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Use of a plastic temperature response function reduces simulation error of crop maturity date by half

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ABSTRACT

Understanding how crop development rate responds to the environment provides the basis for evaluating the impact of climate change on crop yield. In most crop simulation models, temperature response functions of development rate during the reproductive growth period (RGP) are assumed to only vary with temperature and not with other environmental factors. However, studies have indicated that the response functions may be plastic with other factors. Until now, little attention has been paid to this type of response. Here, using extensively collected field observations and data from intentionally designed interval planting experiments with winter wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), and spring maize (*Zea mays* L.), we show that temperature response functions during RGP are plastic with day of year of flowering/heading (DOY_R). Coefficients of determination between DOY_R and development rate were significant for 69% sites. Partial correlation coefficients between development rate, temperature, and DOY_R suggest that DOY_R explains almost the same variability in maturity date as temperature. The plastic model was developed by coupling DOY_R with a linear temperature response function. The model can improve the fitting efficiency by 112%, while dependency between DOY_R and temperature explains less than 25% of this improvement. The average RMSEs of simulated maturity date estimated by the plastic model in the three crops were 2.1, 2.5, and 3.7 d, respectively, while the corresponding values given by widely applied traditional models were 3.1, 6.5, and 7.4 d, respectively. Therefore, the plastic model can reduce simulation error by half. Moreover, simulation errors resulting from the plastic model have less systematic bias than traditional models. The plastic model simply and effectively provides accurate estimates of crop maturity and reduces the system deviation of the estimates. Coupling the plastic model of crop development with crop simulation models will likely decrease uncertainties in simulated yield under warming conditions. Additionally, results of this study will encourage future studies of other phenotype plasticity considered in current crop simulation models.

1. Introduction

As sessile organisms, plants require a tremendous capacity to adjust their phenotype to survive in the environment to which they have been dispersed (Rozendaal et al., 2006). Many kinds of phenotypes in various plant species are plastic to changes in environmental conditions (Nicotra et al., 2010), such as leaf functions (Schmitt et al., 2003; Rozendaal et al., 2006; Poorter et al., 2009), root distribution in soil profiles (Hodge, 2004), optimum temperature of photosynthesis (Kumarathunge et al., 2019), and photosynthetic capacity (Kattge and Knor, 2007). However, plasticity in crop phenology has not been well investigated, especially during the reproductive growth period (RGP, from flowering (for wheat and maize) or heading (for rice) to maturity). Though many crop simulation models are already essential tools for investigating climate change effects on agriculture (Asseng et al., 2015), the thermal time accumulation required to complete RGP for a specific variety is generally assumed to be a constant in these models. As simulation models generally allocate most of the biomass formed during RGP to storage organs such as grain (Jones and Kiniry, 1986; Supit et al., 1994; Mccown et al., 1996; Bouman et al., 2001), the length

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of RGP has a very large impact on crop yield. Understanding the plasticity of development rate to environment during RGP can provide the basis for accurately evaluating the impact of climate change on crop yield.

Three factors are generally considered to impact development rate during the vegetative growth period (temperature, photoperiod, and/or vernalization) (Mouradov et al., 2002). However, most models currently consider only one factor (temperature) to affect development rate during RGP, though soil water condition can also affect development (McMaster and Wilhelm, 2003; Liu et al., 2016b). Three cardinal temperatures are generally used to define the response of development rate to temperature. They are: base temperature (below which development rate is zero), optimum temperature (at which development rate is the maximum), and maximum temperature (above which development rate is zero) (Porter and Gawith, 1999). Response functions can be linear or curvilinear between base temperature and optimum temperature, and between optimum temperature and maximum temperature (Wang et al., 2017). The time scale applied when calculating the thermal time accumulation with a temperature response function is usually daily and hourly (Supit et al., 1994; Yin et al., 1995; Bouman et al., 2001). Maturity date can then be predicted if meteorological data and the starting date of RGP are available. This framework for describing a temperature response function is the most widely accepted and applied method used in crop modeling.

One of the underlying assumptions of this framework is that the assumed temperature response function will remain the same for a given variety and is independent of conditions other than temperature. However, crop maturity is also affected by other factors including unfavorable weather events. For example, wheat originated from the arid countries northwest of the Fertile Crescent (Salamini et al., 2002), where the summer is hot and dry. Wheat has adapted to local climate and evolved to mature before the onset of the unfavorable hot and dry weather. Autumn-harvested crops, including maize and rice, have a vital need to produce progenitive seeds before a killing frost occurs. In fact, it is widely accepted that all plants, including crop species, are already finely tuned to the seasonality of their growing environments (Menzel and Fabian, 1999; Cleland, et al., 2007).

Many phenotypes of plants are plastic to environmental conditions, and the molecular basis of this plasticity has been more and more clearly defined (Valladares et al., 2006; Zhu, 2016; Liu et al., 2017). Like other phenotypes, the temperature response function of development rate may not be a fixed relationship and may be plastic to the signals given by the environment. This shifted temperature sensitivity has been verified by Fu et al. (2015). But unlike other parameters in existing phenology models, the signal may not be quantified adequately by a genetic crop parameter since the time of occurrence of unfavorable events is not determined by crops, but rather is locally dependent.

The underlying assumption of the traditional framework also implies that, for a given variety, the contribution of per unit accumulated thermal time to development rate is equal at any time and in any place. However, after investigating rice phenology responses to historical climate change under conditions in which variety remained the same for 21 years, Zhang et al. (2008) reported that thermal time accumulation from transplanting to maturity has significantly increased with years. In a related modeling study, van Oort et al. (2011) found that the trend in simulation errors caused by the trend in thermal time accumulation could be removed by lowering the base and optimum temperature. However, Wu et al. (2019) carried out an extensive investigation with a similar data set across China and found thermal time accumulation during RGP in four of the seven investigated winter wheat varieties was increased significantly though the base temperature had been set low (0 °C). As shown in previous reports (Hawker and Jenner, 1993; Slafer and Rawson, 1995) for winter wheat, the base temperature during RGP was reported as 5 °C in most cases. Lowering base temperature to remove the increasing trend in thermal time accumulation therefore may not remove the trends in all crops. In addition, after examining the phenology of a spring maize variety across 34 sites in north China, Liu et al. (2013) reported that the thermal time accumulation in RGP significantly decreased with latitude. Consequently, the contribution of per unit accumulated thermal time to development rate may also be plastic with the environment.

In general, one of the important defects existing in the traditional framework is that it considers crop response to environment but not crop adaptation to environment. The key problem in considering crop adaptation is to find out which factors are proper to use to quantify the adaptation. Since phenology has been regarded as a major adaptive trait of plants to environment (Cleland et al., 2007), and the climatic environment under which plants grow changes annually, the day of year of a phenology event (DOY_{ph}) could be used to characterize both the preceding climate that a crop has experienced and the anticipated climate that a crop will experience. Therefore, DOY_{ph} has the potential to act as a signal given by the environment. Several reports have already implied the possible relationships between DOY_{ph} and development rate. Zhao et al. (2016) reported that timing of rice maturity in China was affected more by day of year of transplanting date than by climate change. Fu et al. (2014) showed experimental results from indicating that a warming-induced earlier spring led to earlier autumn senescence in trees. The relationship was then verified by field and satellite observations (Keenan and Richardson, 2015). The model based on the relationships between day of year of spring phenology and autumn senescence has proven to be able to produce accuracy similar to that of traditional models (Keenan and Richardson, 2015). However, until now, there has been very little research on the plastic phenology model in crops.

