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Modelling phasic development in wheat: a conceptual integration of physiological components

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SUMMARY

Simulation of phasic development in wheat is necessary in constructing wheat growth and yield models. It is also useful for evaluating cultivar adaptation and scheduling cultural practices. This paper describes a conceptual model of wheat development based on phenological principles, as affected by vernalization, photoperiod, thermal response and intrinsic earliness, and also reports the results of sensitivity analysis and validation of the model.

The model predicts when the plant will reach double ridge, terminal spikelet and heading. In the model, the daily thermal sensitivity of development following emergence is determined by an interaction of 'relative vernalization completion' and 'relative photoperiod effectiveness' for that day. After complete vernalization is reached, the daily thermal sensitivity is determined only by relative photoperiod effectiveness, which gradually increases from terminal spikelet to heading. A multiplication between the daily thermal sensitivity and thermal effectiveness generated daily flowering time, which was accumulated to trigger a particular developmental stage. Genotypic differences were characterized as vernalization requirement, photoperiod sensitivity and intrinsic earliness.

The model showed a sensitive response to environmental variables of temperature and daylength, and to genetic parameters of vernalization requirement and photoperiod sensitivity. Evaluation of the model using multiple experimental data involving various cultivars and planting dates exhibited a marked goodness of fit between simulation and observation with a root mean square error < 5 days. The results indicate that the model can be used as a predictor for the major flowering stages, as well as functioning as a knowledge base for understanding the characteristics of different development components in wheat.

INTRODUCTION

Prediction of phasic development is essential for the accurate modelling of morphogenesis and yield components in wheat (*Triticum aestivum* L.) and is also helpful for evaluating cultivar adaptation and scheduling cultural practices (Shaykewich 1995). A large number of studies have indicated that vernalization and photoperiod interact to determine the response of the plant to temperature, which is ultimately the driving force of development toward flowering in wheat (Davidson *et al.* 1985; Hay & Kirby 1991; Slafer & Rawson 1994). The literature also suggests that intrinsic earliness (also called basic development rate) is a separate genetic factor influencing the thermal time required for the cultivar to reach flowering (Flood & Halloran 1984; Masle *et al.* 1989; Miao *et al.* 1994). Thus, an ideal wheat development model must be able to provide a quantitative description of how these environmental factors and genetically controlled physiological traits interact during phenological development (Slafer & Rawson 1994). This requires a simulation of the plant's response to temperature and daylength, as well as a characterization of genotypic differences in phasic development.

Heading in wheat is the ultimate indication of the completion of development toward flowering. Thereafter, vernalization and photoperiod no longer have an effect on progress toward maturity (Slafer & Rawson 1994). Current wheat development models use specific combinations of algorithms describing the effect of environmental factors on progress toward heading; however, different models use different combinations of algorithms (Weir *et al.* 1984; Miglietta 1991; Ritchie 1991; McMaster *et al.*

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1992). Thus, there has been a lack of agreement on the fundamental relationships between development processes and environmental variables (Cao 1994). Mechanisms for plant responses to vernalization and photoperiod are not described well in the existing models, and some of the algorithms and parameters of the models lack clear biological meanings.

CERES-wheat (Ritchie 1991) and AFRCWHEAT (Weir *et al*. 1984) are two widely recognized wheat growth and yield models, which both include the development submodels and algorithms influenced by vernalization and photoperiod processes. From emergence through terminal spikelet formation, the CERES-wheat model calculates relative sufficiency factors on 0–1 scales for the daily vernalization and photoperiod response, and then adjusts the daily flowering progress based on the least favourable factor (Ritchie 1991). Thus the algorithms do not allow an interaction between vernalization and photoperiod responses. In contrast, from emergence to double ridge the thermal time response of flowering in AFRCWHEAT is modified by a factor derived from the multiplication of daily vernalization and photoperiod effects; then between double ridge and heading, only a photoperiod response is used to adjust the daily progress toward flowering (Weir *et al*. 1984; Travis *et al*. 1988). The AFRCWHEAT model has been developed for specific winter wheat genotypes, and needs to be modified to predict the development rates of other wheat cultivars. Other models used only photoperiod response (Miglietta 1991) or vernalization degree-days (Craigon *et al*. 1995) to predict development rate toward heading or final leaf appearance in wheat, but do not combine photoperiod response and the vernalization process. None of the existing models characterizes genetic differences in intrinsic earliness. Thus, there is a need to derive a physiologically based conceptual model of wheat development that would account for the interactions of vernalization, daylength and thermal time on the flowering progress.

The primary objective of this paper was to present a fundamental model of wheat phasic development as both a knowledge library of different physiological components and a predictor for major development stages. Also, a series of simulation experiments were conducted to examine the sensitivity of the model to major input variables and to test the model with the data involving various cultivars and planting dates.

