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Improving predictions of developmental stages in winter wheat: a modified Wang and Engel model☆

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Abstract

Accurate simulations of plant development is an important component in crop simulation models and for use in managerial decisions, such as fertilizer applications or pest control. The three major environmental factors that control development in winter wheat (*Triticum aestivum* L.) are temperature, photoperiod, and vernalization. Results from a previous study showed that the prediction of several developmental stages from booting to physiological maturity were better with the Wang and Engel (WE) model compared to CERES-Wheat, but not for the prediction of terminal spikelet initiation (TS). In the WE model, the vernalization function [$f(V)$] is a three-stage linear function and the life cycle of the wheat crop is divided into two phases, vegetative (emergence–anthesis) and reproductive (anthesis–physiological maturity). The objective of this study was to modify the WE model by introducing a nonlinear $f(V)$, and dividing the vegetative phase into two sub-phases (emergence–terminal spikelet initiation and terminal spikelet initiation-anthesis). A series of field experiments were carried out at Lincoln, NE, USA, to provide independent data on the date of developmental stages of two winter wheat cultivars (Arapahoe and Karl 92) for evaluating the original and the modified WE model. The root mean square error (RMSE) with the modified WE model was 5 days for Arapahoe and 6 days for Karl 92 for all developmental stages, which corresponds to a 45% decrease in the RMSE compared with the original WE model.

Keywords: Development; Model; Temperature; Photoperiod; Vernalization; *Triticum aestivum*

1. Introduction

Accurate predictions of plant developmental stages are important in crop simulation models and for crop management. An example of the former application is the partitioning of assimilates to different plant organs, which varies with developmental stage. While selection of appropriate cultivars and scheduling field operations such as fertilizer applications, pest control, and harvest are examples of the latter application.

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Three major environmental factors control development in winter wheat (*Triticum aestivum* L.); temperature, photoperiod, and vernalization (Angus et al., 1981; Slafer and Rawson, 1994; Cao and Moss, 1997). These factors are represented in wheat simulation models by temperature [$f(T)$], photoperiod [$f(P)$], and vernalization [$f(V)$] response functions (Weir et al., 1984; Hodges and Ritchie, 1991; Wang and Engel, 1998). The many existing wheat developmental models use different approaches to combine these factors: limiting factor models (e.g. Ritchie, 1991), additive models (e.g. Perry et al., 1987; Summerfield et al., 1991; Saarikko and Carter, 1996; Kirby and Weightman, 1997; Jamieson et al., 1998), multiplicative models (e.g. Angus et al., 1981; Weir et al., 1984; Ewert et al., 1996; Cao and Moss, 1997), and a combination of both additive and multiplicative approaches (e.g. Yan and Wallace, 1998). The multiplicative approach appears more realistic from a biological point of view because interactions among temperature, photoperiod, and vernalization have been verified in field and controlled environment experiments with wheat (Slafer and Rawson, 1994, 1995c; Ortiz-Ferrara et al., 1995; González et al., 2002). Wheat developmental models also differ with respect to the nature of the response functions $f(T)$ and $f(P)$, from linear to several nonlinear functions (Ritchie, 1991; Wang and Engel, 1998; Yan and Wallace, 1998). The $f(V)$, however, is a three-stage linear function in all wheat models (e.g. Weir et al., 1984; Ritchie, 1991; Cao and Moss, 1997; Wang and Engel, 1998).

The accuracy of different models varies in predicting developmental stages in wheat. For example, heading and ripening have been predicted with a root mean square error (RMSE) of 2–10 days (e.g. Saarikko and Carter, 1996; Cao and Moss, 1997; Yan and Wallace, 1998). Anthesis was predicted with a RMSE of 4–7 days (e.g. Ewert et al., 1996; Kirby and Weightman, 1997; Jamieson et al., 1998).

The Wang and Engel model (WE; Wang and Engel, 1998) is a multiplicative, wheat developmental model that has a nonlinear (β) function for $f(T)$, a nonlinear (negative exponential) function for $f(P)$, and a three-stage linear function for $f(V)$. Xue (2000) compared the predictions of developmental stages of three winter wheat cultivars grown in Nebraska by the WE model with the CERES-Wheat model (Ritchie, 1991), which uses a linear function for $f(T)$, a quadratic function for $f(P)$, and a three-stage linear function for $f(V)$. The predictions of developmental stages from booting (BT) to physiological maturity (PM) were better with the WE model (RMSE = 1–4 days) than with the CERES-Wheat model (RMSE = 5–6 days). The superior performance of the WE model was attributed to the more meaningful relationship between development and environmental variables in the WE model, i.e., the multiplicative approach and the nonlinear $f(T)$ (Xue, 2000). However, the prediction of terminal spikelet initiation (TS), was better with the CERES-Wheat model (RMSE = 6 days) compared to the WE model, which had an overall RMSE of 7 days and up to 11 days for some sowing dates (Xue, 2000). The TS is a key developmental stage since the number of spikelets is defined at this stage (Slafer and Rawson, 1994). Since predictions with the WE model were superior to CERES-Wheat for later developmental stages (BT to PM), but inferior for earlier developmental stages (TS) provides a rationale to improve the WE model.

