional and plastic models.

To further test model accuracy, both traditional and plastic models were tested using leave-one-out cross-validation, which is commonly used to quantify the reliability of a forecasting system in the presence of limited data (Cappelli et al., 2018; Zhang & Tao, 2019). For the four traditional models, the parameterization method was the same as used with the above-mentioned model calibration.

All statistics were done by FORTRAN codes. Results generated by these codes were verified by comparing the results given by statistical functions available in Microsoft EXCEL 2013.

TABLE 4 Slopes, coefficients of determination, and partial correlation coefficients (controlling for temperature) between day of year of date of emergence (for rice, maize, and soybean) or jointing date (for wheat) and development rate

	Crop	Variety	Method 1 Slope ($\times 10^{-3}$)	Method 1 R^2	Method 1 r	Method 2 Slope ($\times 10^{-3}$)	Method 2 R^2	Method 2 r
Field observation	Winter wheat	CZ648	0.755	.501**	0.604**	0.0322	.259*	0.611**
		XY6	0.747	.463**	0.427	0.0280	.270*	0.386
		5819	0.636	.548***	0.683***	0.0277	.330**	0.685***
		71321	0.412	.135	0.361	0.0054	.006	0.363
		YN15(LZ)	0.503	.461***	0.377	0.0220	.386**	0.393
		YN15(FS)	0.409	.343**	0.529**	0.0226	.256**	0.545**
		7464	0.407	.270*	0.407	0.0171	.168	0.378
	Rice	SY397	0.084	.095	0.352	−0.0056	.027	0.322
		QG	0.075	.791***	0.860***	0.0017	.015	0.840***
	Spring maize	DN248	0.044	.055	0.120	−0.0050	.066	0.026
		TD4	0.123	.306*	0.644**	0.0083	.348*	0.655**
		JD101	0.151	.613***	0.511*	−0.0031	.056	0.468*
	Soybean	TF29	0.104	.329*	0.849**	0.0026	.044	0.840**
Interval planting experiment	Spring maize	ZD958	0.087	.825***	0.543*	−0.0002	.004	0.467

Note. In calculating the development rate, both reciprocal of number of growing days (Method 1, using the reciprocal of number of days during vegetative growing period as the development rate) and reciprocal of accumulated temperature (Method 2 using the reciprocal of accumulated temperature during vegetative growing period as the development rate) were used as the development rate. Base temperatures for calculating the accumulated temperature for winter wheat, rice, maize, and soybean were set as 0, 8, 8, and 6 °C, respectively.
*Significant at the .05 probability level. **Significant at the .01 probability level. ***Significant at the .001 probability level.

3 | RESULTS AND DISCUSSION

3.1 | Effect of DOY_v on development rate

All cultivars of the four crops had positive relationships between DOY_v and development rate when using Method 1, of which 11 were significant (Table 4). The average R^2 values for winter wheat, rice, maize (including the interval planting experiment), and soybean were .39, .44, .33, and .83, respectively. When using Method 2, the relationships were positive for 10 cultivars, and six of them were significant. None of the four negative relationships was significant.

All of the partial correlation coefficients were positive for Method 1 and Method 2 (Table 4). The partial correlations were significant in eight and seven cultivars for Method 1 and Method 2, respectively. By using Method 1, the average partial correlation coefficients for the four crops were .48, .61, .45, and .85, respectively; the corresponding values using Method 2 were .48, .58, .40, and .84, respectively. These values suggest that the different methods of representing development rate had little effect on the partial correlation results and suggest that DOY_v explained almost the same amount of variability in heading and flowering date as temperature did for the four examined crops.

3.2 | Improved R^2 after coupling DOY_v with a linear response function

The R^2 value was effectively improved after combining DOY_v in the linear temperature response function for both Method 1 (Figure 2) and Method 2 (Figure 3). For the case of using Method 1, the R^2 values were improved for all cultivars of all crops (Figure 2). Average R^2 values for the four crops were improved by .17, .39, .15, and .27, respectively. Averaged over all crops and cultivars, the R^2 was improved by 70%. The dependency between DOY_v and temperature also partially explains the improved R^2. The quadratic polynomial relationship (Equation 3) showed that after considering this dependency, R^2 values for the four crops were improved by .04, .01, .11, and .21, respectively. Averaged over all crops, the R^2 was improved by .07. Therefore, the dependency between DOY_v and temperature explained one third of the improvement in Equation 3. Paired t test showed that the differences in R^2 between the plastic and quadratic polynomial relationships were significant at $p < .05$.

