Effects of thermal stress on the pre-heading duration and grain production for Mediterranean irrigated durum wheat

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Abstract: *Yields as expressed in terms of Grain Number (GN) in cereals are closely related to the length of the Emergence-Heading period (EH) and the prevailing environmental conditions. The present work investigates the effects of increasing photoperiod, temperature and thermal amplitude on EH duration and GN in durum wheat. Used data related to cv Karim, grown under no limiting water and nutrient conditions in three Tunisian sites: Tunis (16 dates), Kef (8 dates) and Mornag (5 dates). GN varied from 17200 to 800 grains m^{-2} when EH range was 117-32 days, for November and July sowings, respectively. For conventional sowing and under higher temperatures wheat reached heading faster with EH interval reduction around 12 days each 1 °C rise during the phenophase. The modified photothermal unit (MPTU) gave the best predictive phenological results for both conventional and unconventional sowing dates. Results showed the possible substitution of rise in photoperiod effect by rate of rising in temperature in field conditions. GN was found to be correlated to maximum temperatures adjusted by thermal amplitude logarithm. The latter can express the intensity of thermal stress and can be used as a satisfactory predictor of attainable wheat yields in conditions with no water and nutrient limitation and in Mediterranean environments.*
Keywords: *durum wheat, phenology, Thermal indices, grain number, heat stress.*

Riassunto: *I rendimenti espressi in termini di numero di grani (GN) di cereali sono strettamente correlati alla durata del periodo di emergenza - spigatura (EH) e alle condizioni ambientali. Il presente lavoro indaga gli effetti dell'aumento di fotoperiodo, temperatura ed escursione termica sulla durata di EH e sulla resa del grano duro. Sono stati utilizzati dati relativi alla varietà Karim, coltivata senza condizioni limitanti per acqua e nutrienti in tre siti tunisini: Tunisi (16 date), Kef (8 date) e Mornag (5 date). E' stata osservata una variazione di GN compresa fra 17.200 a 800 grani m^{-2} con EH compreso tra 114 e 32 giorni, rispettivamente per semine a novembre e a luglio. La spigatura è stata raggiunta più velocemente per le semine convenzionali e con temperatura più elevata con una riduzione dell'intervallo di EH di circa 12 giorni ogni 1 °C di aumento durante la fenofase. L'applicazione delle unità fototermiche modificate (MPTU) ha dato i migliori risultati predittivi per le date di semina convenzionali e non convenzionali. I risultati hanno mostrato la possibile sostituzione dell'effetto dell'aumento del fotoperiodo con il tasso di incremento della temperatura, GN è risultato correlato alle temperature massime corrette dal logaritmo dell'ampiezza termica, che può esprimere l'intensità dello stress termico e può essere utilizzato come predittore soddisfacente del rendimenti ottenibili in condizioni non limitanti di acqua e di nutrienti e in ambiente mediterraneo.*
Parole chiave: *frumento duro, fenologia, indici termici, numero di cariossidi, stress termico.*

1. INTRODUCTION

Improving cereal yields and production stability are globally important goals, particularly in areas characterized by scarce and variable rainfall regimes (Savin *et al.*, 2015). In the Mediterranean, cereals are frequently exposed to water stress, which often combines with heat stress. Irrigation can relieve the effect of water deficits. However, high temperatures that often occur during the growing season, causing important restrictions of potential yield aren't easy to avoid. Heat stress is not only recurrent during terminal growing periods, affecting basically grain mass (Dias and Lidon, 2008, Mondal *et al.*, 2013), but also during pre-heading stages, impacting essentially grain number (GN) (Fisher and Maurer, 1976; Ugarte *et al.*, 2007; Dolferus *et al.*, 2011, Slafer *et al.*, 2014). Environmental constraints are expected to continue intensifying because of climate change (IPCC, 2013). Some scenarios for the Mediterranean are forecasting major effects on crop production associated to an overall reduction in annual precipitation (about 40mm) and an increase in air temperature from 0.84 to 2.31 °C for the fifty coming years (Saadi *et al.*, 2015).

It has long been recognized that large yield variation for wheat is essentially accommodated by GN rather than grain weight (Fischer, 1985; Peltonen-Sainio *et al.*, 2007; Slafer *et al.*, 2014). Recent studies are

