RESEARCH

Using Stage-Dependent Temperature Parameters to Improve Phenological Model Prediction Accuracy in Rice Models

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ABSTRACT

Crop phenology models that use constant temperature parameters across developmental stages may be less accurate and have temperature-dependent systematic prediction error (bias). Using the DD10 model, we evaluated default and optimized (DD_Opt) temperature parameters using data from seven California rice (*Oryza sativa* L.) cultivars grown in six locations over 3 yr (2012–2014). Furthermore, we evaluated the effect of using stage-dependent temperature parameters on model performance using two- and three-stage optimization approaches. Optimized temperature parameters, or DD_Opt (RMSE: 2.3–5.4 d), performed better than DD10 (RMSE: 2.9–7.3 d). A temperature sensitivity analysis indicated that the time from planting to panicle initiation was most sensitive to temperature (every 1°C increase decreased days to panicle initiation by 1.8 d) while time from heading to R7 (marked by the appearance of one yellow hull on the main stem panicle) was not affected by temperature. Optimized temperature parameters varied between stages, with base temperature decreasing and optimum temperature increasing with plant development. Compared to the DD_Opt, two-stage optimization (planting–heading and heading–R7) reduced the RMSE by 0.8 d and the systematic error by 0.6 d $°C^{-1}$. Three-stage optimization (planting–panicle initiation, panicle initiation–heading, and heading–R7) further reduced RMSE by 1.1 d and systematic error by 1.4 d $°C^{-1}$ for preheading. These results demonstrate the importance of using stage-dependent parameters to improve accuracy of phenological models, which may be important when models are used to study the crop response to climate change, field management options, ecosystem productivity, breeding, and yield gap analysis.

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Abbreviations: DD_Opt, optimized temperature parameters; HD, heading stage; PI, panicle initiation stage; PL, planting.

THE ABILITY to accurately predict crop development is essential for the accuracy of crop growth simulation models (Penning de Vries et al., 1989; Yin et al., 1997). Crop models have been widely used to evaluate crop responses to climate change (Mall and Aggarwal, 2002; Yao et al., 2007; Wang et al., 2014), ecosystem productivity (White et al., 2009), yield gaps (van Ittersum et al., 2013; Espe et al., 2016), management practices (Awan et al., 2014), and technological change (Hijmans et al., 2003). Temperature and photoperiod are the primary environmental factors affecting crop development (Gao et al., 1992; Yin et al., 1996; Streck et al., 2011). While photoperiod only affects photoperiod-sensitive cultivars (and only during a discreet stage of development), temperature affects all cultivars during the entire growing season (Yin and Kropff, 1998). Many crop models simulate crop developmental (i.e., phenological) stages based on temperature and photoperiod, including Oryza2000 (Bouman et al., 2001), CERES-Rice (Jones et al., 2003), the Rice Clock model (Gao et al., 1992), and the β model (Yin et al., 1997). Others, such as DD10 (DD50 for the Fahrenheit scale; Keisling et al., 1984; Counce et al., 2009), simulate based on temperature only. In this study, we only focus on the effect of temperature on crop phenology, as the cultivars of interest were not photoperiod sensitive.

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For temperature-based phenology models (i.e., DD10), developmental rate is generally modeled in relation to thermal time accumulation (Gao et al., 1987; Yin et al., 1996). It is assumed that a certain amount of thermal time (degrees per day, °C d^{-1}) is needed to complete a given developmental stage (Gao et al., 1992; Summerfield et al., 1992). Thermal time accumulation is generally computed as a summation over time (e.g., days) of the temperature above a base temperature (T_b), and capped at an optimum temperature (T_{opt}), with no further development occurring above a maximum temperature threshold (T_{max}) or below T_b (Zhang et al., 2008). These temperature thresholds are known as 'cardinal temperatures.' The development rate parameters are generally computed as the reciprocal of the required thermal time, such that the product of the rate and the required thermal time is one. In this study, we refer to cardinal temperatures and developmental rate constants as 'temperature parameters.'

Most phenological models share the assumption that plants have the same response to temperature across all growth stages (van Oort et al., 2011), and therefore the same temperature parameters are used for pre- and postflowering stages (Timsina and Humphreys, 2006; Yao et al., 2007; Zhang and Tao, 2013). For example, in rice, both Oryza2000 and DD10 use a constant value for T_b and T_{opt} throughout pre- and postflowering (8°C for T_b and 30°C for T_{opt} in Oryza2000; 10°C for T_b and 34.4°C for T_{opt} in DD10).

There is evidence for wheat (*Triticum aestivum* L.; Slafer and Rawson, 1995) and faba beans (*Vicia faba* L.; Ellis et al., 1988) that optimal temperatures (in this case, T_b and T_{opt}) differ among crop developmental stages. For rice, it has been reported that the base temperature is lower during postflowering than during the preflowering stage (Dingkuhn et al., 1995; van Oort et al., 2011). While differential optimum temperatures among development stages have been reported, the effect of stage-dependent temperature parameters in models has not been evaluated. Nonetheless, given the importance of temperature parameters in crop phenology model performance, it is surprising that more attention has not been given to improving phenological model calibration (Mall and Aggarwal, 2002; Confalonieri et al., 2005).

