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Effect of Varying Temperature and Thermal Amplitude on Phenological Accumulated Heat Units for Mediterranean Wheat

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Abstract: Phenological records obtained for wheat (*Triticum durum* Desf., cv Karim) sown at 26 different dates around the year in no limiting water and nutrient conditions were used to investigate the predictive ability of the accumulation heat models and their sensitivity to thermal amplitude. Monitoring of days of Emergence (E), Tiller initiation (T), Jointing (J), Heading (H) and Maturity (M) and meteorological data concerned two different thermal regimes sites: Tunis (18 series) and Kef (8 series). Results show the performance of seven phenology models: the Number of calendar Days (ND), Growing Degree-Days (GDD), Modified Growing Degree-Days (MGDD), Photothermal Units (PTU), Solar Radiation (SR), Solar Thermal Units (STU) and Simplified Beta Function (SFB). For the seeding-emergence and emergence-tiller initiation stages, the GDD gave the best result with significantly the same average index value for the two stations. Because the rate of development is a linear function of temperature, there is no effect of thermal amplitudes on model performances. However, in the case of all phenological phases following tiller initiation all the tested models are sensitive to thermal amplitude presenting significantly different average indices values for the two stations which bring as to conclude that the temperature-growth relationships are non linear. The adjustment of the heat unit models with mathematical functions of thermal amplitudes improves their predictive accuracy. The adjusted thermal indices give significantly the same average values with less variability.

Key words: Durum wheat, phenology, thermal indices, thermal amplitude, Mediterranean, Tunisia

INTRODUCTION

Crop modelling and agriculture operational planning require accurate prediction of crop phenology. For wheat, development is primarily driven by temperature (Friend, 1966), so many different thermal units accumulation methods have been proposed for predictive purposes. The most commonly used method is the Growing-Degree-Day (GDD) which is defined as the difference between the mean daily temperature and a growth threshold value also called base temperature (T_b) which presumably the biological activity is supposed to take place (McMaster and Wilhem, 1997). This index hypothesizes the linearity response of wheat development. However, it was demonstrated by many researcher (Friend, 1966; Sawada, 1970; Angus *et al*., 1981; Slafer and Rowson, 1995a) that wheat development response to temperature is strongly curvilinear and many of biological processes such as photosynthesis increase linearly with temperature between T_b and an optimum temperature Topt and are reduced above Topt. As used in GDD, the mean temperature is simply the average between maximum and minimum air temperatures and does not recognize the effect of daily amplitudes. Indeed for a given mean changing the range of variation of the actual temperature may greatly affect the crop without changing the summation of heat units as suggested by Swan *et al*. (1981) who observed that the rate of leaf emergence of corn was linearly dependent upon diurnal temperature range and photoperiod in controlled environment chamber but the model adjusted from this relation did not well predict the measured leaf growth in the field because of the square wave temperature pattern used in controlled condition. So, one should not expect the response in varying day/night temperature regimes to be well estimated by a linear thermal indices, specially when thermal amplitude is great enough that maximal temperature Tx exceeds Topt in warm conditions. This occurs frequently in both Mediterranean and continental climates, particularly during reproductive wheat phases. T_b and Topt are not constant during the entire plant growing cycle. They are found to increase with development and 25°C is considered as the highest Topt value for all wheat phenophases (Porter and Garwith,

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1999). This can explain the experimental results of Slafer and Rowson (1995a) concerning the non consistent effect of thermal amplitude varying between 0 and 14°C around a common mean of 19°C on phenological development at any stage to anthesis since Tx did not exceed Topt. When Tx exceeds Topt Tamaki *et al.* (1998) found that phyllochron values were greater when day/night temperature is 32/8°C comparing to values measured on plant grown at constant 20°C, then phenological events can be delayed. When Tx exceeds Topt ontogeny durations can also be shortened by thermal stress, this was proven for reproductive phases (Ugarte *et al.*, 2007; Dias and Lidon, 2008).

