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RESEARCH ARTICLE

Prediction of Spring Barley Flowering Time Based on Multiplicative Approach of Temperature × Photoperiod

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ABSTRACT

Accurate predictions of plant developmental stages are important in crop simulation models. Plant development has been measured using the number of days to flowering. The concept of flowering rate defined as the inverse of the time between emergence and flowering. It has long been recognized that photoperiod and temperature interactively modulate plant development. The multiplicative approach simulate the rate of development using a function of temperature multiplied by a function of photoperiod: R= f(T) × f(P). The relationship between temperature and photoperiod with developmental rate has been described with different equations. Our results revealed that between 24 combined models (8 equations for f(T) and 3 equations for f(P))combined model Beta-Negative exponential (B-NE) (as f(T) and f(P), respectively) has a good estimation of flowering date (or rate) in response to temperature and photoperiod. Base, optimum and ceiling temperatures as a cardinal temperatures based on B-NE were (1, 35 and 40 °C, respectively). Minimum biological required days from emergence to flowering, also, was determined as 36.85 days. Critical photoperiod and photoperiod sensitivity obtained (14.27 h and 0.37, respectively). Thermal time from emergence to flowering predicted to 1252.9. This combined model can be used for barley flowering prediction or as a sub model in other barley phonological models, although Assessment of the model using independent data and conducted several studies on other spring barley at different places are needed.

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INTRODUCTION

Accurate predictions of plant developmental stages are important in crop simulation models and for crop improvement and management (such as timing of resource application and yield formation) (Streck *et al*., 2003; Soltani *et al*., 2006; Yan *et al*., 1996). The production and partitioning of dry matter in crop simulation models is regulated to a large extent by the timing of phonological stages (Soltani *et al*., 2006). Plant development has been measured using the number of nodes or leaves to flower (NTF) or the number of days to flowering (DTF) (Yan and Hunt, 1999).Crop duration interactively determined by the genotype and the environment (Vergara, 1976).

In any given environment, photoperiod and temperature are highly correlated. It has long been recognized that photoperiod and temperature interactively modulate plant development (Wallace, 1985; Yan and Wallace, 1995, Hodges, 1991). These factors are represented in simulation models by temperature [f(T)] and photoperiod [f(P)] response functions (Hodges and Ritchie, 1991; Wang and Engel, 1998; Streck *et al*., 2003). Mean temperature influences flowering time of crops such that as mean daily temperature (MDT) increases within a species-specific range, days to flower (DTF) decreases (Vaid and Runkle, 2013). All biological processes respond to temperature, and all responses can be summarized in terms of three cardinal temperatures, namely the base or minimum (T_b), the optimum (T_o), and the maximum or cieling (T_c) temperatures (Yan and Hunt, 1999; Soltani *et al*., 2006). The nature of the response to temperature between these cardinal points, is important for calculating the phenology, adaptation and yield of various crops (Shaykewich, 1995).The base temperature is the minimum temperature below which no development occurs, and thermal time is the summation of all degree-days above T_b required for a particular developmental event to occur.T_b varies among species and possibly cultivars, and likely varies with growth stage or process being considered (Wang, 1960; McMaster and Wilhelm, 1997). When plants are grown at an MDT above the optimum temperature (Topt), the flower development rate (reciprocal of DTF) begins to decline (Blanchard and Runkle, 2011; Cave *et al*., 2013). A decrease in flowering rate at temperatures >Toptis known as heat delay and may be due to a delay in flower induction, initiation, and/or development (Warner and Erwin, 2006). Estimation of Tmin is useful in calculating the thermal time for a particular event and categorizing plants according to their thermal tolerance. Tmin and Topt values within a species can vary with environmental conditions such as photoperiod (Adams *et al*., 1997, 1998a, 1998b) and daily light integral (Adams *et al*., 1997; Pramuk and Runkle, 2005). An understanding of response of crops to photoperiod is essential to accurate modeling of their phenological events (Yin and Kropff, 1998). The critical photoperiod can vary between and within species.