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increasingly focussing on the differential effect of environmental factors on these two yield parameters (Slafer *et al.*, 2014; Talukder *et al.*, 2014). For pre-anthesis period, Ugarte *et al.*, (2007) found that grain yields were more limited by GN penalties than grain weight restrictions when temperature increased. In this work, the highest heat stress effects were noticed during stem elongation and the lowest one during heading-anthesis. Other studies showed also the close relationship between GN and the duration of the early stages of the growing cycle, considering the impact of temperature and photoperiod as the most important variables that regulate pre-heading duration under water and nutrient non limiting conditions (Slafer *et al.*,1996).
Modelling plant phenology is a key issue for plant breeders and agronomists. Although the Growing-Degree-Day (GDD) concept is widely used, GDD supposes a linear relationship between temperature and development while many authors demonstrated that wheat development was reduced when temperature exceeds an optimum temperature (Friend, 1965; Slafer and Rowson, 1995a). In an attempt to improve the predictive ability of this model a variant, called the Modified Growing-Degree-Day (MGDD), limiting the maximum daily temperatures to a threshold, was proposed by Barger (1969). Other indices were also proposed, using a non linear temperature-response in the form of polynomials (Stewart *et al.*, 1998; Streck *et al.*, 2003), exponential function (Angus *et al.*, 1981), simplified beta function (Yin *et al.*, 1995), and exponential sine equation (Longhui *et al.*, 2008). Nevertheless, based on mean temperatures, these models don't incorporate the photoperiod effects. Using more information, the Photo-thermal Unit (PTU) model multiplies GDD by daylength (McMaster and Smika, 1988). Probably PTU brings some improvement, but doesn't overcome the shortcoming of the linear thermal time concept.
Major (1980) approximated the non linear trend of phenophase response to photoperiod with adjacent linear segments with different slopes providing an estimate of the photoperiod sensitivity. Using an important set of data obtained under controlled conditions and field measurements conducted with artificial photoperiod extension (Slafer and Rawson, 1995b), a comprehensive analysis of the interactive effects of photoperiod and temperature on wheat development, was carried out by Slafer and Rawson (1996). They showed that photoperiodic sensitivity is not constant and should be moderated by temperature.
Our work relates to the relationship between photoperiod and thermal regimes in the Mediterranean. We consider that day-length and temperature show increasing pattern during the growing cycle of durum wheat i.e. from December to May in northern Tunisia and Southern Italy. The thermal amplitude increases also during the same period. Based on these hypotheses, this study aims to test a thermal unit accumulation method that can predict EH duration and potential GN for durum wheat using only maximum and minimum temperatures. The modelling effort includes the integration of the thermal amplitude in modelling to account for the differential exposure to heat stress in sites having similar mean temperatures.

2. USED DATA AND METHODS

Data used in this study were obtained on durum wheat (Triticum turgidum L. var. Durum, cv Karim), grown in three agriculture experimental stations in Tunisia. The first site is located in the coastal region of Tunis (36.8°N,10.1°E), the second is in the continental area of Kef (36.1°N, 8.7°E) and the third in the semi-continental area of Mornag (36.4° N,10.1° E). Daily maximum (Tx) and minimum (Tn) temperatures were recorded 2m above the soil surface in conventional meteorological stations, located within the experimental site.
Phenological and production data series related to respectively 16, 8 and 5 sowing spaced out dates under water and nutrient non limiting conditions were recorded respectively in Tunis, Kef and Mornag stations (Khlifa, 1989 ; Melki, 1993, Abdou 2011). The sowing dates for the first two stations were chosen to explore a wide spectrum of plant exposure to climatic conditions, ranging from conventional sowing periods (November-December) to totally unusual time spans (June-July) within the same agricultural year. In Mornag station the sowing dates were related to three different production years 2006 to 2008, selected to enhance variability.
The indicated experiments were conducted in split plot design having $2m^2$ of area for both Tunis and Kef stations and $48m^2$ for Mornag with three replications, except for the 'January 2006 sowing' for Mornag whose plot was $180m^2$ with only one replication. All the treatments were well irrigated and fertilized. 30-50-30 kg N of the nitrogen fertilizer was respectively applied at seeding, tillering and stem elongation and 80 kg P_2O_5 of the phosphorus was applied before sowing. For Kef and Tunis stations one irrigation was applied weekly and for Mornag station one to two irrigations were applied to refill soil to field capacity after heading according to soil moisture measures and no water

stress was detected before heading thanks to wet autumn and winter. The experiments were sprayed with herbicide (active ingredients: Mésosulfuron-Méthyl, anti mono and dicotyledon) and fungicide (active ingredients: epoxiconazole, anti Septoria tritici) during respectively the early tillering and before heading stages. At physiological maturity three samples of 1 m², even for 'January 2006 sowing' for Mornag, were hand harvested and threshed to avoid loss in grain quantity. Grain yield was bulked and kernel weight was determined for one thousand grains counted by seed counter. GN is estimated indirectly by dividing grain yield by kernel weight. The development stages have their corresponding values on the Feekes scale (Large, 1954) as follow: emergence (E,1.0) and heading (H,10.5) observed when 50% of the main stems reached the target stage. Fig. 1 represents the Emergence-heading observed duration related to the different sowing dates.
Six indices were selected to investigate the possible use of meteorological variables to predict the wheat growth period following a given sowing date under a Mediterranean type climate, regardless of the period of the year.
The SGDD is defined as:

$$\Sigma GDD=\sum_{i=s1}^{s2}(T_i - T_0) \qquad (1)$$

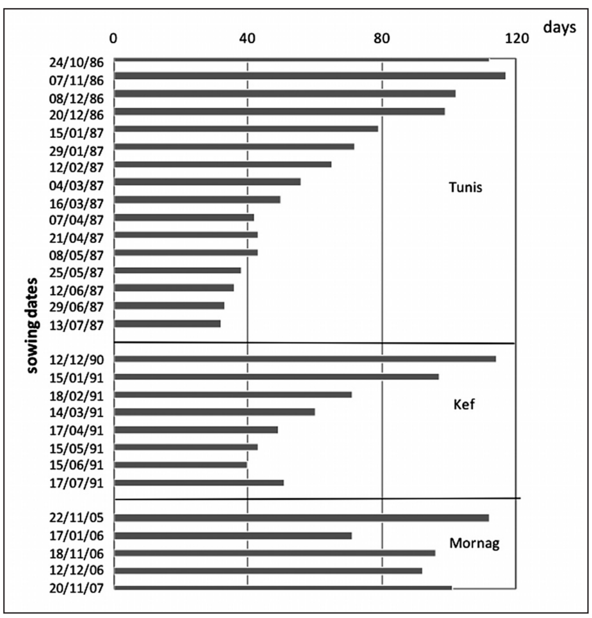

Fig. 1 - Emergence-heading durations related to the 16, 8 and 5 sowing dates of respectively Tunis, Kef and Mornag.
Fig. 1 - Durata della fase di emergenza-spigatura in relazione 16, 8 e 5 date di semina rispettivamente per Tunisi, Kef e Mornag.

