Grain growth and yield formation of durum wheat grown at contrasting latitudes and water regimes in a Mediterranean environment

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SUMMARY

A set of ten durum wheat genotypes was grown in experiments conducted under four contrasting Mediterranean conditions during three years to assess the effect of latitude and water regime on grain growth and grain yield formation. The relationship between grain weight and accumulated growing degree-days (GDD) from anthesis was described by a logistic equation and final grain weight (*W*) and maximum rate (*R*) and duration (*D*) of grain filling were calculated from the fitted curves. Thousand kernel weight (TKW) was positively related to grain yield at both latitudes and water regimes, although the contribution of the number of grains per m^2 to final yield was only significant in the south, where environmental constraints likely limited the achievement of a large grain set. Differences in final grain weight between latitudes could be mostly explained by differences in the grain filling rate, while changes on *W* between water regimes were due to altered grain filling durations. Under northern conditions grain yield was positively associated to grain filling duration but negatively related to the maximum rate of grain filling, while in the south the coefficients of the grain filling curves had little or no effect on final yield. Reductions in grain yield under rainfed conditions were due to the fall in the number of grains per m^2 since TKW was not significantly affected by drought.

*Index words***:** Final grain weight, maximum grain filling rate, grain filling duration.

INTRODUCTION

Under Mediterranean conditions grain filling of durum wheat (*Triticum turgidum* L. var. *durum*) is constrained by abiotic stresses, since it often concurs with rising temperatures and falling moisture supply. Water stress during early grain filling has a marked effect on grain yield through reduced sink capacity to accumulate dry matter (Nicolas et al. 1985).

Final grain weight has two components: rate and duration. Grain filling rate has been associated to higher grain weight in durum wheat (Motzo et al. 1996) although its correlation with grain yield in wheat range from weak (Van Sanford 1985) to significantly positive (Wardlaw & Moncur 1995). The rate of grain growth may be reduced by drought (Nicolas et al. 1985), although some authors have reported that it is relatively insensitive to water stress (Egli, 1998). A significant association between grain filling duration and grain yield has been found in durum wheat (Gebeyehou et al. 1982), but many studies have failed to find significant relationships in bread wheat (Talbert et al. 2001). It is generally accepted that grain filling duration is largely affected by environmental conditions, as its heritability is medium to low (Egli 1998).

The objective of this study was to investigate the effect of latitude and water regime on the relationships between grain yield and the number of grains per m^2, grain weight and the coefficients of the grain filling curves under field Mediterranean conditions.

A set of ten durum wheat genotypes was grown in four contrasting Mediterranean environments, during three years. From the different multipoint functions that have been proposed to evaluate grain growth, we chose the logistic equation suggested by Darroch and Baker (1990), which has been successfully used in small grain cereals (Royo et al., 1996, 2000; Royo & Blanco, 1998).

MATERIALS AND METHODS

Experimental design. Twelve field experiments were carried out during three consecutive years at two different temperature regimes (latitudes north and south) of Spain and under two contrasting water regimes (irrigated and rainfed) at each latitude. The experimental sites and soil characteristics are summarized in Table 1.

In the irrigated trials, additional water was given from 1 to 3 times during late winter and spring. The experimental design in each trial was a randomized complete block design with four replicates in the north and three in the south. Plots were of 12 m^2 (six rows and 20 cm apart). Ten durum wheat genotypes were used: four Spanish commercial varieties (Altaraos, Jabato, Mexa and Vitron) and six advanced lines from the breeding programme of ICARDA (Awalbit, Korifla, Lagost-3, Omrabi-3, Sebah and Waha). Seed rate was adjusted for a density of 550 seed m^{-2} in the north and 350 seeds m^{-2} in the south, according to the standard practices in each zone. The number of spikes per m^2 was calculated by counting the spikes contained in 1 m of one of the central rows in each plot. The number of grains per spike was determined by counting grains on every spike from a subsample of 10 plants randomly taken from the 1 m row-length sample. Thousand kernel weight (TKW) was determined from a sample of the grain obtained by mechanically harvesting each plot at ripening. Grain yield was expressed at 10% moisture level.