A possible reason for the larger RMSE for the TS stage with the WE model, as compared to CERES-Wheat was that the $f(V)$ in the WE model may not be correct, Xue (2000). Also, the linear nature of the three-stage linear $f(V)$ introduces abrupt changes at the transition points of the response function that are not likely to be encountered in the response of biological systems to environmental factors (Shaykewich, 1995). Streck et al. (2003) developed and evaluated a generalized nonlinear $f(V)$ that was superior to the three-stage linear $f(V)$, which requires known coefficients, and described well the vernalization response of different cultivars from around the world.

Another possible reason for the poorer performance of the WE model in the early stages of plant development may be that the maximum development rate (r_{max}) and the cardinal temperatures (minimum, optimum, and maximum) for development did not change from emergence (EM) to anthesis (AN), (Xue, 2000). The development rate in wheat is lower from EM to TS than from TS to AN (Slafer and Rawson, 1995b) and the cardinal temperatures increase with development (Slafer and Savin, 1991; Slafer and Rawson, 1995a; Porter and Gawith, 1999).

The objective of this study was to modify the WE model by introducing a nonlinear vernalization function, and dividing the vegetative phase (EM–AN) into two sub-phases, EM–TS and TS–AN, with increasing cardinal temperatures for each sub-phase. It was hypothesized that these modifications would improve the predictions of developmental stages in winter wheat compared with the original WE model.

2. Materials and methods

2.1. The WE model

The first step in using the WE model is to calculate the daily rate of plant development (r). The developmental stage (DS) is then calculated by accumulating the daily development rate values (i.e. at a 1 day time step, DS $= \Sigma r$). DS is 0 at EM, 1 at AN, and 2 at PM. Other developmental stages in the vegetative phase are 0.4 at TS, 0.8 at late BT, and 0.88 at awns first visible (AFV).

The general form of the WE model is

$$r = r_{\max,v} f(T)\ f(P)\ f(V) \quad (1)$$

for the vegetative phase (EM–AN), and

$$r = r_{\max,r}\ f(T) \quad (2)$$

for the reproductive phase (AN–PM), where r is the daily development rate (per day), $r_{\max,v}$ and $r_{\max,r}$ are the maximum development rate (per day) in the vegetative and reproductive phases, and $f(T)$, $f(P)$, and $f(V)$ are temperature, photoperiod, and vernalization response functions, varying from 0 to 1, Fig. 1. A complete list of model parameters is given in Appendix A.

The values of $r_{\max,v}$ and $r_{\max,r}$ are cultivar specific (Wang and Engel, 1998). Two winter wheat cultivars were used in this study (‘Arapahoe’ and ‘Karl 92’). These cultivars were chosen, because they are widely grown in Nebraska and Kansas, USA, respectively, and they have different pedigrees and developmental patterns. When planted in Nebraska, Karl 92 is one of the earliest flowering cultivars and Arapahoe is medium to medium-late in flowering. Arapahoe is more photoperiod sensitive than Karl 92. These cultivars were also used in the study by Xue (2000), from whom the values of $r_{\max,v}$ and $r_{\max,r}$ were obtained. The $r_{\max,v}$

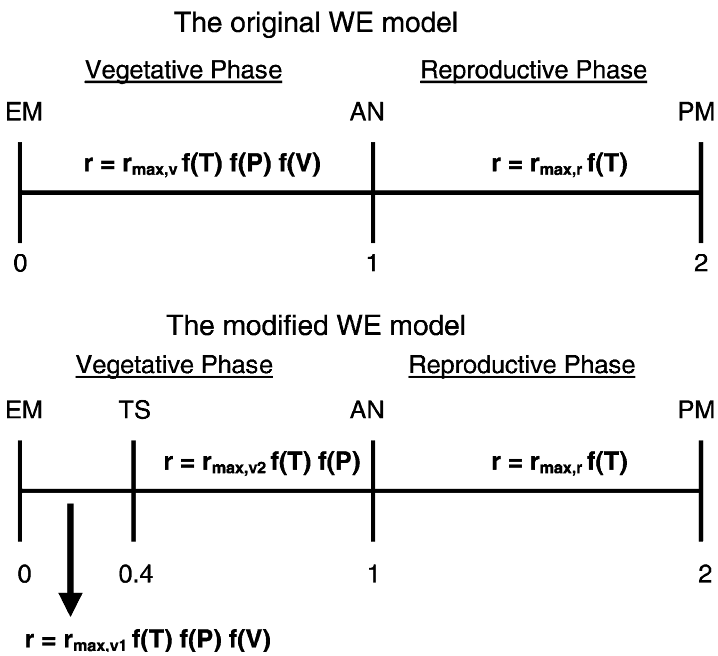

Fig. 1. Schematic diagram of the original and the modified Wang and Engel (WE) model (Wang and Engel, 1998). The developmental stages are EM = emergence, (0); TS = terminal spikelet initiation, (0.4); AN = anthesis, (1); PM = physiological maturity, (2). A list of model parameters is given in Appendix A.

was 0.0294 per day for Arapahoe and 0.0349 per day for Karl 92, and $r_{\max,\mathrm{r}}$ was 0.04545 per day for both cultivars (Xue, 2000).