Where T is the mean temperature in °C calculated as (Tx+Tn)/2 and i is the day beginning at stage (s1) and incrementing daily until reaching stage (s2). Whenever expression (1) produces a negative value then GDD is set equal to zero.
The base temperature (T_0) was determined using a linear regression of the rate of 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 greater than 30°C equal to 30°C (Barger, 1969):

$$\Sigma MGDD=\begin{cases}\sum_{i=s1}^{s2}\left(\frac{Tx_i+Tn_i}{2}-T_0\right) & \text{if} \quad Tx_i<30°C\\ \sum_{i=s1}^{s2}\left(\frac{30+Tn_i}{2}-T_0\right) & \text{if} \quad Tx_i\geq 30°C\end{cases} \qquad (2)$$

The STx cumulates daily maximal temperatures between phenological events.
The SPTU is defined by multiplying the day length in hours (L) with GDD (McMaster and Smika, 1988):

$$\Sigma PTU=\sum_{i=s1}^{s2}L_i(T_i - T_0)=\sum_{i=s1}^{s2}L_i(GDD_i) \qquad (3)$$

The (SMPTU) modifies equation (3) by using MGDD instead of GDD.

The simplified beta function model SBF is a non linear approach represented by Yin *et al.*, (1995):

$$\Sigma SBF=\sum_{i=s1}^{s2}\left(\frac{Tceil - T_i}{Tceil - Topt}\right)\left(\frac{T_i}{Topt}\right)^{\frac{Topt}{Tceil-Topt}} \qquad (4)$$

Topt is the optimum temperature at which the maximum rate of development occurs, Tceil is ceiling temperature at which development ceases. They are fitted to the data in order to minimise the coefficients of variation (CV) of the index.
The actual number of calendar days (ND) for EH durations is compared to predictions of SGDD, STx, SMGDD, SPTU, SMPTU and SSBF. The models' predictive ability is evaluated on the basis of the CV whereas the sensitivity to the thermal regime was assessed by comparing summation values relative to each site.

3. RESULTS

The years of experimentations, the number of sowing dates and mean temperatures values recorded over the respective EH phenological

		Tunis	Kef	Mornag
Year of experiment		86/87		2004-08
Cycles number		03	01	04
	Tx (°C)	15.9	18.7	18.4
Conventional	Tn (°C)	7.6	2.5	7.7
(01 Nov- 31 Dec.)	T (°C)	11.7	10.4	13.0
	(Tx-Tn) (°C)	8.3	15.7	10.7
Cycles number		13	07	01
	Tx (°C)	25.1	31.1	20.5
Non conventional	Tn (°C)	14.0	7.6	8.0
(01 Jan- 30 Oct.)	T (°C)	19.5	19.3	14.3
	(Tx-Tn) (°C)	11.1	23.5	12.5

Tab. 1 - Mean climatic variables averaged over the "Emergence - Heading" recorded periods related to the set of cropping cycles for Tunis, Kef and Mornag stations for conventional (from 1/11 to 31/12) and non conventional sowing dates.
Tab. 1 - Variabili climatiche medie relative ai periodi emergenza - spigatura per l'insieme dei cicli colturali per le stazioni di Tunisi, Kef e Mornag per date convenzionali (dal 1/11 al 31/12) e non convenzionali della semina.

periods are given in Tab. 1. Thermal amplitudes were higher for non conventional sowing, especially for Kef station.

3.1. Grain yield variation

Depending on both sowing date and station thermal regime, grain yield varied between 10.7 to 0.3 t ha^{-1}, however it is linearly related to GN for the three experimental stations (Fig. 2). A variation of 1 t ha^{-1} corresponds to about 1850 grain m^{-2} (slopes of the regression line for all the data reported in Fig. 2).
Maximum GN 17200, 13800 and 13100 grains m^{-2} are obtained with conventional sowings during the months of November-December corresponding to respectively EH durations of 102,114 and 112 days in Tunis, Kef and Mornag, respectively. Minimum grain number values were associated to sowings that took place during the summer hottest months. These were 5900 grains m^{-2} in Tunis station and 800 grains m^{-2} in Kef for a sowing in July. The corresponding observed EH durations were respectively 32 and 51 days. The rate of GN increased linearly by about 150 grains m^{-2} for each day of delay in heading (Fig. 3).

3.2. Phenology response

With sowings spaced out over the different seasons, it has been observed that EH durations could be highly variable, with important impact on grain

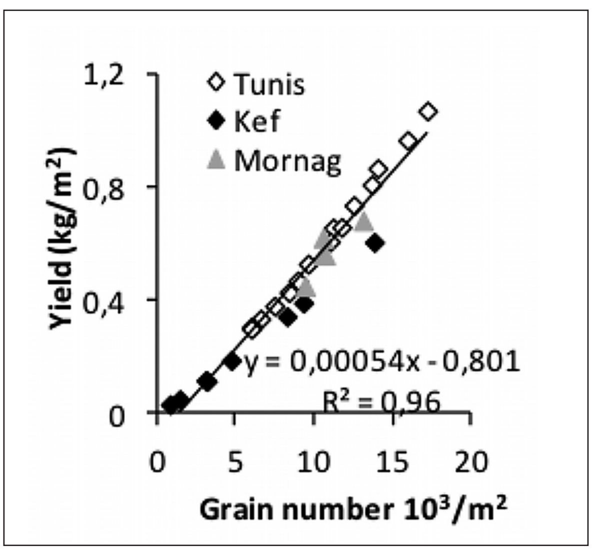

Fig. 2 - Grain yield vs grain number for the different experimental stations.
Fig. 2 - Resa in funzione della granella per le differenti stazioni sperimentali.

