

Old and modern durum wheat varieties from Italy and Spain differ in main spike components

Fanny Álvaro^a, Julio Isidro^b, Dolors Villegas^a,
Luis F. García del Moral^b, Conxita Royo^{a,*}

^aIRTA, Durum Wheat Breeding, Rovira Roure 191, 25198 Lleida, Spain

^bDepartamento de Fisiología Vegetal, Facultad de Ciencias, Instituto de Biotecnología, Universidad de Granada, 18071 Granada, Spain

Received 21 September 2007; accepted 5 November 2007

Abstract

Four field experiments comparing 24 durum wheat varieties grown at different periods during the 20th century in Italy and Spain were carried out to assess the changes caused by breeding activities on the number of grains per main spike and its determinants: number of spikelets per spike, number of grains per spikelet, fertile flowering and grain setting. Increases of 0.14 grains spike⁻¹ year⁻¹ (0.43% year⁻¹ in relative terms) and 0.08 grains spike⁻¹ year⁻¹ (0.22% year⁻¹) were observed in Italian and Spanish varieties, respectively. The overall change in the number of grains per spike in Italian germplasm (29.5%) was due to increases in both, the number of spikelets per spike (7.5%) and the number of grains per spikelet (20.3%), while in Spanish varieties the increase in the number of grains per spike (19.5%) was only attributed to the improvement of the number of grains per spikelet. The increase in the number of fertile florets per spike (about 12%) was similar in both countries, but while it explained more than 70% of the changes in the number of grains per spike in Spanish varieties, grain setting was responsible for most of the improvement in the number of grains per spike in the Italian germplasm. The percentage of florets setting grains was 68 and 64% in modern Italian and Spanish varieties, respectively. Most of the changes in the number of grains per spikelet were found in the upper part of the spike on Italian varieties, whilst they were more evenly distributed in the Spanish ones. The main achievement derived from the introduction of the *Rht-B1* dwarfing gene was an increase in the number of grains per spikelet, but it did not have any effect on the number of spikelets on the main spike. The lack of genetic associations between grain setting and both the number of spikelets per spike and the number of fertile florets per spike suggests that future yield gains may be obtained through increases in the three components independently.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Number of grains per spike; Number of spikelets per spike; Number of grains per spikelet; Fertile florets; Grain setting; *Rht* genes

1. Introduction

Italy and Spain are the largest producers of durum wheat in the Mediterranean basin (Royo, 2005). Yield improvement during the last century has been attained by different breeding strategies in each country. In Italy local breeding programmes were conducted since the beginning of the century. In Spain yield gains have been achieved primarily by introducing germplasm from the International Center for Improvement of Maize and Wheat (CIMMYT). Another important difference between the durum varieties of the two countries is the source of dwarfing genes they contain. In Spain the major advance in durum wheat breeding has been derived from the deployment

of the *Rht* dwarfing genes from the hexaploid wheat variety Norin10/Brevor, largely used by CIMMYT (Rajaram, 2001). The dwarfing genes *Rht-B1* (formerly *Rht1*) and *Rht-D1* (formerly *Rht2*, absent in durum wheat) have a strong effect on plant height (Peng et al., 1999), and a pleiotropic effect on various agronomic and end-use quality traits (Elias and Manthey, 2005). These genes confer gibberellic acid (GA) insensitivity, so the response of seedlings to GA has traditionally been used to test the presence or absence of GA-insensitive *Rht* genes (Gale and Gregory, 1977). Molecular PCR-based markers have been developed more recently to detect them (Ellis et al., 2002). CIMMYT germplasm was also introduced in Italy during the 1970s. However, breeding programmes conducted in this country had already introgressed GA-sensitive *Rht* genes, such as *Rht9* introduced by N. Strampelli from the variety Akagomughi in 1912 (Borghi, 2001).

* Corresponding author. Tel.: +34 9 73 702583; fax: +34 9 238301.

E-mail address: conxita.royo@irta.es (C. Royo).

Increases in the number of grains per unit area have been the main cause of genetic yield gains in bread wheat during the last century (Austin et al., 1980; Siddique et al., 1989; Shearman et al., 2005) while no positive correlations have been found between yield improvement and grain weight (Perry and D'Antuono, 1989; Brancourt-Hulmel et al., 2003; Shearman et al., 2005). Durum wheat has received less attention than bread wheat, but yield genetic gains of Italian varieties have been recently reported to be about 20 kg ha⁻¹ year⁻¹ (De Vita et al., 2007). Durum wheat yield improvements have been associated with positive changes in harvest index and in the number of grains per square meter (Waddington et al., 1987; Pfeiffer et al., 2000; Royo et al., 2007).