The many existing developmental models use different approaches to combine mentioned factors (Streck *et al*., 2003): that multiplicative models (Angus *et al*., 1981; Cao and Moss, 1997; Summerfield *et al*., 1991; Bonhomme *et al*., 1994; Yin *et al*., 1995; Yan and Wallace, 1996; Slafer and Rawson, 1996; Sinclair *et al*., 1991; Wang and Engel, 1998; Streck *et al*., 2003a,b), is one of them. The multiplicative approach appears more realistic from a biological point of view because interactions among temperature and photoperiod have been verified in field and controlled environment experiments (Streck *et al*., 2003; Slafer and Rawson, 1994, González *et al*., 2002). The multiplicative approach simulate the rate of development using a function of temperature multiplied by a function of photoperiod: R= f(T) × f(P). The first model of this category was proposed by Robertson (1968). The models used by Angus *et al.* (1981), Sinclair *et al.* (1991) and Grimm *et al.* (1993), among others, all belong to this category, though the responses were described using different mathematical functions (quadratic, exponential or power, Angus *et al*., 1981). Many current crop system simulation models such as CERES and CROPSIM (Hunt and Pararajasingham, 1995) also adopted this approach. Most phenology models predicting flowering date use mean photoperiod and temperature as input variables, assuming that crop plants are sensitive to photoperiod throughout their vegetative phase from sowing to first flower (Angus *et al*., 1981; Roberts and Summerfield, 1987; Sinclair *et al*., 1991; Yan and Wallace, 1998). Developmental models also differ with respect to the nature of the response functions f(T) andf (P), from linear to several nonlinear functions (Streck *et al*., 2003; Ritchie, 1991; Wang and Engel, 1998; Yan and Wallace, 1998). Various exponential functions have been developed that incorporate parameters such as Tmin, Topt, and an upper temperature threshold at which developmental rate is zero (Tmax) (Hidén and Larsen, 1994). Many models simulate plant phenology based on temperature and photoperiod; most use the inverse of days to flowering (or to other specified stages), which is called the rate of development towards flowering (Summerfield *et al*., 1991). A quadratic function was found to best describe the effect of MDT on DTF of some crops because the decrease in DTF with an increase in MDT was not linear between T_{min} and T_{opt} (Clough *et al*., 2001; Yuan *et al*., 1998). To analyze flowering in soybean, Hadley *et al.* (1984) used the concept of developmental rate (D, day^{-1}), defined as the inverse of the time between emergence and flowering (1/f). The time required for the completion of a developmental event can be converted to a rate by calculating the reciprocal of time (e.g., 1/d). The relationship between MDT and developmental rate has been described with linear, quadratic, cubic, and exponential models (Larsen, 1990; Vaid and Runkle, 2013).

The objectives of this study were modeling of temperature×photoperiod effects on barley flowering rate and introducing best none regression model among available models as a temperature and photoperiod equations (f(T) and f(P), respectively).

MATERIALS AND METHODS

This study was carried out on barley var. Jonoob in 12 sowing dates (May-2013 to Apirl-2014 with one month intervals) with for replication in Ramin University of Agriculture and Natural Resources, Iran (31.5953°N 48.8927°E). During the experiment weeds were hand-controlled several times if needed. 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. After emergence, ten plants in each replication were randomly selected and tagged with colored bands (Streck *et al*., 2003). Based on Zadoks *et al* (1974), When 50% of plants were in the flowering stage, time to flowering was recorded (Sowing dates in July and August were not reach to flowering stage). Flowering rate (R50, h^{-1}) was then calculated as (Soltani *et al*. 2001; Soltani *et al*. 2006):

$$R50 = 1/D50 \qquad \text{(Eq. 1)}$$

Where D50 is the estimation of time taken for cumulative flowering to reach 50% of maximum where interpolated from the flowering progress curve versus time.

In order to formulate and validate mathematical functions that can be used to quantify the effect of temperature and photoperiod on required biological days to flowering of barley, eight and three non-linear regression models, respectively, were fitted to flowering rate as inverse of time from start of emergence date to flowering versus mean temperature and photoperiod (24 combine models) (Table 1 and 2).