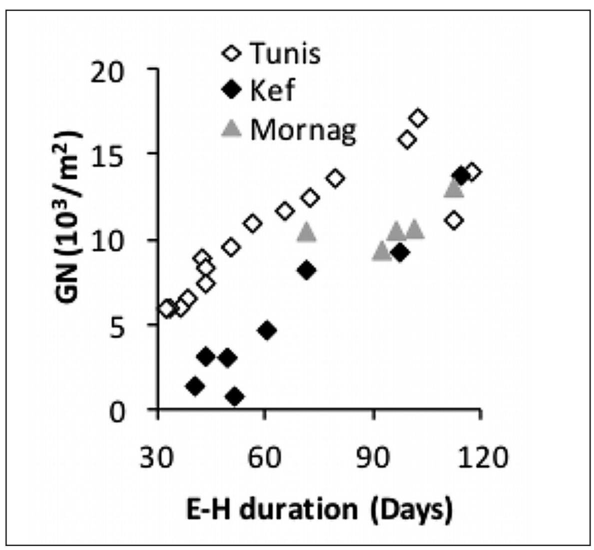

Fig. 3 - Variation of grain numbers in relation to the Emergence - Heading phenophase duration.
Fig. 3 - Variazione della granella in relazione alla durata della fase compresa tra emergenza e spigatura.

production; depending on the station thermal regime we obtained different totals GN for the same calendar duration of the EH phenophase. The length of EH was about 105 days for standard sowing dates (November-December) and reached 117 days for October sowing but with no improvement in yield (Fig. 3). This phenophase was reduced down to only 30-40 days for sowings in June-July with constrained GN. As the GN was highly dependent on EH phenophase duration which was itself determined by prevailing temperature conditions, it is interesting to seek simple models whereby these relationships could be quantitatively determined.

As a starting step, all the data series for Kef, Tunis and Mornag stations were used to compute threshold temperatures relating to the growth and development of the Karim cultivar. Hence, using the statistical procedure recommended by Gbur *et al.*, (1979), a common base temperature of 0°C was obtained for the different stations, with a linear regression determination coefficients of 0.82, confirming the relevance of this value for wheat as pointed out by many authors (Slafer and Rawson, 1995a; Kirby *et al.*, 1999; McMaster and Wilhem, 1997). For optimal and ceiling temperatures obtained values are different from one station to the other. Nevertheless, respectively 28 °C and 42 °C minimize the coefficient of variation for all EH stages, independently to sites. Tab. 2 presents the most relevant results obtained for EH duration modelling, including the average heat accumulation totals, the number of calendar days (ND) and their respective coefficients of variation.

Intermediate calculations showed that GDD index cumulated over EH decreased from 1423°C to 722°C day when sowing dates moved from the beginning of autumn to summer. Averages for EH calendar days obtained for the three stations weren't similar (Tab. 2). Apparently, PTU index seemed to predict this stage with reasonable CVs compared to GDD, although it didn't produce statistically significant similar means. This consolidates that the development rate of Karim variety is sensitive to photoperiod under 10-15 hours of daylength. Similar findings for wheat were reported by many authors (Slafer and Rawson, 1996; Miralles *et al.*, 2001). The non linear thermal models (not based on linear accumulation of mean temperatures) i.e. MGDD, Tx and SBF didn't handle the photoperiod sensitivity so they couldn't improve the coefficients of variation. Fig. 4 presented a general linear decrease of the EH phenophase durations by 17 days when the mean inductive photoperiod progressively rose by one hour. This linear trend consolidates the finding of Slafer *et al.*, (1994) supporting that wheat phenology during the EH stage seems to respond to average photoperiod rather than to its rate of change across the stage.

Phenophase durations decreased also with increasing mean temperature (Fig. 5). For conventional sowing dates EH stage is hastened by around 12 days for each mean temperature increase of 1 °C during EH stage while GN is more reduced in continental zones characterized

		Tunis	**Kef**	**Mornag**
ND	(day)	63a	66b	94c
	CV	0.46	0.41	0.16
∑GDD	(day °C)	993a	1073b	1244b
	CV	0.20	0.18	0.11
∑Tx	(day °C)	1307a	1766b	1762b
	CV	0.21	0.16	0.10
∑MGDD	(day °C)	975a	982a	1243b
	CV	0.21	0.17	0.11
∑PTU	(h day °C)	12522a	14315b	13370b
	CV	0.11	0.17	0.07
∑MPTU	(h day °C)	12268a	13027a	13357a
	CV	0.10	0.11	0.07
∑SBF		35.1a	55.7b	43.1c
	CV	0.15	0.24	0.09

Tab. 2 - Average number of days, thermal indices (respectively, Growth Degree Day; maximal temperature summation; Modified Growth Degree Day; Photo-Thermal units, Modified Photo-Thermal units and Simplified Beta Function) and their respective coefficients of variation (CV) for Tunis (16 data series), Kef (8 data series) and Mornag (5 data series) during Emergence - Heading period. The indices are presented in the text. Stations indices means for the same stage are not significantly different when they are followed by the same letters (one factor analysis of variance test at 5%).

