Photoperiod and Vernalization Effect on Anthesis Date in Winter-Sown Spring Wheat Regions

Michael J. Ottman,* L. Anthony Hunt, and Jeffrey W. White

ABSTRACT

Accurate prediction of phenology is required to guide crop management decisions and to predict crop growth and yield. However, the relative importance of photoperiod and vernalization in predicting anthesis dates for spring bread and durum wheat (*Triticum aestivum* L. and *T. durum* Desf.) sown in the winter has not been reported. The purpose of this research is to determine the improvement in predicting anthesis dates of spring wheat sown in the winter when photoperiod and vernalization are considered. Observed dates of anthesis were obtained from University of Arizona wheat variety trials conducted at Maricopa, Wellton, and Yuma, AZ. The Cropping Systems Model CROPSIM-CERES as released in DSSAT 4.5 was used to simulate days to anthesis based on temperature, daylength, and vernalization. For 12 bread and durum wheat cultivars, the model predicted days to anthesis with a root mean square error (RMSE) of 7.6 d if all cultivar differences were ignored, 6.4 d considering only differences in thermal time (TT), 6.1 d with differences in TT and daylength response, 6.4 d with TT and vernalization, and 6.2 d with TT, daylength, and vernalization. Consideration of cultivar differences in TT and photoperiod response improved the prediction of days to anthesis for winter-sown spring wheat, but there was no benefit from considering effects of vernalization in CROPSIM-CERES.

Accurate prediction of phenology is required to guide crop management decisions and to predict crop growth and yield. The simplest models for time of anthesis or maturity assume that the rate of development is proportional to growing temperature, an approach dating to the work of Reaumur (1735). In bread wheat and durum wheat, anthesis is also affected by photoperiod and vernalization responses. Winter-sown spring wheat crops are grown over millions of hectares globally, being represented in CIMMYT's megaenvironment (ME) 1 and portions of ME 2, 3, 4, and 5 (Hodson and White, 2007). Germplasm for these regions require low photoperiod sensitivity and low vernalization requirement (van Beem et al., 2005). However, it is unclear whether these low levels of responsiveness need to be considered to accurately predict time of anthesis or whether a pure temperature response (e.g., TT, heat unit, or growing degree day) approach is adequate.

Models of wheat flowering time vary in complexity (Jamieson et al., 2007), depending on whether they link development to leaf initiation or appearance and how many discrete phases they recognize from sowing to anthesis. Their core structure typically involves integrating a developmental rate, R, over time. Furthermore, the models usually assume that for a given phase, there is a maximum rate of development, R_{max}, whose effects may be reduced by individual environmental factors. Thus,

$$R = R_{max} \times F(T, D, V)$$

where T is the main effect of temperature, D is the effect of daylength (photoperiod), and V is the effect of vernalization. Vernalization is actually a function of temperature, but for clarity, it is best specified separately from T. The development rate, R is integrated over intervals defined by the two stages that delimit a given phase. The duration of the phase may be expressed in various types of units but most often is expressed in TT.

The underlying physiological question is whether the photoperiod and vernalization responses have agronomically important effects in environments with short daylengths and cool, but typically non-freezing temperatures. This question is important both for characterizing germplasm released for such environments and for devising strategies to increase crop yield. The latter is especially relevant given interest in determining whether global warming would permit earlier sowing dates due to reduced chance of frost damage during early reproductive development (Ottman et al., 2012).

The importance of photoperiod and vernalization in determining flowering time in wheat has been widely researched, but few studies have emphasized quantitative prediction of their effects. The effects of the *Vrn* and *Ppd* loci on anthesis date in wheat have been shown through simulation emphasizing winter wheat (White et al., 2008) and genetic analysis of

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Abbreviations: P, duration from end of juvenile phase to end of spike growth (P1+ P2+ P3); P1, duration from end of juvenile stage to terminal spikelet formation; P1D, daylength coefficient; P1V, vernalization coefficient; P2, duration from terminal spikelet formation to end of leaf growth; P3, duration from end of leaf growth to end of spike growth; RMSE, root mean square error; TT, thermal time; VEFF, maximum allowed reduction in development rate when unvernalized.

Table 1. Latitudes, elevations, air temperatures, and precipitation for the locations used in the study. The temperature and precipitation are from December through April, representative of the wheat growing season.

Location	Latitude	Elevation	Temperature			Precipitation
			Maximum	Minimum	Average	
		m		°C		mm
Maricopa	33°04'07"	361	22.6	5.0	13.5	82
Wellton	32°44'40"	91	24.2	5.1	14.4	35
Yuma Valley	32°42'45"	32	23.8	7.7	15.8	36

spring wheat (van Beem et al., 2005). The importance of daylength and vernalization in predicting anthesis dates for winter wheat grown in Europe has been reported (He et al., 2012; Herndl et al., 2008). Sharma and D'Antuono (2011) showed that a statistical model that included vernalization was superior to a model that only considered temperature and photoperiod in predicting flowering dates of wheat in colder regions of western Australia. Lanning et al. (2012) compared yields of near-isogenic lines that differed in photoperiod sensitivity and determined that photoperiod sensitive lines were superior in the northern regions of the western United States and the Canadian plains.

Spring wheat sown in the winter is generally thought to show little response to vernalization and to be photoperiod insensitive. Although qualitatively true, especially for vernalization, these spring wheat crops do respond to vernalization and photoperiod treatments (Eagles et al., 2010). What remains unclear is whether the levels of response are large enough to affect prediction of anthesis dates for a spring wheat sown in the winter. The purpose of this research is to assess the improvement in predicting anthesis dates of spring wheat sown in the winter when possible cultivar differences in photoperiod and vernalization are considered.