CONCEPTUAL FRAMEWORK

An obligate winter wheat growing under a non-vernalizing temperature remains vegetative and continues to produce leaves and tillers, driven by thermal time, even under an inductive photoperiod (Cao & Moss 1991). Thus, in the absence of vernalization, a long photoperiod has no effect on progress toward flowering in strong winter wheats (Davidson *et al*. 1985; Manupeerapan *et al*. 1992). In contrast, in the presence of vernalization, the response of flowering to long photoperiods is much greater in fully vernalized plants than in partially vernalized plants (Davidson *et al*. 1985; Slafer & Rawson 1994). Therefore, vernalization is a process whereby the plant synthesises a physiological system that enables the plant to sense photoperiod, as far as flowering progress is concerned. Both the vernalization and photoperiod response systems are quantitative: a plant need not be fully vernalized and nor need it be in an optimum photoperiod for it to flower. However, a partially vernalized plant or a plant in a non-optimum photoperiod will require more thermal time to reach flowering than a fully vernalized plant or a plant in an optimum photoperiod. Thus, both vernalization and photoperiod processes determine the efficiency of thermal time for progress toward flowering in the wheat plant.

A re-examination and synthesis of existing literature on wheat development provided a basis for making the following assumptions to conceptualize a general development model for both winter and spring wheats.

1. Double ridge, terminal spikelet, and heading are three major observable developmental stages in the flowering progress with wheat. Double ridge is the beginning of reproductive growth and spikelet initiation. Formation of the terminal spikelet determines number of total spikelets on a spike. Heading indicates a completion of development toward flowering.

2. During phasic development, the wheat plant is able to sense cold (vernalization) temperatures quantitatively and has a system that accumulates the effect of those cold temperatures until the plant is fully vernalized. That effect is to enable the plant to sense photoperiod. Thus, the relative effectiveness of a long photoperiod on development increases with increasing vernalization progress.

3. Relative vernalization and relative photoperiod effectiveness interact to determine the relative efficiency of thermal time in driving the plant's progress toward flowering. Thus, the progress toward flowering each day is determined as a fraction of an optimum flowering day that would be obtained by a fully vernalized plant growing at an optimum temperature and photoperiod. This daily fraction of optimum flowering time is accumulated by the plant.

4. The optimum flowering time to reach a given development stage is constant for a specific genotype, and varies among genotypes. That difference in optimum flowering time is a measure of 'intrinsic earliness' of the genotype.

5. Genotypic differences in development can be quantified using a vernalization requirement, a photoperiod sensitivity and an intrinsic earliness for each genotype.

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DESCRIPTION OF THE MODEL

Diurnal temperatures

The response of a plant to daily mean temperatures is non-linear. Therefore, the temperature values at different times during a day are more closely correlated to plant response than is the mean temperature (Kropff *et al*. 1994; Shaykewich 1995). In this model, the eight temperature factors (TFAC) are calculated per day and used to generate eight 3-h temperature (TEMP) values from daily maximum (TMX) and minimum (TMN) temperatures to describe the diurnal temperature pattern (Manrique & Hodges 1989):

$$\mathrm{TFAC(I)} = 0{\cdot}931 + 0{\cdot}114 \times \mathrm{I} - 0{\cdot}0703 \times \mathrm{I}^2 + 0{\cdot}0053 \times \mathrm{I}^3 \qquad \mathrm{I} = 1, \ldots, 8 \tag{1}$$

$$\mathrm{TEMP(I)} = \mathrm{TMN} + \mathrm{TFAC(I)} \times (\mathrm{TMX} - \mathrm{TMN}) \tag{2}$$

These algorithms produce similar results to the AFRCWHEAT model (Weir *et al*. 1984), but appear more straightforward. The calculated individual temperature values are then used to determine the daily thermal and vernalization responses of the plant. As compared to the method of daily mean temperature, this approach compensates for the non-linearity of the daily temperature fluctuation.

Relative thermal effectiveness

Relative thermal effectiveness (RTE) is calculated from the eight different temperature values each day, using base (TB), optimum (TO) and maximum (TM) temperatures for wheat development. Before terminal spikelet, the TB is 0 °C, TO 22 °C, and TM 32 °C, whereas after terminal spikelet, 3 °C is added to the TB, TO, and TM. Use of lower base and optimum temperatures during early development is based on previous controlled environment studies (Cao & Moss 1989; Slafer & Rawson 1995). Daily thermal effectiveness (DTE) is obtained as an average of eight different values:

$$\mathrm{RTE(I)} = 0 \qquad \mathrm{TB} \geqslant \mathrm{TEMP} \geqslant \mathrm{TM} \tag{3}$$