Tab. 2 - Numero medio di giorni, indici termici (rispettivamente: gradi giorno, somma termica delle massime, gradi giorno modificati, unità fototermiche, unità fototermiche modificate, funzione Beta semplificata) e i rispettivi coefficienti di variazione (CV) per Tunisi (serie di 16 date), Kef (serie di 8 date) e Mornag (serie di 5 date) durante il periodo emergenza - spigatura. Gli indici sono descritti nel testo. Gli indici medi per stazione e per lo stesso stadio non sono significativamente diversi quando sono seguiti dalle stesse lettere (test di analisi della varianza ad un fattore al 5%).

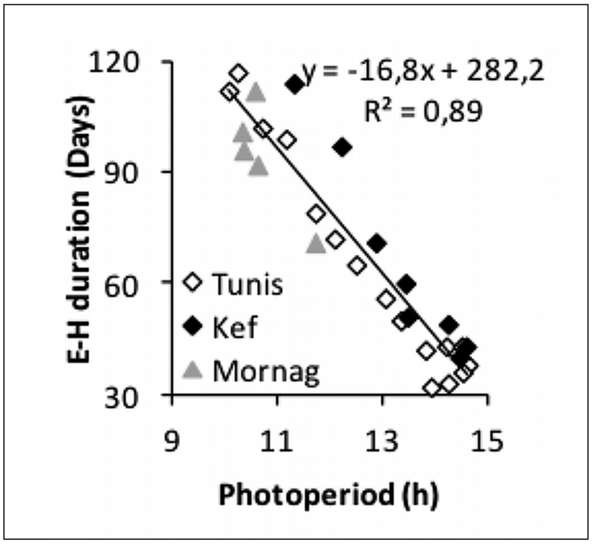

Fig. 4 - Emergence - Heading duration vs prevailing photoperiods.
Fig. 4 - Durata della fase emergenza - spigatura in funzione del fotoperiodo.

by higher thermal range leading to more stressful diurnal thermal regime. The rate of decrease was more gradual under higher temperatures. In our case it changed from -12 day $°C^{-1}$ to -1.3 day $°C^{-1}$ when both average mean temperature and photoperiod increased beyond respectively 15 °C and 13h (Fig. 5). This is conforming to the findings of Slafer and Rawson (1996), who argued for photothermal cultivar response sensitivity to temperature. The decrease of photothermal sensitivity when temperatures increase was also consolidated by results showing some discrepancy between the three stations (Fig. 4), which was reduced when both photoperiods and mean temperatures increased. Even so, longer photoperiods associated with higher temperatures induced exaggerated rise in cumulative PTU index because it is based on linear multiplicative temperature and photoperiod response without taking into account the photothermal sensitivity interaction with increasing temperature whilst the MPTU index reduced the discrepancies of the prediction especially for Tunis and Kef stations where sowing dates were non conventional and linked to more stressful thermal conditions. Modifying the GDD by truncation mean temperature instead of maximum temperature didn't improve the performance of the prediction (results not shown).