The higher grain number in modern bread wheat varieties resulted mainly from a rise in the number of grains per spike and per spikelet (Perry and D'Antuono, 1989; Sayre et al., 1997). Likewise, in durum wheat, the increase in the number of grains per spike has been found to explain up to 50% of genetic gains in the number of grains per unit area (Royo et al., 2007). The higher survival of floret primordia to form fertile florets (Siddique et al., 1989; Slafer et al., 1994) as a consequence of the introduction of dwarfing genes (Miralles et al., 1998) appears to have played a major role in differentiating modern and old bread wheat varieties. The introduction of dwarfing genes and the selection for shorter varieties reduced competition between the growing spike and the growing stem in the few weeks preceding anthesis and, hence, enhanced partitioning of assimilates to the spike (Fischer and Stockman, 1986). The percentage of fertile florets at anthesis that will set grains is close to a 100% in modern bread wheat varieties (Yu et al., 1988; Fischer, 2001). However, in CIMMYT durum wheat varieties, spike sterility is a significant factor in yield potential variation (Fischer, 2001).

This study was undertaken to quantify the relative contribution of the increases in the number of spikelets and grains per spikelet to the grain number of main spikes. A complementary approach, by studying the changes in the number of fertile florets and grain setting was also used to

explain changes in the number of grains per main spike. Modifications in the number of grains and their weight were also assessed at different positions within the spike.

2. Materials and methods

2.1. Plant material

Twelve durum wheat (*Triticum turgidum* L. var. *durum*) varieties from Italy and twelve from Spain were chosen to represent the germplasm grown in both countries throughout the 20th century. Based on the year of release, the varieties were assigned to three periods: old (before 1945), intermediate (from 1950 to 1985) and modern (from 1988 to 2000). Old varieties were landraces or cultivars selected from exotic populations, such as Senatore Capelli. The intermediate group included varieties grown nearby the Green Revolution, some of them carrying GA-insensitive dwarfing genes such as Mexa and Creso. Modern Spanish varieties were chosen among the lately released by local breeding programmes, avoiding the inclusion of varieties of foreign origin (Mexican and Italian), while the modern Italian set included some of the most cultivated varieties in the country. The presence of the *Rht-B1* dwarfing gene in the varieties had been previously determined (Royo et al., 2007) by analyzing the response of seedlings to GA (Table 1).

2.2. Experimental design and management

Four field experiments were conducted during two growing seasons, 2004 and 2005, at two Spanish latitudes representing contrasting environmental conditions: Lleida in the Ebro Valley in the north-east of the country (41°40'N, 0°20'E); and Granada in Andalusia in the south (37°08'N, 3°49'W). The northern area has a Mediterranean-continental climate, with a mean yearly temperature of 19 °C and an average seasonal precipitation of 310 mm, which is irregularly distributed. In the northern site, mean temperature during grain filling was around 21 °C the 2

Table 1
Varieties used in the study

Italian	Year of release	Presence of <i>Rht-B1</i> gene	Plant height (cm)	Spanish	Year of release	Presence of <i>Rht-B1</i> gene	Plant height (cm)
Old							
Balilla Falso	<1930	–	114	Blanco Verdeal	<1930	–	136
Carlojucchi	1945	–	114	Clarofino	<1930	–	137
Razza 208	1930	–	119	Pinet	<1930	–	127
Senatore Capelli	1930	–	133	Rubio de Belalcázar	<1930	–	139
Intermediate							
Adamello	1985	–	73.4	Bidi 17	1950	–	102
Capeti 8	1955	–	99.4	Camacho	1975	+	80.5
Creso	1974	+	73.6	Esquilache	1976	+	74.2
Trinakria	1970	–	104	Mexa	1980	+	79.9
Modern							
Cirillo	1992	+	79.5	Ariesol	1992	+	73.1
Flavio	1992	+	65.1	Astigi	1999	+	83.4
Simeto	1988	+	77.4	Boabdil	2000	+	77.8
Zenit	1992	+	75.5	Senadur	1995	+	75.8

years of this study, with averaged maximum temperatures of 29 °C. Seasonal precipitations were 256 mm in 2004 and 130 mm in 2005. Flood irrigation before anthesis provided additional 150 mm every season. Water input during grain filling were 84 mm and 66 mm in 2004 and 2005, respectively. The southern area has a typical Mediterranean climate, with mild winters and hot, dry summers. Mean temperatures during grain filling were 21 °C in 2004 and 25 °C in 2005, with maximum temperatures up to 34 °C the second year. Seasonal precipitations provided 419 mm of water (81 mm during grain filling) in 2004, and 96 mm (8 mm during grain filling) in 2005. Before anthesis 40 and 120 mm in 2004 and 2005, respectively, were applied by flood irrigation. Soils were mesic Calcixerolic Xerochrept with a fine-loamy texture in the northern site, and a silty-clay, loamy Calcixerolic Xerochrept in the south.