$$\mathrm{RTE(I)} = (\mathrm{TEMP(I)} - \mathrm{TB})/(\mathrm{TO} - \mathrm{TB}) \qquad \mathrm{TB} < \mathrm{TEMP} \leqslant \mathrm{TO} \tag{4}$$

$$\mathrm{RTE(I)} = (\mathrm{TM} - \mathrm{TEMP(I)})/(\mathrm{TM} - \mathrm{TO}) \qquad \mathrm{TO} < \mathrm{TEMP} < \mathrm{TM} \tag{5}$$

$$\mathrm{DTE} = 0{\cdot}125 \times \Sigma(\mathrm{RTE(I)}) \qquad \mathrm{I} = 1, \ldots, 8 \tag{6}$$

Relative vernalization effectiveness

Relative vernalization effectiveness (RVE) is depicted in three linear relationships as shown in Fig. 1. Evidence suggests that spring and winter wheat cultivars exhibit differences not only in vernalization duration requirement, but also in the limits of the effective temperature window for vernalization (Trione & Metzger 1970; Flood & Halloran 1986; Guo *et al*. 1994). In general, the temperature window for vernalization is narrower for winter wheat than for spring wheat (Flood & Halloran 1986; Guo *et al*. 1994). This is particularly apparent in the Chinese literature (Guo *et al*. 1994) which indicates three distinct cold temperature ranges for winter, intermediate and spring wheats, respectively.

This model assumes a minimum temperature of 0 °C and a lower optimum temperature of 1 °C for effective vernalization of all genotypes. However, the upper optimum temperature (TVO) and maximum temperature (TVM) for vernalization decrease with vernalization requirement (VR) of specific genotypes (Eqns 7–8). For a hypothetical spring wheat with a VR of 0, the TVO will be 10 °C and TVM 18 °C. This temperature range does not actually affect the plant's response to cold temperature because development of this spring wheat does not require a cold exposure. For most spring wheat cultivars whose flowering is enhanced by cold temperatures, the VR will be > 0, and thus TVO will be < 10 °C and TVM < 18 °C. For a winter wheat with a VR of 50 days, the TVO and TVM would be 7·5 and 11·8 °C, respectively. Kirby (1992) reported a similar vernalization temperature range for winter wheat, i.e. 8 and 12 °C. The current algorithms use one genetic parameter (VR) to quantify both the temperature window and the duration for vernalization requirement, provide a continuous adjustment of cold temperature responses for a wide range of varieties, and thus minimize the number of genetic coefficients required to run the model.

$$\mathrm{TVO} = 10 - \mathrm{VR}/20 \tag{7}$$

$$\mathrm{TVM} = 18 - \mathrm{VR}/8 \tag{8}$$

$$\mathrm{RVE(I)} = 0 \qquad 0 \geqslant \mathrm{TEMP(I)} \geqslant \mathrm{TVM} \tag{9}$$

$$\mathrm{RVE(I)} = \mathrm{TEMP(I)} \qquad 0 < \mathrm{TEMP(I)} < 1 \tag{10}$$

$$\mathrm{RVE(I)} = 1 \qquad 1 \leqslant \mathrm{TEMP(I)} \leqslant \mathrm{TVO} \tag{11}$$

$$\mathrm{RVE(I)} = (\mathrm{TVM} - \mathrm{TEMP(I)})/(\mathrm{TVM} - \mathrm{TVO}) \qquad \mathrm{TVO} < \mathrm{TEMP(I)} < \mathrm{TVM} \tag{12}$$

Daily vernalization effectiveness (DVE) is obtained as an average from eight different values:

$$\mathrm{DVE} = 0{\cdot}125 \times \Sigma(\mathrm{RVE(I)}) \qquad \mathrm{I} = 1, \ldots, 8 \tag{13}$$

When temperatures are > 27 °C, devernalization (DEV) is assumed to be occurring at a rate of 0·5 per degree > 27 °C. Daily devernalization (DDEV) is obtained as an average of eight DEV values. It should be noted that information on devernalization is limited and the algorithms are only reasonable approxi-

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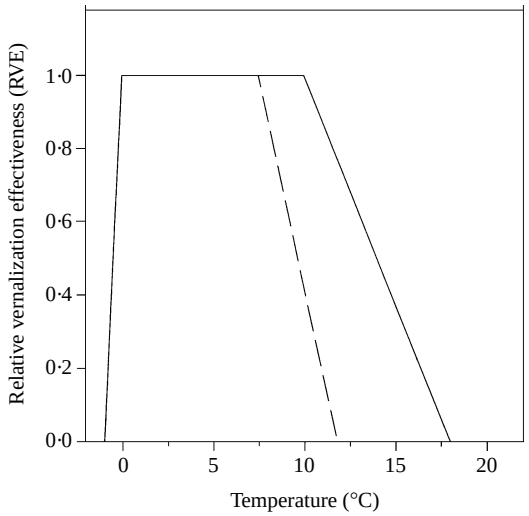


Fig. 1. Relative vernalization effectiveness (RVE) in relation to temperature and genotypes with different vernalization requirement (VR). Solid line: VR = 0; broken line: VR = 50.