Processes such as photosynthesis and transpiration are concentrated in daylight hours and therefore should be more responsive to Tx whereas processes such as respiration or vernalization occur throughout day and night. So, minimal temperature Tn affects also wheat development rates, it can lengthen thermal time when respiration is increased by high night temperatures (Tamaki *et al.*, 1998) and can reduce thermal time by low night temperatures when phenology is sensitive to vernalization that affects, especially the vegetative period (Flood and Halloran, 1984; McMaster *et al.*, 2008). It is known that winter wheat have a strong vernalization response, plants will not flower until after they have been exposed to cold temperatures. But the vernalization response of spring wheat is less well defined. Many spring genotypes do not respond to vernalization (Flood and Halloran, 1984) but some others are reported to have mild sensitivity (Wort, 1940; Mossad *et al.*, 1995; Kirby *et al.*, 1999; Iqbal *et al.*, 2007). The optimum temperature for vernalization of spring wheat is defined by the temperature which most reduces the time between sowing and heading (Rawson *et al.*, 1998) beyond it flowering is not inhibited but delayed. Depending to cultivars, this optimal temperature is suggested to vary between 6-19°C (Rawson *et al.*, 1998). To improve the accuracy of prediction, many variants of thermal units derived from the GDD have been introduced. Modifications that limit the maximum daily temperatures to a threshold such as the Modified Growing-Degree-Day (MGDD) are used to account for plant requirements (Barger, 1969). Although, temperature has a major effect on wheat development day-length and solar radiation are also determinant factors during the reproductive stages. Many researchers suggested alternate indices such as the Solar Thermal Units (STU) that incorporates in addition to temperature, the effect of light by multiplying the solar radiation and the daily mean temperature (Caprio, 1971). The Photo Thermal Unit (PTU) multiplies the GDD by the day-length (McMaster and Smika, 1988). To overcome the shortcoming of the linear thermal time concept other indices using a non linear temperature response such as polynomials (Stewart *et al.*, 1998; Streck *et al.*, 2003), exponential function (Angus *et al.*, 1981), Simplified Beta Function (SBF) (Yin *et al.*, 1995) and exponential sine equation (Longhui *et al.*, 2008) are determined. All these models use the average temperature and do not incorporate the effect of its range of diurnal variation that is related to thermal amplitude and therefore are not well structured to handle the problem of the non linearity temperature responses. Continentalism increases temperature amplitudes and could explain the variability of the accuracy of wheat phenology simulations reported by many resaercher when the models are applied across different agro-ecological zones (Asseng *et al.*, 1998; Angus *et al.*, 1981; Kirby *et al.*, 1999; McMaster and Wilhem, 2003).

The main objective of this study is to determine the thermal unit accumulation methods that can predict accurately the different phases of wheat development whatever seeding date and cultivation site might be and their sensitivity to thermal amplitude. The data concern the commonly grown cultivar in North Africa Karim. They combine a wide range of climatic data because they have been collected for both standard and out of agronomic range sowing dates in continental and coastal sites in Tunisia where average temperature could be similar but amplitudes are different.

MATERIALS AND METHODS

Phenological observations of wheat (*Triticum durum* Desf.) used in this study came from two agriculture experimental stations located in Tunisia. The first site is located in the coastal region of Tunis (36.8°N, 10.17°E) and the second is in the continental area of Kef (36.18°N, 8.7°E). The used spring wheat variety is Karim which is the most used variety in North Africa. The climatic variables recorded 2 m above the soil surface are the daily maximum (Tx) and minimum (Tn) temperatures, precipitation and sunshine duration (l). The solar radiation SR is estimated in this study by the Angstrom type equation:

$$SR_i = (0.25 + 0.5\, l_i / L_i) * Ra_i \quad (1)$$

where, L is the day-length in hours defined as the period from sunrise to sunset and Ra the extraterrestrial radiation in mm day^{-1}. The climatic data shown in Fig. 1 and 2, respectively is Tunis and Kef stations. Their mean values for the phenological recorded periods are shown in Table 1. In both stations, observation series related to respectively 18 and 8 sowing spaced out dates over a

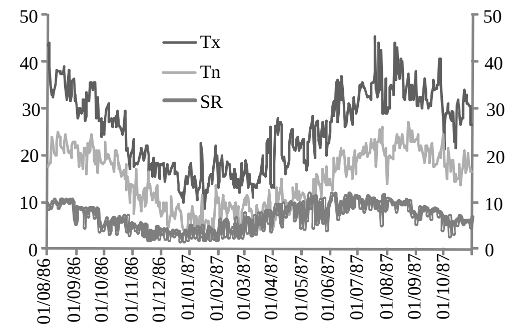

Fig. 1: Maximal (Tx) and minimal (Tn) temperatures (°C) and Solar Radiation (SR) (mm day^{-1}) distribution during Tunis experiment period