In this study, we assume that the temperature response function during RGP of crops is plastic to the day of year of flowering/heading (DOY_R), i.e., the contribution of per unit temperature on development rate is affected by DOY_R. Extensively collected field-observed data were obtained and an intentionally designed interval planting experiment was conducted to compile data sets to verify this assumption. The objectives of this study were to verify the impact of DOY_R on development rate, investigate the independence of DOY_R to temperature in impacting maturity date, and to evaluate the plastic model through comparisons of simulations from three widely applied traditional crop models.

2. Material and methods

2.1. Sites and observations

Two data sets were assembled in which phenology data were observed under varying temperature conditions. The first data set was comprised of phenology observations of three crop species (winter wheat, rice, and spring maize) at 11 sites (Fig. 1). At each site, crop variety remained unchanged for at least 15 years. In total, 12 crop varieties were planted at these sites. There were seven winter wheat sites, two single rice sites, and three spring maize sites. The Tonghua station planted both single rice and spring maize. The start of RGP for winter wheat and spring maize was flowering. For rice, due to lack of observations of flowering date, the start of RGP was set as heading. Day of year of flowering and heading date for the three investigated crops were represented as DOY_R. The end of RGP for the three crops was physiological maturity. Phenological observations were managed by the Chinese Meteorology Administration (CMA). 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). Observations were conducted by trained agricultural technicians following standardized observation methods (CMA, 1993). All phenology observation data were obtained from the National Meteorological Information Center (NMIC). Historical weather data at agro-meteorological observation sites, including mean temperatures and precipitation during the same years as phenology observations were also collected from NMIC. Table 1 shows the site information and

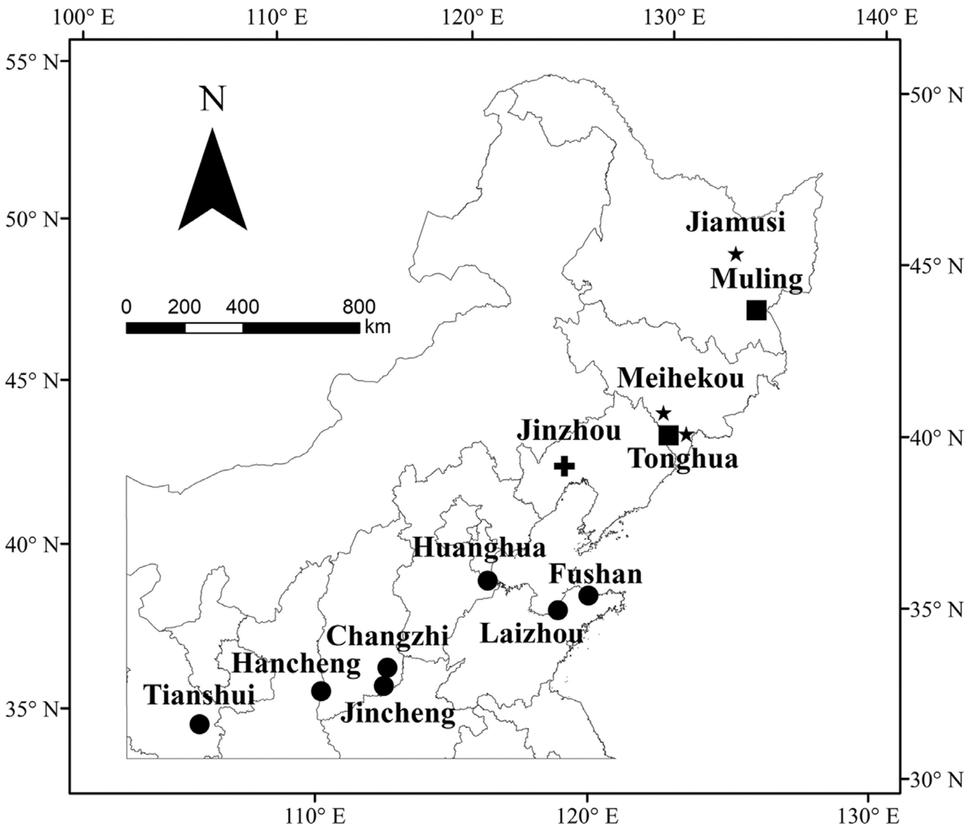

Fig. 1. Locations of 11 agro-meteorological observation sites and one experiment site. + is the site where the intentionally designed interval planting experiment was carried out, ● are winter wheat observation sites, ■ are rice sites, ★ are spring maize sites. Tonghua station had both rice and spring maize observations, with the ★ 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.

summary meteorological information for these sites. Wu et al. (2019) described the phenological characteristics of these crops in more detail. This data set represents the response of maturity date to climate change under normal planting conditions.

The second data set was an intentionally designed interval planting experiment under controlled conditions. This experiment was carried out to observe spring maize phenology response to different sowing dates at Jinzhou Agricultural Ecosystem Experiment Station (41.82° N, 121.20° E, 17 m a.s.l) (Fig. 1) in 2018. Soil at this site is a typical brown soil, with field capacity of 21.6% and wilting point of 6.2% in the 0–50 cm profile. The variety was ZD958, which is a widely planted variety in China (Liu et al., 2013; Hou et al., 2014). The first planting was done at day of year 94. Planting earlier than this day results in poor seedling emergence due to low soil temperatures. Seeds were subsequently planted every five days. The last planting was ended on day of year 149. Planting later than this date results in maize not reaching physiological maturity before a killing frost. Each planting occupied a plot (15 m long and 5.5 m wide), with an in-row plant spacing of 0.5 m and row spacing of 0.3 m. The experiment was managed such that there were no water and nutrient stresses. Management was performed to guarantee optimum growth and to avoid the effects of weeds and pests. Table 2 provides the detailed information for the experiment. There was a national weather station within 50 m of the experiment field. Daily average temperatures were collected from the weather station. This data set characterized the response of maize maturity date to a large variation in flowering date under natural conditions.

Table 1
Summary information for sites in which the planted variety remained unchanged for at least 15 years. Laizhou and Fushan planted the same variety 'YN15'. In order to distinguish between the two, the variety name was marked as 'YN15(LZ)' and 'YN15(FS)', respectively. The definition of reproductive growing season for winter wheat and spring maize is from flowering to maturity, and for rice is from heading to maturity.