MATERIALS AND METHODS

Data Sources

Data on time of anthesis were obtained from University of Arizona wheat variety trials conducted at Maricopa, Wellton, and Yuma, AZ (Table 1). Where only heading dates were recorded, the assumption was made that anthesis occurred 7 d later for durum wheat and 5 d later for bread wheat based on analysis of long-term data where both heading and anthesis dates were recorded. In these trials, the wheat was grown in small plots of approximately 1.5 m width and 6 m length. Seed was planted at a rate of about 120 kg seed ha^{-1} (2.6–3.2 million seed ha^{-1} depending on seed size), about 250 kg N ha^{-1} was applied in applications split over the period from sowing time to anthesis, and about 0.9 m of irrigation water was applied in six to seven border flood irrigations. Most trials were arranged in four randomized complete blocks. Sowing occurred at planting times that are considered optimum or typical for the location except for a 3-yr planting date trial that was included in the data for the cultivars Westbred 881 and Yecora Rojo at the Maricopa location. The cultivars tested in these trials were early to late maturing, semi-dwarf, and commercially available, and they were adapted to the desert regions of the southwestern United States and similar areas throughout the world. Anthesis or heading dates were observed about three times per week and based on all stems in the plot, not just the main stem. Heading date was defined as when the base of the spike had emerged past the leaf collar on 50% of the stems. Anthesis date was defined as when anthers were first visible on 50% of the spikes. Temperature data were obtained from the nearest Arizona Meteorological (AZMET) station, an automated network of weather stations maintained by the University of Arizona (http://ag.arizona.edu/azmet).

Simulation Model

The Cropping Systems Model CROPSIM-CERES as released in DSSAT 4.5 (Hoogenboom et al., 2011) was used throughout. Developmental stages considered include germination, seedling emergence, terminal spikelet initiation, anthesis, and physiological maturity. In CROPSIM-CERES, cultivar differences in vernalization and photoperiod response are specified through ecotype and cultivar parameters (Table 2). Durations of specific stages are variously defined at the cultivar, ecotype, and species level (Table 2).

The model calculates the average daily temperature from the mean of the daily maximum and minimum air temperatures, and all cardinal temperatures for development are based on average temperatures. In the absence of vernalization and photoperiod effects, development does not occur below a base temperature (T_{base}) of 0°C, increases linearly with temperature from 0°C to a lower optimum (T_{optl}) of 26°C, continues at the maximum rate to an upper optimum (T_{optu}) of 50°C, declines linearly from 50°C to the maximum temperature (T_{max}) of 60°C, where development ceases (Fig. 1). Daily TT is calculated from this temperature response function. The daily average temperature for the studies analyzed in this study were between 0 and 26°C, so daily TT was equivalent to daily average temperature. Occurrences of stages are simulated by integrating daily TT over time. A given stage is reached when sufficient progress, quantified as accumulated daily TT, has accrued.

Photoperiod and vernalization affect development from germination to terminal spikelet initiation only (genotype coefficient P1 in Table 2). In the presence of photoperiod and/or vernalization effects, daily thermal time ($TT_{d,v}$, °Cd) is calculated as:

$$TT_{d,v} = TT \times DF \times VF \quad [1]$$

where TT (degree days, °Cd) is the daily thermal time adjusted for daylength and/or vernalization effects, DF (0–1) is the daylength or photoperiod factor, and VF (0–1) is the vernalization factor. The maximum allowed reduction in development rate when unvernalized (VEFF) was set to 0.6. Therefore, the product of DF and VF is never <0.4 when unvernalized. Daily TT is summed and the phase-specific required accumulations of TT are specified as cultivar or ecotype parameters (Table 2).

The daily photoperiod factor (DF) is calculated as:

Table 2. Descriptions of the main coefficients affecting time of flowering in the CSM CROPSIM-CERES model as released in DSSAT (Hoogenboom et al., 2011).

Coefficient	Definition†	Range‡ or default values	Units
Genotype			
P1V	Days at optimum vernalizing temperature required to complete vernalization	0–8.3	days
P1D	Percentage reduction in development rate in a photoperiod 10 h shorter than the optimum relative to the rate at the optimum	9–56	%
Ecotype			
P1	Duration from end of juvenile phase to terminal spikelet	460–600	°C day
P2	Duration from end of terminal spikelet to end leaf growth	328–428	°C day
P2FR1	Duration from end of terminal spikelet to jointing (relative to P2)	0.25	(fraction)
P3	Duration from end of leaf growth to end of spike growth	219–285	°C day
P4	Duration from end of spike growth to end of lag phase for grain fill	200	°C day
P4FR1	Duration from end of spike growth to anthesis (relative to P4)	0.25	(fraction)
P5	Duration from end of lag phase for grain fill to physiological maturity	450	°C day
VEFF	Maximum allowed reduction in development rate when unvernalized	0.6	(fraction)
Species			
PGERM	Duration from planting to germination	10	°C day
PEMRG	Duration from germination to seedling emergence	8.0	°C day cm^{-1} sowing depth
P0	Duration of juvenile phase	0	°C day
P6	Duration from physiological maturity to harvest	200	°C day
PPFPE	Photoperiod factor for pre-emergence development	1	(binary)
PPTHR	Photoperiod threshold above which there is no further effect of daylength	20.0	hour
PPEND	End stage for photoperiod sensitivity (2 = terminal spikelet)	2	(integer)

† Juvenile phase is the period after emergence when the plant is unresponsive to photoperiod and is 0°C day for wheat but is important for other crops modeled by CERES. The terminal spikelet stage signifies the end of initiation of floral primordial and usually occurs by the time the sixth leaf appears. Leaf growth ends when the flag leaf is fully extended. Spike growth ends after the spike is fully extended and before anthesis. The end of the lag phase for grain fill occurs near the end of the kernel watery stage. Physiological maturity is the stage when no more dry matter accumulates in the grain.