Similar results were obtained using Method 2 (Figure 3). For this case, using the plastic relationship improved the average R^2 values for the four crops by 0.23, 0.15, 0.33, and 0.17, respectively, whereas the quadratic polynomial relationship improved average R^2 by .06, .00, .18, and .11,

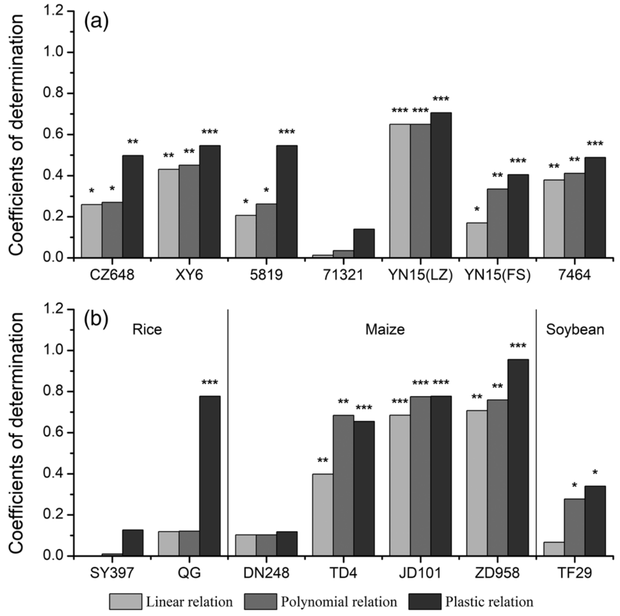

FIGURE 2 Coefficients of determination for three kinds of relationships (linear, polynomial, and plastic) for winter wheat (a) and for rice, maize, and soybean (b) using the reciprocal of number of growing days as the development rate (Method 1). *Statistically significant at $p < .05$. **Statistically significant at $p < .01$. **Statistically significant at $p < .001$.

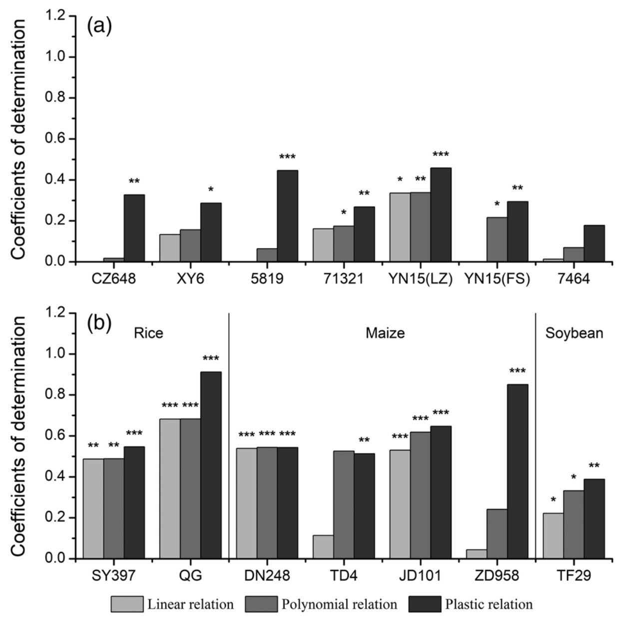

FIGURE 3 Coefficients of determination for three kinds of relationships (linear, polynomial, and plastic) for winter wheat (a) and for rice, maize, and soybean (b) using the reciprocal of accumulated temperature as the development rate (Method 2). The base temperatures used in calculating the accumulated temperatures for winter wheat, rice, maize, and soybean were 0, 8, 8, and 6°C, respectively. *Statistically significant at $p < .05$. **Statistically significant at $p < .01$. ***Statistically significant at $p < .001$.

respectively. On average, the plastic and quadratic polynomial relationships improved R^2 by 100 and 37%, respectively. In this case, dependency between DOY_v and temperature also explained about one-third of the improvement. The paired t test showed that the differences in R^2 produced by the two relationships were significant at $p < .05$. These results indicate that DOY_v and temperature are two almost unrelated yet equally important factors affecting crop development rate and confirm that introducing DOY_v into the linear temperature response function can effectively improve the R^2 in accounting for variation of heading and flowering date.