Site name	Elevation (m)	Number of observations	Variety	Reproductive Growing season duration (d)	Annual temperature (°C)	Reproductive growing season average temperature (°C)	Reproductive growing season rainfall (mm)
Winter wheat							
Changzhi	992	17	CZ648	32.6	9.9	19.2	55
Hancheng	458	15	XY6	32.6	13.8	20.7	63
Jincheng	753	21	5819	35.3	11.9	20.1	69
Huanghua	7	23	71,321	28.0	13.0	21.7	40
Laizhou	48	21	YN15(LZ)	35.3	13.4	21.0	56
Fushan	54	26	YN15(FS)	36.3	12.8	20.9	60
Tianshui	1142	19	7464	40.4	11.5	19.7	71
Rice							
Tonghua	380	26	QG	48.5	6.0	19.1	124
Muling	266	16	SY397	42.6	4.0	19.1	197
Spring maize							
Jiamusi	82	18	DN248	59.9	4.1	18.6	184
Meihekou	341	15	TD4	59.7	5.8	18.7	227
Tonghua	380	20	JD101	51.7	6.0	20.7	319

Table 2

Dates of planting, flowering, and maturity, reproductive growing period (RPG) length, average temperature, and accumulated temperature for maize in interval planting experiment at Jinzhou, China during 2018.

Number of planting	Planting date[b]	Flowering date[b]	Maturity date[b]	RGP Length (d)	Average temperature (°C)	Accumulated temperature (°C·d)[a]
1	94	190	253	64	25.6	1123.7
2	99	192	253	62	25.6	1091.2
3	104	192	255	64	25.5	1119.8
4	109	194	257	64	25.5	1117.1
5	114	195	258	64	25.4	1111.1
6	119	195	258	64	25.4	1111.1
7	124	196	260	65	25.2	1115.1
8	129	200	261	62	25.1	1060.6
9	134	212	263	52	24.4	850.9
10	139	212	266	55	24.1	883.1
11	144	213	271	59	23.4	906.1
12	149	213	273	61	23.0	914.2

[a] The effective accumulated temperature above 8 °C.

[b] day of year.

2.2. Testing the driving effect of DOY_R on development rate

Regression analysis between DOY_R and development rate for each species and at each site was conducted to determine if DOY_R affects the development rate. Significance level of coefficient of determination was determined by two-tailed *t*-test.

Readers should be aware that DOY_R and average temperature in RGP are not totally independent. The relative influence of DOY_R on development rate was tested for each species and at each site using partial correlation analysis (controlling for temperature). The significance level of the partial correlation coefficient was also determined by two-tailed *t*-test.

Because both reciprocal of number of days and reciprocal of thermal time accumulation are widely used to represent development rate, the regression analysis and partial correlation analysis were performed for these two development rate expressions.

2.3. Introduction to the plastic temperature response function

The plastic phenology model was developed by assuming that development rate is linearly related to temperature, but that the linear relationship is affected by DOY_R. Three kinds of regression relationships were designed to investigate how fitting efficiency (R^2) was improved by coupling DOY_R with a linear temperature response function.

The response of development rate to temperature is essentially nonlinear (Bonhomme, 2000), but for ease of application, it is assumed to be linear over a wide temperature range in many crop simulation models (Hodges and Ritchie, 1991; Supit, et al., 1994; Bouman et al., 2001). For simplicity, we assumed a linear response function. The linear relationship is:

$$R = a_1 + b_1 \times T \tag{1}$$

where R is the development rate over a specified growth period (d^{-1}), and a_1 and b_1 are regression coefficients. T is growth period average temperature (°C). Traditional mechanical models can be roughly regarded as a special case of this linear function, since they assume constant thermal time accumulations. However, in this linear function, the thermal time accumulation can be increased or decreased, depending on the linear tendency. The larger the linear tendency, the greater the decrease in thermal time accumulation, and vice versa.

We assumed that the linear tendency (b_1 in Eq. (1)) was affected by DOY_R. Thus we defined the plastic model as:

$$R = a_2 + (b_2 + c_2 \times D) \times T \tag{2}$$

where a_2, b_2, and c_2 are regression coefficients, D is the DOY_R. If DOY_R does affect temperature sensitivity, R^2 of the plastic relation is expected to be much larger than for the linear temperature response function. Obviously, the linear relationship (Eq. (1)) is a special case of the plastic relationship (Eq. (2)). Traditional models, therefore, can be seen as a special case of the plastic model.

Fitting efficiency of Eq. (2) can be partially explained by the linear relationship between DOY_R and T. Thus, we replaced DOY_R in Eq. (2) with the linear regression between DOY_R and T:

$$R = a_3 + (b_3 + c_3 \times (d_3 + e_3 {*} T)) \times T \tag{3}$$

where a_3, b_3, c_3, d_3, and e_3 are regression coefficients.

Reorganizing Eq. (3) and produces the polynomial relationship:

$$R = a_4 + b_4 \times T + c_4 \times T^2 \tag{4}$$

where a_4, b_4, and c_4 are regression coefficients. a_4 equals a_3, b_4 equals $b_3 + c_3 \times d_3$, while c_4 equals $c_3 \times e_3$. If the effect of DOY_R on development rate is not primarily caused by the dependency between DOY_R and average T, R^2 in the plastic relationship is expected to be larger than the polynomial relationship.

The above three regressions were performed for each variety of each crop 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 represent the development rate, regressions were performed on these two development rate expressions. Values of AICc were used to determine whether it was cost-effective to introduce DOY_R in Eq. (1):

$$\mathrm{AICc} = \mathrm{n} \times \ln(1 - R^2) + 2\mathrm{k} + \frac{2k \times (k + 1)}{n - k - 1} \tag{5}$$

where n represents the number of observations, R^2 is the coefficient of determination in each regression, and k denotes the number of parameters needed to be fitted. For Eqs. (1) and (2), k equals 2 and 3, respectively.

2.4. Model comparison

Three commonly applied traditional phenology models (used by crop growth models CERE-Wheat, CERES-Maize, and ORYZA2000) were used to simulate crop phenology. Many reports have described the models in detail (Jones and Kiniry, 1986; Hodges and Ritchie, 1991; Bouman et al., 2001). For all three models, only one parameter affects development rate during RGP. For CERES-Wheat and CERES-Maize, the parameter is the thermal time accumulation. For ORYZA2000, the parameter is the inverse of the thermal time accumulation. Parameters for these models were optimized over a wide range and with a small step. For these three models, parameter ranges were 300–800, 500–1150, and 0.0001–0.0050, respectively. The corresponding steps were 1, 1, and 0.0001, respectively. All observations were used to calibrate the model. The principle of optimization was root mean square

Table 3

Slopes, coefficients of determination and partial correlation coefficients (controlling for temperature) between day of flowering/heading date DOY_R and development rate. In calculating the development rate, both reciprocal of number of growing days and reciprocal of accumulated temperature were used as the development rate. Base temperatures for calculating the accumulated temperature for winter wheat, rice, and spring maize were set as 0, 8, and 8 °C, respectively.