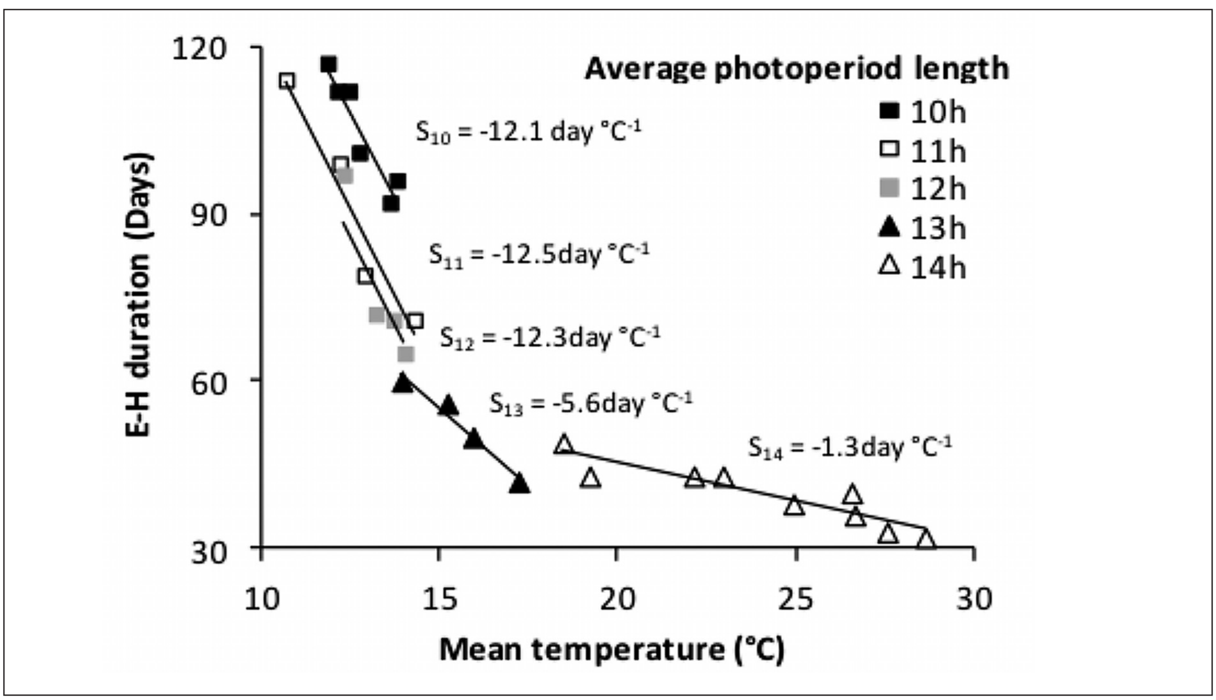

Fig. 5 - Duration intervals for "Emergence - Heading" vs "mean temperatures" grouped according to average photoperiod (the grouped data are in the same photoperiod interval with one hour of amplitude around the average value). Si are the slopes of the regression lines of the grouped data related to average photoperiod i.
Fig. 5 - Intervalli di durata per "emergenza - spigatura" in relazione alle temperature medie, raggruppati secondo il fotoperiodo medio (i dati raggruppati sono nello stesso intervallo di fotoperiodo con un'ora di ampiezza attorno al valore medio). Si sono le pendenze delle rette di regressione dei dati raggruppati in relazione al fotoperiodo medio i.

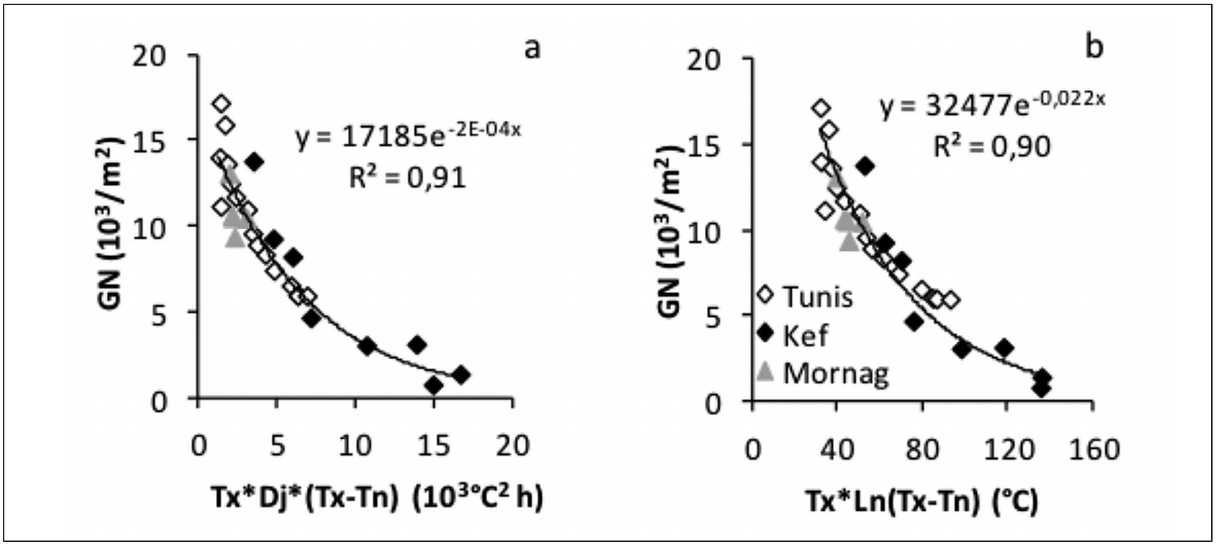

Fig. 6 - Grain number vs a) the mean product of maximal temperature, photoperiod and thermal range, and b) adjusted maximum temperatures averaged over Emergence-Heading stage. Tx and Tn are maximum and minimum temperatures, respectively.
Fig. 6 - Granella in relazione a: a) il prodotto medio di temperature massime, fotoperiodo ed escursione termica, e b) temperatura massima aggiustata e mediata sul periodo emergenza - spigatura. Tx e Tn sono rispettivamente le temperature massima e minima.

3.3. Grain number modelling

GN seemed to be not only driven by EH duration (Fig. 3) but also by the intensity of heat stress during this stage which was more related to maximum temperatures than to mean temperature as found by Ferris *et al.*, (1998) during anthesis process and advanced by Wahid *et al.*, (2007) who described a heat stress plant response as a complex function of heat intensity, exposure duration and rate of increase in temperature. The thermal amplitude can be used to express both the exposure duration differences and the rate of increase in temperature between the three stations.
The multiplication of the different variables controlling developmental and growth processes: maximum temperature, thermal amplitude and photoperiod explained better GN with exponential regression determination coefficient of 0.91 (Fig. 6a). However Tx multiplied by the naperian lorgarithm of thermal amplitude gave also comparable results without taking into account the photoperiod term (Fig. 6b). The logarithmic function was used in phenological thermal time modelling by Heurer *et al.*, (1978) who selected it owing to its ability to describe better the diurnal hourly progression of temperature. When both thermal range and photoperiod are constant, GN is exponentially related to maximum temperature.