The Akaike's information criteria values for Equation 2 were lower than the values for Equation 1 in 11 out of 14 sites (Figure 4a), whereas values for Equation 2 were also lower than the values for Equation 3 in 13 out of 14 sites (Figure 4b). These results further confirm that it is cost effective to introduce DOY_v into Equation 1 and that this cost effectiveness is not mainly caused by the linear relationship between DOY_v and temperature. Results were similar when using the reciprocal of accumulated temperature as the development rate.

3.3 | Model evaluation

Table 5 shows the values of parameters in the plastic model for all cultivars of the four crops. The impact of DOY_v on development rate (parameter c_2 in Equation 2) was positive for all crops and all cultivars. For winter wheat, rice, spring maize, and soybean, the average impacts (c_2 values) were 0.02750×10^{-3}, 0.00495×10^{-3}, 0.00527×10^{-3}, and 0.00459×10^{-3}, respectively. These values indicate that the development rate of these crops will be accelerated if the emergence and jointing dates are delayed, and vice versa.

Averaged over all crops and varieties, the RMSE value found for the simulation of heading and flowering dates by the plastic model (2.81 d) was less than that simulated by the phenology modules in the traditional crop simulation models (3.39 d) (Figure 5a). Paired t test showed that the differences in RMSE between the plastic and traditional models were significant at $p < .01$. Except for one rice cultivar (SY397) and one soybean cultivar (TF29), RMSE values associated with the plastic model were less than simulated by the traditional models at the other 12 sites. On average, the RMSE associated with the plastic model for the four crops were 2.90, 3.44, 2.38, and 2.69 d, respectively, and the values simulated by the traditional models were 3.76, 3.54, 2.88, and 2.50 d, respectively. In summary, the plastic model decreased simulation error in winter wheat and maize by about 20%, whereas simulation error for rice and soybean were similar for both the plastic model and the traditional model.

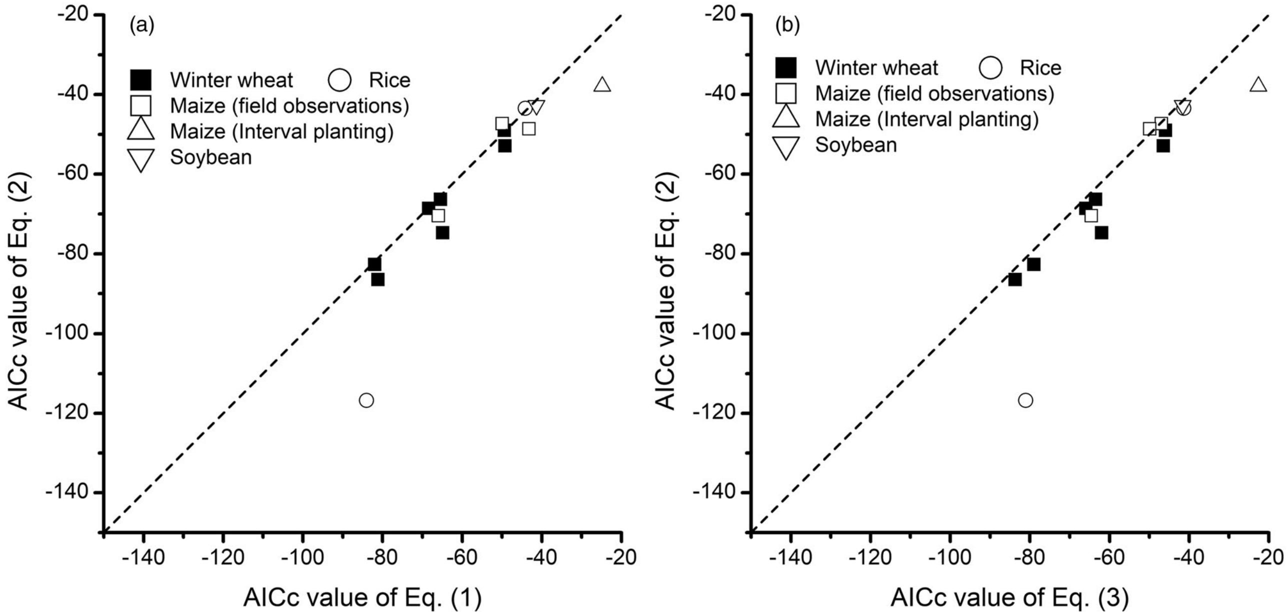

FIGURE 4 Akaike's information criteria (AICc) values for Equations 1, 2, and 3 for all four investigated crops using the reciprocal of number of growing days as the development rate. (a) The AICc values for Equation 1 vs. Equation 2. (b) The AICc values for Equation 3 vs. Equation 2.