	Crop	Variety	Using the reciprocal of number of days during RGP as the development rate			Using the reciprocal of accumulated temperature during RGP as the development rate		
			Slope ($\times 10^{-3}$)	R^2	*r (partial correlation coefficient)*	Slope ($\times 10^{3}$)	R^2	*r (partial correlation coefficient)*
Field observation	Winter wheat	CZ648	0.4372	0.572*	0.429	0.0151	0.241*	0.431
		XY6	0.5180	0.807***	0.734***	0.0150	0.336*	0.726***
		5819	0.6141	0.663***	0.639**	0.0256	0.430***	0.647**
		71,321	0.6014	0.622**	0.215	0.0114	0.138	0.208
		YN15	0.4038	0.754***	0.756***	0.0164	0.455***	0.757***
		YN15	0.4328	0.658***	0.628***	0.0171	0.330**	0.636***
		7464	0.0841	0.263	0.120	0.0012	0.008	0.131
	Rice	QG	-0.0551	0.038	0.391	0.0282	0.553***	0.385
		SY397	-0.0437	0.010	0.240	0.0578	0.429***	0.317
	Spring maize	DN248	0.1700	0.638**	0.765***	0.0382	0.761***	0.797***
		TD4	0.0072	0.032	0.698**	0.0369	0.770***	0.678**
		JD101	0.2241	0.573**	0.691***	0.0410	0.669***	0.712***
Interval planting experiment	Spring maize	ZD958	0.0996	0.605**	0.902***	0.0115	0.924***	0.893***

*, **, ***: statistically significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$ levels.

error (RMSE) minimization. The parameter values that achieved the minimum RMSE were considered as the best values.

Maturity date simulation errors and corresponding RMSE values produced by the traditional models and the plastic model were calculated. Trends of simulation errors over RGP average temperature, DOY_R, and year were calculated to evaluate model performance and compared for both traditional models and the plastic model.

3. Results

3.1. Effect of DOY_R on development rate

When using the reciprocal of number of days from flowering/heading to maturity as the development rate, DOY_R was positively related to development rate for 11 sites, and nine of them were significant (Table 3). Neither of the two negative relationships were significant. The relationships were significant at six winter wheat sites and three spring maize sites (including the interval planting experiment) (Table 3). The averaged R^2 for the three crops were 0.62, 0.02, and 0.46, respectively. When using the reciprocal of accumulated temperature as the development rate, DOY_R was positively related to development rate for all sites (Table 3), and 11 of them were significant. The averaged R^2 for the three crops were 0.28, 0.49, and 0.78, respectively. The interval planting experiment with maize had the highest R^2 (0.923). These results suggest that the development rate is positively related to DOY_R.

Partial correlation coefficients between DOY_R and development rate (controlling for temperature) were also positive for all varieties of all crops, whether the development rate was expressed as the reciprocal of number of days or the reciprocal of accumulated temperature (Table 3). For the two expressions, partial correlation coefficients for the three crops were significant at 57% of winter wheat sites, 0% of rice sites, and 100% of maize sites. When the development rate was expressed as the reciprocal of number of days, averaged partial correlation coefficients for the three crops were 0.50, 0.32, and 0.76, respectively. When controlling for DOY_R in the partial correlation analysis, the averaged correlation coefficients for the three crops were 0.45, 0.56, and 0.65, respectively. These results suggest that DOY_R explains almost the same amount of variability in maturity date as temperature for the three crops.

Additionally, Table 2 shows that for the interval planting experiment with maize, each day delay in flowering date resulted in a decrease of accumulated temperature by 11.4 °C·d ($R^2 = 0.938$, $p < 0.001$). This result indicates that the contribution of per unit accumulated temperature to development rate is positively related to DOY_R.

3.2. Improved fitting efficiency after coupling DOY_R with a linear response function

Based on the observed relationship between DOY_R and development rate, a plastic phenology model was developed, which accounts for the impact of DOY_R on development rate (Eq. (2)). Results showed that fitting efficiency (R^2) can be greatly improved after DOY_R was combined in the linear temperature response function for both the case of using the reciprocal of number of growing days (Fig. 2) as the development rate and the case of using the reciprocal of accumulated temperature (Fig. 3) as the development rate.

For the case of using the reciprocal of number of growing days as the development rate, the R^2 values were improved for all varieties of all crops when DOY_R was included in the relationship compared with the linear function (Fig. 2). Average R^2 values for the three crops were improved by 0.23, 0.06, and 0.49, respectively. The R^2 values in the maize variety ‘DN258’ increased the most (0.59). Averaged over all variety and crops, the R^2 was improved by 112%. Dependency between DOY_R and temperature partially explains the improved R^2. The polynomial relationship showed that after considering this dependency, R^2 values for the three crops were only improved by 0.04, 0.12, and 0.04, respectively. On average, the R^2 was improved by 20%. Therefore, the dependency between DOY_R and temperature explains less than 20% of the improvement resulting from incorporating DOY_R.

Similar results were obtained using the reciprocal of accumulated temperature as the development rate (Fig. 3). For this case, the R^2 values for the three crops were improved by 0.30, 0.03, and 0.18, respectively, while the quadratic polynomial relationship improved R^2 by 0.06, 0.08, and 0.03, respectively. On average, the plastic and polynomial relationships improved R^2 by 65% and 15%, respectively. In this case, dependency between DOY_R and temperature also explained only 25% of the improvement. These results further indicate that DOY_R can be regarded as a relatively independent factor, and confirms that introducing DOY_R into the linear temperature response function can greatly improve model fitting efficiency.

The AICc values for Eq. (2) were lower than the values for Eq. (1) in nine out of 13 sites in the two expressions of development rate (Fig. 4), indicating that introducing DOY_R was effective for explaining maturity

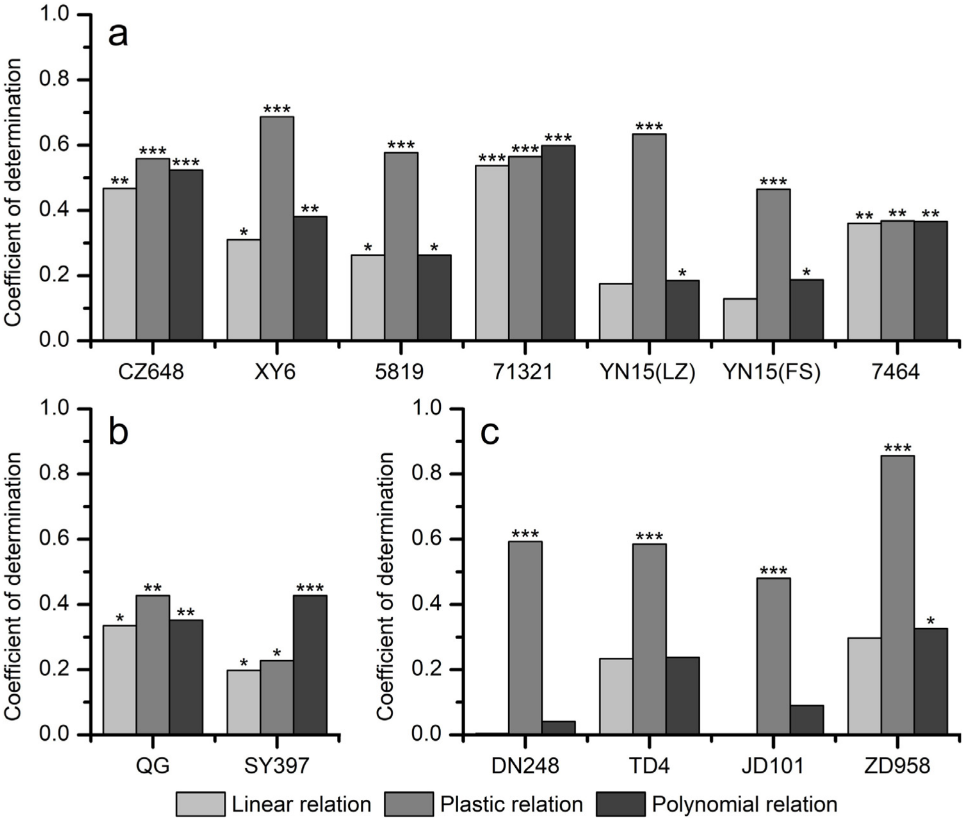

Fig. 2. Coefficients of determination for three kinds of relationships (linear, plastic, and polynomial) for winter wheat (a), rice (b), and spring maize (c) using the reciprocal of number of growing days as the development rate. *, **, ***: statistically significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$ levels.

date variation at most sites.