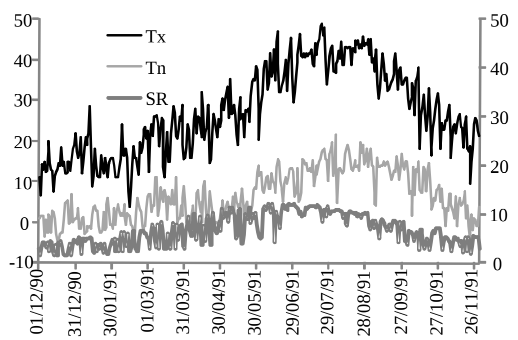

Fig. 2: Maximal (Tx) and minimal (Tn) temperatures (°C) and Solar Radiation (SR) (mm day^{-1}) distribution during Kef experiment period

year in water and nutrient non limiting conditions were obtained. The sowing dates were chosen to explore a wide range of plant exposure to climatic conditions, especially temperature and solar radiation. The years of experimentation campaign, respectively 86/87 and 90/91 are different but this did not inhibit the finding accurate results since the aim of the research is to enhance variability. Experiments were conducted in split plot system with one replication and each plot size is 2 m^2. All plots are regularly irrigated to avoid water stress during the entire growing season. About 66 kg units of Nitrogen (N) are applied at emergence, tiller initiation and jointing and 45 kg units of phosphorus (P_2O_5) are applied at sowing. The phenological events are recorded when 50% of the plants reached successively the stages Seeding (S), Emergence (E), Tiller initiation (T), Jointing (J), Heading (H) and Maturity (M) observed in the main stems. Their corresponding values on the Feekes scale (Large, 1954) were, respectively: (0.0, 1.0, 2.0, 6.0, 10.5 and 11.3). Models predictive ability has been evaluated on the basis of the Coefficient of Variation (CV) associated to the considered phenological stages and sensitivity to thermal amplitudes was assessed by comparing summation values relative to

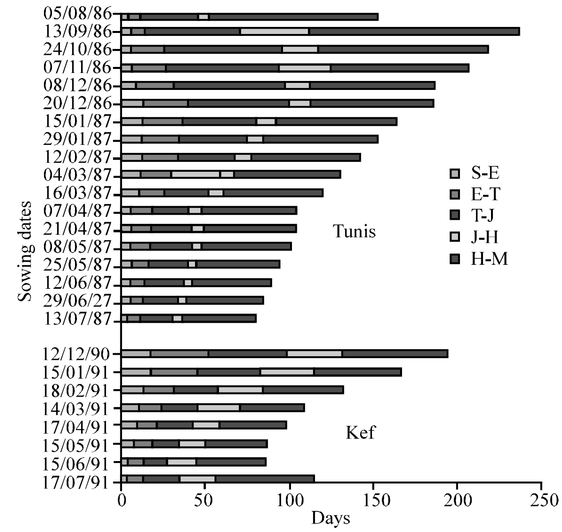

Fig. 3: Sowing dates and variation of the phenophases durations for the 18 data series of Tunis and 8 data series of Kef

both sites (Fig. 3). To account for the effect of amplitude, a general relationship between Heat Units (HU) and temperature amplitude (ΔT) has been investigated in order to have:

$$\sum_{stage1}^{stage2}\left(HU*f(\Delta T)\right)_{station1} = \sum_{stage1}^{stage2}\left(HU*f(\Delta T)\right)_{station2} = \text{Constant} \quad (2)$$

Tested functions f are suggested by the curve's shape describing:

$$1/\sum_{stage1}^{stage2} HU$$

verses the average thermal amplitude calculated over the corresponding phenological period.

Six indices: ΣGDD, ΣMGDD, ΣPTU, ΣSR, ΣSTU and ΣSBF have been selected for this study and their performance were compared to the actual Number of calendar Days (ND). The ΣGDD is defined as:

$$\sum GDD = \sum_{i=s1}^{s2}\left(T_i - T_b\right) \quad (3)$$

Where:

T = Mean temperature in °C calculated as (Tx+Tn)/2

i = Day beginning at stage (s1) and incrementing daily until reaching stage (s2)

Whenever, Eq. 3 produces a negative value then GDD is set equal to zero. The base temperature (T_b) was determined using a linear regression of the rate of

Table 1: Mean Temperature (T), thermal amplitude (Tx - Tn) and Solar Radiation (SR) for the phenological recorded periods during 86/87 and 90/91 and for respectively Tunis (18 data series) and Kef (8 data series) stations