Each experiment consisted of a randomized complete block design with three blocks and plots of 12 m² (eight rows 10 m long and 0.15 m apart). Experiments were planted between 13 November and 16 of December in all cases. Sowing rates were 400 and 350 seeds m⁻² in Lleida and Granada, respectively. Plots were fertilized before planting with 500 and 300 kg ha⁻¹ of complex 15-15-15 at Lleida and Granada, respectively. At the end of tillering the plots were top dressed with ammonium nitro sulphate at a rate of 35 kg N ha⁻¹. Pests, diseases and weeds were chemically controlled following the recommendations at each site. Mean yields of experiments ranged between 1424 and 5580 kg ha⁻¹, indicating that they were conducted under a wide range of environmental conditions.

2.3. Data recording

Three main spikes were randomly chosen from a central row of each plot at anthesis, and the number of fertile florets per spikelet was counted in all the spikelets of the two more homogeneous. A floret was considered to be fertile when male and female reproductive organs had developed green anthers and *bifidum* stigma, respectively (Waddington and Cartwright, 1983).

Two 50-cm-long row were randomly sampled at ripening in each plot, 10 representative plants were selected from them and the number of spikelets and grains were counted on their main spikes. The percentage of grain setting was calculated as the percentage of the number of grains per spike at maturity over the number of fertile florets per spike at anthesis.

A detailed study of the changes in grain number and weight in near-apical, central and basal spikelets of main spikes was conducted in the northern experiments. The number of grains per spikelet was measured in three central, three near-basal and three near-apical spikelets of the same side of three main spikes of each plot, and grains from each group of spikelets were weighted. Plant height was determined at ripening.

2.4. Statistical analyses

Analyses of variance were performed across years and latitudes. All factors were regarded as fixed effects, except

blocks that were nested to year and latitude. Adjusted means were compared by Tukey's Studentised Range test at $P = 0.05$. Absolute and relative genetic gains were computed as the slope of the linear regression between the absolute or relative value of the trait and the year of release of the cultivar. Relative values were computed for each variety as percentages irrespective of the average values of all the varieties for a given country, as described in Royo et al. (2007). Genetic correlations were estimated from the genetic variances and covariances, following the method described by Hanson et al. (1956), as follows

$$r_g = \frac{\sigma_{p_1 p_2}}{(\sigma_{p_1}^2 \sigma_{p_2}^2)^{1/2}}$$

where $\sigma_{p_1 p_2}$ is the genetic covariance component for two traits, and $\sigma_{p_1}^2$ and $\sigma_{p_2}^2$ are the respective genetic variance components. In order to assess the pleiotropic effect of the *Rht1-B1* dwarfing gene on the main spike characteristics, the mean values of the varieties carrying it in each set (see Table 1) were compared with the mean values of the remaining varieties. All analyses were performed with the SAS-STAT package (SAS Institute Inc., 2000).

3. Results

3.1. Number of grains per main spike

The number of grains per main spike increased significantly in varieties from both Italy and Spain as a consequence of the breeding activities conducted during the 20th century (Table 2). However, the rate of increasing grains per spike was greater in Italian (0.143 grains spike⁻¹ year⁻¹, $P < 0.001$) than in Spanish (0.076 grains spike⁻¹ year⁻¹, $P < 0.05$) varieties (Table 3). In Italian varieties, changes in the number of grains were larger between the old and intermediate groups (around 16%) than between the intermediate and modern (about 12%), while in Spanish varieties it increased around 9% in both cases (Fig. 1a).

Table 2

Mean values for each country and period of the main spike traits: number of grains per spike (NGS), number of spikelets per spike (sS), number of grains per spikelet (NGs), fertile florets per spike (FF) and percentage of grain setting (SET)

	NGS	sS	NGs	FF	SET
Italian					
Old	29.1 c	16.0 b	1.82 c	51.0 c	57.6 c
Intermediate	33.7 b	16.9 a	1.99 b	54.1 b	63.9 b
Modern	37.7 a	17.2 a	2.19 a	56.8 a	68.0 a
Spanish					
Old	31.7 c	17.4 a	1.83 c	54.6 b	58.6 b
Intermediate	34.6 b	17.0 a	2.02 b	56.4 b	62.7 a
Modern	37.9 a	16.7 a	2.26 a	61.4 a	63.6 a

Means within a column and country and within countries and periods followed by the same letter are not significantly different according to Tukey's Studentised Range test at 5% probability level.

Table 3
Absolute and relative genetic gain in the main spike components ($n = 12$)

	R^2	Absolute change (year ⁻¹)	Relative change (% year ⁻¹)
Italian			
Grains per spike	0.75***	0.143	0.43
Spikelets per spike	0.27	0.022	0.13
Grains per spikelet	0.55**	0.006	0.29
Fertile florets per spike	0.37*	0.092	0.17
Grain setting (%)	0.69***	0.184	0.29
Spanish			
Grains per spike	0.40*	0.076	0.22
Spikelets per spike	0.08	-0.080	-0.04
Grains per spikelet	0.46*	0.005	0.26
Fertile florets per spike	0.28	0.102	0.18
Grain setting (%)	0.14	0.048	0.07

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

3.2. Number of spikelets per spike and number of grains per spikelet

Spanish old varieties had a larger number of spikelets per spike than the Italian ones. The number of spikelets per spike increased by 7.5% as a consequence of breeding activities during the 20th century in Italy, but it did not significantly change in Spanish varieties (Table 2 and Fig. 1b). Nevertheless, the relative genetic gain was not significant in varieties of either of the two countries (Table 3).