3.3. Model evaluation

Table 4 shows the values of the three parameters in the plastic model. The influence of DOY_R on temperature sensitivity (parameter c_2 in Eq. (2)) was found to be positive for all varieties of all crops. For winter wheat, rice, and spring maize, the average impact of DOY_R on temperature sensitivity was 0.0016×10^{-3}, 0.0058×10^{-3}, and 0.0132×10^{-3}, respectively. We interpret this to mean that the development rate of all three crops will be accelerated if the DOY_R is increased.

Averaged over all crops and varieties, the RMSE found for the simulation of maturity date by the plastic model (2.5 d) was about half of that found for the traditional developmental models used by the three crop simulation models (5.0 d) (Fig. 5a). For all varieties of all crops, the plastic model always resulted in lower RMSE than seen with the traditional models. The average RMSE values resulting from the plastic model were 2.1, 2.5, and 3.7 d for winter wheat, rice, and spring maize, respectively, while the corresponding values resulting from the traditional developmental models were 3.1, 6.5, and 7.4 d, respectively. Therefore, the plastic model was found to be more accurate than the traditional models. This was mainly because traditional models assume that development rate was only affected by temperature and assumed constant thermal time accumulations. In years with later DOY_R, this assumption will lead to a very late simulated maturity date, or even to a situation in which the crop never matures in an extremely cold year. But with the plastic model, later DOY_R will result in greater temperature sensitivity, thus reducing the number of growing days during this period, resulting in simulated plant development always reaching maturity, even in cold years.

Additionally, the simulation error generated by the plastic model was not significantly related to temperature and DOY_R at all sites (Fig. 5b,c), and was significantly related to year at four sites (Fig. 5d). With the traditional models, errors were significantly related to temperature at five sites, to DOY_R at seven sites, and to year at six sites. Therefore, the plastic model can reduce the system error of the simulated maturity date.

The plastic model provided a better fit of simulated maturity dates to observed maturity dates than the traditional models for winter wheat and spring maize, with R^2 values of 0.932 and 0.772, respectively (Fig. 6a, c). For the traditional models, the corresponding R^2 values were 0.884 and 0.633, respectively. As for rice, the ORYZA2000 model ($R^2 = 0.957$) gave a slightly better fit than the plastic model ($R^2 = 0.938$) (Fig. 6b). However, the plastic model gave a better no-bias fit than the traditional models used for the three crops. For winter wheat, rice, and spring maize, when flowering/heading date was delayed by 1 day, the maturity date simulated by traditional models was delayed by 1.13, 1.61, and 1.24 d, respectively, while the plastic model predicted delays of 1.00, 1.07, and 0.91 d, respectively. For spring maize in the interval planting experiment, the systematic biases for the traditional models and the plastic model were 1.81 and 0.86 d, respectively (Fig. 6d). Hence, considering all four data sets, the plastic model gave better unbiased estimates of maturity date than the traditional models.

Observations of rice variety 'QG' at the Tonghua have been reported previously (Zhang et al., 2008; van Oort et al., 2011). In the current study, this site was used as a typical case to show how the plastic model and ORYZA2000 performed in detail. At this site, the RMSE values produced by the plastic model and ORYZA2000 were 1.7 and 6.1 d, respectively (Fig. 5a). The trends of simulation error against year, growth period average temperature, and DOY_R produced by ORYZA2000 were significant, while the only significant trend of simulation error produced by the plastic model was the trend of simulation error against year. Though the error produced by ORYZA2000 was larger than the error produced by the plastic model in 19 out of 26

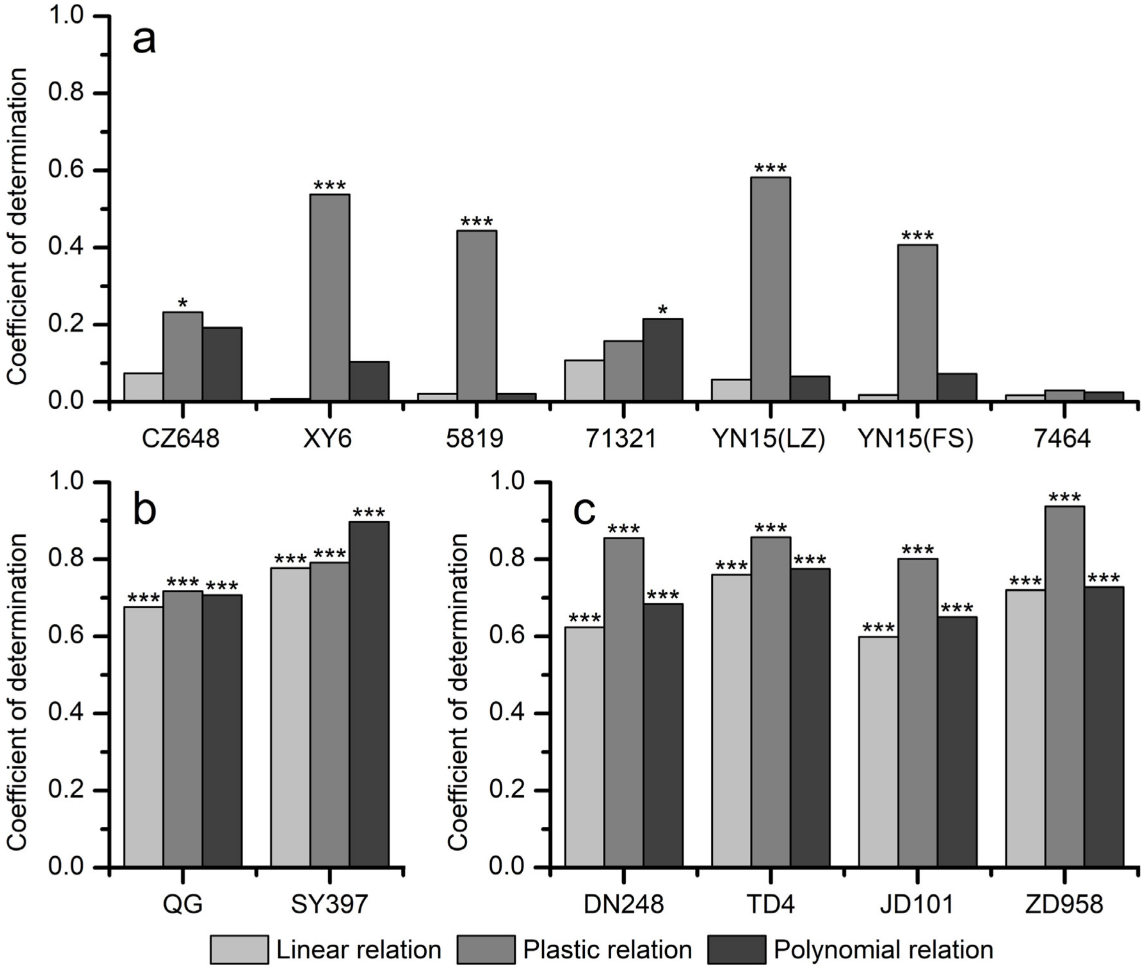

Fig. 3. Coefficients of determination of three kinds of relationships (linear, plastic, and polynomial) for winter wheat (a), rice (b), and spring maize (c) using the reciprocal of accumulated temperature as the development rate. Base temperature used in calculating the accumulated temperatures for winter wheat, rice, and spring maize were 0, 8, and 8 °C, respectively. *, ***: statistically significant at $p < 0.05$ and $p < 0.001$ levels.