The temperature function [$f(T)$] is

$$f(T) = \frac{\left[2(T - T_{\min})^{\alpha}(T_{\mathrm{opt}} - T_{\min})^{\alpha} - (T - T_{\min})^{2\alpha}\right]}{(T_{\mathrm{opt}} - T_{\min})^{2\alpha}} \quad \text{for } T_{\min} \le T \le T_{\max}$$

$$f(T) = 0 \quad \text{for } T < T_{\min} \text{ or } T > T_{\max} \tag{3}$$

$$\alpha = \frac{\ln 2}{\ln\left[(T_{\max} - T_{\min}) / (T_{\mathrm{opt}} - T_{\min})\right]} \tag{4}$$

where $T_{\min}$, T_{opt}, and $T_{\max}$ are the cardinal temperatures for development (minimum, optimum, and maximum), and T is the mean daily temperature calculated from the 24 h temperature (Xue, 2000). For the vegetative phase, $T_{\min}$, T_{opt}, and $T_{\max}$ were 0, 24, and 35 °C, and for the reproductive phase they were 8, 29, and 40 °C, respectively (Xue, 2000).

The photoperiod function [$f(P)$] is

$$f(P) = 1 - \exp[-\omega(P - P_{\mathrm{c}})] \tag{5}$$

where P is the actual photoperiod (h), P_{c} the critical photoperiod (h) below which no development occurs, and ω is a cultivar specific photoperiod sensitivity coefficient (h^{-1}). Using the algorithm by Kiesling (1982), the photoperiod, including civil twilight (when the sun is from 0 to 6° below the horizon), was calculated. Values of P_{c} and of ω were 9.5 h and 0.34 h^{-1} for Arapahoe and 7.0 h and 0.16 h^{-1} for Karl 92, (Xue, 2000).

The three-stage linear vernalization function [$f(V)_{\mathrm{linear}}$] is

$$f(V)_{\mathrm{linear}} = \min\left\{1, \max\left[0, (\mathrm{VD} - \mathrm{VD_b}) / (\mathrm{VD_{full}} - \mathrm{VD_b})\right]\right\} \tag{6}$$

where VD is the effective vernalization days, $\mathrm{VD_{full}}$ is the number of effective vernalization days for the plant to be fully vernalized, and $\mathrm{VD_b}$ is the minimum effective vernalization days, i.e. development begins only after a minimum value of $\mathrm{VD_b}$ has been reached (Weir et al., 1984). The functions max and min in Eq. (6) represent the maximum and minimum values in a string of numbers, respectively. The effective vernalization days, VD, is calculated from sowing as:

$$\mathrm{VD} = \sum fvn(T) \tag{7}$$

where $fvn(T)$ is the daily vernalization rate (per day), calculated using Eqs. (3) and (4) with the cardinal temperatures for vernalization ($T_{\min,vn}$, $T_{\mathrm{opt},vn}$, and $T_{\max,vn}$) being −1.3, 4.9, and 15.7 °C (Porter and Gawith, 1999). Both $\mathrm{VD_b}$ and $\mathrm{VD_{full}}$ are cultivar dependent. The value of $\mathrm{VD_{full}}$ was 46 days for Arapahoe and 40 days for Karl 92 and the values of $\mathrm{VD_b}$ were one-fifth of $\mathrm{VD_{full}}$ (Xue, 2000).

2.2. The modified WE model

The original WE model was modified by dividing the vegetative phase (EM–AN) into two sub-phases, EM–TS, and TS–AN (Fig. 1). The general form of the modified WE model during the vegetative phase is

$$r = r_{\max,\mathrm{v1}} f(T)\, f(P)\, f(V) \tag{8}$$

for the EM–TS vegetative sub-phase, and

$$r = r_{\max,\mathrm{v2}} f(T)\, f(P) \tag{9}$$

for the TS–AN vegetative sub-phase, where $r_{\max,\mathrm{v1}}$ and $r_{\max,\mathrm{v2}}$ are the maximum development rates (per day) in the EM–TS and TS–AN vegetative sub-phases, respectively, all other terms have been previously defined. The general form of the WE model during the reproductive phase Eq. (2) was not modified.

The cardinal temperatures for the $f(T)$ in the EM–TS sub-phase were 0, 19, and 30 °C based on Porter and Gawith (1999). Values of the coefficients of the $f(P)$ for the two winter wheat cultivars used here (Arapahoe and Karl 92) were the same as in the original WE model. The vernalization function [$f(V)$] is the nonlinear response function proposed by Streck et al. (2003)

$$f(V) = \frac{(\mathrm{VD})^5}{(22.5)^5 + (\mathrm{VD})^5} \tag{10}$$

where $f(V)$ is the vernalization function that varies from 0 (unvernalized) to 1 (fully vernalized plants) and VD was previously defined. The coefficient 22.5 is the effective vernalization days when plants are 50% vernalized, and the exponent 5 provides the sigmoidal shape of the response to VD.

The maximum development rate for the EM–TS sub-phase ($r_{\max,\mathrm{v1}}$) for the cultivars Arapahoe and Karl 92 was estimated from the data sets of Xue (2000). These data sets comprise the date of developmental stages measured in field experiments conducted at Lincoln, NE, USA (latitude 40°51′N, longitude 96°36′W, elevation 347 m) during three growing season (1996–1997, 1997–1998, and 1998–1999) and two sowing dates in each growing season. The 1996–1997 growing season (October–June) was cold and dry with an average monthly temperature of 5.7 °C and 388 mm of total precipitation. In contrast, the 1997–1998 and 1998–1999 growing seasons were warmer and wetter with average monthly temperatures of 7.3 and 8.0 °C and 650 and 658 mm of total precipitation, respectively. The SAS-NLIN (SAS Institute Inc., 2001) procedure with the Marquardt method was used to determine $r_{\max,v1}$. The estimates of $r_{\max,v1}$ were 0.0198 per day for Arapahoe and 0.0241 per day for Karl 92. These two values of $r_{\max,v1}$ are approximately 0.7 of the $r_{\max,v}$ that Xue (2000) estimated for the EM–AN phase. Data from Slafer and Rawson (1995b), for the spring wheat cultivar Condor, also showed that the development rate during the EM–TS sub-phase was about 0.7 of the development rate of the EM–AN phase.