The number of grains per spikelet rose dramatically in both sets of varieties (Table 3 and Fig. 1c). The number of grains per spike was more strongly associated to the number of grains per

spikelet than to the number of spikelets per spike (Table 4). No significant association was found between the numbers of spikelets per spike and grains per spikelet (Table 4).

3.3. Fertile florets and grain setting

Durum wheat breeding during the 20th century increased the number of fertile florets per main spike and the percentage of grain setting in varieties from both Italy and Spain (Table 2 and Fig. 1d and e). The number of fertile florets per spike was greater in the Spanish varieties than in the Italian ones in the three periods. Modern Italian and Spanish varieties showed a significant increase in the number of fertile florets per spike (11.4 and 12.4%, respectively) compared to the old cultivars (Table 2). The genetic gain in the number of fertile florets per spike was 0.092 year⁻¹ (0.17% year⁻¹ in relative terms) for the Italian varieties, but it was not significant for the Spanish set (Table 3). In Spanish varieties the greatest increase in the number of fertile florets per spike occurred between the intermediate and modern periods, while the change was more regular within the Italian germplasm (Fig. 1d).

Increases in the percentage of grain setting were greater in Italian than in Spanish varieties (Tables 2 and 3), the highest genetic gain recorded between the old and intermediate periods (Fig. 1e). In Italian varieties the relative change in grain setting (0.29% year⁻¹) was greater than that of the number of fertile florets per spike (0.17% year⁻¹) (Table 3). The relative genetic gain in grain setting was not significant in Spain (Table 3).

The percentage of grain setting was positively associated to the number of grains per spike and per spikelet, but no significant associations were found between grain setting and

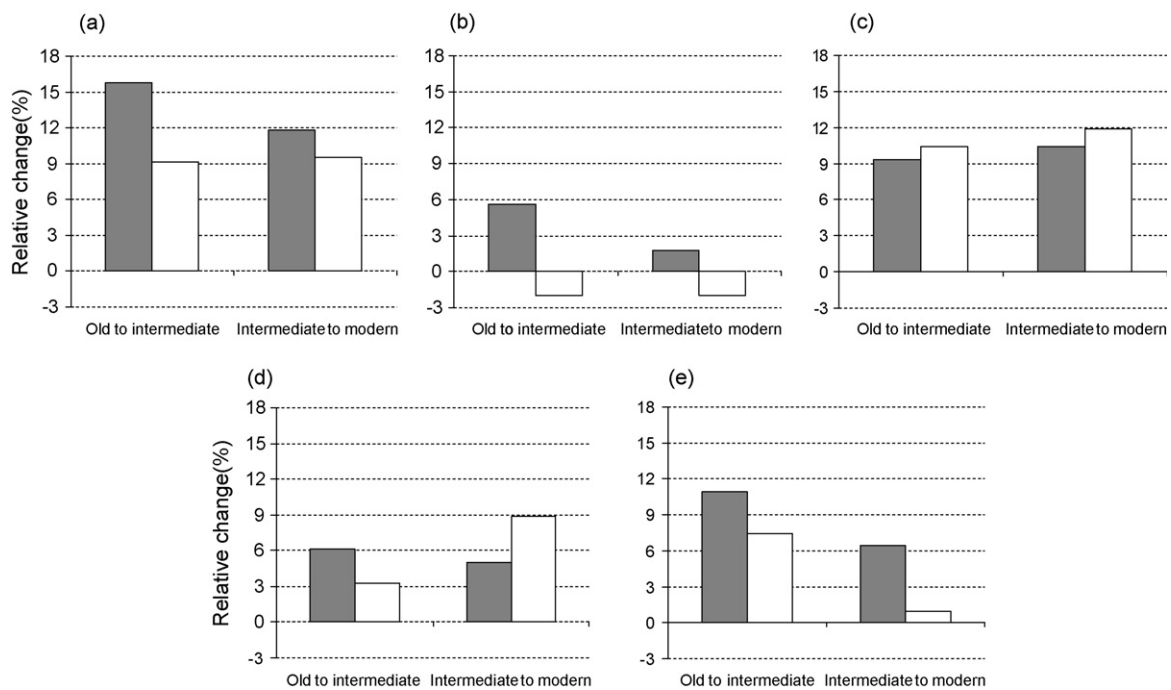


Fig. 1. Relative change in the number of grains per spike and its components in Italian (black) and Spanish (white) durum wheat varieties grown in three periods of the 20th century. (a) Number of grains per spike; (b) number of spikelets per spike; (c) number of grains per spikelet; (d) number of fertile florets per spike; (e) percentage of grain setting.