Another issue to consider in phenology models is temperature-dependent systematic prediction error (henceforth referred to as systematic error). This systematic error is manifest in consistent over- or underpredictions of developmental rate as temperature changes. Others, based on using the Oryza2000 phenology submodel, have suggested that using default cardinal temperature values may result in systematic error (van Oort et al., 2011; Li et al., 2015). van Oort et al. (2011) indicated that it is especially important to evaluate systematic error when models are used outside of their original calibration temperature range. Both van Oort et al. (2011) and Yao et al. (2007) demonstrated that calibration of cardinal temperatures in Oryza2000 increased model accuracy and reduced systematic error compared to using default values.

The DD10 model was first developed in the 1970s by the University of Arkansas, Cooperative Extension Service to help rice growers improving the timing of midseason nitrogen application (Slaton et al., 1993). Since then, the DD10 model has been widely used in rice-producing areas in the southern United States (Keisling et al., 1984; Counce et al., 2015) and is used to predict developmental stages in rice cultivars. Using the thermal time concept employed in the DD10 model, the objectives of this study were (i) to determine if optimal temperature parameter values differ among developmental stages in rice, and (ii) to quantify the effect of using stage-dependent temperature parameters on model performance and systematic error relative to using constant optimized temperature parameters across all stages.

MATERIALS AND METHODS

Data

Field trials were conducted during the 2012 to 2014 growing seasons, next to the California Statewide Variety Trials (http://rice.ucanr.edu/) located in six counties of the Sacramento Valley in California. All fields were managed using the water-seeded system typical of California. That is, fields are preflooded, and presoaked seeds are broadcast via airplane into the flood water. The fields remain flooded throughout the season until about 3 wk before harvest, when the fields are drained in preparation for harvest. To maintain the floodwater height in the field, water continually flows into the field, except for brief periods when the floodwater in the field needs to be lowered for some reason (e.g., herbicide applications). The cultivar plots (each plot was 18.6 m^2) within these fields were managed identically to the main field, except that presoaked seeds were broadcast by hand into the plots. Phenological data were collected for seven rice cultivars with a range of maturation times (Table 1). These cultivars represent the majority of cultivars grown in California. Given the California climate, early-maturing cultivars are preferred and are planted on approximately 70 to 75% of the area. A medium-grain temperate *japonica* cultivar, M-206, is the most common and is planted in approximately 50% of the area (California Cooperative Rice Research Foundation, 2014).

The rice growth staging system developed by Counce et al. (2000) was used to identify three specific rice developmental stages: panicle initiation (PI, or R0), 50% heading (R3), and R7 (marked by the appearance of one yellow hull on the main stem panicle). Crop growth stage data were collected every 2 d during the periods of interest. The time to PI was determined when a dark green circle (i.e., "green ring") formed below the last-initiated leaves of the culm and initiated panicle (Counce et al., 2000). The day for 50% heading was when 50% of the panicles were fully exerted. This occurs about 1 to 3 d before flowering (the R4 stage; De Datta, 1981; Counce et al., 2015). While it would have been ideal for the model to project through to physiological maturity (the point at which

Table 1. Characteristics and duration of various stages of cultivars used in the study.

Cultivar	Maturity	Grain type	Planting to panicle initiation	Panicle initiation to heading)	Heading to R7
			d		
CM101	Very early	Short	46–56	25–36	16–23
L206	Very early to early	Long	46–58	27–39	13–21
M104	Very early	Medium	45–56	22–34	13–27
M202	Early	Medium	47–58	31–45	14–29
M205	Early	Medium	47–58	33–47	16–29
M206	Very early to early	Medium	47–56	26–38	16–27
S102	Very early	Short	46–56	24–35	15–26

carbohydrate accumulation ceases), physiological maturity is difficult to determine (Espe et al., 2016). In this study, R7 was used as a proxy for physiological maturity. Counce et al. (2000) indicated that physiological maturity typically occurs between R7 and R8 (R8 is when one brown hull appears on the main stem panicle). We used R7 because it was more objectively identifiable than R8 for the cultivars in this study. Across field trials, planting dates ranged from 29 April to 29 May, and time to PI from 45 to 58 d, PI to heading (HD) from 22 to 47 d, and HD to R7 from 13 to 29 d (Table 1).

For each location, weather data were obtained from the nearest (always within 20 km) California Department of Water Resources CIMIS (California Irrigation Management Information Systems) weather station (Snyder et al., 2001). California Irrigation Management Information Systems weather stations are a network of 145 automated weather stations in California, with the overall goal of increasing water use efficiency (http://www.cimis.water.ca.gov).