For the TS–AN sub-phase Eq. (9), no vernalization response was assumed because vernalization has been shown to have no significant effect on development during this sub-phase (Slafer and Rawson, 1994; González et al., 2002) as field grown winter wheat is fully vernalized by TS, i.e., $f(V)$ is 1. In the TS–AN sub-phase, the cardinal temperatures were 4, 24, and 35 °C (Slafer and Savin, 1991; Slafer and Rawson, 1995a; Porter and Gawith, 1999). Values of the coefficients of the $f(P)$ were the ones used by Xue (2000) in the original WE model.

It was not possible to estimate the maximum development rate for the TS–AN ($r_{\max,v2}$) from the data of Xue (2000) because there was not enough variation in the duration of this sub-phase, causing no convergence in the statistical procedure for parameter estimation. Slafer and Rawson (1995b) found that the development rate in the TS–AN sub-phase was about 40% greater than the development rate for the EM–AN phase. Thus, the $r_{\max,v2}$ was calculated as $r_{\max,v2} = 1.4\ r_{\max,v}$ and were 0.0412 per day for Arapahoe and 0.0489 per day for Karl 92.

The cardinal temperatures for the reproductive phase (AN–PM) were 8, 24, and 35 °C (Porter and Gawith, 1999). Even though the general form of the original and the modified WE model was the same for the reproductive phase Eq. (2), a new value for the maximum development rate in this phase ($r_{\max,r}$) was estimated for the modified WE model because the cardinal temperatures were modified. The value of $r_{\max,r}$ in the modified WE model was estimated from the data set used by Xue (2000) using the SAS-NLIN (SAS Institute Inc., 2001) procedure and the Marquardt method. The estimate of $r_{\max,r}$ in the modified WE model was 0.0381 per day for both cultivars.

2.3. Field experiments

A series of field experiments was carried out to evaluate the influence of varying temperature and photoperiod on the development of Arapahoe and Karl 92. These experiments were conducted at the Havelock Farm, Department of Agronomy and Horticulture, University of Nebraska-Lincoln, Lincoln, NE, USA, during two growing seasons, 1999–2000 and 2000–2001. There were four sowing dates during the 1999–2000 growing season (13 September 1999, 29 September 1999, 13 October 1999, and 15 November 1999), and two sowing dates during the 2000–2001 growing season (29 September 2000, and 12 October 2000).

The experiments were in a randomized complete block design with four replications. Each plot was 1.2 m × 2.4 m with four rows in each plot in an E–W row direction. The row spacing was 0.30 m and the plant density was about 200 plants m^{-2}. Plants were grown under rainfed conditions and the plots were well fertilized before sowing. The soil at the experimental site is a Butler silt loam (fine, montmorillonitic, mesic Abruptic Agriaquoll).

Emergence was measured in four 0.5 m row lengths in each plot by counting the number of emerged plants on a daily basis. Emergence date was considered when 50% of the plants were emerged from the soil surface. Two days after emergence, six plants located in the center two rows (three plants/row) in each replication were randomly selected and tagged with colored wires. These plants were used to record the dates of major visible developmental stages based on the Zadoks scale (ZS, Zadoks et al., 1974). The following ZS were recorded on the tagged plants: late booting with stem swollen between the penultimate leaf and the lower leaf (BT, ZS = 45), awns first visible (AFV, ZS = 49), anthesis (AN, ZS = 65), and physiological maturity (PM, ZS = 92). The frequency of the ZS measurements was daily. The date of the ZS in each plot was the average date of the individual plants (six plants per plot).

The terminal spikelet initiation (TS) stage was determined by destructive sampling of one or two plants per plot (four replicates for each cultivar) every 2 days, from 15 March to 25 April 2000 in the first year, and from 20 April to 5 May 2001 in the second year. The dissected main stem apex was observed by microscope and evaluated based on Porter et al. (1987).

Hourly meteorological data (air temperature, precipitation, and solar radiation) were measured by an automated weather station about 300 m from the field site.

2.4. Model evaluation

The dates of developmental stages predicted by the original WE model and the modified WE model were compared with the observed values from the field experiments, which were independent data sets. The statistic used to test model performance was the root mean square error (RMSE), calculated as (Janssen and Heuberger, 1995)

$$\mathrm{RMSE} = \left[\frac{\Sigma(p_i - o_i)^2}{N}\right]^{0.5} \tag{11}$$

where p is the predicted data; o the observed data; and N is the number of observations. The smaller the RMSE, the better the prediction.

3. Results

There was a large variation in environmental conditions during the six sowing dates in the two field growing seasons, which provides a rich data set to evaluate the developmental models. The 1999–2000 growing season was warmer and drier than the 2000–2001 growing season (Table 1), leading plants to mature 20–25 days earlier in 2000 as compared with 2001. Different years and sowing dates also resulted in plants that produced different final leaf number (FLN), from 9 to 16 leaves, and plants that were vernalized at different stages (data not shown). Plants from all sowing dates in the 1999–2000 growing season showed mild to severe symptoms of water stress (leaf rolling during the afternoon) during several days in April and May 2000, whereas no water stress symptoms were observed during the 2000–2001 growing season.