‡ Range is from among cultivars considered in this study and is for calibrations including P1, P2, P3, P1D, and P1V.

$$DF = 1 - [(P1D/10{,}000) \times (P1DT - PP)^2] \quad [2]$$

where P1D is the cultivar sensitivity to photoperiod, P1DT (h) is the critical long photoperiod set to 20 h in this study, and PP (h) is the photoperiod. Photoperiod includes twilight and is calculated using a 6° inclination from the horizon. Cultivar sensitivity to photoperiod is mainly determined by the parameter P1D, which specifies the reduction in developmental rate in a photoperiod 10 h shorter than the critical long photoperiod, P1DT.

The effect of vernalization is based on the concept of progress of vernalization as a function of daily mean temperature. The cultivar-specific vernalization coefficient P1V specifies how many days of vernalization are required for reproductive development to proceed at its maximum rate, assuming that temperatures for vernalization are optimal. Vernalization is assumed to occur at temperatures from –5 to 15°C, with the maximum rate between 0 and 7°C (Fig. 2). The vernalization factor (VF) is calculated as the relative development rate when unvernalized plus the ratio of accumulated to required vernalization days:

$$VF = (1–VEFF) + (VEFF \times CUMVD/P1V) \quad [3]$$

where VEFF is the maximum allowed reduction in development rate when unvernalized and was set to 0.6 for this study, CUMVD is the accumulated vernalization days, and P1V is the cultivar specific vernalization coefficient. The daily vernalization progress is accumulated to indicate vernalization status, this value being used to calculate the daily vernalization factor. Because an unsatisfied vernalization requirement generally slows but does not prevent reproductive development, the lowest allowed value of the vernalization factor is specified by the "vernalization effectiveness" parameter, VEFF (the lowest vernalization factor = 1 –VEFF). De-vernalization may occur when <10 d of progress toward vernalization have accumulated, and the maximum temperature exceeds 30°C, which never occurred in the trials analyzed in this study.

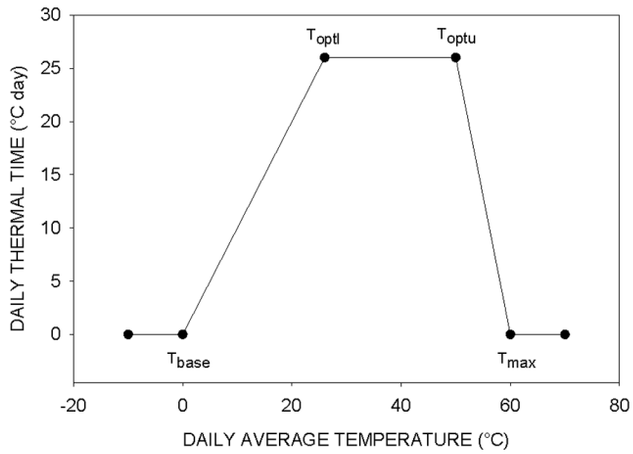

Fig. 1. Daily thermal time (TT) as influenced by daily average temperature. Below a base temperature (T_{base}) of 0°, TT does not accumulate. Between 0°C and the lower optimum temperature (T_{optl}) of 26°C, TT is equivalent to daily average temperature. Between 26°C and the upper optimum temperature (T_{optu}) of 50°C, TT is 26°C day. Between 50°C and the maximum temperature (T_{max}) of 60°C where development ceases, TT has a negative linear relationship with daily average temperature. Daily average temperatures for the trials analyzed in this study were between 0 and 26°C.

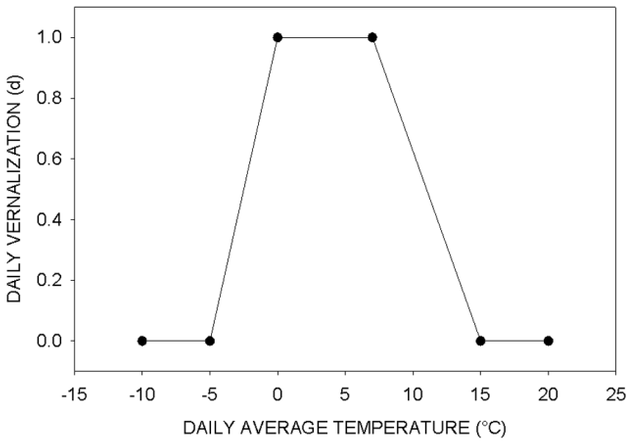

Fig. 2. Vernalization days as affected by daily average temperature. Temperature for vernalization is optimum between a daily average temperature of 0 and 7°C, and vernalization days are 1 in this range. Temperature for vernalization is less effective when daily average temperature is between –5 and 0°C and 7 and 15°C, and vernalization days decreases linearly and is <1 as temperature deviates from the optimum vernalizing temperatures. Vernalization does not occur at daily average temperature below –5 or above 15°C.