	S-E		E-T		T-J		J-H		H-M	
Parameters	Tunis	Kef	Tunis	Kef	Tunis	Kef	Tunis	Kef	Tunis	Kef
T (°C)	18.5	14.9	18.6	16.5	18.8	18.1	19.0	19.9	20.9	21.1
(Tx - Tn) (°C)	10.4	19.3	10.9	20.5	10.6	22.4	11.2	24.3	11.5	19.2
SR (mm day^{-1})	7.0	6.6	7.0	7.4	7.3	8.1	7.8	9.1	8.5	9.5

S: Seeding, E: Emergence; T: Tiller initiation; J: Jointing; H: Heading; M: Maturity

development (i.e., the reciprocal of time between two stages) vs. the average temperature (Gbur *et al*., 1979). The Modified Growing Day Model was obtained by setting any daily maximum temperature ≥30°C:

$$\sum \text{MGDD} = \begin{cases} \sum_{i=s1}^{s2} (T_i - T_b) & \text{if} \quad T_i < 30°C \\ \sum_{i=s1}^{s2} (30 - T_b) & \text{if} \quad T_i \geq 30°C \end{cases} \tag{4}$$

The ΣPTU is defined as:

$$\sum \text{PTU} = \sum_{i=s1}^{s2} L_i (T_i - T_b) \tag{5}$$

The ΣSR is defined by summing the daily solar radiation as:

$$\sum \text{SR} = \sum_{i=s1}^{s2} \text{SR}_i \tag{6}$$

The ΣSTU combines the effect of temperature and solar radiation:

$$\sum \text{STU} = \sum_{i=s1}^{s2} \text{SR}_i T_i \tag{7}$$

The simplified beta function model ΣSBF is a non linear approach represented by:

$$\sum \text{SBF} = \sum_{i=s1}^{s2} \left(\frac{\text{Tceil-T}_i}{\text{Tceil-Topt}} \right) \left(\frac{T_i}{\text{Topt}} \right)^{\frac{\text{Topt}}{\text{Tceil-Topt}}} \tag{8}$$

Topt is the optimum temperature at which the maximum rate of development occurs, Tceil is ceiling temperature at which development ceases. Optimal and ceiling temperatures are fitted to the data in order to minimise the CVs of ΣSBF. Other thermal indices derived from the selected ones are also tested but their results are not interesting to present because of their high coefficient of variance.

RESULTS

The phenophases durations corresponding to the different seeding dates are shown in Fig. 3. The duration of the whole growing cycle from sowing to physiological maturity ranged from 237 days for early Autumn sowing to 81 days for Summer sowing. All the phenophases are hastened by hot conditions. However, for similar sowing dates reproductive continental stages durations are shorter for T-J and H-M stages and longer for J-H phenophase.

Base, optimum and ceiling temperatures: Using all data series for Kef and Tunis, a base temperature of 0°C was obtained for all phenological periods. This value was also the most being used for wheat (Slafer and Rawson, 1995a; Kirby *et al*., 1999; McMaster and Wilhem, 1997). Determination coefficients of regression were >0.95 for sowing-emergence and emergence-tiller initiation periods, and <0.60 for the other stages probably because there is no linear relationship between temperature and the rate of development from tiller initiation to maturity.

Optimal and ceiling temperatures are respectively 27 and 42°C for all phonological periods till heading and 30 and 42°C for H-M stage.

Comparing the models predictive ability for the different phenophase: Table 2 shows average heat accumulation totals and coefficients of variation of the tested models, as they compare to the Number of calendar Days (ND). The coefficient of variation for all the data of two stations together are close to the weighted averages of the two coefficient of variation of two stations calculated separately.

Total GDD units cumulated over the entire cycle decreased from 3548-1847°C when sowing dates moved from the beginning of Autumn (13/09) to Summer (13/07). Tunis results variability is frequently highest than this of Kef because Tunis series explore more wide range of climatic conditions over the experimental year.

