

HEAT STRESS

Daylength, Temperature and Solar Radiation Effects on the Phenology and Yield Formation of Spring Durum WheatD. Villegas¹, C. Alfaro², K. Ammar³, M. M. Cátedra⁴, J. Crossa³, L. F. García del Moral⁵ & C. Royo¹

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Keywords

daylength; harvest index; radiation; temperature; yield components

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Accepted July 3, 2015

doi:10.1111/jac.12146

Abstract

Future food security will depend on crop adaptation to changing environments. We studied the limitations imposed by daylength, temperature and solar radiation on wheat yield in eight field experiments conducted at contrasting northern latitudes and involving 42 adapted spring durum wheat genotypes of divergent phenology, and reduced or without photoperiod sensitivity. Air temperatures averaged from sowing to anthesis (SA) increased from northern to southern sites, while daylength and minimum temperatures from anthesis to maturity (grain filling, GF) followed the opposite trend, due to differences in the latitude of sites. The site effect explained 96 % of the variation in the number of days SA, which was much smaller in southern sites. Average minimum daily temperatures above 6.9 °C before anthesis and below 10.8 °C during GF accompanied by photoperiods during GF of less than 14.2 h resulted in less than 14 000 kernels m⁻², which was the threshold below which kernel number limited yield. Radiation during GF lower than 1.8 kJ kernel⁻¹ day⁻¹ limited kernel weight, which was then a constraint to the achievement of yield potential.

Introduction

Wheat is one of the most important staple crops in the world (FAOSTAT, 2010) and is essential to global food security. In coming decades, increases in wheat production will be needed in order to match the expected population growth, and both agronomic improvements and genetic progress through breeding will be required to meet the resulting increase in global demand (Spiertz 2012). Breeding strategies that seek to achieve large genetic yield gains will depend on the precise knowledge of both genetic and environmental yield-limiting factors (Reynolds et al. 2011).

Most climate change scenarios predict increases in temperatures and in the frequency of extreme events, such as heat waves and longer lasting droughts, as well as more erratic water availability in several major wheat-producing areas of the world (IPCC, 2014). Grain yield in wheat is determined mainly by environmental factors, particularly

under Mediterranean conditions. A study that tested 191 durum wheat accessions in nine Mediterranean environments reported that the percentage of yield variability explained by the environment was 98 %, with mean daily maximum temperature from emergence to heading accounting for 59 % of yield variations (Royo et al. 2010). The uncertainty associated with weather patterns is one of the greatest contributors to the gap present between potential and actual yield (Zhang et al. 2013) – estimated at 20 % by Lobell et al. (2009). Luo et al. (2005) reported that, by 2080, climate change is likely to cause a reduction between 13.5 % and 32 % in wheat yield in Mediterranean-type environments, mostly because of changes in rainfall and temperature.

The site latitude is an important and integrative environmental driver, as it is associated with variations in temperature regimes, photoperiod and radiation intensity, all of which determine growth and development (Craufurd and

Wheeler 2009), and ultimately productivity. Within the range of latitudes of areas devoted to spring cereals, in addition to causing changes in development, latitude may affect biomass production, tiller number (Peltonen-Sainio et al. 2009), grain number (Fischer 1985, 2011) and kernel weight (Menéndez and Satorre 2007). It is also known that latitude-determined photoperiod affects biomass production (Hay 1990). Most studies relating photoperiod or temperature variation to production have considered fixed photoperiod or temperature treatments (Giunta et al. 2001, Chauhan et al. 2005), and field studies are often limited to a small range of latitudes (Penrose et al. 1996, He et al. 2012).

Environmental limiting factors differ from site to site (Ereikul and Köhn 2006). Phenological adjustment, or the optimization of the duration of the different developmental phases, has been one of the most useful strategies available to adapt wheat to harsh or/and highly erratic environmental conditions (Gouache et al. 2012). Time to anthesis is considered a primary trait determining wheat adaptation to a particular set of growing conditions (Worland et al. 1998, Snape et al. 2001). Variability in time to anthesis can be used to fine-tune growth and development patterns to the most prevailing environmental conditions in any particular environment (Blum 2011).

The objective of this study was to ascertain the effect of daylength, temperature and solar radiation on spring durum wheat phenology and to assess the constraints associated with these environmental factors on yield formation.

Material and Methods

Experimental set-up

Eight field experiments involving 42 durum wheat genotypes were performed at four sites with contrasting latitudes in Spain and Mexico in 2007 and 2008 (Table 1). Each experiment consisted of 12-m² plots arranged in a randomized complete block design with three replications. Experiments were planted in autumn except in southern Mexico, where they were planted in May (summer crop cycle). Sowing densities were adjusted to 400 and 275 viable seeds m⁻² in Spain and Mexico, respectively, in order to obtain approximately 450 spikes m⁻². Plot management was implemented to maximize yield at each site, to the extent allowed by local conditions. Soil analyses were performed, and fertilization was provided to cover crop extraction. Plots were irrigated when necessary (required full irrigation in northern Mexico) to prevent significant water deficit. Plots were kept disease and insect free by means of preventive pesticide applications. Lodging was prevented, when needed, using networks of strings to support lodging-prone or tall genotypes.

Table 1 Relevant geographic and environmental descriptors for the 4 testing sites

Site	Site, state or autonomous community	Experimental station (institution's acronym)	Coordinates		Altitude (m asl)	Long-term rainfall (mm/year)	Soil characteristics				Environmental characteristics	
			Lat	Long			Texture	pH	P (ppm)	K (ppm)		O.M. (%)
North Spain	Gimenells, Cataluña	Gimenells (IRTA)	41° 38'N	0° 23'E	200	370	Fine-loamy	8.1	16	134	2.4	Moderate terminal stress. High to medium productivity
South Spain	Jerez de la Frontera, Andalucía	Rancho de la Merced (IFAPA)	37° 0'N	3° 40'W	30	600	Fine-Loamy	7.7	40	155	2.5	Very high terminal stress. Medium productivity
North Mexico	Ciudad Obregón, Sonora	CENEB (CIMMYT)	27° 21'N	109° 54'W	40	32	Clay	8.5	2.4	273	1.2	Very high terminal stress. Mandatory full irrigation. Very high productivity
South Mexico	El Batán – Texcoco, State of Mexico	El Batán (CIMMYT)	19° 31'N	98° 50'W	2249	500	Clay	5.9	65	312	5.0	Initial stress eliminated with irrigation. Medium productivity

O.M., organic matter.