Table 4
Genetic correlations between the number of grains per main spike and its components ($n = 24$)

	Number of grains per spike	Number of spikelets per spike	Number of grains per spikelet	Fertile florets per spike
Number of spikelets per spike	0.48*			
Number of grains per spikelet	0.86***	−0.03		
Fertile florets per spike	0.90***	0.44*	0.78***	
Percentage of grain setting	0.73***	0.40	0.62**	0.36

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

the numbers of spikelets per spike or fertile florets per spike (Table 4). Astigi, a modern Spanish variety showed the largest number of grains per spike (44.0) and per spikelet (2.69), as well as fertile-floret number per spike (72.3).

3.4. Grains per spikelet and grain weight at different positions within the spike

The number of grains per spikelet increased from old to modern Italian varieties by 12 and 7% in near-apical and central spikelets, while no significant change was produced in the near-basal ones (Table 5). The mean grain weight on near-apical spikelets decreased by 7.3% ($P < 0.05$) from old to modern varieties, but on central and basal positions the intermediate group had the lowest grain weight.

In the Spanish set, the number of grains per spikelet increased similarly from old to modern varieties in the three positions within the spike (18.7, 18.2 and 19.8% in near-apical, central and basal spikelets respectively, Table 5). Grain weight did not change from old to intermediate varieties in any position, but

Table 5
Number of grains per spikelet and weight of one grain on near-apical, central and basal spikelets of main spikes from experiments conducted in the north of Spain in 2004 and 2005

		Number of grains per spikelet	Grain weight (mg)
Italian			
Apical	Old	2.17 b	53.2 a
	Intermediate	2.28 b	48.2 b
	Modern	2.43 a	49.3 b
Central	Old	2.71 b	57.2 a
	Intermediate	2.78 ab	55.1 b
	Modern	2.91 a	56.0 ab
Basal	Old	2.68 a	55.9 a
	Intermediate	2.67 a	53.8 b
	Modern	2.69 a	56.6 a
Spanish			
Apical	Old	2.09 c	52.3 a
	Intermediate	2.26 b	52.5 a
	Modern	2.48 a	48.3 b
Central	Old	2.63 b	55.7 a
	Intermediate	2.80 b	57.1 a
	Modern	3.11 a	52.1 b
Basal	Old	2.42 c	54.1 a
	Intermediate	2.59 b	55.6 a
	Modern	2.90 a	50.7 b

Means within a column and group followed by the same letter are not significantly different according to Tukey's Studentised Range test at 5% of probability level.

it decreased in the three positions between intermediate and modern varieties (Table 5). Differences in the yield per spikelet (calculated as product of the number of grains per spikelet and the mean grain weight), indicated that in both Italian and Spanish varieties, and in the three periods considered, central and basal spikelets contributed more to the yield of the main spike than those of the apical section.

3.5. Effect of *Rht-B1* dwarfing gene on spike components

The number of grains per main spike was significantly greater for the genotypes carrying the *Rht-B1* gene (Fig. 2a), given the larger number of grains per spikelet recorded in varieties carrying it (Fig. 2c). However, it did not change the number of spikelets per spike. The effect of the *Rht-B1* gene on the number of fertile florets per spike and grain setting differed between the Italian and Spanish varieties. In Italian varieties grain setting was the main trait affected by the introduction of this dwarfing gene, while in Spanish varieties the trait mostly affected was the number of fertile florets per spike (Fig. 2d and e).

4. Discussion

The number of grains per main spike increased by 29.5 and 19.5% from old to modern Italian and Spanish varieties respectively, with a rate of 0.14 grains spike^{−1} year^{−1} (0.43% year^{−1} in relative terms) in Italian varieties, and 0.08 grains spike^{−1} year^{−1} (0.22% year^{−1}) in the Spanish set. Part of this increase can be attributed to a pleiotropic effect of the *Rht-B1* dwarfing gene, as the varieties carrying it increased the number of grains per main spike by 20% in Italian varieties and 13% in the Spanish ones. Contrasting changes were observed in varieties of the two countries in the components of the number of grains per main spike. Within the Italian varieties the gain in the number of grains per spike was due to an increase in both the number of spikelets per spike and in grains per spikelet. However, the contribution of the former to the increases in the number of grains per spike was more than double than that of the number of spikelets per spike. Although studies evaluating the breeding work done in Italy *a posteriori* did not reveal any clear trend in spike size over time (Canevara et al., 1994), it has been reported that Italian breeders were mainly concerned with improving the yield per spike; and that the number of fertile spikelets per spike and grains per spike were considered essential selection traits (Canevara et al., 1994). Within the Spanish varieties the improvement in the number of grains per spike was only due to an increase in the number of grains per spikelet. Differences