Table 1
Monthly mean air temperature (T_{air}) and total monthly precipitation (Precip) during the two growing seasons at Lincoln, NE

Season	Month	T_{air} (°C)	Precip (mm)
1999–2000	October	12.0	1
	November	8.4	24
	December	0.2	15
	January	−1.9	2
	February	3.0	40
	March	7.2	20
	April	11.4	38
	May	19.4	46
	June	22.1	104
	Mean/total	9.1	290
2000–2001	October	13.8	70
	November	0.1	27
	December	−8.9	16
	January	−2.7	23
	February	−5.5	46
	March	2.2	34
	April	13.2	68
	May	17.7	203
	June	22.0	71
	Mean/total	5.7	558

The comparison between observed and predicted day of the year (DOY) of the TS, BT, AFV, AN, and PM developmental stages for the original and the modified WE models for the two winter wheat cultivars is illustrated in Fig. 2. Data from all sowing dates were pooled. The original WE model over predicted the date of the developmental stages for all sowing dates and cultivars (data above the 1:1 line). Predictions were greatly improved with the modified WE model, with data falling closely below and above the 1:1 line. The RMSE calculated using all developmental stages for the original and modified WE model decreased from 9 to 5 days for Arapahoe and from 11 to 6 days for Karl 92, respectively. Comparing observations of different developmental stages throughout the season with the predictions from the original WE model, predictions were relatively better at intermediate (BT, AFV, and AN) developmental stages (RMSE was between 6 and 10 days), than at earlier (TS) and late (PM) developmental stages (RMSE was between 12 and 14 days). The improvement in the predictions with the modified WE model was in all developmen-

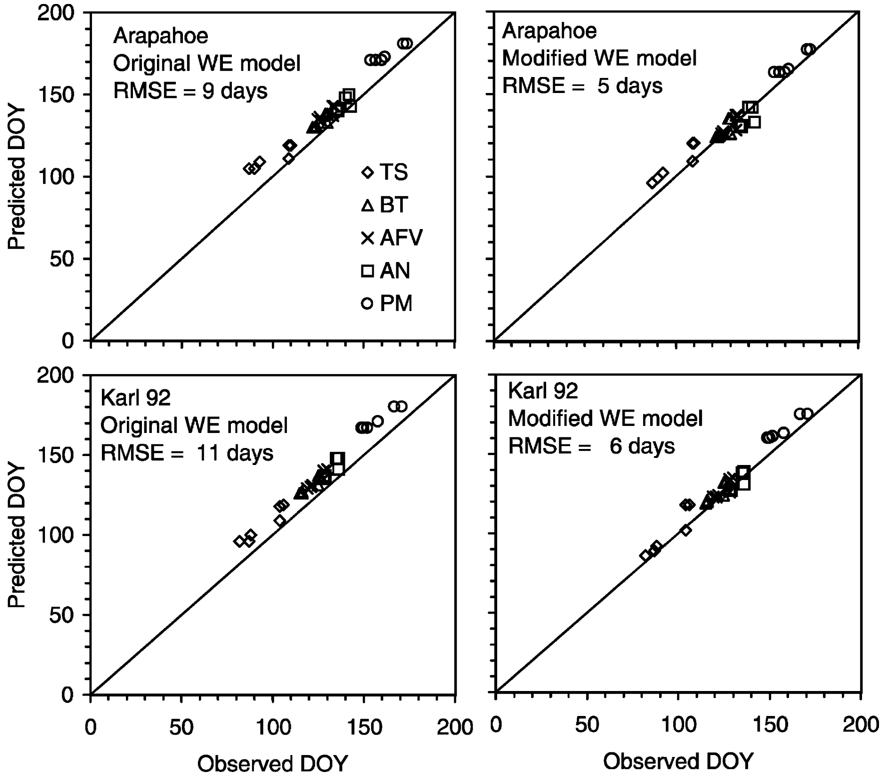

Fig. 2. The predicted vs. observed day of year (DOY) of terminal spikelet initiation (TS), booting (BT), heading (HD), awns first visible (AFV), anthesis (AN), and physiological maturity (PM) for two winter wheat cultivars (Arapahoe and Karl 92) grown at Lincoln, NE. The line is the 1:1 line. Data from four sowing dates during the 1999–2000 growing season and from two sowing dates during the 2000–2001 growing season were pooled.

tal stages, with RMSE values between 5 and 8 days for TS and PM, and RMSE between 3 and 5 days for BT, AFV, and AN.

The RMSE for the different developmental stages with the modified WE model obtained in this study were similar, and in some cases better, than the RMSE reported in other studies with different cultivars and developmental models. For example, Saarikko and Carter (1996), predicted heading in three winter wheat cultivars grown in Finland with a RMSE of 4 days and ripening with a RMSE between 5 and 9 days. Cao and Moss (1997) predicted heading of seven cultivars grown in China and 20 US cultivars with a RMSE of 4–5 days. Kirby and Weightman (1997) predicted anthesis of one winter wheat cultivar grown in six locations and three growing seasons in the UK with a RMSE of 7 days. Jamieson et al. (1998) predicted anthesis of two cultivars in several years in New Zealand and the UK with a RMSE of 6 days. Yan and Wallace (1998) predicted heading of four cultivars from published data with a RMSE between 2 and 10 days.