Plant material

Thirty-nine inbred lines and three controls (Mexa-early, Simeto-medium late and Anton-late) with contrasting time to anthesis were used. Thirty-seven inbred lines resulted from divergent selection for time to anthesis, initiated in F_4 and continued until F_8 , in crosses between five German genotypes and five CIMMYT lines. Two additional CIMMYT sister lines, derived from the cross-CF4-JS 40/3/Stot//Altar84/Ald, were also included in the collection. The genotypes included were characterized by weak or no vernalization requirements and reduced to no photoperiod sensitivity. The collection evaluated was purposely selected to include genotypes with the widest possible range of flowering dates, including the earliest types (exemplified by the check Mexa) and very late types (similar to the check Anton), the latter possibly having adaptation only to the highest latitudes (northern Spain) within the range examined in this study.

Data recording

Anthesis and physiological maturity dates were recorded in each experimental plot when approximately 50 % of the main spikes reached Zadoks stages 65 and 87, respectively (Zadoks et al. 1974). Plots were divided in two sections of 6 m², one used for destructive sampling and the other left untouched for mechanical harvest and estimation of grain yield at full maturity (g m⁻²), subsequently adjusted to a 10 % moisture basis.

At maturity, a 1-m row length of a central representative section was uprooted, and a subsample of 10 randomly selected stems was weighed after being oven-dried at 70 °C for 48 h. The harvest index (HI) was calculated from the subsample as the ratio between kernel weight and total stem weight. Biomass (crop dry weight, CDW g m⁻²) was computed for each plot as the product of average dry stem weight and number of stems m⁻². Thousand-kernel weight (TKW, g) was obtained by weighing a randomly drawn sample of 200 kernels from harvested grain of each plot. The number of kernels m⁻² was computed as the ratio between grain yield and TKW.

Data on daily maximum and minimum temperatures, rainfall, daylength and radiation were obtained from meteorological stations located less than 3 km away from the experimental plots. Thermal time (growing degree-days, GDD) was calculated by summing the daily values of mean temperatures (T_m , °C) minus the base temperature. The limits for the maximum and minimum temperatures used to calculate T_m were 37 °C and 0 °C, respectively (Gallagher 1979). Daylength, including civil twilight (h), was computed daily following Forsythe et al. (1995). Environmental variables were averaged from sowing to anthesis

(SA) and from anthesis to maturity (AM), considering the mean phenological data of each experiment. The daily post-anthesis radiation per kernel was calculated for each experiment by dividing the mean radiation received during the anthesis–maturity period (MJ m⁻² day⁻¹) by the mean number of kernels m⁻².

Statistical analyses

Environmental variables were coupled with crop phenology by averaging their values on each plot to the length of the periods sowing–anthesis and anthesis–maturity. The GLM procedure of the SAS statistical package (SAS Institute Inc. 2009) was used to perform a combined ANOVA for environmental and agronomic variables. A mixed model was fitted, in which year and site were fixed factors, while genotype and block (nested to site and year) were considered random factors. Means were compared by Least Significant Difference's (LSD) multirange test at $P = 0.05$.

Pearson correlation coefficients between yield and yield components were calculated for each experiment using the genotype means. To identify the environmental variables discriminating between sites, principal component analysis (PCA) was performed on the correlation matrix, calculated from the mean data of each experiment. Linear regression models were fitted to the relationships between variables using the mean data of each experiment and the forward selection option of the REG procedure of the SAS-STAT statistical package (SAS Institute Inc 2009). From the regression equations, boundary values for environmental variables were those at which the coefficients of correlation between yield and the corresponding yield component became significant at $P = 0.05$.

Results

Environmental conditions

Mean temperatures from sowing to maturity ranged from 10.0 °C, recorded in northern Spain in 2007, to 17.7 °C, registered in northern Mexico in 2008 (Table 2), with the latter site showing the greatest difference between years for this variable. Daily minimum averages increased as site latitude decreased, with southern Spain and northern Mexico being relatively similar, while there was close to a twofold difference for this variable between northern Spain and southern Mexico. A similar trend was observed for daily maximum averages for the first three sites, but this variable decreased while moving from northern (40 m asl) to southern Mexico (2249 m asl, Table 1). Thermal amplitude (average daily maximum–minimum temperatures) also increased with decreasing site latitude, with a substantial increase when moving from southern Spain to northern

Table 2 Summary of environmental conditions prevailing at each testing site and main agronomic data

Site	Year	Sowing date	Period sowing–physiological maturity							Yield (g m ⁻²)	
			Water input (mm)		Temperature (°C)		Net radiation (MJ m ⁻²)	Daylength ¹ (h)			Range of days sowing – anthesis ²
			Mean	Max	Min	Max		Min	Max		
North Spain	2007	24/11/2006	463	15.9	4.8	10.0	2576	10.2	16.2	152–171	661
	2008	19/11/2007	640	16.3	5.5	10.3	2990	10.2	16.3	159–177	705
South Spain	2007	12/12/2006	299	19.5	6.9	12.9	2667	10.6	15.4	116–139	648
	2008	30/11/2007	343	19.9	7.7	13.7	2706	10.6	15.3	107–139	525
North Mexico	2007	30/11/2006	384	25.4	7.7	15.9	2390	11.3	13.3	81–114	526
	2008	22/12/2007	507	27.4	8.1	17.7	3212	11.3	14.4	83–115	646
South Mexico	2007	18/5/2007	670	24.4	10.3	17.3	2481	12.9	13.9	59–87	402
	2008	28/5/2008	482	23.6	10.4	17.0	2319	12.8	14.1	65–90	485

¹Including twilight.²Indicates the range of means observed in the 42 genotypes at each site/year.

Mexico and then a slight decrease when moving down to southern Mexico.

Daylength increased during the growth cycle except in the spring planting site of southern Mexico (Fig. 1). The average daylength amplitude from sowing to maturity narrowed sharply with decreasing latitude, from 6.05 h in northern Spain to 1.15 h in southern Mexico (two-year average, deduced from Table 2). Sharp differences were observed between sites and close similarity between years at each site. A similar trend was observed when considering average daylength from anthesis to maturity (data not shown).

In terms of solar radiation, the lowest and highest values accumulated during the entire growth cycle were recorded in 2008 in southern Mexico and northern Mexico, respectively (Table 2). A substantial year-to-year variability was observed for this trait, especially in site in northern Mexico. Water input ranged from 299 mm in southern Spain (2007) to 670 mm in northern Mexico (2007). All experimental plots were irrigated either fully (northern Mexico) or in a complementary manner, except in southern Spain, where the water content in the effective root zone (according to Aquacrop model) was high enough to avoid stomata closure during all growth cycle (data not shown). These values of total water input and the distribution of watering events should not have resulted in significant water stress, even for southern Spain, where the 2-year average yield level was equal to that of the typically high-yielding site of northern Mexico (Table 2).