Grain filling curves. Time to anthesis was recorded when half of the plants in the plot reached the stage 65 of Zadoks'scale (Zadoks et al. 1974). At anthesis, 100 main spikes were tagged in each plot. Five tagged spikes were removed at random once per week from anthesis to ripening, and six grains were taken from the central spikelets of each spike. Grains were oven dried at 70ºC for 48 h to determine grain weight. Growing degree days (GDD) from anthesis were calculated assuming a base temperature of 9ºC (Weir et al. 1984). Grain dry weight data were fitted to the logistic curve proposed by Darroch and Baker (1990), the coefficients of the grain filling curves being determined for each plot by using the algorithm of Levenberg-Marquardt (Marquardt 1963). Final grain weight (W) was estimated in mg. The maximum rate of grain filling (R) was mathematically determined and was expressed as mg of grain GDD^{-1}. Duration of grain filling (D) was considered to be the time in accumulated GDD required for grain weight to reach 0.95 W, and was derived from the curve. It was divided in two periods: D_1 or the time in GDD from anthesis to the inflexion point of the curve, when the grain reaches the maximum rate of grain filling, and D_2 or the time in GDD from this point to 0.95 W.

Statistic analysis. Fixed models were used in combined ANOVA over latitudes, water regimes, years and genotypes. Means were compared by Duncan's multiple-range test at P = 0.05. Pearson correlation coefficients between traits were calculated for each environment. Calculations were done using the SAS/STAT package (SAS Institute Inc. 1996).

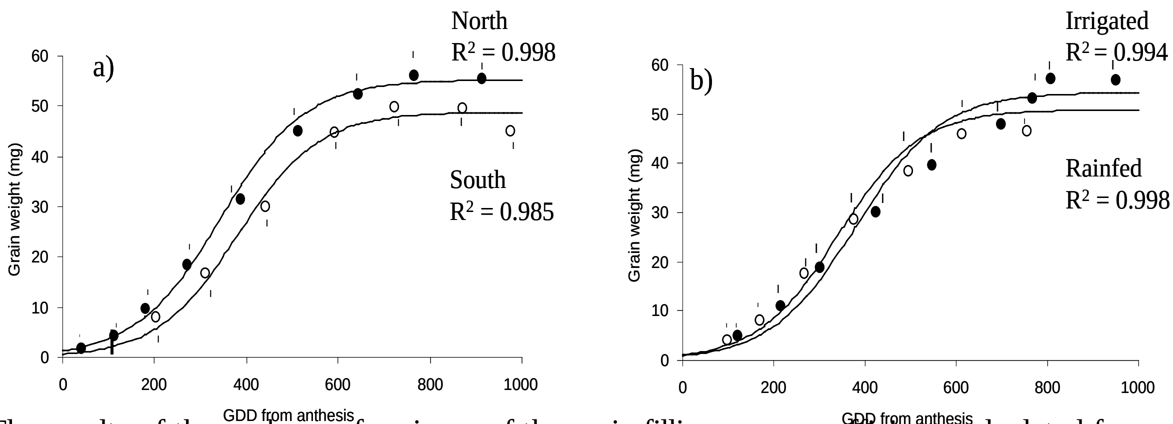
Table 1. Description of the environments used in the study.

Environment	North (cooler environment)			South (warmer environment)		
		Irrigated	Rainfed		Irrigated	Rainfed
Site		Gimenells	El Canós		Granada	Ventas Huelma
Coordinates		41º40'N;0º20'E	41º41'N;1º13' E		37º21'N;3º35'W	37º10'N;3º50'W
Altitude (m a.s.l.)		200	440		650	720
Soil type		Calcixerolic-Xerochrept	Fluventic-Xerochrept		Typic Xerofluvent	Loamy Carcixerolic Xerochrept
Texture		fine-loamy	loamy-fine		silty clay	silty clay
pH		8.1	8.2		8.0	8.2
P(ppm)		16	12		50	27
K(ppm)		134	184		88	210
Organic matter (%)		2.40	2.10		2.01	1.86
Mean temperatures	97	17.3	16.5	98	19.2	21.3
during grain filling	98	17.2	16.3	99	21.9	21.6
(ºC)	99	19.2	19.2	00	20.1	21.7
Long-term seasonal rainfall, mm		283	304		363	323
Seasonal rainfall +	97	364	206	98	412	183
irrigation (mm)	98	386	184	99	423	187
	99	397	255	00	403	160
Fertilisers (kg ha^{-1}) N (seed bed + top	97	(50+100), 120, 165	(32+84), 60, 60	98	(60+20), 60, 60	(45+20), 45, 45
dressing), P_2O_5, K_2O	98	(45+100), 115, 120	(32+84), 60, 60	99	(75+20), 75, 75	(49+20), 49, 49
	99	(24+100), 45, 45	(32+60), 60, 60	00	(60+20), 60, 60	(52+20), 52,52
Sowing time	97	3 Dec. 96	3 Dec. 96	98	11 Dec. 97	12 Jan. 98
	98	23 Nov 97	17 Nov. 97	99	15 Dec. 98	25 Nov. 98
	99	10 Nov. 98	3 Nov. 98	00	23 Nov. 99	10 Dec. 99