The durations of specific phases are specified through cultivar, ecotype, and species parameters (Table 2). The ecotype coefficients P1, P2, and P3 are values of TT from seedling emergence to terminal spikelet, terminal spikelet to the end of leaf growth, and the end of leaf growth to the end of spike growth, respectively. Their sum, here identified as P, determines TT from the emergence to the end of spike growth. The terminal spikelet stage signifies the end of initiation of floral primordial and usually occurs by the time the sixth leaf appears. Leaf growth ends when the flag leaf is fully extended. Spike growth ends after the spike is fully extended and before anthesis. Actual time of anthesis from emergence is estimated as P plus a fraction (P4FR1, 0.25) of the time from the end of spike growth to the end of lag phase for grain (P4, 200°Cd).

Simulations

Simulations assumed no water or nitrogen limitations since crops in the target megaenvironment are typically well irrigated and fertilized to obtain near-maximum yields. The depth of sowing was assumed to be 4 cm.

Cultivar parameters were calibrated using the GenCalc tool (Hunt et al., 1993) of DSSAT (Hoogenboom et al., 2011). Briefly, GenCalc executes a series of gridded searches of possible parameter values starting from initial, user-selected values and search criteria. The user also determines the maximum number of iterations to be executed. In each cycle, GenCalc defines an N-dimensional grid of possible values, where N is the number of parameters to be estimated. For each combination of parameter values, GenCalc simulates values for the target variable (e.g., days to anthesis) for all experiments and treatments being considered and then estimates the goodness of fit (as RMSE) for the measured vs. simulated values. GenCalc then selects the set of parameters values giving the smallest RMSE to define the center of the next search grid using the new selected values as the center. The new grid is evaluated, and the cycle of testing is continued until the RMSE reaches a constant minimum value or the maximum allowed iterations is reached.

Four sets of calibrations were conducted. In all calibrations, P1, P2, and P3 were varied proportionally based on reference values of 400, 285, and 190, their sum being defined as P. The first set assumed that cultivars differed only for TT requirement and thus fitted only P. The second set fitted both P and P1D to allow for an effect of photoperiod. In the third set, P and P1V were fitted, excluding photoperiod but considering vernalization, and in the fourth set P, P1D, and P1V were fitted, representing the full model for temperature, photoperiod, and vernalization effects. To assess how well coefficients from a single, generic cultivar could predict phenology, the coefficient P for such a cultivar was estimated as the mean of values for all cultivars for the calibrations that only considered variation in TT (e.g., assuming P1D = 0 and P1V = 0). Similarly, a generic cultivar with a photoperiod response was created using mean values of P and P1D, while setting P1V = 0. For both generic cultivars, all other species, ecotype, and cultivar parameters (Table 2) were held constant.

To assess the impact of the various combinations of coefficients on variability in anthesis date, a sensitivity analysis was conducted using hypothetical combinations of P1V and P1D, while assuming VEFF = 0.6 and P = 1270. Sowing dates were varied from 1 November to 28 February for a 19-yr series of weather data from the Yuma Valley.

Goodness-of-Fit Evaluation

Goodness of fit was judged by comparing means of observed vs. simulated anthesis dates, r^2 values, slopes of bi-variate linear regressions, and RMSE. Multiple linear regression was used to assess the relative predictive capability of cultivar coefficients estimated through the different approaches, as in the approach of White et al. (2007) and using the GLM procedure of the SAS package (SAS Institute, 2009). For all regressions, sums of squares were values for sequential entry of dependent variables (Type I).

RESULTS AND DISCUSSION

Measured Days to Anthesis

The mean measured days to anthesis for all cultivars varied from 104 to 119 d after planting (Table 3). Cultivars Yecora Rojo and Westbred 881 showed over a 60-d range, reflecting their inclusion in 3 yr of planting date studies at Maricopa, which included plantings in February that resulted in rapid flowering.

Model Coefficients

Within each calibration approach, the fitted coefficients affecting anthesis varied considerably among wheat types and cultivars (Table 4). As expected, the sums of P1, P2, and P3 were lower when photoperiod, vernalization, or their combined effects were considered since these effects reduce the effectiveness of TT (i.e., slow development). For the complete model, the sum ranged from 1010 for Yecora Rojo to 1310 for three of the durum cultivars. The values for the bread wheat cultivars were similar to the earliest of the durums.

In the case of calibrations that considered effects both of vernalization and photoperiod (Table 4), the values for the photoperiod response, P1D, varied from 9 for Mohawk to 56 for Yecora Rojo. Mohawk has a small response to photoperiod

Table 3. Summary of bread and durum wheat cultivars assessed including the number of trials at each location for each cultivar; mean, minimum, and maximum days from planting to anthesis.

	Number of trials			Days to anthesis		
Cultivar	Maricopa	Wellton	Yuma	Mean	Minimum	Maximum
Bread						
Brooks	4	1	3	111	93	123
Cavalier	4	1	3	113	93	123
Yecora Rojo	29	1	3	104	61	133
Durum						
Crown	13	1	8	116	97	136
Duraking	12	1	8	115	98	136
Havasu	6	0	4	111	100	126
Kofa	12	1	7	113	95	127
Kronos	12	1	8	111	91	132
Mohawk	12	1	7	112	94	129
Ocotillo	11	1	8	113	96	128
Orita	10	1	7	116	100	131
Platinum	12	1	8	114	96	132
Sky	9	1	6	112	98	127
Topper	6	1	3	119	100	134
Westbred 881	43	0	7	110	64	133

Table 4. Values for the coefficients derived from GenCalc for thermal time (TT) from seedling emergence to end of spike growth (P1+P2+P3), for response to daylength (P1D), and for vernalization requirement (P1V) from the four calibration approaches.