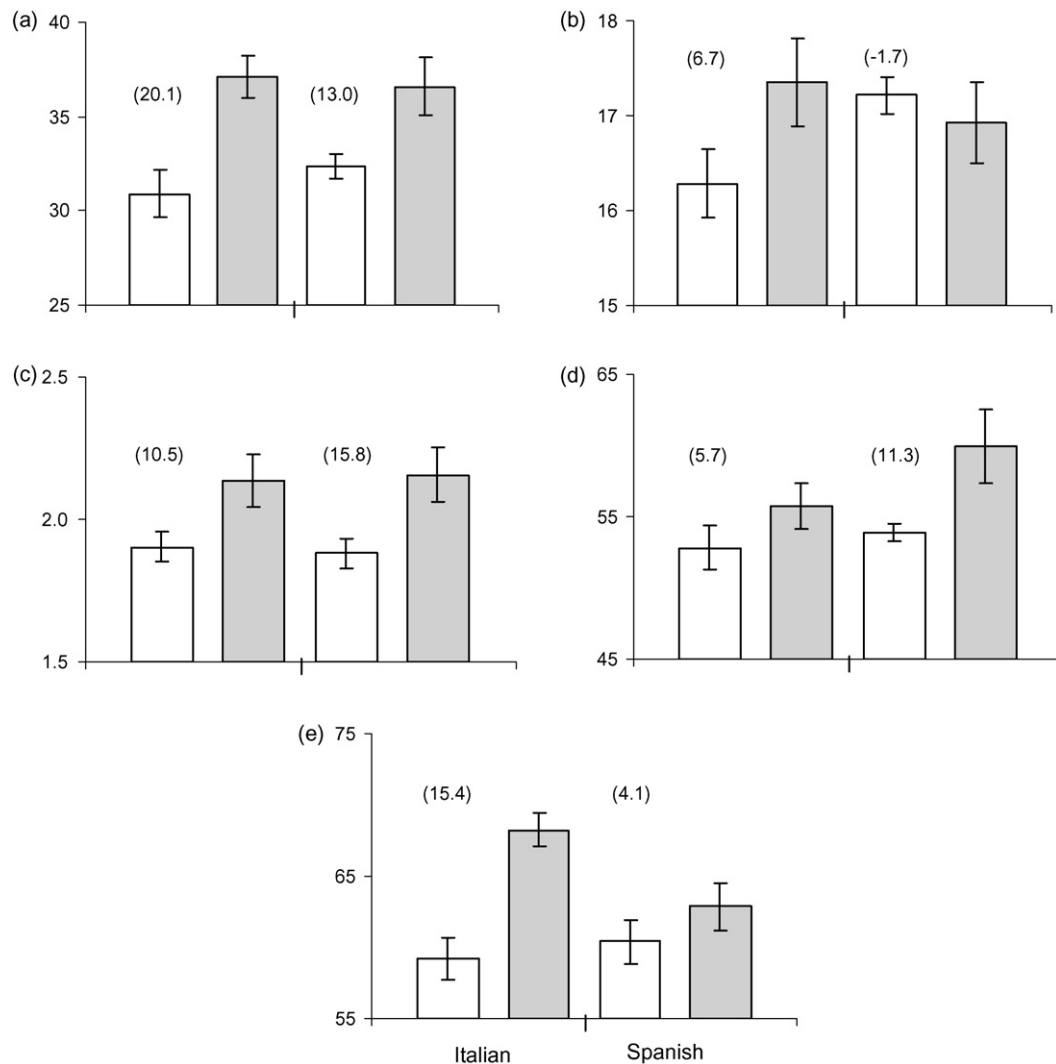


Fig. 2. Effect of *Rht-B1* gene on main spike components of Italian and Spanish varieties. Bars are the average value of the durum wheat varieties carrying the *Rht1-B1* dwarfing gene (dark bars) or not (white bars), from experiments conducted in the north and south of Spain. Numbers in parenthesis indicate the percentage of change in each case. Vertical bars indicate SE. (a) Number of grains per spike; (b) number of spikelets per spike; (c) number of grains per spikelet; (d) number of fertile florets per spike; (e) percentage of grain setting.

between the Italian and Spanish varieties may be interpreted in the framework of the breeding strategies followed. Italian breeding efforts started earlier in the 20th century and selection for short straw involved dwarfing genes from the Japanese varieties Akagomughi (*Rht9*), Saitama 27 (*Rht1s*), and probably other minor genes (Borghini, 2001). On the other hand, breeding progress in Spain relied on CIMMYT germplasm introduced during the second half of the century (Royo, 2005), mostly carrying the GA-insensitive gene *Rht-B1*. The largest effect of the *Rht-B1* dwarfing gene seems to have been an increase in the number of grains per spikelet.