DD10 Model

Recently, Counce et al. (2015) used DD10 to present a thermal time sum data set on rice reproductive developmental stages for six rice cultivars in Arkansas. In DD10, daily thermal time accumulation is used to model rice development. A certain amount of thermal time is needed to complete a given developmental stage. The thermal time accumulated in each time step (in this case, t = 1 d) is calculated as follows:

$$\mathrm{TT}_t = \max(0, [0.5(T_{\max} + T_{\min}) - T_{\mathrm{b}}]) \qquad [1]$$

$$T_{\min} = T_{\mathrm{l}} \text{ if } T_{\min} > T_{\mathrm{l}}$$

$$T_{\max} = T_{\mathrm{opt}} \text{ if } T_{\max} > T_{\mathrm{opt}}$$

where TT_t is the thermal time at time t, $T_{\max}$ is the daily maximum temperature, $T_{\min}$ is the daily minimum temperature, T_{b} is the base temperature, T_{l} is the lower threshold, and T_{opt} is the optimum threshold. There is no development (i.e., TT_t below zero is set to zero) below T_{b} (here 10°C), and since $T_{\max}$ that are greater than T_{opt} are set equal to T_{opt}, there is no increase in development for daily maximum temperatures above T_{opt}. Similarly, for $T_{\min}$, since $T_{\min}$ that are greater than T_{l} are set equal to T_{l}, there is no increase in development for daily minimum temperatures above T_{l}. The default values for these 'cardinal temperatures' are T_{b} = 10°C, T_{l} = 21.1°C, and T_{opt} = 34.4°C (Counce et al., 2009). These values were obtained using common cultivars and weather data from 13 sites in Arkansas (Slaton et al., 1993).

Model Optimization and Systematic Error

Model Optimization and Evaluation

We first evaluated the DD10 model with its default cardinal temperature values using the 2012 to 2014 California data. To obtain the optimal temperature parameter values and evaluate the effect of stage-dependent temperature parameters on model performance and systematic error, three model simulations were conducted using the same thermal time concept as described for the DD10 model: single-stage, two-stage, and three-stage model simulations. In all simulations, we optimized all parameters (cardinal temperatures and thermal times) in the model (see below). In the single-stage simulation model (default and optimized, DD_Opt), the thermal time was calculated based on the assumption that cardinal temperature parameters are constant across all developmental stages (from PL to R7). In the two-stage simulation (DD_2S), the model was expanded such that the thermal time accumulation was based on stage-dependent cardinal temperature parameters for preheading (from PL to HD) and postheading (from HD to R7) stages. The three-stage simulation model (DD_3S) uses stage-dependent cardinal temperature parameters for three developmental stages: from PL to PI, PI to HD, and HD to R7.

We used a fivefold cross-validation statistical procedure to assess the prediction accuracy of optimized model parameters in DD10, DD_Opt, DD_2S, and DD_3S for all developmental stages. In this procedure, the data is randomly divided into K-fold (in this paper K = 5) datasets of approximately equal size (Jones and Carberry, 1994; Kohavi, 1995). Model results are presented as the mean of the resulting five sample RMSEs (James et al., 2013).

The *R* environment for statistical computing was used to implement and optimize the parameter values of the models (cardinal temperatures and thermal times), using the 'optim' function with the default method of Nelder and Mead (R Core Team, 2015). The optimization objective was set to minimize the RMSE (Eq. [2] below) for duration of a development stage (d) and systematic error (Eq. [3] below), minimizing the slope of the regression line between RMSE and average seasonal temperature in a given stage. Root mean square error was calculated as:

$$\mathrm{RMSE} = [n^{-1}\sum(\mathrm{SIM} - \mathrm{OBS})^2]^{0.5} \qquad [2]$$

where n is the number of observations, SIM is the predicted duration (d), and OBS is the observed duration (d).

Stage-Dependent Temperature Sensitivity

The observed duration of a given phenological stage was plotted against the mean temperature during the same period, which allows for an evaluation of whether that stage is sensitive to temperature (van Oort et al., 2011). An analysis of covariance was used to determine if the resulting slopes of the regression lines for stage were different from one another (Chatterjee and Hadi, 2015).

Systematic Error

For a given stage, we calculated the systematic error by fitting a linear regression model of RMSE as a function of mean temperature (van Oort et al., 2011). Systematic error is calculated using the following equation:

$$E = \alpha + \beta(T) \qquad [3]$$

where E is the prediction error (SIM − OBS), T is the average temperature during a given stage, α is the intercept (the random error),β is the slope, and $\beta(T)$ is the systematic error. The larger the β, the larger the temperature-dependent systematic error; thus, a β closer to zero is preferred. The unit for β is days per 1°C change in temperature (d °C^{-1}).

RESULTS

Single-Stage Models: DD10 versus DD_Opt

Optimal Temperature Parameters

For DD_Opt, with the exception of T_{opt} in cultivar M205, there was little difference in optimized temperature parameters among cultivars for the values of T_b, T_l, and T_{opt} (Table 2). Optimized values across cultivars averaged 11.5°C (range:11.2–11.9°C) for T_b, 13.2°C (range: 13–13.5°C) for T_l, and 32.7°C (range [not including M205]: 32.5–32.9°C) for T_{opt}. The largest difference between DD10 and DD_Opt was for T_l (21.1 versus 13.2°C). Cultivar M205 was different than the other cultivars with respect to T_{opt} which was 29.3°C—almost 3°C lower than the cultivar mean of 32.2°C; however, its T_b and T_l values were similar to those of other cultivars.