The GDD Model gave the least variability for Seeding-Emergence (S-E), Emergence-Tiller initiation (E-T) and Heading-Maturity (H-M) periods and no significant differences were found between GDD and PTU results for these stages. The longest H-M stage presents the lowest variability among all phenophases whereas Tiller-Jointing (T-J) and Jointing-Heading (J-H) stages have the most variable indices particularly those considering a linear

Table 2: Average number of days, heat units and their respective Coefficients of Variation (CV) for Tunis (18 data series) and Kef (8 data series)

	S-E		E-T		T-J		J-H		H-M	
Parameters	Tunis	Kef	Tunis	Kef	Tunis	Kef	Tunis	Kef	Tunis	Kef
ND										
Day	9.00^{a}	11.00^{a}	15.00^{a}	17.00^{a}	38.00^{a}	25.00^{b}	12.00^{a}	23.00^{b}	69.00^{a}	47.00^{b}
CV	0.38	0.46	0.41	0.57	0.47	0.42	0.79	0.30	0.31	0.20
$\sum_{GDD}$										
°C	135.00^{a}	134.00^{a}	237.00^{a}	227.00^{a}	624.00^{a}	416.00^{b}	191.00^{a}	430.00^{b}	1419.00^{a}	1063.00^{b}
CV	0.15	0.08	0.15	0.18	0.29	0.25	0.45	0.14	0.07	0.09
$\sum_{MGDD}$										
°C	131.00^{a}	130.00^{a}	232.00^{a}	216.00^{a}	610.00^{a}	383.00^{b}	187.00^{a}	388.00^{b}	1369.00^{a}	918.00^{b}
CV	0.13	0.13	0.16	0.21	0.29	0.24	0.47	0.13	0.08	0.13
$\sum_{PTU}$										
h, °C	1663.00^{a}	1661.00^{a}	2910.00^{a}	2883.00^{a}	7798.00^{a}	5511.00^{b}	2413.00^{a}	5920.00^{b}	19325.00^{a}	14805.00^{b}
CV	0.23	0.15	0.11	0.18	0.23	0.24	0.29	0.12	0.08	0.08
$\sum_{SR}$										
mm	51.00^{a}	61.00^{a}	89.00^{a}	105.00^{a}	241.00^{a}	188.00^{b}	77.00^{a}	203.00^{b}	563.00^{a}	436.00^{b}
CV	0.22	0.14	0.20	0.17	0.14	0.17	0.35	0.17	0.19	0.17
$\sum_{STU}$										
mm, °C	918.00^{a}	890.00^{a}	1568.00^{a}	1682.00^{a}	4411.00^{a}	3389.00^{a}	1323.00^{a}	3928.00^{b}	12230.00^{a}	10110.00^{b}
CV	0.46	0.45	0.31	0.39	0.33	0.39	0.15	0.20	0.16	0.14
$\sum_{SBF}$										
	5.2.00^{a}	4.80^{a}	9.20^{a}	8.40^{a}	24.40^{a}	16.00^{b}	7.50^{a}	16.70^{b}	45.60^{a}	35.50^{b}
CV	0.12	0.13	0.18	0.14	0.29	0.21	0.44	0.10	0.08	0.08

The mean of the two stations for the same stage and index are significantly similar when they are followed by the same letters (one factor aNOVa test at 5%). Results having the smallest CV are underlined. S: Seeding; E: Emergence; T: Tiller initiation; J: Jointing; H: Heading; M: Maturity

developmental relationship with temperature. For these phenological events (T-J) and (J-H), the SR and STU indices present the lowest coefficients of variation, respectively. PTU Model seems to predict T-H and J-H stages with reasonable CVs, compared to those obtained when using GDD Models. However, we think that this improvement is in fact due to the effect of solar radiation rather than to the photoperiod. This explains why STU has better predictive ability than PTU with lowest variability for the J-H stage. The photoperiod sensitivity of the rate of development for all phenological phases for Karim variety seems to be small under 9-14 h of day-length. It is also important to notice that till tiller-initation the similarity between MGDD and GDD summations indicates that Tx rarely exceeds 30°C, so plants are not exposed to severe thermal stress that can impair development rates. This is not the case during the reproductive period when Tx exceeds frequently 30°C as reflected by the significant differences between the MGDD and the GDD summations, especially for the continental station of Kef (Table 2). When plants are exposed to severe thermal stress the curvilinear model SBF improves the prediction accuracy compared to both GDD and MGDD and if not their CVs are similar. If the rate of development is linearly related to temperature, the same GDDs should be obtained regardless of the seeding dates and thermal amplitudes. This is the case of the two first phenological periods in spite of the observed differences between the temperature regimes (Table 1). Growth response to temperature seems to be linear from sowing to tiller initiation. The thermal time from sowing to emergence is about 135°C. This value was also found by Miralles *et al.* (2001) for spread out sowing dates. From emergence to tiller initiation, 240°C is obtained similarly to the values found by McMaster and Simka (1988) and Gonzalez *et al.* (2002) for unvernalized wheat. For the following stages (T-J, J-H and H-M), the Kef and Tunis stations have significatively the same mean average temperatures but large differences in thermal amplitudes (Table 1). Since, GDDs for these periods present high coefficients of variation, it could be concluded that for this stages development are not linearly related to temperature as advanced by many researchers (Friend, 1966; Sawada, 1970; Angus *et al.*, 1981; Slafer and Rowson, 1995a) or temperature interacts with other factors so mean temperatures do not have the same effectiveness and different accumulation heat values could be therefore obtained depending to thermal amplitudes.