The relative contribution of the number of fertile florets and the capacity to set grains in determining the final number of grains also differed between Italian and Spanish varieties. In Italian varieties, the increase in the number of grains per main spike was explained by both significant increases in the number of fertile florets and the percentage of grain setting, being the contribution of the last one much higher than that of fertile florets

(63 and 37%, respectively). This result underlines the success of the efforts made by Italian breeders during the first decades of the 20th century to improve the capacity of setting grains. Increases in grain setting have probably improved the adaptation of Italian durum wheats to Mediterranean environments, where abiotic stresses during grain filling are the main cause of floret abortion. In the Spanish varieties the overall increase in the number of fertile florets per spike explained more than 70% of the changes in the number of grains per spike, while changes in grain setting had less importance. Nevertheless, differences between old and intermediate Spanish varieties were higher for grain setting than for the number of fertile florets. This result may be explained by the shorter duration to anthesis of intermediate varieties when compared to the old ones (Miralles et al., 2002) that likely allowed grain setting to be fixed under more favourable environmental conditions, thus avoiding the negative effect of high temperatures during the linear phase of the grain filling period (Tashiro and Wardlaw, 1990).

Improvements in fertile florets were probably also a pleiotropic effect of the *Rht-B1* gene, since higher floret survival due to a larger partitioning of assimilates to the spike during the preflowering period has been attributed to the introduction of *Rht* dwarfing genes (Flintham et al., 1997; Miralles et al., 1998). Significant differences in the number of fertile florets between old and modern Spanish varieties have been associated with a higher survival of floret primordia in the modern ones (Miralles et al., 2002). The distinct effect of the *Rht-B1* gene on Italian and Spanish varieties may be due to differences in the genetic background of the varieties from one and the other countries. Three of the intermediate Italian varieties proved to be sensitive to exogenous GA and were shorter than the old ones. This indicates that they carry other sources of dwarfness, such as the *Rht9* gene. The variety Adamello is the clearest example, which even has a similar height to the modern varieties carrying *Rht-B1*. Gibberellic acid-sensitive dwarfing genes have been proved to have a similar pleiotropic effect on the number of grains and grain yield (Rebetzke and Richards, 2000) and may be partially responsible of the changes observed between old and intermediate Italian varieties.

Among Spanish modern varieties, Astigi showed the largest number of fertile florets at anthesis that, together with a capacity of setting grains similar to the other Spanish modern varieties, resulted in a larger number of grains per spikelet and per spike. Astigi could be an interesting parent for breeding programmes aiming to increase these traits, and demonstrates that genetic diversity exists among the varieties currently cultivated.

The percentage of florets setting grains changed from 58% in old Italian varieties to 68% in modern ones, and from 59% in old Spanish varieties to 64% in modern ones. These values are far from those reported for bread wheat in Australia (from 85% of fertile florets setting grains in old varieties to 93% in modern ones; Siddique et al., 1989), Argentina (from 63% in old varieties to 90% in modern ones; Slafer and Miralles, 1993), and the modern dwarf varieties from CIMMYT (below 80%, Fischer, 2001). Future yield improvements in durum wheat may be achieved by increasing the capacity of setting grains after anthesis, as the percentage of grain setting of modern durum varieties are still far from those of modern bread wheat.

Increases in the number of grains per spikelet in the Italian varieties were mainly found in the upper half of the main spike, whereas in the Spanish varieties the number of grains per spikelet increased evenly throughout the spike. The increase in the number of grains per spikelet between old and intermediate Italian varieties was associated with large decreases in grain weight, mostly in the upper part of the spike. This decrease cannot be attributed to the presence of *Rht-B1*, but it may be a consequence of the increase in the number of grains in positions with a lower potential grain weight (Slafer et al., 1994). The increase in the number of grains per spikelet in all positions within the main spike of Spanish varieties was found between all three periods considered, indicating that not only has *Rht-B1* influenced the number of grains per spikelet, but also the continued breeding activity has enhanced this trait. Increases in

grain number per main spike during the last decades have been associated to reductions in grain weight in the Spanish varieties constraining main spike yield increases.

5. Concluding remarks

The results of this study have to be interpreted taking into consideration that the experiments were conducted in Spain, where the degree of adaptation of Spanish varieties may differ from that of the Italian. Genetic gains in the number of grains per main spike were double in Italian than in Spanish varieties probably as consequence of the Italian largest investment in durum wheat breeding programmes. Improvements in the number of grains per spikelet explained most of the raises in the number of grains per spike. Breeding programmes conducted in Italy in the target environments resulted in grain setting improvements in the main spike much larger than the accomplished in Spain by the introduction of foreign germplasm. The main achievement derived from the introduction of the *Rht-B1* dwarfing gene was an increase in the number of grains per spikelet, but it did not have any effect on the number of spikelets on the main spike.

The lack of genetic associations between grain setting and both the number of spikelets per spike and the number of fertile florets per spike suggest that future improvements in durum wheat grain yield may be obtained through increases on the three main spike components independently, since negative effects in one component when the other increases are not expected.

Acknowledgements

This study was partially funded by CICYT, under projects AGL-2002-04285 and AGL-2006-09226. Fanny Álvaro and Julio Isidro were recipients of PhD grants from IRTA and CICYT, respectively. The skilled technical assistance of the staff of Cereal Breeding of IRTA is greatly acknowledged.