DD_Opt versus DD10

The ability of the DD_Opt to predict time to various stages was similar for all cultivars in terms of accuracy (RMSE) and systematic error (β, Table 3, Fig. 1). Given these results and that there was almost no difference among cultivars in terms of optimal temperature parameters, we will focus on results averaged across cultivars. The DD_Opt model improved accuracy compared with the default parameters of DD10, particularly for the PI to HD and HD to R7 stages, where the RMSE was reduced by 1 and 1.3 d, respectively (Table 3). The DD_Opt also improved the RMSE for PL to PI stage, but to a smaller degree (0.6 d).

The bias in developmental rates in response to temperature (β) averaged less than 2.5 d °C^{-1} for both models and across all growth stages (Table 3). Systematic error was highest for PL to PI (2.4 and 1.8 d °C^{-1} in DD10 and DD_Opt, respectively) and between 0.1 and 1.5 d °C^{-1} for the other stages. Nonetheless, the DD_Opt model improved systematic error by reducing β from 2.4 to 1.8 d °C^{-1} for PL to PI, 1.5 to 0.1 d °C^{-1} for PI to HD, and 0.9 to 0.5 d °C^{-1} for the HD to R7 stage (Table 3).

Two- and Three-Stage Models: DD_2S and DD_3S

Optimal temperature parameters

The DD_2S model optimizes temperatures separately for two stages (PL–HD and HD–R7), while the DD_3S model divides the PL to HD stage into two stages and thus optimizes for three stages (PL–PI, PI–HD, and HD–R7). On average, compared with DD_Opt, DD_2S had higher T_b values (1.8°C) during PL to HD than HD to R7, while T_{opt} values were 3.8°C higher during HD to R7 than in PL to HD (Table 2). Variation in the cardinal temperature parameters among cultivars was greater for DD_2S than for DD_Opt, particularly for T_l during PL to HD (range: 13.1–18.2°C), T_b during HD to R7 (range: 6.0–9.9°C), and T_{opt} during HD to R7 (range: 29.4–38.7°C).

Since the only difference between the DD_2S and the DD_3S models is before HD, output results are identical for these models in the HD to R7 stage. In the DD_3S model, variability in temperature parameters among cultivars was less in the PL to PI and PI to HD stages as compared with the HD to R7 stage (Table 2).

DD_2S and DD_3S Models Performance

Compared to DD_Opt, DD_2S improved prediction accuracy (RMSE) of PL to HD from 4.2 to 3.4 d, while the RMSE was identical (4.9 d) for HD to R7 (Table 3). In addition, DD_2S reduced systematic error during PL to HD by 0.6 d °C^{-1}—from 2.0 to 1.4 d °C^{-1}—but was similar for both models for the HD to R7 stage.

Relative to DD_Opt, the DD_3S model improved prediction accuracy by 0.4 d during the PL to PI stage, but there was little difference for the PI to HD (0.1 d difference) and HD to R7 stages (Table 3). During PL to PI, systematic error was reduced to 0.6 d °C^{-1} (range: 0.4–1.3 d °C^{-1}) using DD_3S and to 1.8 d °C^{-1} (range: 1.2–2.2 d °C^{-1}) using DD_Opt.

Directly comparing DD_2S with DD_3S indicates that the DD_3S model had better prediction accuracy (3.4 versus 2.8 d) and β (1.4 versus 0.9 d °C^{-1}) for the PL to HD stage (Fig. 2). Both models resulted in similar RMSE and β during the HD to R7 stage.

In the DD_2S model, for all cultivars (and in particular for L206 and S102), changes in T_{opt} did not significantly affect the overall model performance during HD to R7 as compared with DD_Opt, in which there was no difference between cultivars in T_{opt} values (Table 3). Root mean square error was only reduced by 0.2 d for L206 and was increased by 0.3 d for S102 during HD to R7 in DD_2S as compared with DD_Opt.

Table 2. Default and optimized model parameters for the planting to panicle initiation (PL–PI), panicle initiation to heading (PI–HD), HD to R7, PL to HD, and PL to R7 stages for the various optimization models. T_b, T_l, and T_{opt} are the base, lower, and optimum temperatures, respectively.