To identify the combination of variables that better explained the environmental variation, we conducted PCA on the mean values of environmental variables for each experiment. The first two axes of the PCA shown in Figure 2 accounted for ca. 77.1 % of the total variance (axis 1, 52.8 %; axis 2, 24.3 %), indicating that most of the information held in the data could be summarized by projecting the points on the plane determined by these two axes. The eigenvectors of the various components are shown in Figure 2a. Principal component 1 (PC1) was related to all the variables included in the analysis, but with a negligible effect of the average daily maximum temperature from anthesis to maturity. Increases in PC1 were related to increases in average daily minimum and maximum temperatures and in daylength from sowing to anthesis. The negative direction of PC1 was related to mean daylength and average daily minimum temperature from anthesis to maturity, and accumulated radiation both before and after anthesis (Fig. 2a). Increases in principal component 2 were related mostly to average daily maximum temperatures and accumulated radiation. However, it should be noted that the variance information content of axis 2 was less than half that of axis 1.

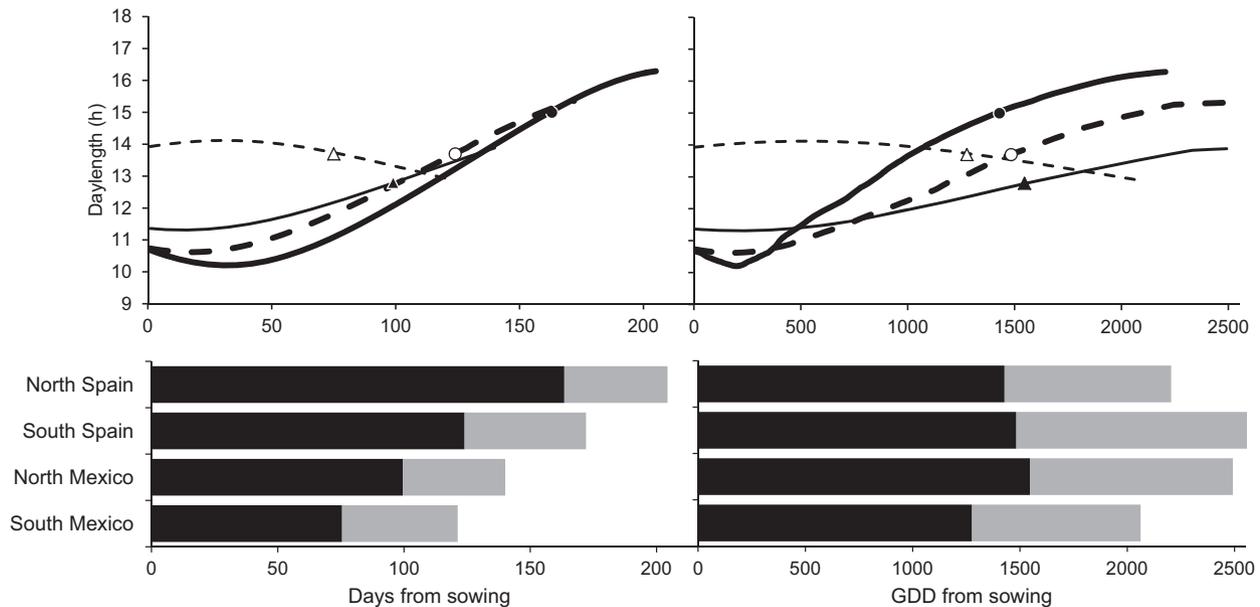


Fig. 1 Mean daylength and cycle duration at each testing site. Data are means of experiments involving 42 durum wheat inbred lines and conducted in 2007 and 2008. For daylength, northern Spain: ● and thick solid line; southern Spain: ○ and thick discontinuous line; northern Mexico: ▲ and light solid line; and southern Mexico: △ and light discontinuous line. Black bars indicate cycle duration from sowing to anthesis; grey bars indicate duration from anthesis to maturity.

The points corresponding to each experiment are plotted in Figure 2b. The relatively lower distance between points representing years within sites compared to the distances between sites indicates a generally weaker effect of years compared to that of sites. The first axis was related to site, shifting from negative to positive values along the axis with movement from the highest to the lowest latitude. The site in the bottom left of Figure 2b of the points corresponding to northern Spain indicates that this site is characterized by long daylength and high minimum temperatures from anthesis to maturity, in agreement with the daylength data shown in Figure 1. The points corresponding to the site in southern Spain were located in-between those of northern Spain and southern Mexico. The points belonging to the last two sites were located in the right part of Figure 2b, indicating long days and high temperatures from sowing to anthesis in this location, in agreement with the spring planting at this site. The points corresponding to northern Mexico were located in the upper part of Figure 2b, mostly because of the high maximum temperatures recorded at this site.

The combined ANOVA across experiments showed that site was the most important variation factor influencing temperature and daylength (Table 3). The only exception to this trend was minimum temperatures in the anthesis–maturity period, which depended on site and on year \times site interaction to the same extent. This pattern was also shown by accumulated radiation in the sowing–anthesis period. The year factor explained a notable fraction of variability for radiation in the anthesis–maturity period,

while the interactions year \times genotype and year \times site \times genotype explained less than 5 % of the observed variation.

The average minimum and maximum temperatures from sowing to anthesis increased when moving from northern to southern sites, while from anthesis to physiological maturity daylength decreased in the same direction (Table 4). Southern Mexico experienced long days from sowing to anthesis, consistent with the spring planting at this site.

Agronomic performance and yield formation

The combined ANOVA across experiments for agronomic traits showed that the site effect explained 96 % of the variability for the number of days from sowing to anthesis (Table 3). The variability induced by site was also the most important variable explaining variations in thermal time from sowing to anthesis, kernels m^{-2} and ultimately yield. Variation in the duration of the anthesis–maturity (AM) period, biomass, HI and TKW was explained to a greater extent by variance components other than site, although site did significantly affect all these traits. The year effect was substantial in explaining variation in the duration of the anthesis–maturity period and in biomass, although it was significant for all variables except the number of kernels m^{-2} . When second to the site effect, the magnitude of genotype effect was relatively substantial for kernel weight, thermal time from sowing to anthesis, HI, kernels m^{-2} , and to some extent yield (Table 3).