A multiplicative relationship (Hammer *et al*., 1989) was used to compute the development rate as a function of temperature and DL (Eq.2) (Jonoob is a spring variety of barley and so has not need to vernalization period, that is f(V), (Yan and Wallace, 1998) :

$$R_t = f(T) \times f(P) \times R_{max} \qquad \text{(Eq. 2)}$$

Where R_t is development rate on Day t, R_{max} the maximum rate of development at optimum temperature and DL, f(T) the temperature function, and f(P) is the DL function. Using the algorithm by Kiesling (1982), the photoperiod, including civil twilight (when the sun is from 0 to 6◦ below the horizon), was calculated using PP_calc program by Soltani (Soltani and maddah, 2010).

Daily thermal time (DTT) for a given phenological stage is also calculated as f(P)×f(T)×(T_o-T_b), where f(P) is the DL function, f(T) is the temperature function, T_o is the optimum temperature, and Tb is the base temperature (Clarkson and Russel, 1975; Soltani *et al*., 2006).

The statistic used to test model performance was the root mean square error (RMSE) (Streck *et al*., 2003), calculated as (Janssen and Heuberger, 1995). Mean Absolute Error (MAE), Relative Mean Absolute Error (RMAE) (Mayer and Butler, 1993), also, were used as the statistical criteria to recognize the best estimates of parameters by non-linear models. RMSE is a measure of the accuracy of the prediction that represents a mean weighted difference between predicted and observed data. MAE avoids compensation between probable under- and over-prediction. Each combination model with lower root mean square error, Mean Absolute Error (MAE) and Relative Mean Absolute Error (RMAE) of estimation, higher determination coefficient (R^2) of flowering response to the temperature and photoperiod; higher Pearson correlation coefficient and lower bias of linear regressed line between observed versus predicted emergence rate values from the 1:1 line, was selected as the best model to estimate emergence rate. *a* and *b* (as intercept and slop values of linear regression between observed versus predicted values of flowering rate) were compared with zero and 1. A closer a to 0 and closer b to 1 indicate better estimates of models.

RESULTS AND DISCUSSION

Statistical parameters of estimation based on superoir combined models are presented in table 3a and b coefficient (intercept and slope, respectively, of regression trend line between observed and predicted flowering rate) showed that all models has an acceptable prediction of flowering rate. Note that if differences of these coefficients with 0 and 1, respectively, was significant for each combined model, that model has been removed. Regression coefficient (R^2) was differed from 69-97 in various combined model. Least R^2 was related to Q-Q and highest value of R^2 was related to SI-NE, SI-S and B-NE. for correlation coefficient (r), also similar results were obtained (SI-NE, SI-S and B-NE with 0.98 have highest r). Based on R^2 and r mentioned models have been chosen as a superior models. These models have a least C.V, RMSE, MAE, RMAE and RMSD showing precision prediction of flowering development. Least RMSD in B-NE indicated that this model able to predict the flowering date with 3.37 days tolerance.

As show in table 4, based on combined models, TbBased on superior model (B-NE) it was 1°C.The value of T_o in B-NE was obtained 35°C. The value of T_c based on selected model was 40°C. The number of biological day from emergence till flowering (fo) was obtained in range 31.05 to 36.90 days after emergence date. Based on B-NE, fo was predicted as 36.85 days. The accuracy of different models varies in predicting developmental stages in different crops (Streck *et al*., 2003). For example, heading and ripening predicting in wheat, have been predicted with a root mean square error (RMSE) of 2-10 days (Cao and Moss, 1997; Yan and Wallace, 1998). Anthesis was predicted with a RMSE of 4-7 days (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) (Streck *et al*., 2003).

Critical photoperiod (CPP) for spring barley Var. Jonoob was calculated 14.27-16.90 h. its value in B-NE was equal to 14.27 h. photoperiod sensitivity (ppsen) for that critical photoperiod varied among models from 0.13 to 0.37. ppsen was 0.37 in B-NE. a coefficient in B-NE that determined shape of curve, was related to -0.25. Soltani *et al*., (2006) and Ritchie (1991) were obtained 21 and 20 h CPP for chickpea and wheat, respectively. Thermal time predicted by B-NE was 1252.9.