RESULTS

The logistic equation proposed by Darroch & Baker (1990) proved to be useful to fit the grain weight data of the present study, since the convergence criteria used to fit the curves was reached in 98% of the cases. The average R^2 values were 0.97 ± 0.05. Curves fitted to the mean observed values for each latitude and water regime are shown in Figure 1.

Figure 1. Grain filling curves of the central grains of the main spike for the two latitudes and both water regimes. Lines represent the predicted values obtained by fitting the logistic curve to the mean observed values across genotypes and years (indicated by dots). Vertical bars represent SE.



The results of the analyses of variance of the grain filling curve coefficients calculated for each plot indicated that the latitude (Lat), year and genotype (Gen) effects were significant for all the coefficients, whereas the water regime (WR) affected all the coefficients except the duration of the last part of the grain filling period (D_2) (Table 2).

Table 2. Mean squares of the combined analysis of variance for yield, yield components and the coefficients of the grain filling curves fitted to the grain weight data. See text for the interpretation of abbreviations.

Source	d.f.	Yield $x10^5$	N of grains m^{-2} x 10^6	TKW	*W*	*R* ($x10^{-3}$)	*D* ($x10^3$)	D_1 ($x10^3$)	D_2 ($x10^3$)
Lat	1	329^{***}	337^{***}	2622^{***}	1891^{***}	391^{***}	264^{***}	67.7^{***}	64.2^{***}
WR	1	7841^{***}	3480^{***}	0.126	642^{***}	7.2^{**}	30.1^{***}	24.6^{***}	0.3
Lat x WR	1	119^{***}	38.8^{**}	78.2^{**}	504^{***}	51.3^{***}	36.5^{***}	2.2^{***}	20.6^{***}
Year (Lat)	4	625^{***}	483^{***}	1470^{***}	1534^{***}	62.9^{***}	97.7^{***}	34.6^{***}	19.6^{***}
WR x Year (Lat)	4	141^{***}	67.7^{***}	629^{***}	620^{***}	56.4^{***}	20.4^{***}	7.8^{***}	16.2^{***}
Gen	9	13.0^{*}	33.1^{***}	444^{***}	430^{***}	7.7^{***}	6.1^{***}	2.6^{***}	1.0^{**}
Gen x Lat	9	10.6	10.2^{**}	32.1^{**}	64.3^{***}	1.2	2.7^{***}	0.9^{***}	1.0^{**}
Gen x WR	9	13.0^{*}	11.4^{**}	36.4^{**}	48.2^{***}	2.0^{*}	1.8^{**}	0.6^{**}	0.6
Gen x WR x Lat	9	5.7	11.9^{**}	11.9	15.5	1.2	1.8^{**}	0.8^{***}	0.6
Gen x Year (Lat)	36	14.0^{***}	12.3^{***}	21.0^{**}	33.7^{***}	1.3	2.0^{***}	0.6^{***}	0.7^{***}
GenxWRxYear(Lat)	36	7.9	9.0^{***}	12.0	26.9^{**}	1.8^{**}	1.6^{***}	0.4^{***}	0.7^{**}
Block(YearxLatxWR)	30	18.0^{***}	12.6^{***}	8.9	14.8	1.2	0.7	0.4^{**}	0.3
Residual	270								
Total	419								

* $P< 0.05$, ** $P< 0.01$, *** $P< 0.001$

Final grain weight (*W*) and *R*, as well as grain yield, NG and TKW were higher in the north than in the south, while grain filling duration was longer under southern conditions, due to the lengthening of both parts of the curve in this latitude (Table 3). Mean yield of genotypes ranged from 3840 kg ha^{-1} (Lagost-3) to 4403 kg ha^{-1} (Korifla). However, the highest yielding variety had not the average heaviest grains (the mean *W* of Korifla was 53.1 while *W* ranged from 48.0 to 61.4 mg) nor the highest grain filling rate or grain filling duration.