Site means across years indicated a shorter growing period, from sowing to anthesis measured in days, and fewer

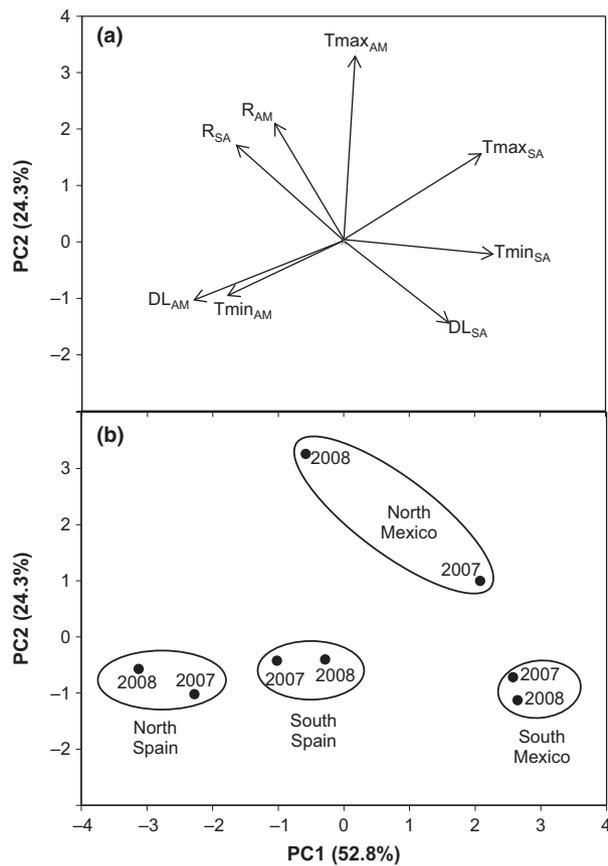


Fig. 2 Plot of the first two axes of the principal component analysis for the following environmental variables from sowing to anthesis (subscript SA) and from anthesis to maturity (subscript AM): Tmin, mean of daily minimum temperatures; Tmax, mean of daily maximum temperatures; DL, mean daylength, including twilight; R, accumulated solar radiation. (a) Eigenvectors of the variables considered. (b) Eigenvalues for the experiments conducted at each site and year.

kernels m^{-2} with decreasing site latitude, independently of sowing time (southern Mexico did not show a reversed trend, Table 4 and Fig. 1). A similar tendency was observed for yield, except that the differences between the sites in southern Spain and northern Mexico were not statistically significant. Thermal time of the two developmental periods (SA and AM) as well as TKW increased when the site latitude decreased in the fall-sown experiments. However, the trend was reversed (decreasing) in the spring-sown experiment in the site in southern Mexico (Table 4). Biomass increased with increasing site latitude, the difference between southern Spain and northern Mexico not being statistically significant. The lowest values for all agronomic variables except grain-filling duration (days from anthesis to maturity) were recorded in southern Mexico.

In order to identify the yield component most associated with yield at each site, Pearson correlation

Table 3 Percentage of the sum of squares of the combined ANOVA for environmental and agronomic variables determined at maturity, for 42 durum wheat inbred lines grown in 2007 and 2008 at 4 sites

Source of variation	d.f.	Tmin _{SA}	Tmin _{AM}	Tmax _{SA}	Tmax _{AM}	R _{SA}	R _{AM}	DL _{SA}	DL _{AM}	Day _{SA}	Day _{AM}	GDD _{SA}	GDD _{AM}	Biomass	HI	TKW	Yield		
Year	1	0.005*	5.54***	0.09***	0.02*	6.07***	17.3***	0.00 ^{ns}	0.28***	0.01***	21.0***	2.93***	24.7***	32***	1.34**	0.10 ^{ns}	3.31***	1.38*	
Site	3	98.2***	35.8***	98.3***	85.0***	26.9***	27.4***	97.6***	92.4***	95.5***	16.8***	42.2***	6.15***	3.8**	20.6***	32.6***	15.7***	41.3***	
Genotype	41	0.16***	11.7***	0.17***	0.75***	32.3***	7.73***	0.35***	0.88***	2.83***	11.6***	37.2***	8.78***	6.4*	29.1***	21.8***	54.8***	9.79***	
Year × Site	3	1.42***	30.5***	1.27***	12.7***	20.1***	31.1***	1.68***	5.10***	0.30***	30.1***	1.27***	40.7***	20***	1.36 ^{ns}	16.1***	4.94***	12.3***	
Year × Genotype	41	0.01 ^{ns}	0.71 ^{ns}	0.00 ^{ns}	0.11 ^{ns}	0.48 ^{ns}	2.02 ^{ns}	0.01 ^{ns}	0.02 ^{ns}	0.03 ^{ns}	1.86 ^{ns}	0.47 ^{ns}	1.95 ^{ns}	2.6 ^{ns}	1.53 ^{ns}	1.11 ^{ns}	1.02 ^{ns}	1.04 ^{ns}	
Site × Genotype	123	0.10 ^{ns}	9.65***	0.09***	0.68 ^{ns}	11.0***	5.46 ^{ns}	0.28***	1.06***	0.90***	7.75***	12.5***	6.08***	8.6 ^{ns}	16.1***	5.79***	6.76***	9.28***	
Year × Site × Genotype	123	0.08***	4.06***	0.02***	0.61***	1.73***	4.58***	0.02***	0.13***	0.15***	5.01***	1.60***	5.00***	6.9***	7.29**	4.62***	3.52***	6.33***	
Genotype	16	0.001***	0.23***	0.00 ^{ns}	0.04***	0.05 ^{ns}	0.49***	0.001**	0.01***	0.005*	0.51***	0.06 ^{ns}	0.68***	2.99***	1.83***	3.02***	0.42*	4.75***	
Block (Year × Site)	656	0.01	1.76	0.01	0.19	1.41	3.91	0.02	0.16	0.32	1.74	1.74	5.92	16.0	20.8	14.8	9.58	13.8	
Total	1007																		

Tmin, mean of daily minimum temperatures; Tmax, mean of daily maximum temperatures; R, accumulated solar radiation; DL, mean daylength, including twilight; GDD, growing degree-days; HI, harvest index; TKW, thousand-kernel weight. Subscripts: SA, period from sowing to anthesis; AM, period from anthesis to physiological maturity. *P < 0.05; **P < 0.01; ***P < 0.001.