		PL–PI			PI–HD			HD–R7			PL–HD			PL–R7		
Cultivar	**Model**	T_b	T_l	T_{opt}	T_b	T_l	T_{opt}	T_b	T_l	T_{opt}	T_b	T_l	T_{opt}	T_b	T_l	T_{opt}
		°C														
Cultivar mean	DD10	–	–	–	–	–	–	–	–	–	–	–	–	10	21.1	34.4
	DD_Opt	–	–	–	–	–	–	–	–	–	–	–	–	11.5	13.2	32.7
	DD_2S	–	–	–	–	–	–	8.9	15.9	32.9	10.7	16.1	29.1	–	–	–
	DD_3S	9.9	14.2	27.7	8.6	16.2	31.2	8.9	15.9	32.9	–	–	–	–	–	–
CM101	DD10	–	–	–	–	–	–	–	–	–	–	–	–	10	21.1	34.4
	DD_Opt	–	–	–	–	–	–	–	–	–	–	–	–	11.5	13.5	32.7
	DD_2S	–	–	–	–	–	–	9.7	16.7	31	10.1	14.3	29.9	–	–	–
	DD_3S	10	14.8	28.1	7.8	17.5	32	9.7	16.7	31	–	–	–	–	–	–
L206																
	DD10	–	–	–	–	–	–	–	–	–	–	–	–	10	21.1	34.4
	DD_Opt	–	–	–	–	–	–	–	–	–	–	–	–	11.5	13.2	32.7
	DD_2S	–	–	–	–	–	–	6	14.9	38.7	10.2	14.3	29.1	–	–	–
	DD_3S	10	14.4	28.2	9.2	16.5	32.7	6	14.9	38.7	–	–	–	–	–	–
M104																
	DD10	–	–	–	–	–	–	–	–	–	–	–	–	10	21.1	34.4
	DD_Opt	–	–	–	–	–	–	–	–	–	–	–	–	11.4	13.1	32.6
	DD_2S	–	–	–	–	–	–	9.8	16.1	32.2	9.8	13.1	29.8	–	–	–
	DD_3S	9.3	13.1	27	7	17.7	29.9	9.8	16.1	32.2	–	–	–	–	–	–
M202																
	DD10	–	–	–	–	–	–	–	–	–	–	–	–	10	21.1	34.4
	DD_Opt	–	–	–	–	–	–	–	–	–	–	–	–	11.9	13.1	32.5
	DD_2S	–	–	–	–	–	–	9.4	16.2	34.7	11.5	17.7	29.1	–	–	–
	DD_3S	9.8	13.5	27.7	10.2	16	30.2	9.4	16.2	34.7	–	–	–	–	–	–
M205																
	DD10	–	–	–	–	–	–	–	–	–	–	–	–	10	21.1	34.4
	DD_Opt	–	–	–	–	–	–	–	–	–	–	–	–	11.2	13	29.3
	DD_2S	–	–	–	–	–	–	7.8	16.4	31.2	11.8	18.2	29.8	–	–	–
	DD_3S	10.3	15.1	28	9.6	13.6	28.9	7.8	16.4	31.2	–	–	–	–	–	–
M206																
	DD10	–	–	–	–	–	–	–	–	–	–	–	–	10	21.1	34.4
	DD_Opt	–	–	–	–	–	–	–	–	–	–	–	–	11.7	13.1	32.9
	DD_2S	–	–	–	–	–	–	9.5	15.2	33.2	11.2	17.7	30.3			
	DD_3S	9.9	14.3	27.5	9.6	16.5	33.1	9.5	15.2	33.2	–	–	–	–	–	–
S102																
	DD10	–	–	–	–	–	–	–	–	–	–	–	–	10	21.1	34.4
	DD_Opt	–	–	–	–	–	–	–	–	–	–	–	–	11.5	13.2	32.7
	DD_2S	–	–	–	–	–	–	9.9	15.6	29.4	10.2	17.5	29.5	–	–	–
	DD_3S	9.8	14.3	27.5	6.7	15.5	31.6	9.9	15.6	29.4	–	–	–	–	–	–

Stage-Dependent Temperature Sensitivity

For the sensitivity analysis, mean temperatures during PL to PI, PL to HD, and HD to R7 ranged from 20.5 to 23.1, 22.5 to 25.8, and 21.2 to 25.9°C, respectively (Fig. 3). Across cultivars, the duration of PL to PI was most affected by temperature, with every 1°C change in mean temperature changing time to PI by 1.8 d. For the PI to HD stage, a 1°C change in mean temperature resulted in a 1.2-d change in days to HD. The HD to R7 stage was not affected by temperature. Using analysis of covariance to compare the slopes of regression lines indicated that slopes were not significantly ($p = 0.3$, data not shown) different for PL to PI and PI to HD; however, slopes are significantly ($p = 0.015$, data not shown) different for PL to PI and HD to R7.

DISCUSSION

The DD10 model using default cardinal temperatures values had poor predication accuracy and higher systematic error for California cultivars and climate. This may be due to higher diurnal mean temperature in the southern United States than in California, under which conditions the southeastern cultivars were developed and for which

Table 3. Model simulation results from the cross-validation procedure for all models. Systematic error (β, d °C⁻¹) is the slope of the regression line between RMSE (prediction accuracy, d) and average temperature for the given stage. The stages are: planting to panicle initiation (PL–PI), panicle initiation to heading (PI–HD), PL to HD, and HD to R7.