4. DISCUSSION

Results indicated the importance of considering the possible effect of heat stress when using mean temperature data to predict crop development and grain yield.
EH phenophase duration, essentially driven by photoperiod, is sensitive to thermal regimes so calendar day couldn't be adopted as a good estimator of GN in variable climate conditions as Mediterranean ones. Indeed, during EH period two concomitant development processes occurred, vegetative and reproductive. The vegetative development, essentially driven by temperature, is crowned by the final number of leaf always linearly related to time to heading as affirmed by Slafer and Rawson (1995b). Whereas, the reproductive ontogeny, characterised by the number of the spikelet and floret set, is driven essentially by the duration of the spike growth period which is essentially affected by both photoperiod and its temperature sensitivity as affirmed by many authors (Slafer *et al.*, 2001; Gonzalez *et al.*, 2005).
The duration of the spike growth period is associated to phenological processes whereas optimal temperature for the vegetative growth is associated to net photosynthesis processes that ensure the availability of carbohydrate needed later for the development of floret which competed for assimilates resulting in final GN. Bancal (2009) advanced that when developmental processes are

accelerated by stressful environmental conditions without substantial increase in photosynthesis, trophic competition induces primordial floret abortion that occurs during rapid stem and spike elongation.

Good predictor of GN based on simultaneous phenological and photosynthesis processes were also championed by many other authors among them Fischer (2011) used the dry mass of spikes at anthesis and explained that for the same wheat cultivar these spikes mass are related to both the spike growth period duration and the rate of accumulation of dry matter then. Higher GN is then ensured by higher available assimilates associated to optimal condition for net photosynthesis-temperature processes during longer EH event. Many authors (Friend 1965; Todd, 1982) found that the optimum temperature for photosynthesis during leaf and ear wheat development was about 15 to 25 °C with a substantial decline at 30 °C. For the three agro-climatic sites, mean maximal temperature over EH stage were above 15 °C. The logarithm amplitude adjustment may express the intensity of stressful temperature condition for photosynthesis process. In warm conditions, larger thermal amplitudes could be associated to longer plant exposure to high temperatures. Indeed, over EH period, cumulative thermal unit of maximum temperatures beyond a threshold of 15 °C, supposed to be stressful units, was closely related to the mean thermal amplitudes (R^2=0.80) rather than cumulative entire maximum temperatures (R^2=0.05) and thermal range related to non conventional sowing dates, and associated to more heat stressful conditions, are higher than for conventional dates. The thermal amplitudes are furthermore correlated to the photoperiods (R^2=0.88, 0.82, 0.80 for respectively Tunis, Kef and Mornag stations). In Mediterranean and field conditions it is then difficult to dissociate rise in photoperiod and the rate of temperature rise.

The high determination coefficient of the exponential relation GN-adjusted Tx (Fig. 6b) assumed that it is possible to substitute rise in photoperiod by rate of temperature rise in field conditions and thermal amplitude can be a good indicator related to both of them. This hypothesis warrants further investigations with more precise data. However Tx adjusted by thermal amplitude and averaged over EH stage remains satisfactory and especially a simple predictor of GN for different Mediterranean agro-climatic zones under non limiting water conditions. The proposed model would help in predicting global warming effects on crop growth and development, especially when only maximum and minimum temperature are available without precise evaluation of heat time exposure.

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REFERENCES

Abdou H., 2011. Effect of some climatic factors on the Stability of durum wheat production under rainfed and irrigated conditions in the north of Tunisia. PH-D. INAT. Tunisia.

Angus J. F., Mackenzie D. H., Morton R., Schafer C.A., 1981. Phasic development in field crops. II. Thermal and photoperiodic responses of spring wheat. Field Crop. Res., 4: 269-283.

Bancal P., 2009. Early development and enlargement of wheat floret primordia suggest a role of partitioning within spike to grain set. Field Crop. Res., 110: 44-53.

Barger G. L., 1969. Total growing degree days. Weekly Weather Crop Bulletin, 56: 5-10.

Dias A. S., Lidon F. C., 2008. Evaluation of Grain Filling Rate and Duration in Bread and Durum Wheat, under Heat Stress after Anthesis. J. Agron. Crop Sci., 195: 137-147.

Dolferus R., Ji. X., Richards R. A., 2011. Abiotic stress and control of grain number in cereals. Plant Science, 181:331-341.

Ferris R., Ellis R. H., Wheeler T. R., Hadley P., 1998. Effect of high temperature stress at anthesis on grain yield and biomass of field-grown crops of wheat. Annals of Botany, 82: 631-639.

Fischer R. A., 2011. Wheat physiology: a review of recent developments. Crop and Pasture Science, 62: 95-114.

Fischer R. A., 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. Journal of Agricultural Science, Cambridge, 105: 447-461.

Fischer R. A., Maurer R., 1976. Crop temperature modification and yield potential in a dwarf spring wheat. Crop Science, 16: 855-859.