Table 3. Mean values of grain yield, number of grains m^{-2}, TKW and the grain filling curve coefficients, for each latitude and water regime. See text for the interpretation of abbreviations.

	Yield (kg ha^{-1})	Number of grains m^{-2}	TKW (g)	*W* (mg)	*R* (mg GDD-^{1})	*D* (GDD)	D_1 (GDD)	D_2 (GDD)
Latitude								
North	4340 a	11445 a	50.2 a	54.8 a	0.309 a	286 b	153 b	133 b
South	3774 b	9652 b	43.3 b	49.7 b	0.240 b	342 a	183 a	160 a
Water regime								
Irrigated	5499 a	13542 a	46.7 a	54.3 a	0.281 a	322 a	174 a	147 a
Rainfed	2696 b	7821 b	47.2 a	51.2 b	0.280 a	297 b	157 b	140 b
Environment								
North irrigated	5887 a	14050 a	49.7 b	57.5 a	0.302 b	306 b	165 c	142 c
North rainfed	2792 c	8861 c	50.7 a	52.2 b	0.317 a	266 c	142 d	124 d
South irrigated	4981 b	12871 b	42.7 d	49.8 c	0.251 c	344 a	188 a	156 b
South rainfed	2567 d	6433 d	43.8 c	49.7 c	0.228 d	341 a	178 b	163 a

Means within columns and effects with different letters are significantly different at 5%.

The maximum rate of grain filling (*R*) and TKW were the only traits not affected by differences in water input (Table 3). Because of the significance of the interaction between latitude and water regime for grain yield, correlation coefficients were calculated for each environment (Table 4).

Table 4. Pearson correlation coefficients between yield and yield components and the grain filling curve coefficients for each latitude and water regime. See text for the interpretation of abbreviations.

Latitude	North		South	
Water regime	Irrigated	Rainfed	Irrigated	Rainfed
NG	-0.19	-0.34	0.57^{**}	0.75^{***}
TKW	0.63^{***}	0.42^{*}	0.65^{***}	0.55^{**}
W	0.23	0.58^{***}	0.47^{**}	0.09
R	-0.53^{**}	-0.53^{**}	-0.15	0.33
D	0.77^{***}	0.72^{***}	0.35^{*}	0.08
D_1	0.82^{***}	0.75^{***}	-0.17	0.29
D_2	0.66^{***}	0.65^{***}	0.60^{***}	-0.21

* $P< 0.05$, ** $P< 0.01$, *** $P< 0.001$

The number of grains per m^2 (NG) was significant in explaining differences in yield in the south, but not in the north. Contrarily, TKW was significantly related to grain yield in the four environments. A negative association existed between TKW and NG in the north (r=-0.43, *P*<0.05 and r=-0.50, *P*<0.05 for irrigated and rainfed sites, respectively), although any relationship existed between both components in the south.

Grain yield was more related to the grain weight of the whole spikes (TKW) than to the weight of the central grains of the main spike (W) (Table 4). Correlation coefficients between grain yield and TKW were higher under irrigated than under rainfed conditions. The relationship between grain yield and the coefficients of the grain filling curves depended widely on the latitude. In the north, grain filling duration was positively associated to grain yield, while the maximum rate of grain filling was negatively associated (Table 4). Contrarily, in the south nor the maximum rate or the duration of grain filling exerted a strong influence on yield, excepting the duration of the second part of the grain filling curves under irrigated conditions. Correlation coefficients between *R* and *D* in the four environments ranged from r=–0.52, *P*<0.01 to r=–0.83, *P*<0.001.