Table 4 Mean values for each site of environmental and agronomic variables determined at maturity, for 42 durum wheat inbred lines grown in 2007 and 2008 at 4 sites

Site	Tmin (°C)				Tmax (°C)				DL (h)				Day (h)				Biomass (g m ⁻²)				Yield (g m ⁻²)	
	Tmin _{SA}	Tmin _{AM}	Tmin _{SA}	Tmin _{AM}	Tmax _{SA}	Tmax _{AM}	Tmax _{SA}	Tmax _{AM}	DL _{SA}	DL _{AM}	Day _{SA}	Day _{AM}	GDD _{SA}	GDD _{AM}	GDD _{SA}	GDD _{AM}	HI	Kernels m ⁻²	TKW (g)	Yield		
North Spain	3.3 ^d	11.8 ^a	14.1 ^d	24.8 ^b	11.9 ^b	15.8 ^a	164 ^a	40.9 ^c	1457 ^c	744 ^d	1490 ^a	0.49 ^a	17 879 ^a	38.8 ^c	683 ^a							
South Spain	6.0 ^c	10.9 ^b	18.3 ^c	23.6 ^c	11.8 ^d	14.6 ^b	124 ^b	48.0 ^a	1499 ^b	825 ^b	1438 ^b	0.45 ^c	14 395 ^b	41.1 ^b	587 ^b							
North Mexico	7.0 ^b	10.2 ^d	24.6 ^a	30.4 ^a	11.9 ^c	13.4 ^c	99 ^c	40.6 ^c	1573 ^a	832 ^a	1447 ^b	0.46 ^b	13 244 ^c	45.4 ^a	586 ^b							
South Mexico	10.2 ^a	10.5 ^c	24.3 ^b	23.5 ^d	14.2 ^a	13.3 ^d	75 ^d	45.7 ^b	1296 ^d	778 ^c	1314 ^c	0.43 ^d	12 096 ^d	37.4 ^d	444 ^c							

Tmin, mean of daily minimum temperatures; Tmax, mean of daily maximum temperatures; DL, mean daylength, including twilight; GDD, growing degree-days; HI, harvest index; TKW, thousand-kernel weight. Subscripts: SA, period from sowing to anthesis; AM, period from anthesis to physiological maturity. Different letters within columns indicate significant differences according to LSD's test at P < 0.05.

coefficients between yield and yield components were calculated. Biomass and HI were in all cases positively and significantly correlated with yield (Table 5). Correlation coefficients with kernels m⁻² were significant at both sites in Mexico, but not in those in Spain. The relationship between TKW and yield was highly significant in Spain, decreasing in magnitude from north to south. In Mexico, this relationship was significant only in the spring-sown experiment in the southern Mexico site.

The relationships between phenological variables and yield components were studied through linear regression models, and the statistically significant ones (P < 0.05) are shown in Figure 3. The most significant positive associations were found between the number of days from sowing to anthesis and both the number of kernels m⁻² (Fig. 3a) and HI (Fig. 3b). While the number of days from sowing to anthesis increased with increasing latitude, the length of this period measured in thermal time did not follow the same pattern (Table 4), but was nevertheless positively related to TKW (Fig. 3c). Large differences in sowing dates between years within sites (from 5 to 18 days, Table 2) resulted in small differences in the number of days from sowing to anthesis (from 1 to 5 days, Fig. 3).

Relationships between environmental variables and agronomic traits

Regression models fitted to the relationships between environmental variables and agronomic traits revealed that the number of days from sowing to anthesis was strongly and negatively related to the temperature during the same period, particularly the mean daily minimum temperature (Table 6). However, the duration of the same period expressed in thermal time was explained mainly by daylength – which accounted for 74 % of variation – and by average daily maximum temperature. Both of these variables had a decreasing effect of the duration of sowing to anthesis. Accumulated radiation and average minimum temperature, on the other hand, had positive, moderate,

Table 5 Pearson correlation coefficients between yield and its components for experiments conducted at 4 sites in 2007 and 2008 involving 42 durum wheat inbred lines (n = 42)

Site	Biomass	HI	Kernels m ⁻²	TKW
North Spain	0.74***	0.50***	-0.27	0.74***
South Spain	0.34*	0.53***	0.15	0.36*
North Mexico	0.32*	0.50***	0.40**	0.20
South Mexico	0.61***	0.59***	0.36*	0.53***

*P < 0.05; **P < 0.01; ***P < 0.001. HI, harvest index; TKW, thousand-kernel weight.

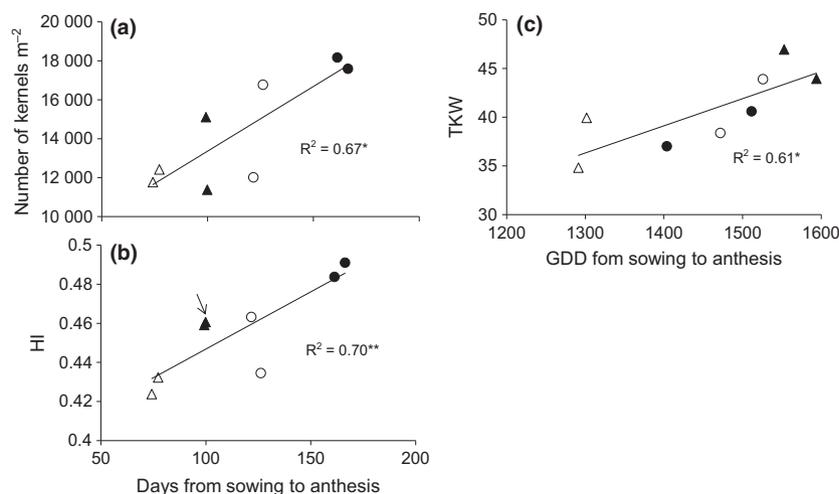


Fig. 3 Statistically significant linear regression models fitted to the relationships between phenological and agronomic variables. Each point represents the mean value for one of eight experiments involving 42 durum wheat inbred lines and conducted at four sites (●: northern Spain; ○: southern Spain; ▲: northern Mexico; and △: southern Mexico) in 2007 and 2008. The arrow in Figure 2b indicates the overlapping of two points.

increasing effects on the sowing to anthesis duration. No environmental variable could explain variation in the number of days from anthesis to maturity, with the exception of accumulated radiation and mean daylength – which jointly explained 96 % of the variation of this period – but only when expressed in thermal time (Table 6). HI and yield were negatively associated with minimum temperatures in the sowing–anthesis period, while mean daylength from anthesis to maturity positively affected the number of

kernels m^{-2} (Table 6). None of the environmental variables studied explained variations in biomass or kernel weight.

The influence of the environmental variables on the relationship between yield and the number of kernels m^{-2} was examined through linear regression models. Long days and high daily minimum temperatures after anthesis were associated with high kernel number (Fig. 4a and b). For sites with a mean daylength shorter than 14.2 h and average daily minimum temperatures lower than 10.8 °C, the relationship between yield and kernels m^{-2} became statistically significant ($P < 0.05$) (Fig. 4d and e). On the other hand, low minimum temperatures averaged over the pre-anthesis period were associated with a high number of kernels m^{-2} (Fig. 4c) and low correlation coefficients between this yield component and yield itself (Fig. 4f). Yield became significantly associated with kernels m^{-2} for average daily minimum temperatures above 6.9 °C before anthesis (Fig. 4b). The boundary value for the number of kernels m^{-2} from which these relationships became statistically significant, calculated from the equations shown in Figure 4, was 14 118 kernels m^{-2} .