Cultivar	Model	PL–PI		PI–HD		PL–HD		HD–R7	
		β	RMSE	β	RMSE	β	RMSE	β	RMSE
		d °C⁻¹	d	d °C⁻¹	d	d °C⁻¹	d	d °C⁻¹	d
Cultivar mean	DD10	2.4	3.3	1.5	4.8	3.3	4.5	0.9	6.2
	DD_Opt	1.8	2.7	0.1	3.8	2	4.2	0.5	4.9
	DD_2S	–	–	–	–	1.4	3.4	0.6	4.9
	DD_3S	0.6	2.3	0.3	3.7	0.9	2.8	0.6	4.9
CM101	DD10	2.1	2.9	2.3	3.7	3.7	3.6	0.5	5.6
	DD_Opt	1.9	2.4	1.2	3	1.5	3.4	0.3	4.7
	DD_2S	–	–	–	–	1.3	2.5	0.4	4.4
	DD_3S	0.6	2	1.4	3	0	2.5	0.4	4.4
L206	DD10	2.1	2.9	0.8	4.4	3.2	4.5	0.1	5.8
	DD_Opt	1.7	2.3	−0.3	4.2	1.8	4.4	−0.2	4.7
	DD_2S	–	–	–	–	1.1	3.7	0	4.9
	DD_3S	0.5	2.5	0.2	4.1	0.7	2.7	0	4.9
M104	DD10	2.7	3.2	1.5	4.6	3.1	4.4	0.3	7
	DD_Opt	2.2	2.7	0.5	4.1	2.1	4.1	0.1	5.2
	DD_2S	–	–	–	–	1.3	3.2	0.2	5.5
	DD_3S	0.4	2	0.8	3.9	0.4	3.1	0.2	5.5
M202	DD10	2.4	3.8	2.1	5.9	3.8	5.5	1.1	6.6
	DD_Opt	2.1	3.1	0.5	4.8	2.5	4.8	0.8	4.7
	DD_2S	–	–	–	–	2	4.4	1	4.7
	DD_3S	0.6	2.6	0.8	4.4	1.9	3.2	1	4.7
M205	DD10	2.8	3.7	1.3	5.9	4.2	5.6	2.3	7.3
	DD_Opt	1.2	2.7	−0.8	3.8	2.7	5.0	1.9	5.4
	DD_2S	–	–	–	–	3	4.3	1.9	5.3
	DD_3S	1.3	2.5	−0.7	4.2	2.1	3.5	1.9	5.3
M206	DD10	2.2	3.5	0.5	4.5	2.2	4.1	1.7	5.7
	DD_Opt	1.8	2.7	−0.8	3.8	2.3	4.2	1	4.7
	DD_2S	–	–	–	–	0.2	3.0	1.2	4.4
	DD_3S	0.4	2.5	0	3.5	1	2.4	1.2	4.4
S102	DD10	2.4	3.3	1.8	4.3	3.3	3.6	0.4	5.6
	DD_Opt	2	2.7	0.5	2.9	1.5	3.0	−0.1	5
	DD_2S	–	–	–	–	0.6	2.8	−0.2	4.8
	DD_3S	0.6	2.2	0.2	3.1	0.5	2.4	−0.2	

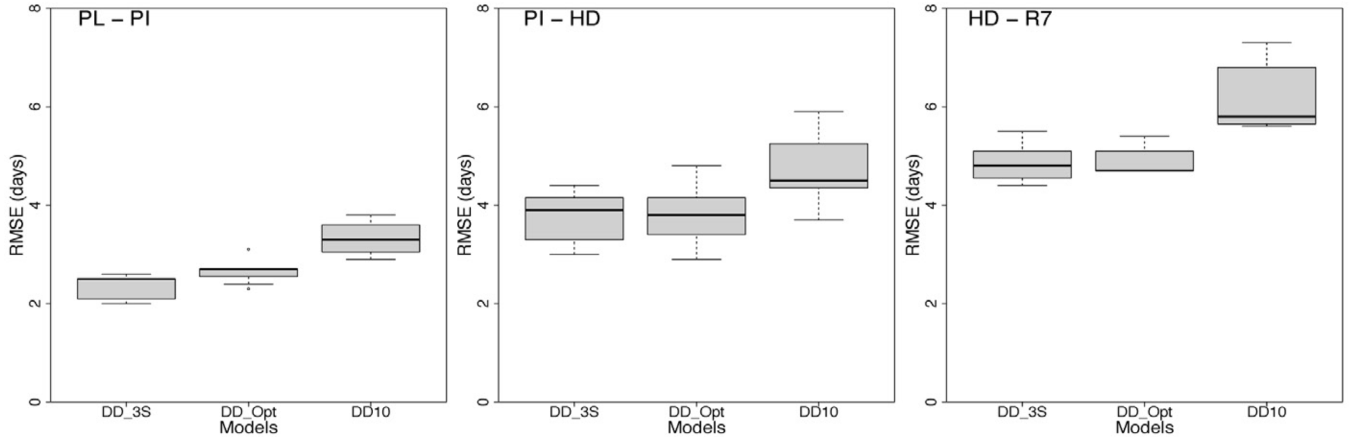

Fig. 1. Box and whisker plots of the cultivar mean RMSE (d) for planting (PL) to panicle initiation (PI), PI to heading (HD), and HD to R7 stages for the DD_3S, DD_Opt, and DD10 models. The horizontal line within the box indicates the median, the boundaries of the box indicate the 25th and 75th percentile, and the whiskers indicate the highest and lowest values of the results.