	Calibration approach							
	TT only	TT and daylength		TT and vernalization		TT, photoperiod, and vernalization		
Cultivar	P1+P2+P3	P1+P2+P3	P1D	P1+P2+P3	P1V	P1+P2+P3	P1D	P1V
Bread								
Brooks	1378	1160	43.1	1378	0.0	1200	34	0.0
Cavalier	1400	1138	48.7	1400	0.0	1140	51	0.0
Yecora Rojo	1269	1028	49.9	1269	0.0	1010	56	0.0
Durum								
Crown	1488	1182	54.0	1444	3.6	1250	36	2.3
Duraking	1465	1225	46.4	1400	3.2	1200	38	3.7
Havasu	1444	1313	27.4	1378	4.2	1230	23	8.3
Kofa	1400	1269	30.2	1357	3.3	1290	15	2.7
Kronos	1400	1247	29.9	1335	2.0	1290	12	1.4
Mohawk	1400	1247	29.9	1335	5.0	1290	9	3.6
Ocotillo	1444	1290	29.9	1335	9.0	1310	12	6.9
Orita	1510	1313	38.4	1465	2.7	1250	40	2.7
Platinum	1444	1313	29.9	1400	3.2	1310	16	5.7
Sky	1444	1247	37.0	1378	4.1	1310	15	2.3
Topper	1488	1160	58.0	1510	0.0	1160	53	3.7
Westbred 881	1313	985	64.4	1290	0.0	1120	42	0.0

while the response of Yecora Rojo is quite large. A small response to photoperiod implies that TT to anthesis is affected little by the short daylengths associated with winter-sown spring wheat cropping. Photoperiod sensitivity was expected to be low in these spring wheat crops because of shuttle breeding, whereby during selection, the lines were exposed to short daylengths that is, selecting in a low latitude location in the winter/spring and a high latitude location in the spring/summer (Braun et al., 1996).

The vernalization coefficient, P1V, varied from 0 d for the three bread wheat cultivars and WestBred 881 to 8.3 d for the durum wheat Havasu. These values are quite low compared to expected values over 20 d for winter wheat and thus are in agreement with the expected lack of vernalization requirement for spring wheat. However, some spring wheat flower somewhat earlier when exposed to vernalizing temperatures (Wort, 1939).

A broad optimum exists where many combinations of TT, daylength, and/or vernalization result in relatively small differences in the fit of the model as measured by RMSE. Therefore, the values of TT and P1D are not necessarily the same when P1V is 0 or not included at all. The starting point and calculation matrix in Gencalc can be different depending on whether or not P1V is included.

The fact that the model calculated a wide range of coefficients for the cultivars tested at the three locations suggests that consideration of photoperiod response is important in predicting time to flower in spring wheat. However, it must be kept in mind that these coefficients were estimated through a

Table 5. Summary of comparisons of measured vs. simulated values of days to anthesis for models considering only thermal time (TT) or combinations of TT plus daylength (D) or vernalization (V) responses. The generic TT model used the averages for each of the coefficients P1, P2, and P3, and the generic daylength model used the average of the TT and daylength coefficients.

Model	Mean of measurements	Mean of simulations	r^2	Slope	Intercept	RMSE
		d				d
Generic TT	111.8	113.1	0.66	0.90	10.6	7.6
TT	111.8	111.9	0.76	0.94	5.9	6.4
Generic daylength	111.8	112.4	0.68	0.86	15.2	7.4
TT + D	111.8	112.0	0.78	0.88	13.5	6.1
TT + V	111.8	112.0	0.76	0.96	4.1	6.4
TT + D + V	111.8	112.8	0.78	0.92	8.3	6.2

best fit procedure that might confound true genetic differences with differences related to unintended effects of location or observers. Furthermore, the parameters are not readily associated with errors of estimation, so the apparent differences cannot be subjected to statistical tests.

Model Fit

The relationship between the observed and simulated data was analyzed by linear regression (Table 5, Fig. 3). The mean observed days to anthesis was 112 d, and the mean simulated days to anthesis ranged from 112 to 113 d depending on the model. The model with the poorest fit (Generic TT) slightly overestimated days to anthesis. The r^2 ranged from 0.66 to 0.78 and the RMSE ranged from 6.1 to 7.6 d. The lowest predictive capability was with the generic TT model, which assumed no differences among cultivars (constant P) and no effect of daylength or vernalization. Allowing for cultivar differences by varying P improved the RMSE from 7.6 to 6.4 d (Table 5). Adding daylength, vernalization, and both daylength and vernalization gave RMSE of 6.1, 6.4 and 6.2 d, respectively, suggesting that considering the effect of cultivar differences in photoperiod sensitivity is warranted.

Table 6. Analysis of variance of the effects of location, thermal time (TT), daylength (D), and vernalization (V), assuming various combinations of these factors. Generic TT and generic daylength effects are from simulations where single mean values of P or P1D were used for all cultivars. Daylength and vernalization effects include cultivar differences in TT (through variation in P).