4. Discussion

The results from the field experiments in this study showed that the modifications introduced in the original WE model improved the predictions of all developmental stages in winter wheat, with an overall decrease of about 45% in the RMSE for both cultivars. Among the developmental stages, the prediction of TS was of special interest in this study. The predictions of TS with the original WE model was inferior to CERES-Wheat in a previous study (Xue, 2000). The prediction of TS with the original WE model in this study was also poor, with RMSE greater than 12 days in both cultivars. The modified WE model reduced the RMSE for TS to 7 days in both cultivars.

The modifications introduced to the original WE model are biologically meaningful. One modification was the vernalization function. The nonlinear vernalization response function Eq. (10) is more realistic than the three-stage vernalization response function Eq. (6), because biological systems respond to environmental factors more likely in a smooth and continuous fashion rather than in a step fashion (Shaykewich, 1995). Eq. (10) is also cultivar independent (Streck et al., 2003) decreasing the number of input data necessary in crop simulation models.

The second modification to the original WE model was the division of the vegetative phase into two sub-phases (EM–TS, TS–AN). This modification was based on previous observations that the development rate before TS was lower than after TS in wheat (Slafer and Rawson, 1995b). It is reasonable to assume that before TS a slower development rate is advantageous, since the plant prioritizes the growth of leaves and the photosynthetic apparatus in order to accumulate carbohydrates and nutrients for future use (Spiertz and Ellen, 1978; Penning de Vries et al., 1989). After TS, an increased development rate towards anthesis is advantageous to avoid possible adverse environmental conditions during the reproductive phase such as high temperatures and soil water stress, commonly encountered in semiarid regions where wheat is grown.

The third modification introduced to the original WE model was a gradual increase in the cardinal temperatures as development progressed. This modification was based on previous studies with wheat (Slafer and Savin, 1991; Slafer and Rawson, 1995a; Porter and Gawith, 1999). One reason suggested to explain the gradual increase in the cardinal temperatures with development in wheat is that it may reflect an adaptation to low temperature during early developmental stages, and to warmer temperatures during the reproductive phase (Angus et al., 1981). Another suggested reason is that metabolic activity may be higher during culm and spike growth and during grain filling than during the early vegetative stages (Slafer and Savin, 1991).

There is often confusion and misuse of the terms plant growth and development (Wilhelm and McMaster, 1995). Plant growth (irreversible changes in biomass, length, volume, or area) and development (cell differentiation and organ initiation, events related to time) are related, but independent processes (Hodges, 1991). Hence, a growing plant may not necessarily be a developing plant. To illustrate this point, daily values of the temperature function $f(T)$, the photoperiod function $f(P)$, and the vernalization function $f(V)$ calculated with the modified WE model for the cultivar Arapahoe on two sowing dates (13 September 1999 and 13 October 1999) at Lincoln, NE, are illustrated in Fig. 3. Observed dates of major developmental stages (EM, TS, AN, and PM) and the observed number of fully expanded leaves on the main stem leaves (MSL) for each sowing date are also indicated in Fig. 3.

In the earlier sowing date, plants started to be vernalized when they had already five fully expanded leaves, about 30 days after emergence (Fig. 3). The plants were growing (i.e. adding leaves) but not developing (i.e. plants were not progressing toward TS from DOY $=$ 264 to about DOY $=$ 294). From a simulation perspective, the vernalization function was zero, and therefore r was 0 Eq. (8). In the later sowing date, plants started to be vernalized immediately after emergence; plants were growing and developing at the same time. When plants from both sowing dates were fully vernalized, about 20 December 1999 (DOY $=$ 354), there were eight MS leaves on the earlier sown plants and four MS leaves on the plants from the later sowing date. At TS and AN, plants from the earlier planting date had three and four more leaves than the plants from the later planting dates, respectively, even though plants in both sowing dates reached TS and AN on the same date (measured and predicted with the modified WE model).

The results in Fig. 3 also illustrate synchronism in winter wheat development under field conditions, i.e. different sowing dates in the fall result in similar flowering and maturation date in the following spring and summer (Hay and Kirby, 1991). During the period DOY $=$ 364 to DOY $=$ 50, although plants were fully vernalized, development was low because both $f(T)$ and $f(P)$ were low (Fig. 3). For example, during this period, $f(T)$ was lower than 0.5 and most of the days it was zero, and $f(P)$ was lower than 0.5. During the period DOY $=$ 50–100, when temperature and photoperiod increased, plants from both sowing dates developed at the same rate because plants from both sowing dates were fully vernalized. As a conse-