TABLE 5 Values of parameters in the plastic model (Equation 2) for all varieties of winter wheat, rice, maize, and soybean

		Parameter values for the plastic model ($\times 10^{-3}$)		
Crop	**Variety**	a_2	b_2	c_2
Winter wheat	CZ648	23.921	−3.422	0.04006
	XY6	0.466	−0.450	0.02990
	5819	13.666	−2.294	0.03620
	71321	53.348	−3.311	0.02633
	YN15(LZ)	−16.359	1.576	0.01602
	YN15(FS)	10.672	−1.311	0.02499
	7464	2.623	−0.165	0.01904
Rice	QG	9.284	−0.441	0.00396
	SY397	15.979	−0.985	0.00595
Maize	DN248	11.156	0.078	0.00121
	TD4	−0.512	−0.098	0.00568
	JD101	9.032	−0.350	0.00456
	ZD958	73.306	−3.488	0.00962
Soybean	TF29	14.962	−0.571	0.00459

Simulation errors associated with the plastic model were less related to temperature (Figure 5b), DOY_V (Figure 5c), and year (Figure 5d) than the simulation errors found for the traditional models. Simulation errors produced by the plastic model were not significantly related to temperature and DOY_V and were significantly related to year for three cultivars (two winter wheat cultivars and one spring maize cultivar) (Figure 5). However, simulation errors produced by the traditional models were significantly related to temperature for four cultivars (one winter wheat cultivar, two rice cultivars, and one maize cultivar), to DOY_V for six cultivars (four wheat cultivars and two maize cultivars), and to year for seven cultivars (four wheat cultivars, two rice cultivars, and one maize cultivar). It can be concluded that the plastic model reduced the systematic deviation of phenology simulations.

The plastic model better estimated the observed heading and flowering dates than the traditional models for wheat (Figure 6a), maize (Figure 6c), and soybean (Figure 6d), with R^2 values of .800, .787, and .875, respectively, but gave a poorer fit to observed values for rice (Figure 6b), with an R^2 value of .467. For all four crops, when the measured heading and flowering dates were delayed by 1 d, the heading and flowering dates simulated by the plastic model were delayed by 0.792, 0.516, 0.843, and 1.363 d, respectively (see slopes of regression lines). These slope values associated with the plastic model were closer to 1.000 than the slope values associated with the traditional models for wheat (0.830), rice (0.644), and maize (0.931) but further from 1.000 for soybean (0.597).

One of the main advantages of the plastic model is that it can produce accurate simulation of heading and flowering dates in extremely cold and hot years (Table 1). For example, winter wheat cultivar YN15 was planted in Laizhou during 1990–2010. During the entire 21-yr period, 1994 and 2001 had the warmest and coolest growing season temperatures, respectively. In 1994, the jointing date was very