Source	df	SS†	SS	*F* value	P
			%		
No location effect considered					
Generic TT	1	33,579	66.0	945.9	<0.0001
TT only	1	5,049	9.9	142.2	<0.0001
Daylength	1	1,729	3.4	48.7	<0.0001
Vernalization	1	16	0.0	0.5	0.4984
TT + D + V	1	111	0.2	3.1	0.0782
Residual	292	10,365	20.4		
Location then other effects					
Location	2	3,477	6.8	72.8	<0.0001
Generic TT	1	36,921	72.6	1546.2	<0.0001
TT only	1	3,291	6.5	137.8	<0.0001
Daylength	1	189	0.4	7.9	0.0053
Vernalization	1	9	0.0	0.4	0.5389
TT + D + V	1	37	0.1	1.6	0.2136
Residual	290	6,925	13.6		
Daylength, then location and their interaction					
Daylength	1	39,890	78.4	1583.8	<0.0001
Location	2	3,551	7.0	70.5	<0.0001
Daylength by location	2	54.3	0.1	1.1	0.3419
Residual	292	7,354	14.5		
Generic daylength effect, daylength by cultivar, and TT + D + V					
Generic daylength	1	34,581	68.0	944.5	<0.0001
Daylength	1	5,378	10.6	146.9	<0.0001
TT + D + V	1	127	0.2	3.5	0.0640
Residual	294	10,764	21.2		

† SS, sequential sum of squares.

The improvement in the ability of the model to predict anthesis date by including genetic coefficients for each variety may not be particularly great for three reasons. First, the durum varieties tested may have been fairly similar since they are all commercial varieties developed for high input, irrigated agriculture in the desert Southwest. The range in anthesis dates for these varieties averages about 7 d. Second, the range in planting dates is relatively small for the data tested, about 1 mo for each location, except for the cultivars Westbred 881 and Yecora Rojo, which were included in a planting date study at Maricopa with dates ranging from early November to mid-February. Third, the environmental conditions at Maricopa and Yuma differ less than between Arizona and other states in the United States, Mediterranean regions, and southern Asia, where these or similar varieties are also grown.

The RMSEs we reported are somewhat similar to those from others using models that include daylength and vernalization along with temperature to predict anthesis dates. For example, White et al. (2008) reported RMSE varying from 6.6 to 10.4 d using a gene-based model where parameters were estimated based on the *Vrn* and *Ppd* loci, which affect vernalization and photoperiodism. He et al. (2012) reported a RMSE of 3.9 d using a hybrid genetic algorithm with vernalization and daylength as parameters in the model, Sirius.

Location Bias

Our results may have been confounded by differences among locations that were not captured by the model. Notably, the model overestimated the time to anthesis at Maricopa, and underestimated the time at Yuma (Fig. 3). The Maricopa location had a greater range of time to anthesis than Yuma due to inclusion of planting date trials. Nevertheless, the model still overestimated time of anthesis over the entire range of planting times at Maricopa. The location bias was small relative to the combined effect of temperature and daylength, according to multiple regression techniques as will be discussed near the end of this section.