In order to quantification of temperature and photoperiod effects on development rate, various equations have been used by different scientists (hammer *et al*., 1989; piper *et al*., 1996; Robertson *et al*., 2002 a b). Suggestion one general equation for all crops and all phonological stages is very difficult (Soltani *et al*., 2006). Quadrative equation used in present study is similar to used equation in CERES-Wheat (Ritchie, 1991), and also have been used by Soltani *et al*., (2006). In Soltani *et al*., (2006) RMSD of predicted versus observed days from emergence to flowering was 6.5-14.8 days for chickpea varieties. B-NE has the best prediction of days to flowering (Fig. 1).

There is reason to believe that the temperature response of a given process should be a smooth curve (Cross and Zuber, 1972), rather than rigid combinations of linear equations, which introduce abrupt changes (Yan and Hunt, 1999). Beta distribution models are characterized by a unimodal response to an independent variable x in the range of [0, 1]. The function has a density of zero when x≤0 or x≥1 and a maximum density at an optimum x between 0 and 1. Replacing the dependent variable x with temperature (T) between a base temperature (Tmin) and a maximum temperature (Tmax) leads to an expression that can be used to describe a temperature response (Yin *et al*., 1995).Here, we report on the effectiveness of this simplified equation in temperature response for the development of barley.

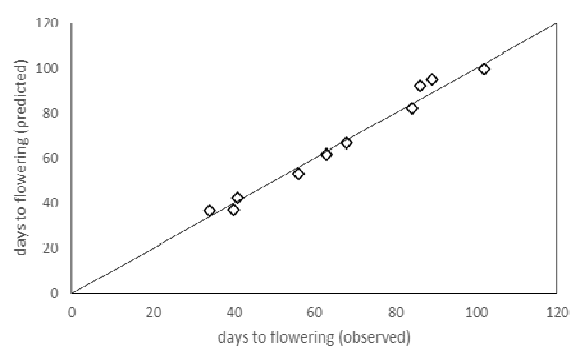

Fig 1: Predicted days of emergence to flowering versus observe values (squares). Line is the 1:1 line based on Beta-Negative Exponential model as the best combined model.

Table 1: Segmented (S), Beta (B), Flat (F), Curvilinear (C), Logistic (L), Quadratic (Q), Sigmoid (SI), Dent-like (D), functions formula as a temperature equations (f(T)) that were used in combination equation of f(T)×f(P)

Function	Equation	if
Segmented	$f(T)=\frac{(T-T_b)}{(T_o-T_b)}$	$T_b \le T \le T_o$
	$f(T)=\left[1-\left(\frac{T-T_o}{T_c-T_o}\right)\right]$	$T_o \le T < T_c$
	f(T)=0	$T \le Tb$ or $T \ge T_c$
Beta	$f(T)=\left[\left(\left(\frac{(T-T_b)}{(T_p-T_b)}\right)\times\left(\frac{(T_c-T)}{(T_c-T_p)}\right)\right)^{\left(\frac{(T_c-T_p)}{(T_p-T_b)}\right)^a}\right]$	
Flat	$f(T)=\frac{(T-T_b)}{(T_o-T_b)}$	$T_b < T < T_o$
Curvilinear	$f(T)=\left[\left(1\Big/\left((T_o-T_b)\times(T_c-T_o)^{\left(\frac{T_c-T_o}{T_o-T_b}\right)}\right)\right)\times(T-T_b)\times(T_c-T)^{\left(\frac{T_c-T_o}{T_o-T_b}\right)}\right]$	
	f(T) =1	$T \ge T_o$
Logistic	$f(T)=\left[1/(1+\exp(-a\times(T-T_o)))\right]$	
Quadratic	$f(T)=\left[(T-T_b)\times(T_c-T)\times\left(\frac{T_c-T_b}{2}\right)^{-2}\right]$	
Sigmoidal	$f(T)=C+(1-C)/(1+\exp(-b\times(T-a)))$	
Dent-like	$f(T)=\frac{(T-T_b)}{(T_{o1}-T_b)}$	$T_b < T \le T_{o1}$
	$f(T)=\frac{(T_c-T)}{(T_c-T_{o2})}$	$T_{o2} < T \le T_c$
	f(T)=1	$T_{o1} < T \le T_{o2}$
	f(T)=1	$T \le Tb$ or $T \ge T_c$

where T, T_b, T_o, T_{o1}, T_{o2} and T_c for Quadratic (Q), Dent-like (D), Segmented (S), Sigmoid (SI), Curvilinear (C), Logistic (L) and Beta (B) and Cubic (Cu) models are mean temperature, base temperature, optimum temperature, lower optimum temperature, and upper optimum temperature, respectively.