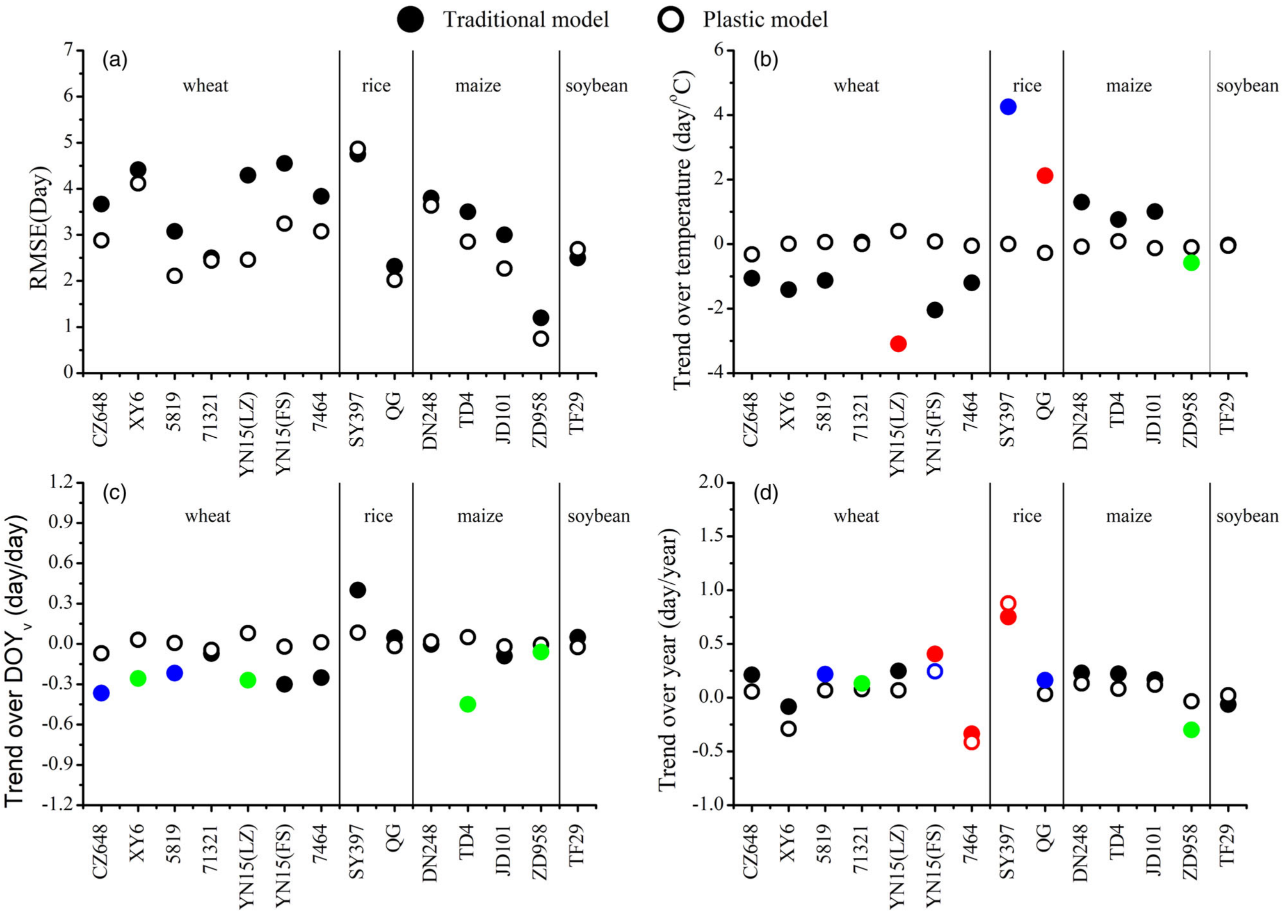

FIGURE 5 Simulation accuracy of heading and flowering date from the plastic model and four traditional phenology modules applied in crop models (WOFOST, ORYZA2000, CERES-Maize, and DSSAT-Soybean) for varieties of winter wheat, rice, maize, and soybean. (a) Simulation RMSE. (b) Trend of simulation error against growth period average temperature. (c) Trend of simulation error against day of year (DOY) of emergence (for rice, maize, and soybean) or jointing (for winter wheat) date. (d) Trend of simulation error against year. Green, blue, and red symbol colors indicate the trends are statistically significant at $p < .05$, .01, and .001, respectively

late (DOY 99), and the subsequent wheat growth occurred at a higher-than-average temperature, causing the growing season average temperature to be 17.0 °C, which was the highest value of all 21 yr. Effective accumulated temperature in this year was 441 °C d^{-1}, which was much lower than the average value (511 °C d^{-1}). Therefore, the simulation error produced by the traditional model in this year was very large (−7 d, measured date minus simulation date) (Figure 7a). In contrast, the later jointing date in the plastic model indicated larger DOY$_v$, which led to increased temperature sensitivity and decreased the needed days to flowering, resulting in a simulation error of only −1 d. In contrast, the year 2001 had the lowest average growing season temperature (13.2 °C) and a large effective accumulated temperature (579 °C d^{-1}) because it had a very early jointing date (DOY 85). In this year, the simulation error produced by the traditional model was 8 d, whereas the corresponding simulation error produced by the plastic model was still only −1 d. The large differences of simulation errors generated by the traditional model under contrasting conditions led to the significant relationship between simulation errors and temperature (Figure 7b) and DOY of jointing date (Figure 7c). Because the plastic model considered the adaptation of crop development to environment, the relationship between the simulation errors and DOY$_v$, temperature, and year were greatly reduced (Figure 7a–c).

The results of leave-one-out cross-validation for the plastic and traditional models showed that for 8 of 14 varieties, the RMSE values associated with the plastic model were smaller than the values associated with traditional models, especially for maize (Figure 8). For all four maize cultivars, the plastic model had smaller RMSE than the traditional models. Figure 8 shows that, the plastic model was generally better than the traditional models, although it was somewhat different among crops.