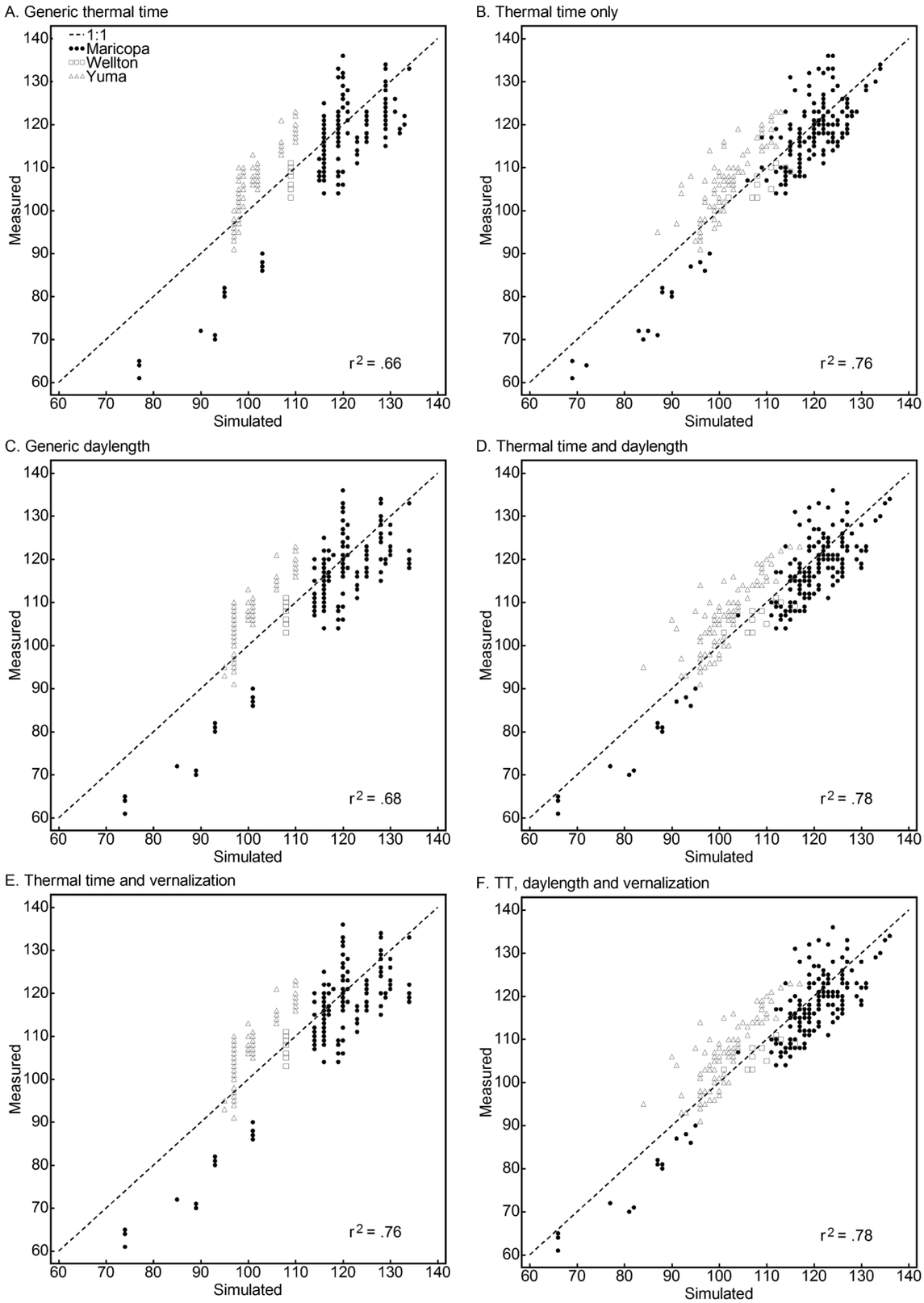

Fig. 3. Measured vs. simulated days to anthesis at Maricopa, Wellton, and Yuma using six modeling approaches, (A) a generic thermal time (TT) and no effects of daylength and vernalization, (B) cultivar differences for TT only and no effects of daylength and vernalization, (C) cultivar differences for TT, a generic daylength response, and no effects of vernalization, (D) cultivar differences for TT, cultivar differences for daylength, and no effects of vernalization, (E) cultivar differences for TT, cultivar differences for vernalization, and no differences for daylength, and (F) cultivar differences for TT, daylength, and vernalization. Generic TT and generic daylength effects are from simulations where single mean values of P or P1D were used for all cultivars. The dashed line in the figure indicates the 1:1 correspondence of measured vs. simulated days to anthesis. Data from Maricopa, Wellton, and Yuma are represented by closed circles, open squares, and open triangles, respectively.