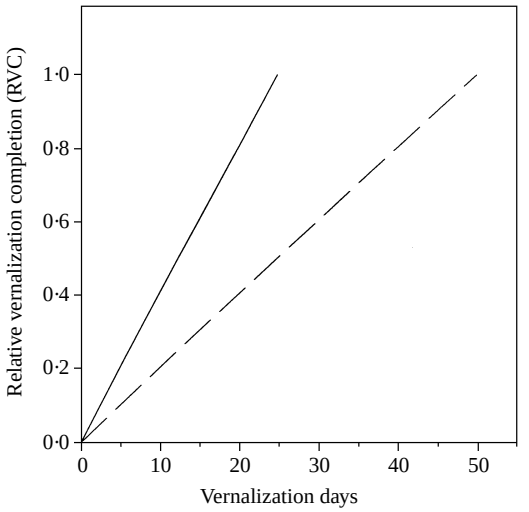


Fig. 2. Relative vernalization completion (RVC) in relation to accumulated vernalization days and genetic vernalization requirement (VR). Solid line: VR = 25; broken line: VR = 50.

mations based on available literature and field experiment data (Flood & Halloran 1986; Ritchie 1991; Lu & Zhang 1992).

$$\mathrm{DEV(I)} = ((\mathrm{TEMP(I)} - 27)) \times 0{\cdot}5 \quad \mathrm{TEMP(I)} > 27 \tag{14}$$

$$\mathrm{DDEV} = 0{\cdot}125 \times \mathrm{S(DEV(I))} \qquad \mathrm{I} = 1, \ldots, 8 \tag{15}$$

Relative vernalization completion

The daily vernalization effectiveness is accumulated to generate a value for vernalization days (VD), which is negatively affected by devernalization. When accumulated VD reaches 30% of the VR, devernalization is no longer effective. The relative vernalization completion (RVC) is calculated as the fraction of VD/VR for each genotype (Fig. 2). The VR for a winter wheat is usually < 60 VD, a cultivar specific character that can be estimated from phenological data by physiologists or breeders. This algorithm differs from that used in the CERES-wheat model (Ritchie 1991), although both can generate a similar result. In CERES-wheat, a fixed value for vernalization days and varied vernalization coefficients are used for different genotypes so that all genotypes finish vernalization when calculated vernalization days reach 50.

$$\mathrm{VD1} = \mathrm{SUM\ (RVE - DEV)} \qquad 0 < \mathrm{VD} < 0{\cdot}3\mathrm{VR} \tag{16}$$

$$\mathrm{VD2} = \mathrm{SUM\ (RVE)} \qquad 0{\cdot}3\mathrm{VR} \leqslant \mathrm{VD} < 1\mathrm{VR} \tag{17}$$

$$\mathrm{RVC} = (\mathrm{VD1} + \mathrm{VD2})/\mathrm{VR} \qquad (\mathrm{VP} = 1 \text{ at } \mathrm{VR} = 0) \tag{18}$$

Relative photoperiod effectiveness

Daily photoperiod changes regularly with seasonal progress and latitude. The actual daily photoperiod for development response can be calculated using the equations in the CERES-wheat model (Ritchie 1991).

$$\mathrm{DEC} = 0{\cdot}4093 \times \mathrm{SIN}(0{\cdot}0172 \times (\mathrm{DOY} - 82{\cdot}2)) \tag{19}$$

$$\mathrm{DLV} = (-\mathrm{SIN}(0{\cdot}01745 \times \mathrm{LAT}) \times \mathrm{SIN(DEC)} - 0{\cdot}1047)/(\mathrm{COS}(0{\cdot}01745 \times \mathrm{LAT}) \times \mathrm{COS(DEC)}) \tag{20}$$

$$\mathrm{PHOT} = 7{\cdot}639 \times \mathrm{ACOS(DLV)} \tag{21}$$

where DEC is sun declination in radians, DOY day of year, DLV daylength variable, LAT latitude in degrees, and PHOT is the effective photoperiod in hours.