Models adjustment to account for thermal amplitude: The daily amplitudes range between 2 and 26°C for Tunis station and reach 40°C for Kef station their mean values for all the experimental periods are respectively 10 and 20°C. Larger thermal amplitudes are associated with higher solar radiation. To have the same heat summation units for both locations were adjusted to account for thermal amplitude differences between Tunis and Kef stations. Adjustments, as explained before were suggested by the statistical curve tendency representing the inversed indices vs. mean thermal amplitudes corresponding to each phenological period considered separately (Fig. 4). The adjusted models giving the best results presented in

Table 3: Adjusted models, the corresponding heat accumulation values and coefficients of variation for Tunis (18 data series) and Kef (8 data series) stations

Parameters	T-J		J-H		H-M	
	Tunis	Kef	Tunis	Kef	Tunis	Kef
$\sum_{SR*Ln(Tx-Tn)}$						
mm	559^{a*}	577^{a*}	183^{a}	645^{b}	1368^{a}	1409^{a}
CV	0.12*	0.15*	0.29	0.15	0.19	0.17
$\sum_{STU/exp[(Tx-Tn)/L]}$						
mm, °C	1902^{a}	615^{b}	580^{a*}	659^{a*}	5201^{a}	1650^{b}
CV	0.29	0.23	0.16*	0.07*	0.16	0.14
$\sum_{GDD*Ln(Tx-Tn)}$						
°C	1423^{a}	1270^{b}	442^{a}	1365^{b}	3418^{a*}	3420^{a}
CV	0.25	0.26	0.35	0.16	0.06*	0.09

*Results having the smallest CV. T: Tiller initiation; J: Jointing ; H: Heading ; M: Maturity. The mean of the two stations for the same stage and index are significantly similar when they are followed by the same letters (one factor ANOVA test at 5%)

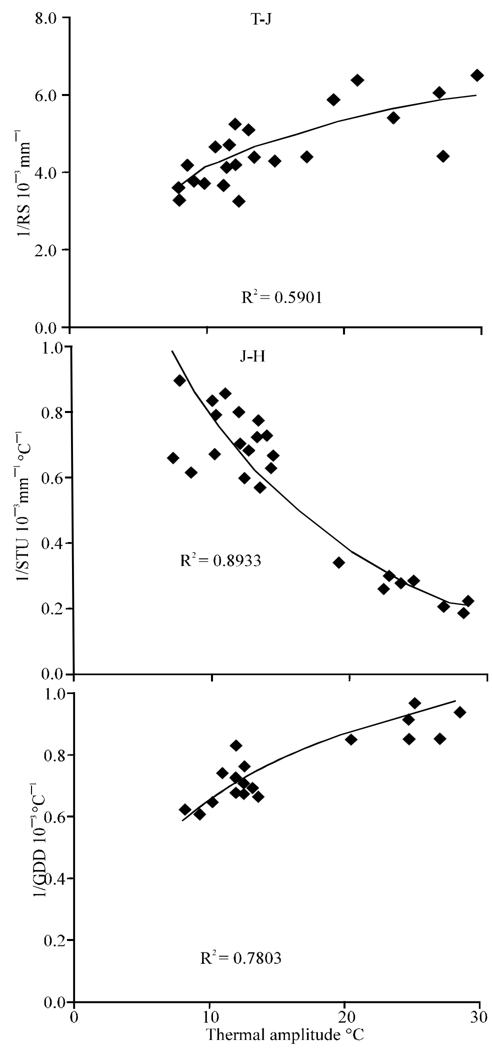

Fig. 4: Variation of the reciprocal indices of SR, STU and GDD for T-J, J-H and H-M periods with the average thermal amplitudes calculated over the corresponding phenological periods for the 26 data series. T-J and H-M data sets present a logarithmic tendency. J-H data set present an exponential tendency