years, this large RMSE was mainly attributed to the very large error observed in 1986 when the simulation error produced by the plastic model and by ORYZA2000 were 1 and 18 d, respectively (Fig. 7a). In this year, measured effective accumulated temperature above 8 °C was 355 °C·d. This was the lowest value during the entire 26 years. The average value during these years was 473 °C·d. Average heading and maturity dates were 7 August and 17 September, respectively. Hence, during this period, temperature was decreasing, and the effective temperature accumulated for each day was also gradually decreasing. According to the assumption used in ORYZA2000, the model needed 473 °C·d to reach maturity in every year. In 1986, ORYZA2000 needed extra days to accumulate the additional 118 °C·d, thus the simulation

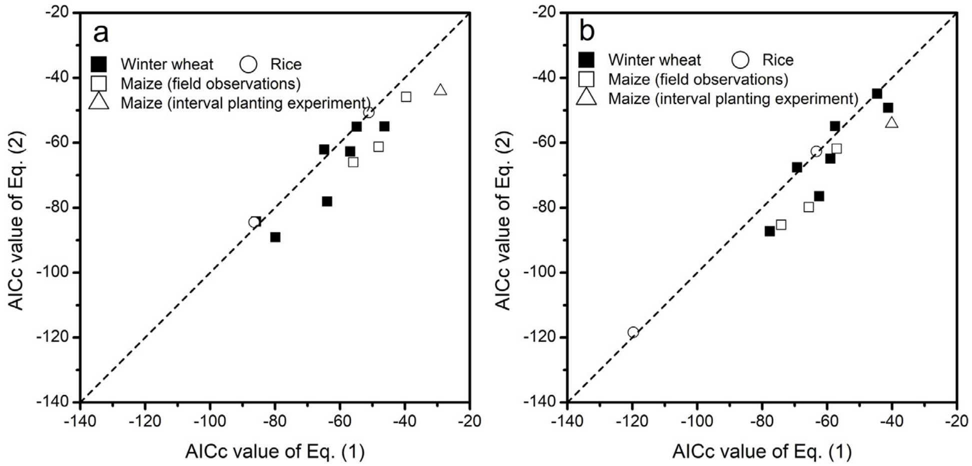

Fig. 4. AICc value of Eqs. (1) and (2) using the reciprocal of number of growing days as the development rate (a) and using accumulated temperature as the development rate (b).

Table 4
Values of the three parameters in the plastic model for all varieties of winter wheat, rice, and spring maize.

	Crop	Variety	Parameter value in plastic model ($\times 10^{-3}$)		
			a_2	b_2	c_2
Field observation	Winter wheat	CZ648	−3.356	−0.02	0.01334
		XY6	20.256	−2.172	0.02268
		5819	1.584	−2.124	0.02675
		71,321	−5.737	0.605	0.01023
		YN15(LZ)	16.592	−1.706	0.01784
		YN15(FS)	16.427	−2.033	0.01929
		7464	4.557	0.834	0.00148
	Rice	QG	3.162	−0.462	0.00648
		SY397	12.923	−0.574	0.00514
	Spring maize	DN248	3.68	−2.307	0.01441
		TD4	0.696	−1.498	0.01118
		JD101	6.711	−2.78	0.01658
Interval planting experiment	Spring maize	ZD958	−26.176	−0.388	0.01051

error was very large. In contrast, the plastic model assumes that the later the DOY_R is, the larger the temperature sensitivity. In 1986, the DOY_R was the latest of all 26 years (14 August), thus the temperature sensitivity was also the highest. Consequently, less accumulated temperature was required in this year. Hence, the simulation error given by the plastic model in this year was only 1 d. The huge simulation error in this one year also contributed to the significant trend of simulation error against average temperature (Fig. 7b) and against DOY_R (Fig. 7c). In this case, the plastic model showed the typical advantage in a year with extreme climate.

4. Discussion

The accurate and unbiased estimation of crop phenology response to climate variation is essential for correctly and reliably estimating crop yield response to future climate change. Previous studies indicate that crop yields will likely decline in the context of climate warming, mainly due to shortened growth periods (Challinor et al., 2016; Liu et al., 2016a). However, in this study, we found that the response of development rate to temperature in RGP is plastic with DOY_R. This plastic relationship indicates that under warmer conditions, crop growing season length during RGP will not likely be shortened as much as traditional models predict.

Previous studies have shown that many phenotypes of plants are plastic to environments (Sultan, 2000; Pigliucci, 2005). For example, root distribution in the profile is plastic to cope with the naturally occurring heterogenous supplies of water and nutrients (Hodge, 2004). Light was also found to have significant effects on leaf functions. Specific leaf area, the key phenotype used in current crop models, has also been shown to be plastic with irradiance (Rozendaal et al., 2006). Temperature response of photosynthesis varies temporally, as a result of adaption to changes in ambient temperature (Kumarathunge et al., 2019). Two main parameters representing photosynthetic capacity have been observed to adapt to plant growth temperature (Kattge and Knor, 2007). The plasticity we found in temperature sensitivity of development rate is consistent with the general conclusions in the field of genetics (Queitsch et al., 2002) and evolutionary biology (Franks, 2011).

The plastic temperature response function that we developed was based on and is an extension of the traditional temperature response framework. In traditional models, temperature sensitivity is always assumed to be in a fixed form in any year. Our plastic model extended this assumption and assumed that the sensitivity varied in different years. With the plastic assumption, if the DOY_R remained the same in every year, then the temperature sensitivity would also remain unchanged. Therefore, the traditional assumption is a special case of the plastic assumption. Some traditional models provide for physiological maturity when temperature is too low to accumulate sufficient thermal time accumulation, especially for autumn-harvested crops (Jones and Kiniry, 1986). This special rule is consistent with the assumption of the plastic model, i.e., allowing crops to mature before a killing frost.