The critical photoperiod for wheat development is ≈ 20 h, below which development rate will be inhibited (Slafer & Rawson 1994). The degree of this inhibition depends on photoperiod sensitivity (PS) of a particular genotype (Fig. 3). The PS here is a second genetic coefficient introduced in this model. The relative photoperiod effectiveness (RPE) for a day is calculated using Eqn 22, identical to the CERES-wheat model (Ritchie 1991):

$$\mathrm{RPE} = 1 - \mathrm{PS}(20 - \mathrm{PHOT})^2 \tag{22}$$

Daily thermal sensitivity

Vernalization and photoperiod response systems determine the physiological sensitivity of the plant to

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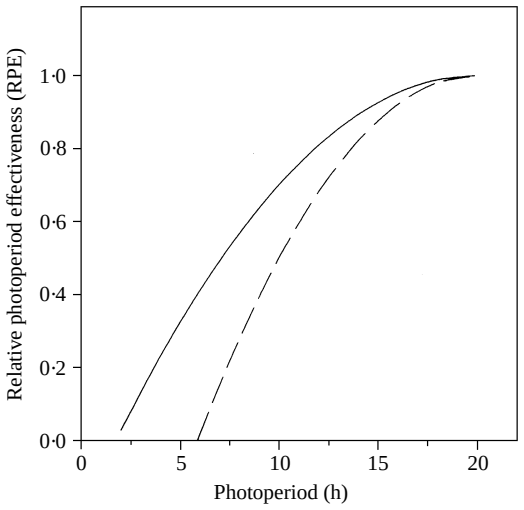


Fig. 3. Relative photoperiod effectiveness (RPE) in relation to photoperiod and genetic photoperiod sensitivity (PS). Solid line: PS = 0.003; broken line: PS = 0·005.

daily thermal effectiveness, defined as daily thermal sensitivity (DTS). It is proposed that before completion of vernalization, the impact of photoperiod on DTS is modified by the relative vernalization completion (RVC, Eqn 18) and that after vernalization is complete, photoperiod effectiveness becomes a dominant factor to regulate the DTS. However, from terminal spikelet to heading, the photoperiod response gradually declines (Slafer & Rawson 1994). This implies that the impact of photoperiod on the DTS is getting smaller and actual DTS is increasing toward 1 at heading. As a result, the differences in DTS caused by different photoperiods are most significant between vernalization completion and terminal spikelet formation (Fig. 4).

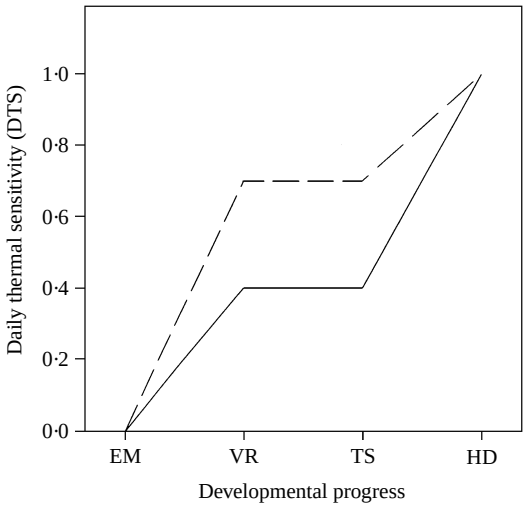


Fig. 4. Daily thermal sensitivity (DTS) during phasic development under hypothetical constant relative photoperiod effectiveness (RPE). Solid line: RPE = 0·4; broken line: RPE = 0·7. EM: emergence, VR: vernalization requirement, TS: terminal spikelet, HD: heading.

$$\mathrm{DTS} = \mathrm{RPE} \times \mathrm{RVC} \qquad \mathrm{VD} < \mathrm{VR} \tag{23}$$

$$\mathrm{DTS} = \mathrm{RPE} \qquad \mathrm{VD} \geqslant \mathrm{AVR} \text{ and } \mathrm{AFT} \leqslant \mathrm{FTTS} \tag{24}$$

$$\mathrm{DTS} = \mathrm{RPE} + (1 - \mathrm{RPE}) \times (\mathrm{AFT\text{-}FTTS}) / (\mathrm{FTHD} - \mathrm{FTTS})$$
$$\mathrm{FTTS} < \mathrm{AFT} < \mathrm{FTHD} \tag{25}$$

where AFT is accumulated flowering time to be obtained from Eqns 26 and 27, and FTTS and FTHD are flowering time requirement for terminal spikelet and heading stages, respectively.