Friend D. J. C., 1965. Ear length and spikelet number of wheat grown at different temperatures and light intensities. Can. J. Bot., 43: 345-353.
Gbur E. E., Thomas G. L., Miller F. R., 1979. Use of segmented regression in the determination of the base température in heat accumulation models. Agron. J., 71: 949-953.
Gonzalez F.G., Slafer G.A., Miralles D.J., 2005. Photoperiod during stem elongation in wheat: is its impact on fertile floret number and grain number determination similar to that of radiation. Functional Plant Biol., 32: 181-188.
Heurer G. R., Heermann D. F., McKee T. B., Benci J. F., 1978. Predicting winter wheat phenology using temperature and photoperiod. Climatology Report 78-2. Colorado State University, Colorado. 81 pp.
IPCC (Intergovernmental Panel on Climate Change), 2013. Climate Change 2013. The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press. New York.
Khlifa K., 1989. Comportement des céréales en semis échelonnés et possibilité de deux cultures par an sous des conditions non limitantes d'eau. Thèse de troisième cycle. INAT. Tunis. Tunisie.
Kirby E. J. M., Spink J. H., Frost D. L., Sylvester-Bradley R., Scott-R. K., Foulkes M. J., lare R. W., Evans E. J., 1999. A study of wheat development in the field: analysis by phases. Eur. J. Agron., 11: 63-82.
Large E. C., 1954. Growth stage in cereals: Illustrations of Feeks scale. Plant Pathology, 3: 128-129.
Longhui L., McMaster G. S., Yu Q., Du J., 2008. Simulating winter wheat development response to temperature: Modifying Malo's exponential sine equation. Computers and Electronics in Agriculture, 63: 274-281.
Major D. J., 1980. Photoperiod response characteristics controlling flowering of nine crop species. Can. J. Plant Sci., 60: 777-784.
McMaster G. S., Wilhem W. W., 1997. Growing degree-days : One equation, two interpretations. Agric. For. Meteorol., 87: 291-300.
McMaster G. S., Smika D. E., 1988. Estimation and evaluation of winter wheat phenology in the central great plains. Agric. For. Meteorol., 43: 1-18.
Melki M., 1993. Effet de la variabilité saisonnière des facteurs climatiques sur les rythmes de croissance des céréales et leur potentiel de production de grains. Thèse de troisième cycle. ESAK. KEF. Tunisie.
Miralles D.J., Brenda C. F., Slafer G. A., 2001. Developmental responses to sowing date in wheat, barly and rapeseed. Field Crop. Res., 71: 211-223.
Mondal S., Singh R. P., Crossa J., Huerta-Espino J., Sharma I., Chatrath R. *et al.*, 2013. Earliness in wheat: A key to adaptation under terminal and continual high temperature stress in South Asia. Field Crop. Res., 151:19-26.
Peltonen-Sainio P., Kangas A., Salo Y., Jauhiainen L. 2007. Grain number dominates grain weight in temperate cereal yield determination: Evidence based on 30 years of multi-location trials. Field Crop. Res., 100: 179-188.
Saadi S., Todorovic M., Tanasijevic L., Pereira L. S., Pizzigalli C., Lionello P., 2015. Climate change and Mediterranean agriculture: Impacts on winter wheat and tomato crop evapotranspiration, irrigation requirement and yield. Agricultural Water Management, 147: 103-115.
Savin R., Slafer G. A., Cossani C. M., L. Abeledo G., Sadras V. O., 2015. Chapter 7 - Cereal yield in Mediterranean-type environments: challenging the paradigms on terminal drought, the adaptability of barley vs wheat and the role of nitrogen fertilization. Crop Physiology, 141-158.
Slafer G. A., Savin R., Sadras V. O., 2014. Coarse and fine regulation of wheat yield components in response to genotype and environment. Field Crop. Res., 157: 71-83.
Slafer G. A., Abeledo L. G., Miralles D. J., Gonzalez F. G., Whitechurch E. M., 2001. Photoperiod senstitvity during stem elongation as an avenue to raise potential yield in wheat. Euphytica, 119: 191-197.
Slafer G. A., Calderini D. F., Miralles D. J., 1996. Yield components and compensation in wheat: Opportunities for further increasing yield potential. In: Reynolds, M.P., Rajaram, S., McNab, A. (Eds.), Increasing Yield Potential in Wheat: Breaking the Barriers. Mexico, D.F.: CIMMYT. pp. 101-133.
Slafer G. A., Rawson H. M., 1996. Response to photoperiod change with phenophase and temperature during wheat development. Field Crop. Res., 46: 1-13.
Slafer G. A., Rawson H. M., 1995a. Rates and cardinal temperatures for processes of development in wheat: effects of temperature and thermal amplitude. Aust. J. Plant Phys., 22: 913-926.

Slafer G. A., Rawson H. M., 1995b. Photoperiod x temperature interactions in contrasting wheat genotypes time to heading and final leaf number. Field Crop. Res., 44: 73-83.

Slafer G. A., Halloran G. M., Connor D. J. 1994. Development rate in wheat as affected by duration and rate of change of photoperiod. Annals of Botany, 73: 671-677.

Stewart D. W., Dwyer L. M., Carrigan L. L., 1998. Phenological temperature response of maize. Agron. J., 90: 73-79.

Streck N. A., Weiss A., Xue, Q., Baenziger P. S., 2003. Incorporating a chronology response into the prediction of leaf appearance rate in winter wheat. Ann. Bot., 92: 181-190.

Talukder A. S., McDonald G. K., Gill G. S. 2014. Effect of short-term heat stress prior to flowering and early grain set on the grain yield of wheat. Field Crop. Res., 160: 54-63.

Todd G. W. 1982. Photosynthesis and respiration of vegetative and reproductive parts of wheat and barly plants in response to increasing temperature. Proc. Okla. Acad. Sci., 62: 57-62.

Ugarte C., Calderini D. F., Slafer G. A., 2007. Grain weight and grain number responsiveness to pre-anthesis temperature in wheat, barley and triticale. Field Crop. Res.,100: 240-248.

Wahid A., Gelani S., Ashraf M., Foolad M. R., 2007. Heat tolerance in plants: An overview, Environmental and Experimental Botany, 61: 199-223.

Yin X., Kropff M. J., McLaren G., Visperas R. M., 1995. A nonlinear model for crop development rate as a function of temperature. Agric. For. Meterol., 77: 1-16.