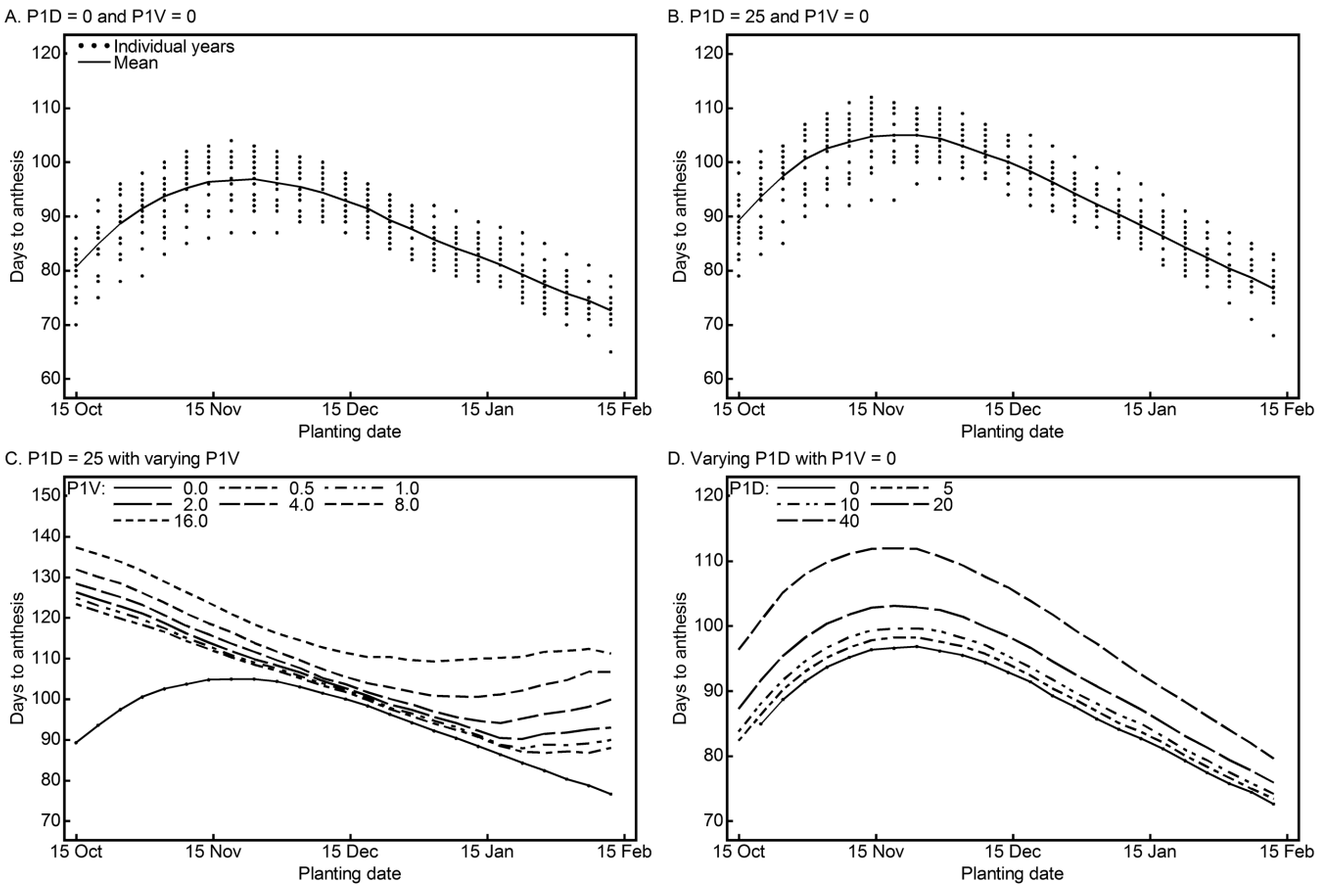

Fig. 4. Planting date effect on days to anthesis at Yuma for 19 yr for differing values of daylength response (P1D) and vernalization requirement (P1V). (A) Assuming only a thermal time response (P1V = 0 and P1D = 0) and showing data for individual years. (B) Assuming no vernalization response (P1V = 0) but including an effect of daylength (P1D = 25) and showing data for individual years. (C) Varying P1V while holding P1D at a constant value of 25. D. Varying P1D and assuming no vernalization requirement (P1V = 0). Data in C and D are means of 19 yr.

Temperature data for each location were obtained from the nearest AZMET weather station and may not have accurately reflected the temperature in the experiments due to distance or to local microclimates affected by air flow patterns. Determinations of heading and anthesis dates also may have differed among personnel at the respective locations. Crop growing practices at each location could differ and introduce bias such as seeding depth, irrigations, and fertilizations. Also, we assumed the crops did not experience water or nutrient deficits, but slight water deficits likely occurred.

Multiple regression using Sequential Sum of Squares (Type I) allowed testing effectiveness of the calibration approaches, as well as examining possible bias associated with locations (Table 6). Considering first a regression without a location effect, the value of calibrating for individual cultivars rather than using a generic temperature model was readily confirmed (Table 6). The benefit of including daylength was also apparent. As expected, a location effect was significant, representing <10% of the total sum of squares (Table 6). Focusing on predictions from the approach considering daylength (including temperature), an effect of location persisted after accounting for the daylength effect. No daylength × location interaction was detected.

Although there was considerable variation in values of P1D (Table 4), the possibility existed that using a single mean effect of photoperiod would provide adequate predictions. An additional set of simulations were conducted using a generic value of P and P1D (Table 5 and Fig. 3C). While the generic daylength approach explained about 68% of the sums of squares, allowing for variation in P1D explained an additional 11%, confirming the need to consider cultivar differences. Overall, the multiple regressions supported using a model that considers cultivar differences in P and P1D to predict days to anthesis. The regressions further indicated that while location bias was present, it was small relative to the overall variation.

Sensitivity Analysis

Anthesis date over a range of years and planting dates was simulated using 19 yr of historical weather data from the Yuma Valley and using combinations of the calibrated temperature, daylength, and vernalization responses for hypothetical cultivars (Fig. 4). When P1V is set to 0 and P1D is either 0 or 25, (i) predicted days to anthesis peaked at planting times near mid-November, (ii) variation in days to anthesis ranged from about 12 d for planting dates in mid-December to 20 d for planting dates earlier than December, and the annual variation in days to anthesis increased for planting dates earlier and later than mid-December (Fig. 4a and 2b).

The vernalization and photoperiod coefficients, P1V and P1D, have differing effects on the predicted days to anthesis (Fig. 2c and 2d). Vernalization coefficients varying from 0 to 16 result in a graph of predicted days to anthesis inverse of

that where P1V is set to 0. That is, days to anthesis peaks at the earliest and latest planting times simulated rather than near 15 November. Furthermore, with larger values of P1V, simulated days to anthesis increase for planting times after 15 December. Varying the photoperiod coefficient from 0 to 40, by contrast, increased the simulated days to anthesis but roughly in proportion to where P1D is set to 0.

General Discussion

The results demonstrate that predicting flowering time of spring durum and bread wheat based solely on temperature would result in large errors (RMSE of 7.6 d). Nonetheless, the RMSE value for the best model which included daylength was not much better and was large enough (RMSE of 6.1 d) to raise two concerns. The first is whether the total effort required to evaluate new cultivars and then calibrate the simulation model justifies expected benefit from providing growers or crop consultants with improved forecasts. This would require a more detailed analysis that considers the value of predicted phenology in farm management decisions, the accuracy of local weather data, and possible impacts of crop management on phenology. The second concern is whether the poor accuracy is due more to bias in weather data and measurements or to errors in CSM-CROPSIM-CERES. Resolving this concern would require a coordinated set of multi-environment trials where extra care was taken to ensure comparability of temperature data and measurements of anthesis date. The temperature data used in this experiment was air temperature, although the growing point is below-ground for much of the time between planting and anthesis, and this could have led to inaccuracies in predicting anthesis date.

We note that it seems feasible and desirable to seek a standard system for quantifying earliness per se, photoperiod response, and vernalization requirement (Herndl et al., 2008; White and Dierig, 2011). Ideally such a classification would rely primarily on functional markers (White et al., 2008; Liu et al., 2012), reducing the need for field testing.

CONCLUSIONS

In conclusion, considering cultivar differences in temperature and photoperiod responses improved the prediction of days to anthesis for spring wheat grown in winter-sown, high input system corresponding to CIMMYT's ME 1. This partially contradicts the expectation that spring wheat bred for this region are photoperiod insensitive but agrees with the assumption that they have a low response to vernalization. Knowledge of temperature and photoperiod responses of spring wheat is important for (i) crop management decisions such as optimum sowing date and timing of fertilizer and water applications and (ii) interpretations of phenological data from plant breeding nurseries at diverse locations.

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