Table 2: Day length functions (f(P)) used in combined models. PP is photoperoid, CPP the critical day length below which development rate decreases due to long day length, and PPsenthe day length sensitivity coefficient.

function	Equation	if
Quadratic	$f(P)=\left[1-\left(PPsen\times\left((CPP-PP)^2\right)\right)\right]$	PP<CPP
	f(P)=1	PP≥CPP
Negative exponential	$f(P)=\left[\exp(-PPsen\times(CPP-PP))\right]$	PP<CPP
	f(P)=1	PP≥CPP
Segmented	$f(P)=\left[1-((CPP-PP)\times PPsen)\right]$	PP<CPP
	f(P)=1	PP≥CPP

Table 3: Statistical parameters of superior combined equations between observed and predicted flowering rate. Equations of temperature include sigmoidal (SI) and beta (B. Equations of photoperiod include negative exponential (NE) and segmented (S). Intercept (*a*) and slope (*b*) of regression trend line, regression coefficient (R^2), correlation coefficient (r), coefficient of variance (C.V), root mean square of errors (RMSE), mean absolute of error (MAE) and relative mean absolute of error (RMAE) between observed and predicted flowering rate, were used for best appropriate model for flowering rate prediction. Root mean square of deference (RMSD) indicated the difference of day to flowering between observed and predicted values. (Data for other 21 combined models were not shown)

Equation	a±SE	b±SE	R^2	r	C.V	RMSE	MAE	RMAE	RMSE	RMSD
SI-NE	0.0004±0.001	0.97±0.06	97	0.98	7.59	0.02	0.001	0.05	0.001	3.73
SI-S	0.0008±0.001	0.95±0.07	97	0.98	8.90	0.02	0.001	0.07	0.001	6.71
B-NE	0.0003±0.005	0.98±0.06	97	0.98	7.12	0.02	0.0009	0.05	0.001	3.37

Table 4: Predicted parameters based on superior combine equations. Base temperature (Tb), optimum temperature (To), ceiling temperature (Tc), The number of biological required days from emergence to flowering (fo), photoperiod sensitivity (ppsen), critical photoperiod (cpp), thermal time (TT), constant coefficient (a, b, and c), lower and upper optimum temperature for dent-like (to1 and to2) (Data for other 21 combined models were not shown).

Equation	a	b	c	Fo	CPP	ppsen		TT
SI-NE	39.34	2.48	1.00	36.90	14.29	0.33		-
SI-S	35.52	2.93	1.28	31.05	16.90	0.13		-
	T_b	T_o	T_c	Fo	CPP	ppsen	a	
B-NE	1.00	35.00	40.00	36.85	14.27	0.37	-0.25	1252.9

This work showed that a beta distribution equation, describes well the temperature response of flowering rate. For importance of temperature in flowering rate of barley, a good model that allows for summarization and simulation of the temperature response of barley development would be valuable in several applications. Knowledge of the optimum and maximum temperatures of the growth and development of a genotype is of vital importance to the successful prediction of its maturity, adaptation and yield in a particular environment. It seems that can be concluded that combined model Beta-Negative exponential (f(T) and f(P), respectively) has a good estimation of flowering date (or rate) in response to temperature and photoperiod. T_b, T_o and T_c as a cardinal temperatures based on B-NE were (1, 35 and 40°C, respectively). fo, also, was determined as 36.85 days. cpp and ppsen as a photoperiod parameters obtain from f(P) (NE) were (14.27 and 0.37, respectively).This combined model can be used for barley flowering prediction or as a sub model in other models, although Assessment of the model using independent data and conducted several studies on other spring barley at different places are needed.

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