Table 3 for the three last phenophases of wheat are related to the models presenting the smallest coefficient of variation in Table 2. For T-J multiplying the SR by the neperien logarithm of the thermal amplitude helped obtaining the same mean heat totals for the two locations. For J-H phase, dividing STU with an exponential function of thermal amplitude give better results. SR adjusted index gives also the same means for the H-M stage but the least variability for this phenophase is obtained when multiplying the GDD by the neperien logarithm of the thermal amplitude. The adjusted models improve the accuracy of the prediction. Indeed researcher obtain the same mean sums with better coefficients of variation. The amelioration is more noticeable for the J-H stage in Kef station where the thermal amplitude is the largest one (Table 1). More maximum and minimum temperatures diverge from the average temperature, the larger the thermal amplitudes are the shorter the T-J and H-M periods are and the longer the J-H period is.

DISCUSSION

Depending to temperature responsiveness wheat development of Karim variety is found to be divided in two main phenology periods from seeding to the first tiller appearance and then to maturity. The former period contrary to the latter is linearly driven by temperature and covers the early vegetative development. These findings are in agreement with many other researchers (Hundal *et al*., 1997; Haider *et al*., 2003) which found also that the delay in sowing reduced the cumulative energy attained for the entire cycle but no such trend was observed during the vegetative phase. The higher CV values of the PTU comparing to GDD index for S-E period and the non-significant difference between them for E-T period supported the non sensitivity of Karim to photoperiod during the juvenile vegetative development. Miglietta (1989) and Stefany (1993) observed also this insensitivity and found that the photoperiod affects the final leaf number rather than the rate of leaf appearance on the main culm. Even when plant response to day-length was reported, the vegetative phenophase was less sensitive to the reproductive development, especially for Spring wheat (Slafer and Rawson, 1996; Miralles *et al*., 2001). The vegetative phase for this research is assessed up to double ridge and not till the first tiller appearance that precede this stage.

The reproductive period is also subdivided in two periods according to solar radiation responsiveness: from tiller initiation to heading and then to maturity. The first stage durations are affected by solar radiation and cover the late vegetative development, spikelet initiation and their growth processes where as the grain filling periods seems to be not affected by both photoperiod and solar radiation. The rate of development for T-H period is sensitive to solar intensity rather than photoperiod or sunshine duration (the CVs of heliothermal index ΣI*GDD are high). Many researches deal about the effect of solar radiation on wheat phenology. Friend (1965) found that higher solar radiation extend the duration of developing inflorescence and ear, however other researchers (Rahman *et al*., 1977; Rawson, 1993) found that lower light level lengthens it. Slafer (1995) found no effect of solar radiation on wheat development.

Although, these results seem to be conflicting, they are more understandable when coupled with the temperature regime of the experiments. The extended duration of the phenophase with low solar radiation is associated with high temperature (27°C) and short day-length (9 h), the inversed situation is associated with low temperature and the non effect of solar radiation can be associated with optimal development temperature (17-21°C) and long photoperiod (16 h). The reproductive development appears then to be more dominated by the non linear effect of temperature than solar radiation and high irradiance emphasizes this non-linearity as found by Sinclair (1994) for photosynthesis response. The interaction between temperature and radiation intensity can present different patterns according to being above or below optimal temperature. In field condition, plant exposure to high solar irradiance increases the bias between plant apex and air temperatures (Vinocur and Ritchie, 2001), so the temperature of the apex can get more closer to optimal temperature when air temperature is low and become more stressful when temperature is high. Consequently high solar radiation is expected to accelerate the rate of development and to shorten the phenophases durations in the two cases. In Mediterranean areas later sowing results in plant exposure to coupled higher temperature and solar radiation so the delay in sowing causes the decrease of the accumulation GDD and STU units required to attain different phonological stages as observed also in many researches (Rajput *et al*., 1987; Hundal *et al*., 1997; Kirby *et al*., 1999; Haider *et al*., 2003). These climatic conditions are also favourable to larger daily thermal amplitudes that affect plant response.