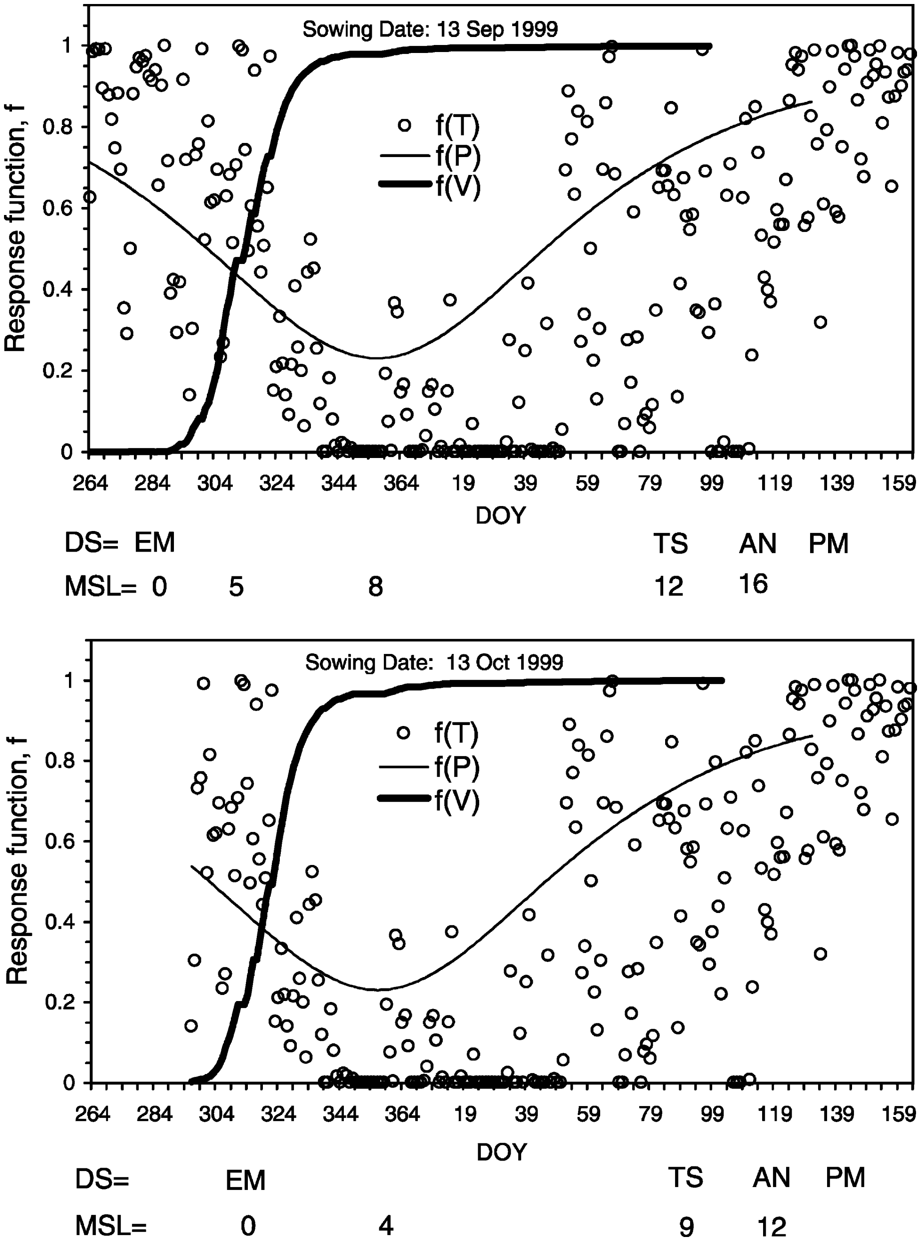

Fig. 3. Daily values of the temperature response function [$f(T)$], the photoperiod response function [$f(P)$], and the vernalization response function [$f(V)$] calculated with the modified WE model for cultivar Arapahoe on two sowing dates (13 September 1999 and 13 October 1999) at Lincoln, NE. Observed dates of major developmental stages (DS) [emergence (EM), terminal spikelet initiation (TS), anthesis (AN) and physiological maturity (PM)], and the number of fully expanded leaves on the main stem leaves (MSL) are also indicated for each sowing date.

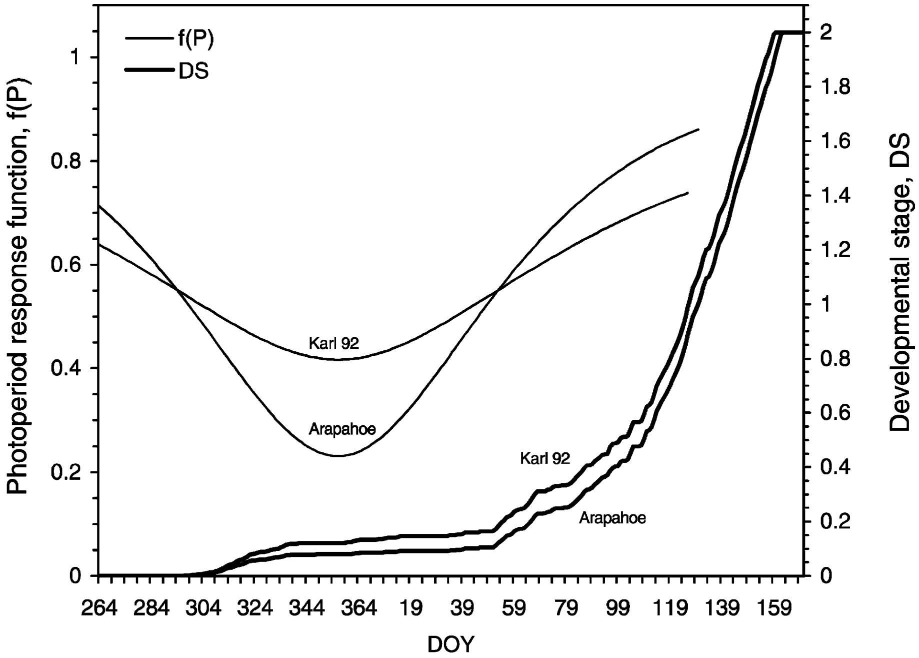

Fig. 4. Daily values of the photoperiod function [$f(P)$] and developmental stage (DS) calculated with the modified WE model for the cultivars Arapahoe and Karl 92 on the 13 September 1999 (DOY = 256) sowing date. Emergence, DS = 0 (occurred on DOY = 264 for both cultivars), terminal spikelet initiation occurs at DS = 0.4, anthesis at DS = 1.0, and physiological maturity at DS = 2.0.