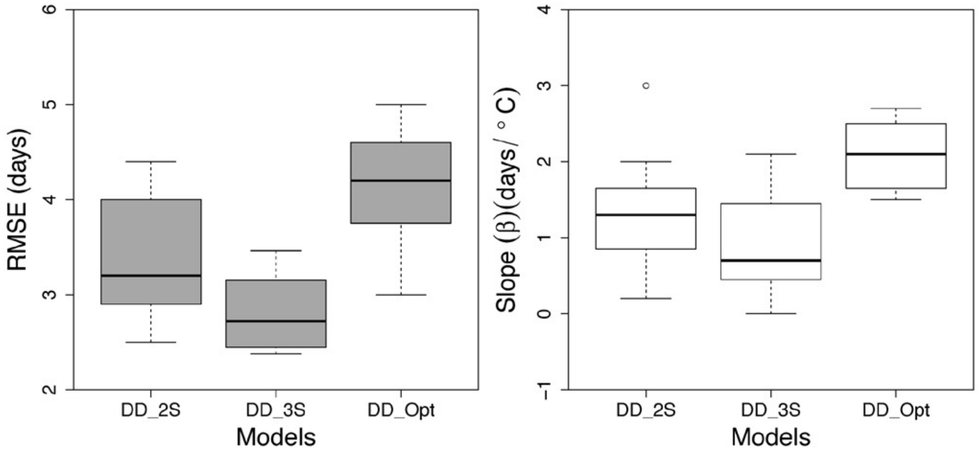

Fig. 2. For the planting (PL) to heading (HD) stage, box and whisker plots of the cultivar mean RMSE (d) and β (days °C^{-1}, β is the slope of the regression line between RMSE and average seasonal temperature) for the DD_2S, DD_3S, and DD_Opt models. The horizontal line within the box indicates the median, the boundaries of the box indicate the 25th and 75th percentile, and the whiskers indicate the highest and lowest values of the results.

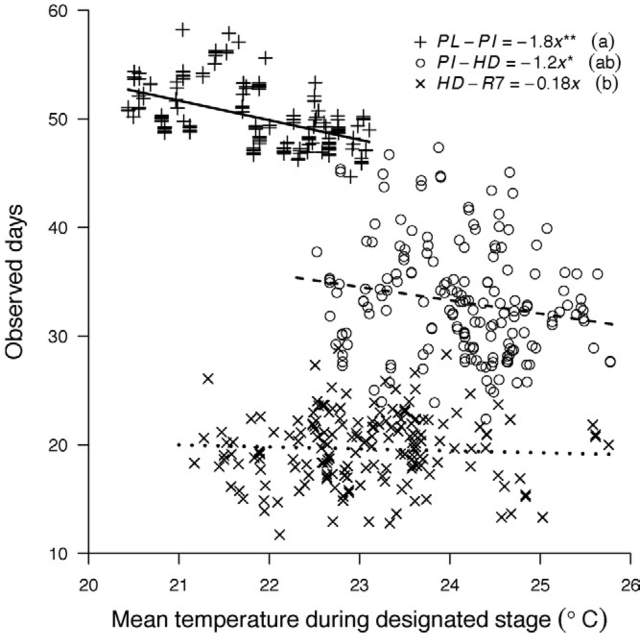

Fig. 3. Temperature sensitivity analysis showing observed duration from planting to panicle initiation (PL–PI), panicle initiation to heading (PI–HD), and heading to R7 (HD–R7) versus mean temperature during that stage. Regression slope coefficients are indicated for each stage with a * and **, indicating significance at $p < 0.05$ and $p < 0.001$, respectively (the coefficient of HD–R7 was not significant). Slope coefficients followed by the same letter are not significantly different ($p < 0.05$) from one another based on an analysis of covariance.

the model was originally calibrated (Slaton et al., 1993). Furthermore, cultivars in the southeastern United States are predominately derived from tropical *japonica* cultivars, while California cultivars are temperate *japonica* (Lu et al., 2005). Temperate *japonica* cultivars are mainly found in temperate regions such as northern Japan and California (Mackill and Lei, 1997). Mackill and Lei (1997) characterized a diverse set of mainly *japonica* rice cultivars for traits related to adaption to low temperature. They found that tropical *japonica* cultivars were usually intermediate between temperate *japonica* and *indica* cultivars with respect to adaptation to temperate regions.

Optimizing temperatures in the various models (DD_Opt, DD_2S, and DD_3S) resulted in improved prediction of duration to various phenological stages, with the RMSE values ranging from 2 to 5 d (Fig. 1, 3). The model accuracy is comparable with, or better than, other studies in which RMSE ranged from 2 to 7 d for Oryza2000 (Zhang et al., 2008; Wikarmpapraharn and Kositsakulchai, 2010; Zhang and Tao, 2013) and CERES-Rice (Alocilja and Ritchie, 1991; Timsina and Humphreys, 2006; Yao et al., 2007) for both pre- and postheading stages.

There was no difference in response to temperature between PL to PI and PI to HD; however, PL to PI was significantly different than HD to R7 and was thus most likely to be responsive to stage-dependent cardinal temperature parameter optimization (Fig. 3). Our result substantiated the results of van Oort et al. (2011), showing that the postheading stage is not responsive to temperature, and therefore most variation in crop development occurs before flowering (Roberts et al., 1993). The mean temperature in the temperature sensitivity analysis of van Oort et al. (2011) ranged from 17.8 to 31.4°C for the preflowering and 17 to 33°C for the postflowering stage—a wider temperature range than in our study (range: 20–26°C), which suggests the applicability of results across wider temperature ranges.