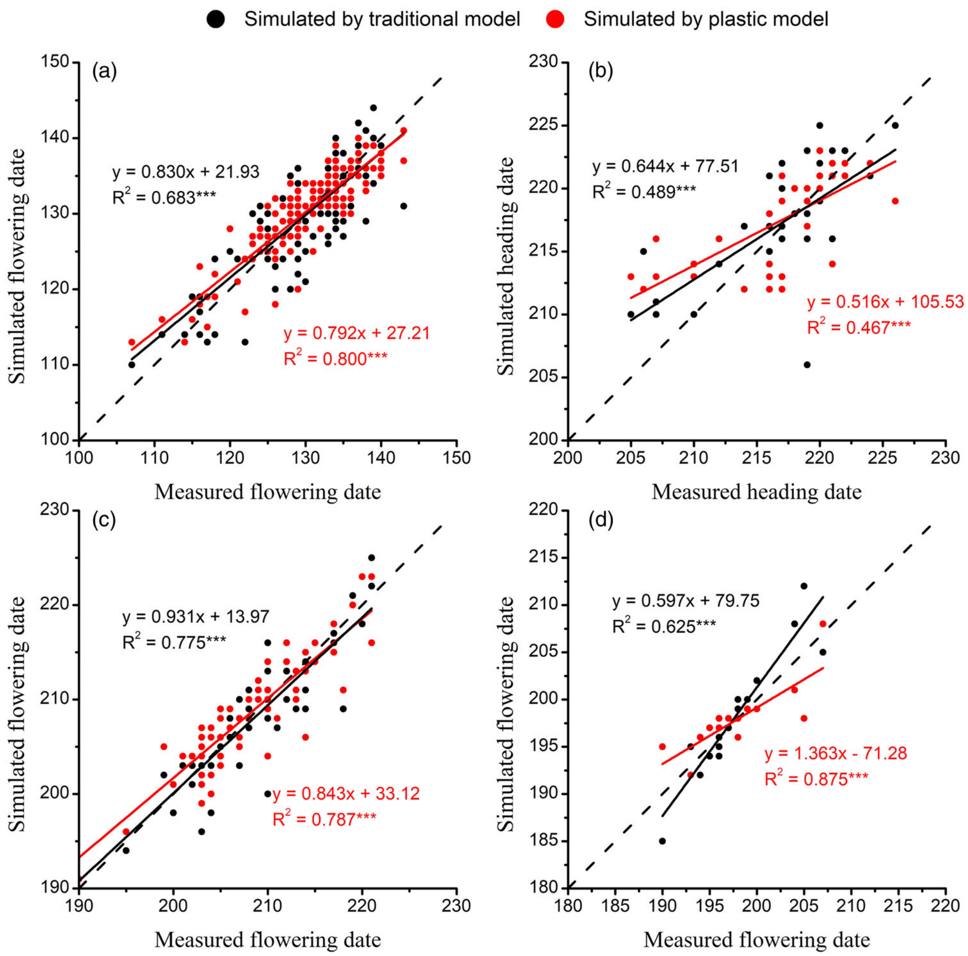

FIGURE 6 Measured and simulated heading and flowering dates (day of year) for winter wheat (a), rice (b), maize (c), and soybean (d). Data are from historical field observations for all four crops, and the maize data included observations from an interval planting experiment. The black points, regression lines, and regression equations are for the traditional model comparison; the red points, lines, and regression equations are for the plastic model comparison. The dashed line is the one-to-one line. ***Statistically significant at $p < .001$.

3.4 | Discussion

Wu et al. (2019a) developed a plastic model that assumed that the response of development rate to temperature was affected by DOY of the start date of RGP. In this study, we tested whether the DOY_v affects the development rate in VGP. Results verified that DOY_v affects the development rate in VGP. The effect was similar to the results reported for RGP (i.e., the values of c_2 in Equation 2 were positive for all cultivars of all examined crops in both growth periods).