Flowering time

Multiplication of relative thermal effectiveness by thermal sensitivity gives a daily flowering time (DFT), which is accumulated to generate accumulative flowering time (AFT). This AFT is essentially a description of the hypothetical optimum flowering days under optimum flowering environments:

$$\mathrm{DFT} = \mathrm{RTE} \times \mathrm{DTS} \tag{26}$$

$$\mathrm{AFT} = \mathrm{SUM}\ (\mathrm{DFT}) \tag{27}$$

A constant AFT is used to predict a particular development stage for a given genotype, which depends on the intrinsic earliness (EN) of the genotype. The AFT values of 9, 15 and 25 in Eqns 28–30 are assumed to be minimum time period required to reach double ridge (FTDR), terminal spikelet (FTTS) and heading (FTHD) stages for a very early genotype without limitations of vernalization and photoperiod. The literature suggests that these AFT values could be 40% greater for winter wheat from northern latitudes (Flood & Halloran 1984; Davidson *et al.* 1985). Thus, the EN could change between 0·6 and 1 for different genotypes.

$$\mathrm{FTDR} = 9/\mathrm{EN} \tag{28}$$

$$\mathrm{FTTS} = 15/\mathrm{EN} \tag{29}$$

$$\mathrm{FTHD} = 25/\mathrm{EN} \tag{30}$$

Programming and implementation

The model is coded in standard FORTRAN 77 and runs on machines with MS-DOS operating systems. To run the model, a weather file containing Julian day number or day of year and daily maximum and minimum temperatures is established and input values are provided as latitude, emergence date and cultivar coefficients of vernalization requirement, photoperiod sensitivity and intrinsic earliness. The output from the

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simulation includes double ridge, terminal spikelet, and heading stages in day of year. The programmed model was then used to conduct a series of simulation experiments to examine the sensitivity of the model to major input variables and to test the model with data involving various cultivars and planting dates.

SENSITIVITY ANALYSIS OF THE MODEL

Sensitivity analysis was carried out by changing four major input variables: temperature and daylength in weather data, and vernalization requirement and photoperiod sensitivity as genetic parameters. As shown in Table 1, the double ridge, terminal spikelet and heading stages were all advanced with increasing temperature and daylength, and delayed with increased vernalization requirement and photoperiod sensitivity. Thus the model exhibited a sensitive response to major environmental variables as well as genetic parameters. It is also obvious that the changes in the development stages were becoming less with development progress, largest at double ridge and smallest at heading. This is consistent with observed phenological development in the field environment (Lu & Zhang 1992). The double ridge stage was most sensitive to temperature reductions, suggesting that thermal time in the winter season was a limiting factor for wheat development in the Nanjing area. In contrast, promotion of double ridge by increased temperature was less significant, probably because vernalization progress was slightly retarded under the higher temperature, thus cancelling out the enhanced thermal effect on development. These results indicate that sensitivity analysis with the model can provide additional insights into dynamic plant–environment relations.

MODEL TESTING

Sources of data

To test the performance of the model under different environments, phenological and weather data were obtained from different sowing date experiments with multiple genotypes at two different locations. The first set of data was from Nanjing Agricultural University (NAU), China with a latitude of 32 °N. The experiments included four sowing dates between October and February, and seven cultivars in two seasons during 1983–85. Detailed phenological data were collected for different development stages at shoot apex including double ridge, terminal spikelet and heading dates (Lu & Zhang 1992). Weather data were obtained from a meteorological station near the NAU. The mean temperature for the planting month varied from 3 to 15 °C. The second data set was from Oregon State University (OSU), Corvallis, Oregon with a latitude of 44·5 °N, including 14 sowing dates from October to March and using 20 cultivars in the 1991/92 season (Baloch 1994). Emergence and heading dates in the experiments were obtained from Baloch (1994) and R. S. Karow at the OSU (personal communication) and weather data were from a local weather station. The mean temperature for the planting month varied from 3 to 10 °C. All the experiments at NAU and OSU were managed using recommended practices for the local production systems.

The genotypes in the NAU and OSU experiments represented a wide range of spring and winter wheats. Three genetic coefficients for each of the genotypes were roughly estimated first from the literature and breeders' experiences, and then determined by simulation experiments by a trial and error process using the field data of the specific genotype from the earliest

Table 1. *Sensitivity of the model to environmental variables of temperature and daylength, and to genetic parameters of vernalization requirement and photoperiod sensitivity*

		Change in development stages		
		Double ridge	Terminal spikelet	Heading
Variable	Change*	(Days)		
Temperature (°C)	−2	+25	+10	+10
	+2	−14	−15	−11
Daylength (h)	−2	+10	+6	+4
	+2	−7	−5	−4
Vernalization requirement	−10	−9	−3	−2
	+10	+8	+3	+1
Photoperiod sensitivity	−0·002	−9	−5	−4
	+0·002	+9	+5	+3

* Control simulation was based on the environment of Nanjing, China with vernalization requirement of 20, photoperiod sensitivity of 0·004.