Keenan and Richardson (2015) developed a phenology model for trees to relate autumn senescence with timing of spring phenology. In their model, if spring phenology events appeared earlier, autumn senescence would also appear earlier, and vice versa. Generally, one day earlier of spring events would result in about 0.6 day earlier autumn senescence. Both our plastic model and their model use day of year of a previous phenology event as input, so the two models are related. But

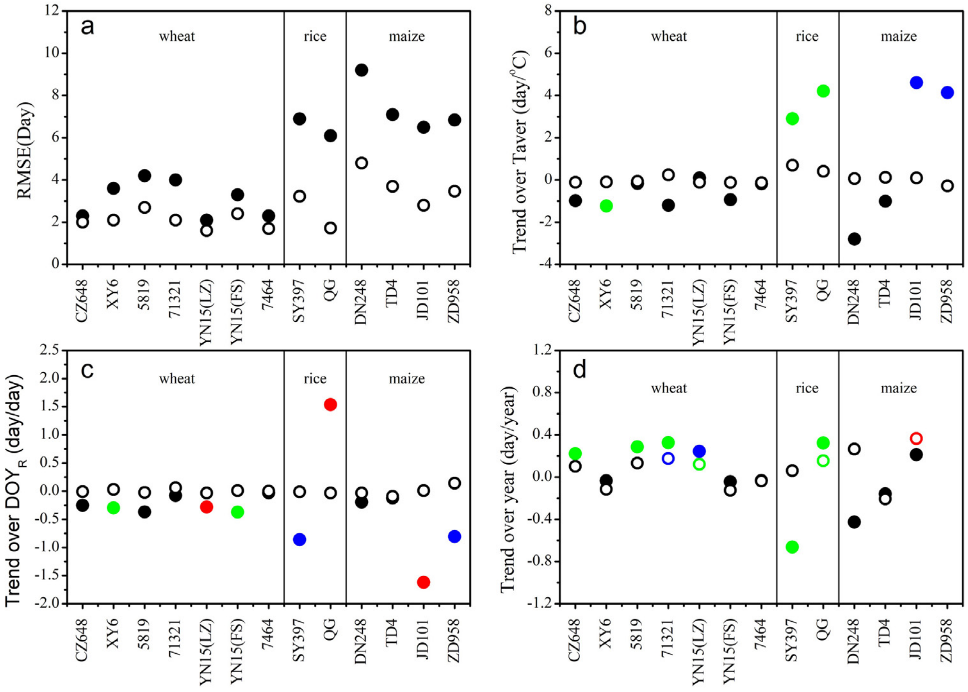

Fig. 5. Simulation accuracy of maturity date from the plastic model and three traditional phenology models (CERES-Wheat, CERES-Maize, and ORYZA2000) for varieties of winter wheat, rice, and maize. Panel a is the simulation root mean square error (RMSE); panel b is the trend of simulation error against growth period average temperature; panel c is the trend of simulation error against day of year of flowering/heading date; panel d is the trend of simulation error against year. The solid and hollow circles are for the traditional and plastic model, respectively. Green, blue, and red symbol colors indicate trend differences between the plastic model and the traditional phenology models that are statistically significant at $p < 0.05$, 0.01, and 0.001, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

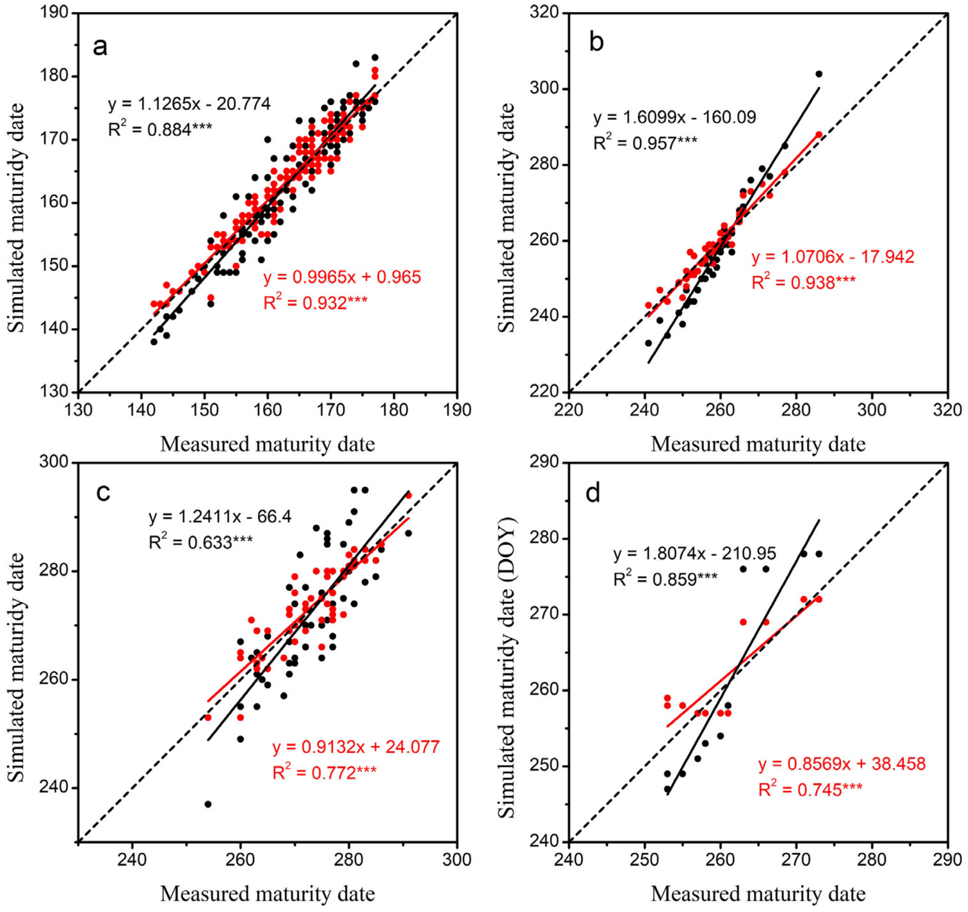

Fig. 6. Measured and simulated maturity date for winter wheat (a), rice (b), and spring maize (c) from field observations, and for spring maize (d) from the interval planting experiment. The maturity date was expressed as the day of year. The black points and regression lines are for the traditional model comparison and the red points and regression lines are for the plastic model comparison. ***: statistically significant at $p < 0.001$ levels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

one of the disadvantages of their model was that their model didn't take into account the effects of temperature on development rate. Our plastic model addresses this disadvantage by combining a linear temperature response function to determine maturity date, since it is well known that temperature plays an important role in determining crop development rate (Porter and Gawith, 1999; Siebert and Ewert, 2012).

There was a significant relationship between DOY_R and day length at each investigated site. Therefore, using day length in the plastic model instead of DOY_R can result in similar results. But doing so is equivalent to assuming that development rate during RGP is photoperiod sensitive. However, this assumption is contrary to current perceptions that development rate during RGP is not sensitive to day length. In addition, using day length in the model would result in a greater number of model parameters and generate additional computations. Therefore, in this study we used DOY_R, and propose that this parameter is a comprehensive indicator of many possible environmental factors. However, it is still not clear what exactly these factors are. Further research will be needed to explore the phenology plasticity.

Values of the three parameters determined for the plastic models in ‘YN15(LZ)’ and ‘YN15(FS)’ were very similar (Table 4). There are two possible reasons. The first is that both sites used the same wheat variety (‘YN15’) (Table 1) and this similarity may indicate that the parameter values of the plastic model will remain stable among different sites. The second reason may be that the two sites are not far apart (linear distance between sites is about 115 km) and both sites are located in the North China Plain (Fig. 1). Therefore, the climate at both sites is very similar (Table 1), resulting in the wheat variety showing similar plasticity in developmental response to temperature.