Although coupling DOY_v also improved simulation accuracy in VGP (Figure 5a), the improvement was not as good as reported in RGP (Wu et al., 2019a). One of the reasons may be that in VGP, the effect of DOY_v is similar to the effect of photoperiod, a factor that has been well considered in current models (Bouman et al., 2001; Ceglar et al., 2019; Jones et al., 2010). For example, in the northern hemisphere, for a long-day species such as winter wheat, longer day length will increase the temperature sensitivity. Because the jointing to flowering period for winter wheat occurs in the first half of the calendar year (Table 1), the longer day length means larger DOY_v. In the plastic model, longer day length will also increase the temperature sensitivity because c_2 values are positive (Table 5). Therefore, coupling DOY_v in the plastic model has a similar effect as coupling day length in the traditional models. However, this similarity will be diminished after considering the c_2 values in RGP. Wu et al. (2019a) verified that c_2 values are also positive during RGP for all cultivars. This consistency in VGP and RGP indicates that the effect of DOY_v on development rate is similar in both VGP and RGP, and for different crops. However, most models assume that there is no photoperiod response in RGP, including WOFOST (Supit et al., 1994), ORYZA2000 (Bouman et al., 2001), CERES-Maize (Jones & Kiniry, 1986), and SPASS (Wang & Engel, 2000). As the results showed, although photoperiod may

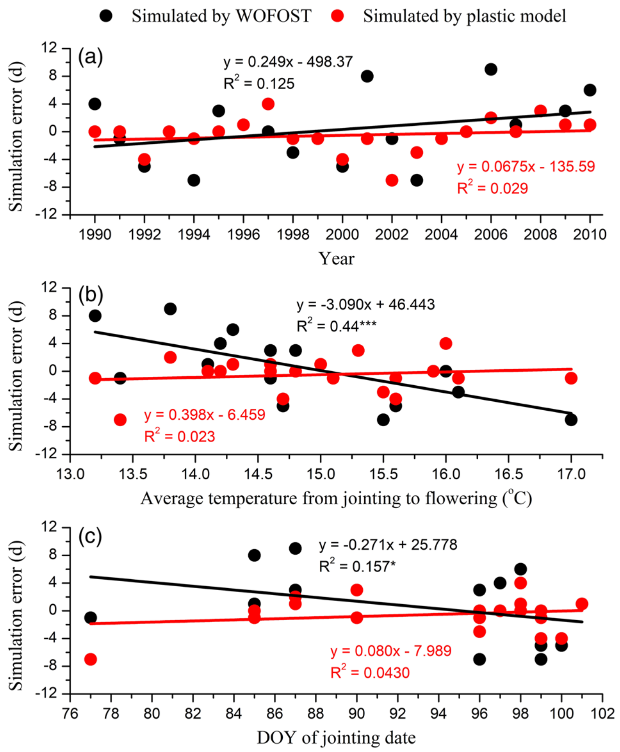

FIGURE 7 Trends of wheat flowering date simulation error over year (a), growth period average temperature (b), and day of year (DOY) of jointing date (c) produced by the plastic model and WOFOST. The black points, regression lines, and regression equations are for the traditional model; the red points, regression lines, and regression equations are for the plastic model. *Statistically significant at $p < .05$. ***Statistically significant at $p < .001$.

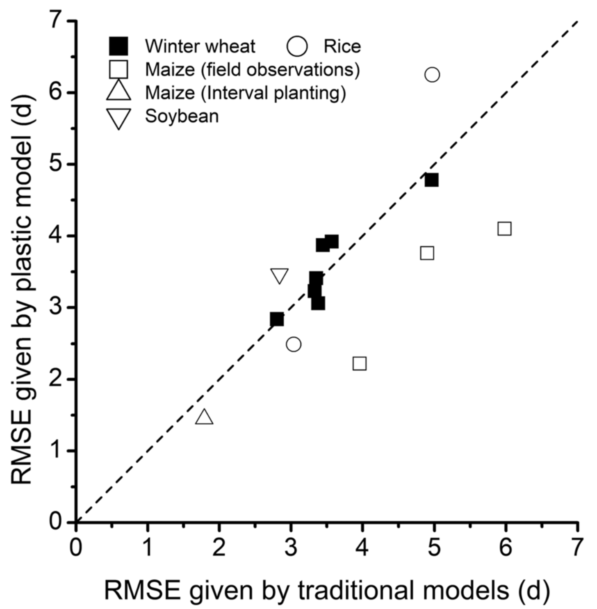

FIGURE 8 Root mean square error associated with the plastic and traditional models calculated by leave-one-out cross-validation.

partially contribute to the plasticity, the plasticity could not be mainly caused by photoperiod. Additionally, these models need to identify the short-day and long-day species and define the photoperiod sensitivity. In contrast, the plastic model does not need this information. According to the rule of Occam's Razor, among competing hypotheses that predict equally well, the one with the fewest assumptions should be selected (Parent et al., 2016; Sinclair & Muchow, 1999). Therefore, the plastic model is preferred over traditional models because it simulated development rate throughout the entire development period for the examined crops using only DOY_V to explain the similar effects of day length for both long-day and short-day species in both VGP and RGP phases.