No environmental variable was found to be significantly related to kernel weight (Table 6), but a positive and significant relationship was found between TKW and the amount of incoming radiation per kernel during the anthesis–maturity period (Fig. 5a). In experiments with radiation values lower than 1.8 kJ per kernel and day, the relationships between kernel weight and yield were statistically significant ($P < 0.05$), but not for radiation greater than this threshold value (Fig. 5b).

Table 6 Coefficients of the forward regression models fitted to the relationships between agronomic traits as dependent variables, and environmental data as independent variables. Fitted data were means across 42 genotypes and 3 blocks for experiments conducted in 4 sites during 2007 and 2008 ($n = 8$)

Dependent variable	Step	Independent variable	Regression coefficient	Partial R^2	Model R^2
Days _{SA}	1	Tmin _{SA}	−8.1	0.95	0.95***
	2	Tmax _{SA}	−3.0	0.04	0.99**
GDD _{SA}	1	DL _{SA}	−167	0.74	0.74**
	2	Tmax _{SA}	−7.3	0.16	0.90*
	3	R _{SA}	0.5	0.07	0.97*
	4	Tmin _{SA}	61	0.03	1.00**
Days _{AM}	–	–	–	–	–
GDD _{AM}	1	R _{AM}	0.77	0.78	0.78**
	2	DL _{SA}	58	0.18	0.96**
Biomass	–	–	–	–	–
HI	1	Tmin _{SA}	−0.01	0.71	0.71**
Kernels m^{-2}	1	DL _{AM}	2200	0.77	0.77**
TKW	–	–	–	–	–
Yield	1	Tmin _{SA}	−36	0.81	0.81**

GDD, growing degree-days; HI, harvest index; TKW, thousand-kernel weight; Tmin, mean of daily minimum temperatures; Tmax, mean of daily maximum temperatures; DL, mean daylength, including twilight, R, accumulated solar radiation. Subscripts: SA, period from sowing to anthesis; AM, period from anthesis to physiological maturity. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Discussion

The global classification and worldwide distribution of wheat into growth-habit classes, or groups characterized by

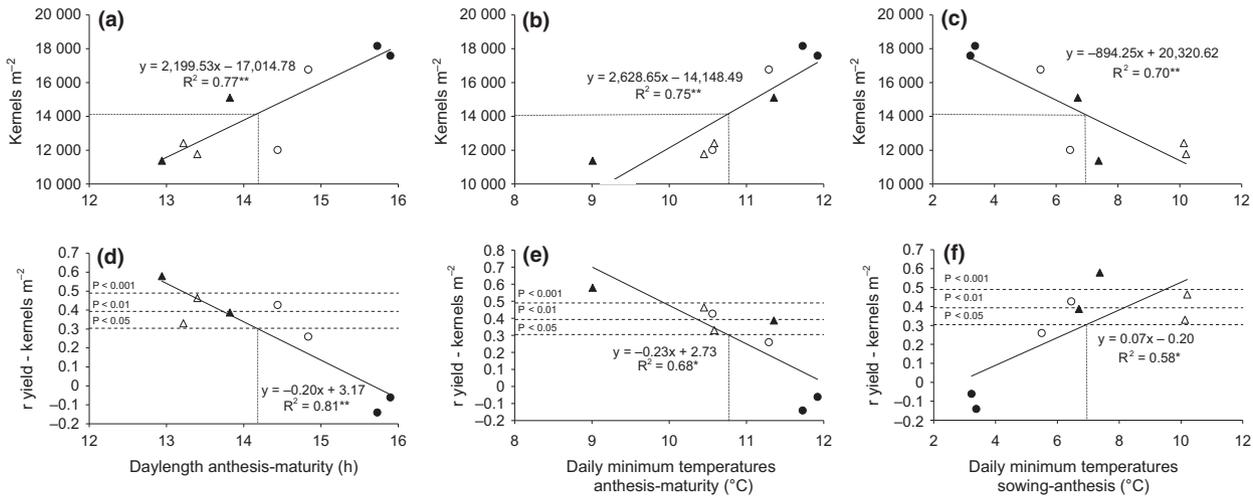


Fig. 4 Statistically significant linear regression models fitted to the relationships between environmental variables and the number of kernels m^{-2} or the Pearson correlation coefficient (r) between yield and the number of kernels m^{-2} . Each point represents the mean value for one of eight experiments involving 42 durum wheat inbred lines and conducted in four sites (●: northern Spain; ○: southern Spain; ▲: northern Mexico; and △: southern Mexico) during 2007 and 2008. Solid lines represent the fitted linear regression equations; dotted lines indicate the abscise values from which regression equations become significant in Figure 4d, e, and f, and the corresponding number of kernels m^{-2} in Figure 4a, b, and c. Levels of significance are shown by discontinuous lines in Figure 4d, e, and f.

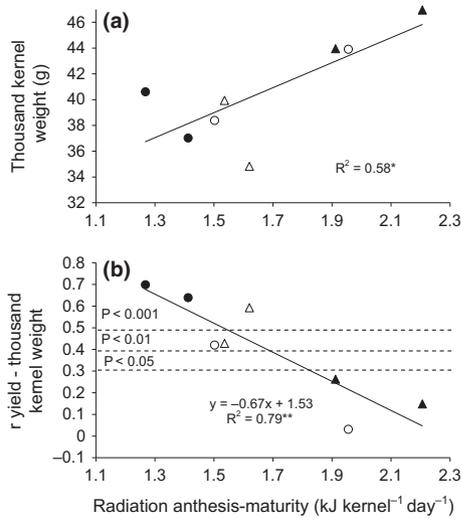


Fig. 5 Statistically significant linear regression models fitted to the relationships between the mean daily radiation per kernel from anthesis to physiological maturity and, (a) thousand-kernel weight, and (b) Pearson correlation coefficient (r) between yield and kernel weight. Each point represents the mean value for one of eight experiments involving 42 durum wheat inbred lines and conducted in four sites (●: northern Spain; ○: southern Spain; ▲: northern Mexico; and △: southern Mexico) during 2007 and 2008.

various combinations of vernalization requirements and photoperiod sensitivity, is known to be related to a great extent to environmental variables associated with latitude (Cockram et al. 2007, Casas et al. 2011). The differences between the classes are well defined in terms of major

‘qualitative’ genetic variations (*Vrn* and *Ppd* genes) that determine the adaptation of a given genotype to a given ‘mega-environment’. However, the environmental variation – which is more ‘quantitative’ in nature – present within growth-habit classes and within latitudes below 45° is less well characterized, particularly in the case of fall-sown, spring habit durum wheat.

The present study is an attempt to provide this missing information by examining key environmental variables, some of them strongly linked to latitude, and their general effects on the duration of developmental phases (pre- and post-anthesis), yield and yield formation of durum wheat.