The traditional models have only one fitting parameter, less than the three parameters required for the plastic model. This is likely the primary reason that the plastic model was more accurate than the traditional models. However, the traditional models have three other implicit parameters, i.e., the three cardinal temperatures. We used their default values for model validation. For winter wheat, rice, and spring maize, their values were 0, 26, and 34 °C; 8, 30, and 42 °C; and 8, 34, and 44 °C, respectively, for the base, optimum, and maximum temperatures (Jones and Kiniry, 1986; Hodges and Ritchie, 1991; Bouman et al., 2001). Therefore, there is a chance to further reduce the simulation error by adjusting these values. For example, van Oort reported that by lowering the base and optimum temperature, the simulated RMSE produced by ORYZA2000 could be reduced (van Oort et al., 2011). However, the physiological meanings of the three cardinal temperatures are very clear. Determining their values cannot rely only on fitting the observed data. Adjusting parameter values casually can impair model function. In addition, finding the best cardinal temperature values is time-consuming work. Furthermore, multiple combinations of parameters may lead to the same simulation accuracy which will further lead to huge uncertainty in model results, especially with these nonlinear functions (He et al., 2017). Therefore, reducing simulation error by adjusting cardinal temperatures is much less desirable than reducing simulation error by directly assuming plastic temperature sensitivity.

There exists potential for improving accuracy of the plastic model. Using a more complicated temperature response function instead of a linear relationship may be one of the most promising ways. Many kinds of curvilinear functions have been applied in traditional models (Wang et al., 2017), which have proven to be more effective than linear functions. Therefore, there is reason to believe that curvilinear functions can be more effective than linear functions. However, in this study our use of linear functions was reasonable for the temperatures that most crops experience during RGP. All of the sites in our study were located in north China, where the chance of daily average temperatures

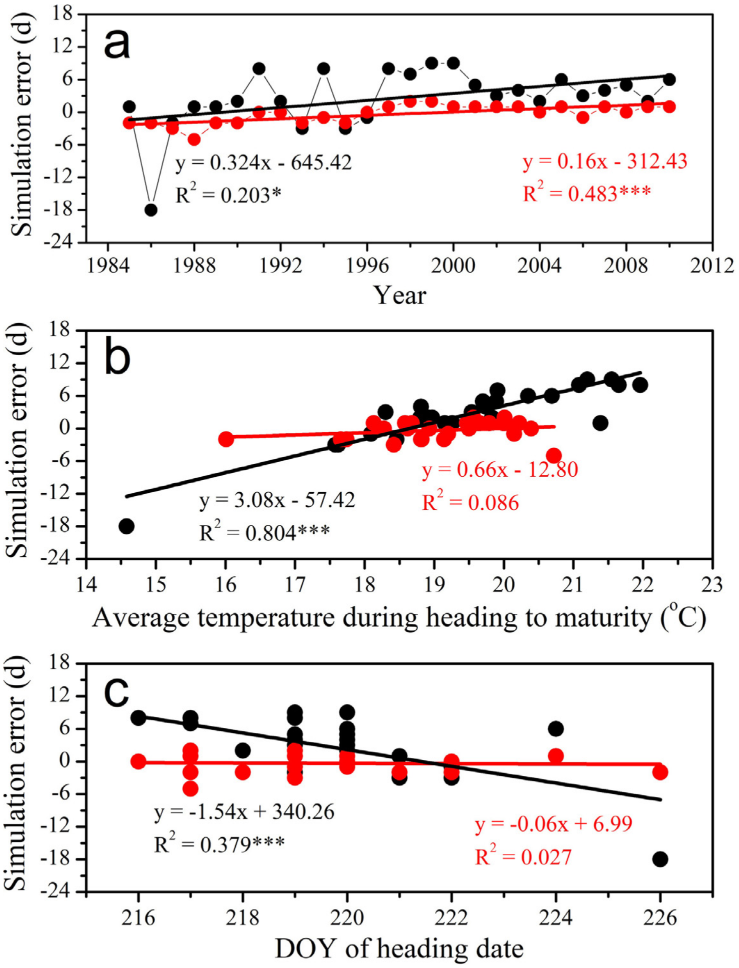

Fig. 7. Trends of rice maturity date simulation error over year (a), growth period average temperature (b), and day of year of heading date (c) produced by the plastic model and ORYZA2000. The black solid circles, regression lines, and regression equations are for the ORYZA2000 model, while the red solid circle, regression lines, and regression equations are for the plastic model. * and ***: statistically significant at $p < 0.05$ and $p < 0.001$ levels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

exceeding the optimum temperature are low, especially for rice and spring maize.

A second way to improve the plastic model is to use a nonlinear function instead of the linear relationship between DOY_R and temperature sensitivity, since the responses of development rate to environmental factors are very complicated, and the linear relationship is a simplified form of the actual relationship. However, using nonlinear functions will likely increase the number of fitting parameters and reduce model applicability.

Our findings indicated that warming-induced yield loss may be less than currently forecasted. This can be explained as a result of the trend for date of flowering/heading to occur earlier (Tao et al., 2013; Wu et al., 2019), which will reduce development rate temperature sensitivity, and thus stabilize the development duration and thereby benefit crop yield. Additionally, the reduction in temperature sensitivity may be beneficial for crops to maintain adaptability to climate. Rahmstorf and Coumou (2011) reported that occurrences of extreme weather have increased over the past few decades and will likely continue to increase in the future, especially associated with warm winter and warm spring events. By adjusting the temperature sensitivity of crop development rate, the improved phenology plasticity will prevent simulated maturity dates from appearing too late in cool years (thereby avoiding the risk of killing frost), and also prevent simulated maturity date from appearing too early in warm years, thereby making the most efficient use of thermal resources and accurately simulating the accumulation of more dry matter.

The plastic model of plant development that resulted from this study has potential for improving calculations of regional and global carbon uptake and emission. Moreover, other important processes simulated by crop models, such as dry matter allocation among different plant structures, specific leaf area, etc., may also be plastic to environmental factors such as irradiance, water availability, and nutrient status. If these additional plastic responses are accurately accounted for in crop models, uncertainties and errors in simulated yield responses to future climate change will likely be effectively reduced.

5. Conclusions

Based on field observations and data from an interval planting experiment, we found that the sensitivity of crop development rate to temperature during RGP was positively plastic with DOY_R for winter wheat, rice, and spring maize. Partial correlation analysis showed DOY_R can be regarded as an impact factor that is independent of temperature. Therefore, DOY_R can be used as the indicator to represent the phenological adaptive response of a crop to the local environment. The plastic phenology model, which was developed by coupling DOY_R with a linear temperature response function, can greatly improve the model fitting efficiency. The dependency between DOY_R and temperature explained only a small part of this improvement. Compared with traditional phenology development methods used in three widely used crop simulation models, the plastic phenology model reduced the simulation error by nearly half, and can effectively reduce the systematic tendency of simulation error in a simple and effective way. The future use of this plastic model of crop development will improve estimates of crop yield produced by simulation models, thereby more accurately predicting the impacts of future climate change.

Acknowledgments

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