In the early stage of VGP, vernalization also affects the response of winter wheat development to temperature (Hodges & Ritchie, 1991; Supit et al., 1994; Yan, Cao, Luo, & Jang, 2000). This effect was not directly considered by the plastic model. However, theoretically, the effect of vernalization on the development rate can be reflected by the plastic model. For example, in hot years, jointing date tends to be advanced, whereas number of vernalization days is likely to be less than that in cold years. The effect of temperature on development rate thus tends to be decreased, resulting in a delayed flowering date. By using the plastic model, the advanced jointing date results in decreased temperature sensitivity, which delays flowering. Consequently, although vernalization is not directly considered by the plastic model, the model can achieve a similar effect. Furthermore, the effect in this case is very similar to the effect of day length (i.e., advanced jointing date will result in decreased temperature sensitivity). Thus, it may be possible to combine both effects (vernalization and photoperiod) in one explanation, just as the plastic model did.

Based on the following three reasons, the default cardinal temperatures were used to optimize the traditional models rather than calibrating the temperatures. First, cardinal temperature values are not independent of other parameter values (He et al., 2017), such as with P1 and P2 in the CERES-Maize model. For example, if optimum and maximum temperatures remain unchanged, a lower base temperature will result in higher P1 and P2. The effect of adjusting cardinal temperatures can be partially achieved by adjusting the values of P1 and P2. This dependence between parameters has also been mentioned previously by Supit et al. (1994). Second, if the three cardinal temperatures were included among the values to be optimized, model calibration would take more time to optimize the values of all of the parameters. Third, cardinal temperatures have very clear physiological meanings (Porter & Gawith, 1999; Sanchez et al., 2014). Modifying these values should not be based on fitting the predictions to the observed data.

Two obvious advantages of the plastic model can be identified. The first advantage is that it provides unbiased predictions of heading and flowering dates (Figures 5 and 7). The unbiased predictions are required to improve the yield estimates. The second advantage is that the model needs fewer parameters and is easy to optimize, both of which are valuable for model application, especially when models are applied at regional scales and under climate change scenarios.

Although the plastic model performed well in simulating crop phenology, there are three points that users need to be aware of. The first is that the plastic model did not simulate the detailed molecular processes that lead to phenology plasticity. Instead, the model simulated the final behavior of numerous complicated molecular biological processes. As a result, the molecular mechanisms of the model are not clear. However, from a practical point of view, it may be easier to simulate the final behavior than to simulate each biochemical process affecting plant development. The second point is that the model does not take into account the effects of soil water content on plant development (Chauhan, Ryan, Chandra, & Sadras, 2019; Liu et al., 2016). The third point is that even though the model worked well over a wide latitude range in the northern hemisphere, model performance in the southern hemisphere is uncertain.

Because temperature sensitivity is plastic with DOY_v, the heading and flowering dates predicted by the plastic model will not be prolonged or shortened as much as predicted by traditional models under cold or hot years. Therefore, the growing season simulated by the plastic model will remain relatively stable during extreme temperature events. As a result, it is logical to infer that current estimates of yield loss due to future climate change may be overestimated (Challinor, Koehler, Ramirez-Vilegas, Whitfield, & Das., 2016; Liu et al., 2016).

4 | CONCLUSIONS

Field observations of crop phenology under actual planting conditions and from an interval planting experiment verified that DOY_v was positively related to development rate for four crops (winter wheat, rice, maize, and soybean). Partial correlation analysis (controlling for temperature) showed that DOY_v and temperature were two almost unrelated yet equally important factors that affect development rate. The plastic model achieved better simulation accuracy of heading or flowering dates than traditional models for wheat and maize and achieved similar accuracy for rice and soybean. Additionally, simulations of heading and flowering dates provided by the plastic model were less biased with DOY_v, temperature, and year. The plastic model explained the mechanisms of temperature and photoperiod with one equation. Advantages of the plastic model are simplicity, few assumptions, effectiveness, and less biased simulations. These advantages make this model an ideal tool for predicting regional crop phenology under varying environmental conditions, and hence yield response, especially for future climate change scenarios.

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