DISCUSSION

Grain yield was significantly affected by both latitude and water regime. The experiments carried out in the north outyielded 15% the southern experiments, due to similar reductions in the two main components of yield, the number of grains per m^2, that was reduced 16%, and TKW, that decreased 14%. However, both yield components played a different role on grain yield formation at the two latitudes. While in the south both the number of grains per m^2 and TKW were significantly related to grain yield, in the north grain yield depended mostly on grain weight, since it was not significantly associated to the number of grains. Under southern conditions, where high temperatures likely limited the number of grains per m^2, this yield component played an important role on grain yield formation, while in the north, where the number of grains was less constrained, the weight of the grain became a much more important yield component. The significant associations found between yield and the curve coefficients in the north, while no associations appeared in the south, support a relatively more important role of grain weight on grain yield at higher latitudes.

The effect of water stress on grain yield was much more dramatic than the effect of latitude, since a reduction in grain yield of 51% was recorded under rainfed conditions in comparison with the irrigated environments. Reductions in grain yield were due to a decrease of 42% in the number of grains per m^2 given that TKW was not affected by water regime, probably because under irrigated conditions the contribution of grains from tillers, with lighter grains than those of the main stem, was higher than in the rainfed environments.

The results of the ANOVA showed that of the two components of final grain weight, grain filling duration was more affected by environmental conditions than grain filling rate, as it has been shown in other cereals under Mediterranean conditions (Royo et al. 2000). The fact that TKW was not affected by water regime as it was *W* suggests that, for the analyzed environments, a higher grain potential capacity was expressed under irrigation that under rainfed environments, especially for the north, where *W* was reduced 9% by water shortage, while TKW was increased by 2%. However, the effect of latitude on *W* was higher than the effect of water regime, since this coefficient was 9% higher in the north than in the south, but under irrigated conditions it was superior only 6% than in the rainfed environments. The effect of latitude on final grain weight may be associated to the higher temperatures prevalent in the south compared to the north, since high temperatures enhance movement of photosynthate from the flag leaf to the spike, but do not necessarily increase *R* because of increased respiratory losses of C also occur at high temperatures (Wardlaw et al. 1980). This was the case of our experiments, since *R* was even lower in the south than in the north, suggesting large losses of C due to plant respiration. Moreover, the higher grain weight reached in the north was attributable to changes in grain filling rates.

Differences in final grain weight between irrigated and rainfed conditions were caused by the differences in the duration of the grain filling period, the rate of grain filling being not affected. Under rainfed conditions, the reduction of assimilate supply caused by the decrease in canopy photosynthesis, induced by water deficit, was probably compensated by a higher mobilization of vegetative reserves assimilated before anthesis (Blum et al. 1994; Royo et al. 1999).

The results of the ANOVA showed that the first part of the grain filling curve, from anthesis to the inflexion point of the curve (D_1), was more sensitive to changes in the different factors considered and their interactions than the second phase (D_2).

Under irrigated conditions grain yield was more related to TKW than to *W*, suggesting that the weight of central grains of the spike was less relevant to explain differences in yield than the weight of all the grains of the spike. Grain yield is conformed by contribution of grains from main stems and tillers, the last ones with a lower potential sink capacity, and since water availability strongly modified the number of grains per m^2, the contribution of tillers under dry conditions seems to have been reduced in relation to that under irrigation.

The relationship between yield and the curve coefficients *R* and *D* depended on the latitude. Under northern conditions grain yield was positively correlated with grain filling duration (and with each of its two components), but negatively correlated to the maximum rate of grain filling. The opposite sign of both correlations was expected given the negative relationship found between *R* and *D*. Given that under Mediterranean conditions the end of grain filling period is largely determined by the high temperatures reached at the end of the spring, this result may indicate that under northern conditions the varieties with longer grain filling duration, due to earlier anthesis date, were capable to reach higher yields in spite of having lower rates of grain filling. A positive association between earlier heading and longer grain fill has been reported in spring wheat (Talbert et al. 2001). Contrarily, in the south nor the maximum rate or the duration of grain filling were strongly related to grain yield, suggesting that under southern conditions, where yield was largely determined by the number of grains per m^2, the coefficients of the grain filling curves had little o no effect on final yield.

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