In the condition diurnal temperatures during the reproductive period exceed frequently 30°C, especially for the continental station of Kef. For T-H period radiation thermal indices give better results than the GDD because they might assess better the apex temperature. For T-J, although higher solar radiations accelerate the rate of development in both stations it is more rapid in continental than costal one. This can be explained by the vernalization effect of night temperature more cold in continental station. Small but consistent effect of vernalization on spring wheat has been noticed in many researches (Rawson *et al*., 1998; Kirby *et al*., 1999; Gonzalez *et al*., 2002). For J-H period the continental rate of development is slower than the costal contrary at it was expected for higher heat stress conditions. Miralles *et al*. (2001) found also that comparing to standard sowing results, for late sowing dates, relatively high temperatures (up to 25°C) and long photoperiods (up to 14.5 h) shorten the double ridge to terminal spikelet thermal times but lengthen the terminal spikelet to flowering thermal times. Kirby *et al*. (1999) found that the thermal times of double ridge to terminal spikelet and then to ear emergence phase are affected by photoperiod but are not similar between 2 years at comparable photoperiods and this can be also explained by solar radiation inter-year variations. These researchers found also that when merging the two successive phenophases the durations of double ridge to ear emergence responded similarly to photoperiod >2 years. This advantage may hide successive antagonist combined effect of temperature and solar radiation on development as observed in the research for T-J and J-H stages so it is obtained on the detriment of loss of phenological informations. The development during J-H stage can be affected by the environment during earlier phases particularly the T-J phase as proposed by Kirby *et al*. (1999) or can be slowed down by more source limitation as proposed by Rawson (1993) who hypothesized the possible variation of development with source/sink ratio. The weight of photosynthesis is very important for this period because of the acceleration of biomass production and any limitations in photosynthetic sources can slow down development. For H-M, the continental development is faster than the costal and this reflect the effect of the maximum temperatures that are known to accelerate maturity by increasing the rate of grain growth (Sofield *et al*., 1974; Dias and Lidon, 2008). This phase is not sensible to solar radiation intensity as found by Sofield *et al.* (1974). For the reproductive development the use of simple thermal time equation ignores the range of temperature between day and night which has been shown to affect plant response, so the biases between the thermal indices are greater between continental and costal zones. Discrepancies between the two climatic zones are reduced when the indices are adjusted with thermal amplitude (Table 3).

For T-J period, SR was adjusted using the neperien logarithm of the thermal amplitude. We believe that the new expression incorporates both the concurrent requirements of vernalization and vegetative development. Temperatures reached generally at night are lower when thermal amplitudes are larger and this accelerates the rate of vernalization. In the same time temperatures reached generally at day are higher when thermal amplitudes are larger and this increases the number of leaves initiated by the shoot apex prior to floral initiation. Chujo (1966a) found that the vernalizing effect of cold nights is not reduced by day temperatures up to 30°C provided they are not prolonged beyond 8 h each day. The differences in the number of leaf primordium initiation as a result of the balance between the concurrent processes of vegetative development and vernalization affect in turn the subsequent rate of development to ear emergence and anthesis (Chujo, 1966b; Brooking, 1996; Miralles *et al*., 2001). The continental temperature regime enhances more production of vegetative primordia, so the subsequent J-H period can be extended to cover their growth processes. Time to heading was always linearly related to final leaf number as affirmed by Slafer and Rawson (1995b). This can explain also the further duration of J-H period for continental station. For this phase, dividing STU with an exponential function of thermal amplitude gave better results. The exponential function in contrast to logarithmic one reflects great sensitivity of this period to temperature change. In this function dividing thermal amplitude by day length allows taking into account both sources limitation proposed by Rawson (1993) who found that the development source limitation associated with high temperature (27/22), short photoperiod (9 h) and low natural radiation extend the thermal time to ear emergence. When thermal amplitude are larger daily temperature are higher and exceed frequently photosynthesis optimal temperature proposed between 10 and 25°C (Friend, 1966; Sawada, 1970), so the rate of photosynthesis decreases as the rate of development.

Less inductive photoperiod limits also photosynthesis source and decrease also the rate of development. For the H-M period multiplying the neperien logarithm of the thermal amplitude by the GDD helped obtaining the same mean heat totals for the two locations. The thermal amplitude in this period reflects the effect of heat stress more pronounced in continental areas. The adjustment of thermal indices with thermal amplitudes gives more weight to Tx or/and Tn according to development processes requirements.

CONCLUSION

Results indicate the usefulness of considering amplitude when using the mean temperature to predict crop development. When a no linear temperature-growth relationship is hypothesised, the classical heat accumulation models need to be adjusted in order to have the same totals when moving from coastal to inland areas. Conversely when the development is linearly related to temperature, a simple heat unit model like the GDD is sufficiently accurate for predicting phenological stages. The thermal amplitude that are usually larger when both solar radiation and Tx are higher can be used to express thermal stress effect but plant responses can be different according to plant exposure duration and intensities to heat shock. Further studies must be done for more phonological models accuracy.

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