Although other factors such as soil condition, water input or agricultural practices could induce variability between sites and years, the results of the PCA showed that 77.1 % of the environmental variation was explained by the environmental variables considered in the study, which provides reliability to the results presently obtained, and robustness to the inferences made, for ‘favourable’ environments, where water or other production inputs (such as nitrogen) are not limiting the expression of yield potential. Water or input scarcity are known to accelerate plant development whenever they occur, which results in shorter than normal developmental phases. Consequently, the relationships described in the present study may not hold, and the resulting inferences made may or may not be confirmed under severely water or input-limited conditions.

The genotypes used in the present study were adapted to latitudes roughly up to 40 degrees, which represent the majority of the fall-sown durum wheat grown worldwide.

This excludes the types grown at high latitudes above 45° (Canada, North-Dakota, Kazakhstan and Russia) where photoperiod sensitivity is either required or highly beneficial, and the winter or facultative types sown in northern and central Europe and parts of central Asia, where a combination of significant vernalization needs and photoperiod sensitivity are required. The main environmental variables differentiating between sites were temperature and daylength, as shown by ANOVA (Table 3) and PCA (Fig. 2). However, differences between sites were much better explained by differences in average daily temperatures from sowing to anthesis (which increased from the north to the south) than from anthesis to maturity. The dependence of daylength on sites was expected given the wide range of site latitudes and the existing relationship between daylength and latitude (Forsythe *et al.* 1995). On the other hand, solar radiation showed a considerable year-to-year difference within each site, in accordance with the yearly variations in cloudiness (Stanhill and Cohen 2001). Although some models use minimum and maximum temperatures to estimate solar radiation, Trnka *et al.* (2005) showed that the deviation of such estimations may be substantial, that is, radiation and temperature do not follow the same pattern, as observed in this study.

The ANOVA of phenological traits revealed that the latitude effect explained 96 % of variations in the number of days from sowing to anthesis, suggesting a cause–effect between site and pre-anthesis duration, in calendar terms (Table 3). Low temperatures from sowing to anthesis, particularly the average daily minimum temperatures during this period, increased the number of days required for flowering. Plant development has a universal response to temperature, and therefore, the relationship between temperature and development is a common component of phenology prediction models (White 2003). Our results support previous studies demonstrating that high average temperatures (minimum or maximum) reduce the duration of the pre-anthesis phase (White 2003, McMaster *et al.* 2008) and go further in linking this result primarily to site, with year-to-year variation within a single site being much less significant.

While the number of sites evaluated in the present study may not be considered theoretically large enough to sample the majority of the ‘favourable’ (in terms of water and input availability) spring durum wheat growing environments, 2 of them have been shown to be highly representative of a wide portion of the durum wheat growing area worldwide: in fact, results from a study involving CIMMYT’s International Durum Wheat Yield Nurseries, distributed to 145 locations worldwide from 1983 to 2003, using both classification and ordination approaches of pattern analysis to cluster sites based on performance of uniform sets of genotypes, indicated that the northern Mexico

testing site (Obregón) coclustered with several irrigated and high rainfall sites worldwide, while the northern Spain site (Gimenells) was highly representative of most Mediterranean environments, irrespective of their year-to-year variation in water availability (Ammar *et al.* 2006).

On the other hand, we found no relationship between the number of days pre-anthesis and thermal time during the same period (Table 4). This is attributed to the fact that thermal time from sowing to anthesis was almost equally affected by genotype as well as by site, while days from sowing to anthesis was hardly affected by genotype (Table 3). Our results show that the effect of site on the thermal time from sowing to anthesis is more associated with daylength than with temperature (Table 6). The long daylength during the sowing–anthesis period because of spring planting in southern Mexico (14.2 h in average) explains the short duration of this phase at this site, for wheat types that do not require any vernalization like the ones used in this study. The effect of daylength on development has previously been demonstrated (Whitechurch *et al.* 2007a). Moreover, delayed development and late dates to anthesis have been associated with short daylength during the sowing–anthesis phase (Kirby *et al.* 1999). The long photoperiod recorded in southern Mexico accelerated development, thus resulting in low biomass, lower kernels m^{-2} , lower HI and reduced overall yield (Table 4).

The duration of the anthesis–maturity period was environmentally controlled by the year \times site interaction and to a lesser extent by the two main factors of this interaction (Table 3). Nevertheless, none of the environmental variables studied could be associated with the duration of the anthesis–maturity period, measured in days (Table 6). However, as expected, thermal time from anthesis to maturity was positively and significantly associated with the accumulated radiation in the same period ($R^2 = 0.78$, $P < 0.01$, Table 6), which depended much more on the year than on the latitude (Table 2).

The effect of environmental variables associated with site latitude on yield formation was elucidated by PCA and regression analysis. We dissected yield formation through two alternative approaches extensively used in simulation models. Both consider yield as the product of: (i) biomass and HI; and (ii) number of kernels per unit area m^{-2} and TKW. Our results showed that the components of the second approach were better explained in terms of environmental variables than those in the first.

In the present study, variation in aboveground biomass at maturity was explained mostly by year and the year \times site interaction, with site alone explaining less than 4 % of its variation even if statistically significant (Table 3). Biomass was positively correlated with yield in all sites but was not associated with any of the environmental variables studied (Table 6). These results suggest that biomass did not follow

a pattern directly associated with the site latitude but that it was strongly affected by year-to-year environmental variations at the same site. The quantitative nature of biomass production (Quarrie et al. 2006) makes it strongly influenced by other factors affecting growing conditions, including crop management practices such as water supply and nitrogen fertilization (Villegas et al. 2001).

The site effect accounted for 15 % of the variance in HI (Table 3), but the pattern of variation of HI according to site was not straightforward (Table 4). HI was found to be negatively related to both average minimum temperatures in pre-anthesis (Table 6) and the duration of pre-anthesis measured in days (Fig. 3). These results indicate that the influence of environmental variables on HI resulted mostly from the effect of minimum temperatures on the duration of the pre-anthesis phase. As biomass was not associated with environmental variables, the impact of minimum temperature on the pre-anthesis phase is likely to affect HI through the number of kernels m^{-2} by increasing the opportunity for floret formation.

Environment strongly influenced the number of kernels m^{-2} , due to the effect of daylength on the anthesis–maturity period and minimum temperatures before and after anthesis (Table 6 and Fig. 4). The decreasing daylength and average minimum daily temperatures after anthesis when moving from northern to southern latitudes, as well as increases in the temperatures before anthesis, resulted in a reduction in the number of kernels m^{-2} . It has been demonstrated that final kernel number is affected by environmental conditions both before and after anthesis (Abbate et al. 1995, Fischer 2011) and that high temperatures during pre-anthesis cause a reduction in the number of kernels per unit area (Ugarte et al. 2007). Our results suggest that average minimum temperatures lower than 6.9 °C during pre-anthesis contribute to reach a high potential kernel number, while average minimum temperatures above 10.8 °C and daylength superior to 14.2 h post-anthesis also favour grain setting. These boundary values in environmental variables corresponded to about 14 000 kernels m^{-2} , a critical value below which the number of kernels m^{-2} became a limiting factor for yield, as revealed by the significant correlations found between the number of kernels m^{-2} and yield for values below this level (Fig. 4).