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Table 2. *Genetic coefficients* (*vernalization requirement*, *photoperiod sensitivity and intrinsic earliness*) *of different wheat genotypes estimated for model evaluation*

Location	Genotype	Vernalization requirement	Photoperiod sensitivity	Intrinsic earliness
			($\times 10^3$)	
Nanjing China	Liaochun 6	0	3·8	0·98
	Mianyang 11	8	3·4	0·92
	Yangmai 3	8	3·1	0·88
	Fengchan 3	24	2·8	0·80
	Taishan 1	31	3·9	0·78
	Dongfenghong 3	40	5·1	0·72
	Xindong 2	42	4·7	0·72
Corvallis USA	Owens	1	8·0	0·97
	Wadual	1	9·3	0·95
	Treasurer	4	7·0	0·90
	OR 8313	10	9·0	0·85
	Whitman	14	6·7	0·80
	Overson	22	9·0	0·75
	WA 7662	29	7·6	0·70
	Stephens	30	6·0	0·65
	Malcolm	33	8·3	0·80
	OR 855	34	8·2	0·85
	ORFW 301	34	8·2	0·80
	ORFW 75336	37	8·4	0·80
	OR 801	37	6·1	0·80
	Daws	38	8·9	0·80
	Dusty	40	7·5	0·70
	Hill 81	42	8·0	0·75
	Yamhill	43	4·0	0·60
	Hyak	44	5·2	0·75
	Eltan	46	8·0	0·70
	Leujain	53	8·2	0·75

planting and the latest planting. In particular, cultivar-specific photoperiod sensitivity was largely determined from the phenological data of the earliest planting and vernalization requirement was from the data from the latest planting. The values for different genotypes were found to be $\approx$ 0–55 days for vernalization requirement, 0·003–0·009 for photoperiod sensitivity and 0·6–1·0 for intrinsic earliness (Table 2). In general, the vernalization requirement was negatively related to intrinsic earliness. Also, photoperiod sensitivity was higher for the cultivars at the northern latitude (OSU) than for those at NAU.

Results

To compare the predicted with the observed developmental stages using different sowing dates and genotypes, statistical analyses were performed in order to obtain root mean square error (RMSE) between simulated and observed calendar days. The RMSE was calculated using Eqn 31 (McMaster *et al.* 1992), for both the NAU and OSU data sets that included the two plantings used for estimating the genetic coefficients. A smaller RMSE indicates a smaller deviation between the simulated and observed values.

$$\text{RMSE} = \left[\frac{\sum_{i-1}^{n} [OBS_i - SIM_i]^2}{n} \right]^{\frac{1}{2}} \tag{31}$$

With the NAU data, the simulated days for the three developmental stages of double ridge, terminal spikelet and heading changed consistently with the observed days, as the timing for the different stages varied from $\approx$ 15 days to 200 days after emergence (Fig. 5). The overall plotting of simulation against observation exhibited a significant 1:1 relationship in Fig. 5, with a RMSE of 4·9. The absolute errors between predicted and observed days for the three stages were generally $<$ 8 days, and RMSE was $\approx$ 6 days for double ridge, 5 days for terminal spikelet and 4 days for heading. Thus, it appears that this model accurately predicts the major apex development stages, double ridge, terminal spikelet and heading. This provides a basis for quantifying the dynamics of shoot apex development, such as leaf initiation, spikelet initiation and floret differentiation.

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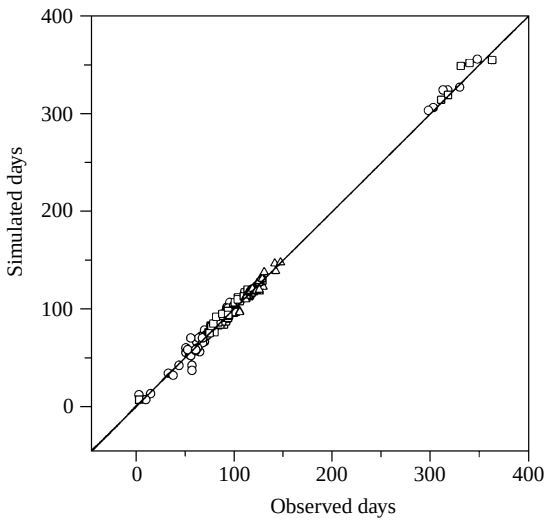


Fig. 5. Comparison of simulated with observed calendar days for different developmental stages including double ridge (○), terminal spikelet (□), and heading (△) ($n = 162$, root mean square error = 4·9). The observed data were obtained with different genotypes and sowing dates in the 1983–85 seasons at Nanjing, China with a latitude of 32 °N.