Contrary to what is often assumed (Summerfield et al., 1992; Bouman and van Laar, 2006; Ahmad et al., 2012), we found that optimal temperature parameters are not the same across phenological stages. The physiological basis for differences in cardinal temperature between stages is unknown (White et al., 2012). Cardinal temperatures have been linked to enzyme kinetics (Parent and

Tardieu, 2012), in which there is no metabolic activity under T_b, and metabolic activity slows down above T_{opt}. More complex mechanisms, such as changes in membrane state (Hughes and Dunn, 1996) and regulation through "thermostat genes" (Deal and Henikoff, 2010), have been suggested. Optimization of the DD_2S and DD_3S models identified different optimal temperatures for pre- (PL–PI and PI–HD) and postheading (HD–R7) stages. Employing stage-dependent temperature parameters in the DD_2S model for pre-and postheading stages improved the model performance for the PL to HD stage compared with DD_Opt. Going further to a three-stage optimization (DD_3S) resulted in higher model accuracy (RMSE and β) than DD_2S for the PL to HD stage. Improved model precision with DD_3S and the results of the temperature sensitivity analysis suggest that development of stage-dependent temperatures is important for improving model accuracy, and that the benefits of this are primarily seen in the early season (PL–PI). However, for the PI to HD and HD to R7 stages, which are less sensitive to temperature, DD_3S was comparable with DD_Opt. Given the difficulty of identifying PI, this data is not commonly collected; however, HD or flowering data is routinely collected. Our data clearly indicate that, in the absence of PI data, the DD_2S approach is still better than the DD_Opt in terms of both accuracy and systematic error for estimating time to heading.

Results from the DD_2S and DD_3S models show that T_b is highest early in the season (Table 2). In the DD_2S model, the cultivar average T_b for the preheading stage (PL–HD) was 10.7°C, compared with 8.9°C during the HD to R7 stage. The DD_3S model further refined this result to demonstrate that higher T_b occurs primarily during the PL to PI stage. Similar results have been shown for wheat (Slafer and Rawson, 1995; Wang and Engel, 1998). These results also substantiate the findings of van Oort et al. (2011) that T_b in the postflowering stage (HD–R7) is noticeably lower than in the preflowering stage.

Our results (DD_3S, Table 3) also show that cultivar average T_{opt} increased from PL to R7. Slafer and Rawson (1995) also reported a similar trend in wheat. Most studies assume that T_{opt} is constant across crop development and that it varies between 28 and 30°C, depending on cultivar (Gao et al., 1992; Yin et al., 1997; Zhang et al., 2008). Across cultivars, the DD_3S model estimates for T_{opt} were 27.7°C for PL to PI, 31.2°C for PI to HD, and 32.9°C for HD to R7. The decreases in T_b and the increases in T_{opt} from PL to PI, PI to HD, and HD to R7 indicate that the slope of thermal time accumulation between T_b and T_{opt} is less steep in PI to HD and HD to R7 (i.e., the rate of development is slower) than in the PL to PI stage, and that thermal time increases less with each 1°C increase in temperature during PI to HD and HD to R7 than during PL to PI (van Oort et al., 2011).

Compared with DD_3S, the DD_Opt model had significantly higher β during PL to PI and lower β during PI to HD. For example, a 4°C difference in average temperature between cold and warm years, and a systematic error of 1.8 d $°C^{-1}$ (as for PL–PI), results in a model phenology prediction bias of 7.2 d (4°C × 1.8 d $°C^{-1}$). A reduction of β to 0.6 d $°C^{-1}$ in DD_3S reduces the phenology prediction bias to 2.4 d (4°C × 0.6 d $°C^{-1}$). All optimized models showed similar systematic error in HD to R7 ($\beta = 0.5$–0.6 d $°C^{-1}$). Furthermore, our results from the DD_3S model for P to PI suggest that the higher systematic error in DD_Opt during PL to PI may in fact be due to using constant temperature parameters. Using stage-dependent temperature parameters in DD_3S reduced β by 1.2 d $°C^{-1}$. Overall, the systematic error observed in this study was much smaller ($\beta < 2$ d $°C^{-1}$ and mostly close to zero) than error observed by van Oort et al. (2011), who reported β between −6.7 and 3.5 d $°C^{-1}$. Nevertheless, the results clearly show the importance of optimization of cardinal temperatures, plus the use of stage-dependent temperature parameters, in reducing systematic error.

CONCLUSION

Optimizing cardinal temperature parameters in the DD_Opt model improved model accuracy and decreased systematic error (especially during PI-HD stage) compared with DD10. Models that predict crop phenological stages based on temperature ignore the critical changes in crop response to temperature at different developmental stages. We demonstrated that plant response to temperature decreases with development towards R7; HD to R7 is not responsive to temperature and preheading stages are most responsive to temperature. Consequently, results also show that optimal temperature values differed across developmental stage. The base temperature is lower in the postheading stage than in the preheading stage, while optimum temperature is lower in preheading and is higher in postheading. Improved model accuracy with DD_2S and DD_3S and the results of the temperature sensitivity analysis suggest that using stage-dependent temperatures is important for improving model accuracy, especially in the early season (reducing systematic error during PL–PI). These results have implications for the performance of climate change-related studies, breeding, and yield gap analysis that utilize models such as DD10 and Oryza2000.

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