TKW was the agronomic trait that showed the greatest genetic control as genotype effects accounted for 55 % of its sum of squares, with latitude effect nevertheless explaining 16 % of the same statistical parameter (Table 3). No significant relationship was detected between TKW and the environmental variables studied. This result disagrees with the conclusions drawn by Ugarte et al. (2007), who reported that kernel weight responds to temperature variations in pre-anthesis. Nevertheless, our results reveal that, for fall-sown experiments, the TKW increased when mov-

ing southward (Table 4), but its relationship with yield decreased in the same direction (Table 5), and both effects were associated with the radiation per kernel and day during the period anthesis–maturity (Fig. 5). These results suggest that low radiation per kernel constrained TKW, thereby making it a limiting factor for yield formation in some environments. The location of the points in Figure 5b corresponding to the spring planting in southern Mexico confirmed that the relationship between kernel weight and yield depended on the available radiation per kernel during the anthesis–maturity period, this relationship being associated with the site latitude for similar planting dates. Our findings show that the minimum radiation required to ensure proper kernel filling and to prevent kernel weight from becoming yield-limiting was approximately 1.8 kJ day^{-1} (Fig. 5). It could be hypothesized that low kernel weights resulted from the number of kernels m^{-2} being too high to be filled with the available incoming radiation. In a study conducted at high latitudes (52–57°N), Bingham et al. (2007) reported similar results in barley, but in this case, the positive relationship between radiation per single kernel and kernel weight was limited to a short period around anthesis and not to the whole grain-filling period as in the present study. In a study also conducted at high latitude (45°N), Takahashi and Kanazawa (1996) found that a reduction in radiation at the end of grain filling caused lower kernel weights as a result of smaller starch granules. On the other hand, recent studies at lower latitudes (around 32°N) have reported that great reductions in radiation during grain filling caused only small reductions in yield (Li et al. 2010, Mu et al. 2010) and kernel weight (Li et al. 2010). All these results suggest that the limitation that radiation exerted on yield formation increased at sites located at higher latitudes.

The site effect was the most important in explaining yield variations (Table 3) through the effect of minimum temperatures pre-anthesis. The negative effects of high temperatures before heading on durum wheat yield (Royo et al. 2010) and the implication of minimum temperatures in pre-anthesis on the genotype \times environment interaction for wheat yield (Sanchez-Garcia et al. 2012) have been reported. However, none of the previous studies identified the effect of minimum temperatures before anthesis on yield components. This study demonstrated that yield reductions were related mostly to lower number of kernels m^{-2} under high pre-anthesis temperatures, which in turn previous studies have associated with an acceleration of spike growth (Fischer 1985, 2011). This acceleration results in a decrease in the potential number of florets (González et al. 2011) and consequently of kernels m^{-2} , which is not fully compensated later by kernel weight (Peltonen-Sainio et al. 2007, Foulkes et al. 2011). In fact, lengthening of the stem elongation phase has been

proposed as a strategy to increase yields in the future (Whitechurch *et al.* 2007a,b) as has been achieved in the past (Isidro *et al.* 2011). Higher temperatures during grain filling have also been associated with lower yields (Feng *et al.* 2014). However, this was not observed in the present study, probably because the anthesis–maturity period in all experiments occurred at ranges of temperatures considered not to result in significant heat stress and therefore in yield reduction. However, at the higher temperatures predicted by some climate change models (Gouache *et al.* 2012), this variable can become yield-limiting and the interaction of environmental variables during the grain-filling period may become more critical for yield formation.

The results of this research provide scientific explanations based on environmental factors for the findings of previous studies concluding that grain yield of durum wheat is determined mostly by kernel weight in the cooler conditions of northern environments, while the number of spikes per unit area predominantly influences grain production in the warmer southern environments (García del Moral *et al.* 2003). Additional evidence supporting this statement comes from the study by Moragues *et al.* (2006), who reported that grain yield of durum wheat Mediterranean landraces was related mainly to variations in kernel size among those from the northern side of the basin, while spikes per unit area was the most important determinant of yield among those from the southern part.

Conclusions

Our results indicate that low minimum temperatures during the pre-anthesis period as the occurring in the northern Spain site favoured the formation of a large kernel number, but the insufficient radiation per kernel during grain filling limited the realization of genetic potential, in terms of kernel weight, to maximize yield potential. Accordingly, kernel weight became a limiting factor for yield in northern Spain, as shown by the significant correlation coefficient between yield and kernel weight. In contrast, the high minimum temperatures in pre-anthesis registered in northern Mexico resulted in a reduced number of kernels m^{-2} , which, below a certain value, became a limiting factor for yield. However, the high level of solar radiation per kernel during the grain-filling period favoured the formation of heavy grains, possibly more than compensating for the reduced kernel numbers and ultimately allowing to the achievement of high yields under non-water-limited conditions.

In quantitative terms, our empirical results suggest that, for the range of environments addressed in this study, the number of kernels became a yield-limiting factor for values lower than ca. 14 000 kernels m^{-2} . Such values occurred in environments with average daily minimum temperatures greater than 6.9 °C from sowing to anthesis and lower than

10.8 °C from anthesis to maturity, with average daylength of less than 14.2 h during this period. Moreover, kernel weight was a limiting factor for yield when radiation values from AM were lower than ca. 1.8 kJ kernel⁻¹ day⁻¹. These threshold values may be useful for growth models that attempt to estimate the effect of global climatic change on the productivity of spring growth-habit durum wheat.

Acknowledgements

This work was conducted in the framework of the agreement INIA (Spain)-CIMMYT and was partially funded by INIA under projects RTA2009-00085-00-00 and RTA2012-00011-00-00, and CICYT project AGL2012-37217. C. Alfaro is recipient of a PhD grant from INIA-Chile. Thanks are given to Dr. Kling from Hohenheim University and to Dr. Wolfgang Pfeiffer (formerly durum breeder at CIMMYT, now at CIAT-Colombia) for providing parental germplasm and resulting segregating populations for this study, and to Chafik Harrathi for his contribution to this work. The Centre UdL-IRTA forms part of the Centre CONSOLIDER INGENIO 2010 on Agrigenomics funded by the Spanish Ministry of Education and Science.

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