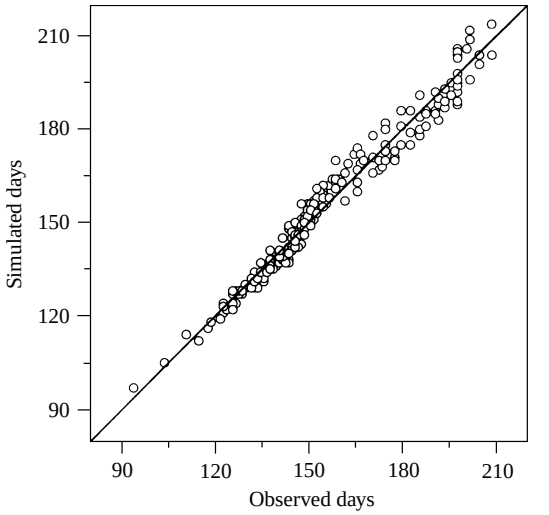


Fig. 6. Comparison of simulated with observed calendar days for heading ($n = 233$, root mean square error = 4·1). The observed data were obtained with different genotypes and sowing dates in the 1991/92 season at Corvallis, Oregon with a latitude of 44·5 °N.

With the OSU data, a good fit was also found between simulated and observed heading days for different sowing dates and cultivars, as shown by the 1:1 relationship in Fig. 6. and a RMSE of 4·1. Although the whole data set indicated a large range of heading stages from 50 to 200 days after emergence, the prediction errors were normally within ± 6 days.

These results indicate that the model is suitable for different growing environments and wheat genotypes. The results also suggest that predictions for winter plantings in January tend to be greater than observations (Fig. 6). These errors were found to be much smaller for wheats with vernalization requirements < 20 days. Therefore, further improvement in the model needs to be made for faster development in strong winter wheat sown in winter although, in practice, winter planting is seldom done in these environments.

DISCUSSION

A general mechanistic model has been proposed to conceptualize the flowering processes and predict major phasic stages of the apex, double ridge, terminal spikelet and heading of wheat, in response to major environmental variables. The model incorporated some algorithms that have been successful in existing models and introduced some new approaches and algorithms to represent the unique development system in wheat. As compared to previous work, this wheat development model exhibits four significant features.

1. The relative impact of vernalization and photoperiod on flowering development differs with developmental progress toward heading. In particular, effects of long photoperiods are most significant between vernalization completion and terminal spikelet formation. This phasic pattern is consistent with the conclusions of a recent literature review (Slafer & Rawson 1994), but differs from the CERES-wheat (Ritchie 1991) and AFRCWHEAT models (Weir *et al.* 1984).

2. Daily flowering time is used to integrate interactions between relative vernalization completion, photoperiod effectiveness and thermal effectiveness. This optimum flowering day concept has removed the impact of vernalization and photoperiod response, and thus is physiologically meaningful. In addition, the optimum flowering time (days) to reach a given development stage is constant for a specific genotype, and can be measured by growing a fully vernalized plant under an optimum temperature and photoperiod. Thus, this system provides a measurable simple scale for predicting development stages.

3. Full vernalization is not required for flowering under effective photoperiods and temperatures. Yet, from double ridge until terminal spikelet a partially vernalized wheat plant still responds to vernalization temperatures to enhance the effect of photoperiod on flowering. Also, most spring wheats require a certain degree of vernalization and thus exhibit an enhanced development rate under a cool environment during the early growth period.

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4. Characterization of such genetic traits as vernalization requirement, photoperiod sensitivity and intrinsic earliness is consistent with current literature and can possibly be estimated from field data and controlled environment experiments both by physiologists and by breeders.

The establishment of fundamental relationships in the model has been based on a synthesis and generalization of existing knowledge and literature reports. Thus, the model represents a general pattern of wheat development and provides a tool for understanding general characteristics and conceptual interactions of different development components and/or processes: vernalization, photoperiod, thermal response and intrinsic earliness. This study indicates that a mechanistic analysis and quantification of a plant system is necessary for describing dynamic relationships between physiological processes.

The model used as few parameters as possible in order to simplify the model structure and to minimize the amount of work needed for determination of the parameters. Most parameters in the algorithms were estimated from available literature and personal knowledge or judgment, and thus were only best reasonable approximations for modelling purposes. The three genetic coefficients were estimated from two field plantings among four and 14 plantings at two different latitudes, and thus are not truly independent estimates. To be fully independent and accurate, for instance, intrinsic earliness would have to be estimated from experiments involving fully vernalized plants grown in non-limiting photoperiods. Clearly, additional work and data sets are needed to obtain accurate parameters and coefficients and to independently evaluate the performance of the model under diverse environments. Therefore, although the model was evaluated with data sets involving 27 different genotypes and two different latitudes in two countries, this paper has not attempted to provide a comprehensive validation of the model, but rather has tried to show a conceptual model of physiological processes in wheat phasic development. Also, the model may have not incorporated some phenomena unique to certain wheats, such as short-day-vernalization, as indicated by Evans (1987). To make the model meet particular circumstances depends on adequate knowledge accumulation from modelling support research.

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