quence, the measured and predicted (by the modified WE model) dates of TS, AN, and PM were the same for both sowing dates, even though there was a 30-day difference in the sowing dates. Similar results were obtained when comparing the 13 September 1999 and 15 November 1999 sowing dates. A difference of 63 days between sowing dates resulted in only 7 days difference in anthesis and physiological maturity (measured and predicted with the modified WE model) between the two sowing dates (data not shown). Comparing the MS leaves at anthesis in the 13 September 1999 and the 15 November 1999 sowing dates, the latter had 9 leaves compared to 16 MS leaves in the former.

Field observations indicate that Karl 92 flowers and matures earlier than Arapahoe. The reason for this difference in developmental patterns is the different development rates in the vegetative phase (EM–TS, TS–AN) between these two cultivars, not in the reproductive phase (AN–PM). The measured length of the reproductive phase was the same for both cultivars. In the modified WE model, Karl 92 has a higher $r_{\max,v1}$ and $r_{\max,v2}$ than Arapahoe. Photoperiod also plays an important role in determining the rate of plant development. Arapahoe is more sensitive to photoperiod, with a higher ω and P_c than Karl 92. The daily values of $f(P)$ and the developmental stage calculated with the modified WE model for both cultivars sown on 13 September 1999 are presented in Fig. 4. The $f(P)$ is greater for Karl 92 than Arapahoe during the period between 21 Oct (DOY = 294) and 21 February (DOY = 52). During this period, the development rate (and consequently the developmental stage) is somewhat higher for Karl 92 because of both a greater $f(P)$ and a greater $r_{\max,v1}$. After DOY = 52, $f(P)$ is lower for Karl 92, but the higher $r_{\max,v1}$ and $r_{\max,v2}$ compensates for the lower $f(P)$ resulting in an almost equal development rate and, therefore, a developmental stage that remains higher for Karl 92 than for Arapahoe for any given temperature. Thus, the modified WE model predicts that the developmental stage is greater for Karl 92 than for Arapahoe until anthesis, and therefore Karl 92 flowers earlier than Arapahoe. After anthesis, since Karl 92 flowers earlier and both cultivars have the same $r_{\max,r}$ and $f(T)$, the modified WE model predicts that Karl 92 matures earlier than Arapahoe. The modified WE model predicted that AN was 3 (±1) days earlier in Karl 92 than in Arapahoe, while the observed data showed that Karl 92 reached AN 6 (±1) days earlier in the two growing seasons. The modified WE model predicted that PM was 4 (±1) days earlier in Karl 92 compared with Arapahoe whereas the observed data showed that Karl 92 reached PM 5 (±1) days earlier in the two growing seasons. These results indicate that the modified WE model described well the different developmental patterns of the two cultivars.

5. Conclusions

The predictions of major developmental stages in winter wheat were greatly improved with the modified WE model under the contrasting field conditions of this study. The RMSE for all developmental stages was 5 days for Arapahoe and 6 days for Karl 92, which corresponds to a 45% decrease in the RMSE compared to the original WE model. The modified WE model described well the different developmental patterns of the two cultivars in the field, i.e. Karl 92 flowers and matures earlier than Arapahoe. Photoperiod is an important factor determining the developmental pattern of the two cultivars.

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Appendix A. List of model parameters

Parameter	Description	Unit
DS	Developmental stage	–
$f(P)$	Photoperiod function, varies from 0 to 1	–
$f(T)$	Temperature function, varies from 0 to 1	–
$f(V)$	Vernalization function, varies from 0 to 1	–
$fvn(T)$	Daily vernalization rate function, varies from 0 to 1	–
P	Actual photoperiod	h
P_c	Critical photoperiod below which no development occurs, cultivar dependent	h
r	Daily development rate	Per day
$r_{max,r}$	Maximum daily development rate in the anthesis-physiological maturity phase, cultivar dependent	Per day
$r_{max,v}$	Maximum daily development rate in the emergence-anthesis phase, cultivar dependent	Per day
$r_{max,v1}$	Maximum daily development rate in the emergence-terminal spikelet initiation phase, cultivar dependent	Per day
$r_{max,v2}$	Maximum daily development rate in the terminal spikelet initiation-anthesis phase, cultivar dependent	Per day
T_{min}	Minimum temperature for development, dependent on developmental phase	°C
T_{opt}	Optimum temperature for development, dependent on developmental phase	°C
T_{max}	Maximum temperature for development, dependent on developmental phase	°C
VD	Effective vernalization days	Days
VD_b	Minimum effective vernalization days, below which no development occurs, cultivar dependent	Days
Vd_{full}	Number of effective vernalization days for the plant to be fully vernalized, cultivar dependent	Days
ω	Photoperiod sensitivity coefficient, cultivar dependent	h^{-1}

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