References

- Austin, R.B., Bingham, J., Blackwell, R.D., Evans, L.T., Ford, M.A., Morgan, C.L., Taylor, M., 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *J. Agric. Sci.* 94, 675–689.
- Borghi, B., 2001. Italian wheat pool. In: Bonjean, A.P., Angus, W.J. (Eds.), *The World Wheat Book, a History of Wheat Breeding*. Lavoisier Publishing, Paris, pp. 289–309.
- Brancourt-Hulme, M., Doussinault, G., Lecomte, C., Bérard, P., Le Buanec, B., Trotter, M., 2003. Genetic improvement of agronomic traits of winter wheat cultivars released in France from 1946 to 1992. *Crop Sci.* 43, 37–45.
- Canevara, M.G., Romani, M., Corbellini, M., Perenzin, M., Borghi, B., 1994. Evolutionary trends in morphological, physiological, agronomical and qualitative traits of *Triticum aestivum* L. cultivars bred in Italy since 1900. *Eur. J. Agron.* 3, 175–185.
- De Vita, P., Li Destri Nicosia, O., Nigro, F., Platani, C., Riefolo, C., Di Fonzo, N., Cattivelli, L., 2007. Breeding progress in morpho-physiological, agronomical and qualitative traits of durum wheat cultivars released in Italy during the 20th century. *Eur. J. Agron.* 26, 39–53.
- Elias, M.E., Manthey, F.A., 2005. Durum wheat breeding at North Dakota State University. In: Royo, C., Nachit, M.M., Di Fonzo, N., Araus, J.L., Pfeiffer,

- W.H., Slafer, G.A. (Eds.), *Durum Wheat Breeding: Current Approaches and Future Strategies*. Food Products Press, New York, pp. 939–962.
- Ellis, M.H., Spielmeier, W., Gale, K.R., Rebetzke, G.J., Richards, R.A., 2002. “Perfect” markers for the *Rht-B1b* and *Rht-D1b* dwarfing genes in wheat. *Theor. Appl. Genet.* 105, 1038–1042.
- Fischer, R.A., 2001. Selection traits for improving yield potential. In: Reynolds, M.P., Ortiz-Monasterio, J.I., McNab, A. (Eds.), *Application of physiology in wheat breeding*. CIMMYT, Mexico, pp. 148–159.
- Fischer, R.A., Stockman, Y.M., 1986. Increased kernel number in Norin-10 derived dwarf wheat. Evaluation of the cause. *Aust. J. Plant Physiol.* 13, 767–784.
- Flintham, J.E., Borner, A., Worland, A.J., Gale, M.D., 1997. Optimizing wheat grain yield: effects of *Rht* (gibberellin-insensitive) dwarfing genes. *J. Agric. Sci.* 128, 11–25.
- Gale, M.D., Gregory, R.S., 1977. A rapid method for early generation selection of dwarf genotypes in wheat. *Euphytica* 26, 733–738.
- Hanson, C.H., Robinson, H.F., Comstock, R.E., 1956. Biometrical studies of yield in segregating populations of Korean Lespedeza. *Agron. J.* 48, 268–272.
- Miralles, D.J., Katz, S.D., Colloca, A., Slafer, G.A., 1998. Floret development in near isogenic wheat lines differing in plant height. *Field Crops Res.* 59, 21–30.
- Miralles, D.J., Rharrabti, Y., Royo, C., Villegas, D., García del Moral, L.F., 2002. Grain setting strategies of Mediterranean durum wheat cultivars released in different periods (1900–2000). In: *Genotype-phenotype: Narrowing the gaps*. The Royal Agricultural College, Cirencester, UK, Dec 16–18, Association of Applied Biologists.
- Peng, J.R., Richards, D.E., Hartley, N.M., Murphy, G.P., Devos, K.M., Flintham, J.E., Beales, J., Fish, L.J., Worland, A.J., Pelica, F., Sudhakar, D., Christou, P., Snape, J.W., Gale, M.D., Harberd, N.P., 1999. ‘Green revolution’ genes encode mutant gibberellin response modulators. *Nature* 400 (6741), 256–261.
- Perry, M.W., D’Antuono, M.F., 1989. Yield improvement and associated characteristics of some Australian spring wheat cultivars introduced between 1860 and 1982. *Aust. J. Agric. Res.* 40, 457–472.
- Pfeiffer, W.H., Sayre, K.D., Reynolds, M.P., 2000. Enhancing the genetic gain yield potential and yield stability in durum wheat. In: Royo, C., Nachit, M.M., Di Fonzo, N., Araus, J.L. (Eds.), *Durum Wheat Improvement in the Mediterranean Region: New Challenges*. Options méditerranéennes, vol. 40, pp. 88–93.
- Rajaram, S., 2001. Prospects and promise of wheat breeding in the 21st century. *Euphytica* 119, 3–15.
- Rebetzke, G.J., Richards, R.A., 2000. Gibberellic acid-sensitive dwarfing genes reduce plant height to increase kernel number and grain yield of wheat. *Aust. J. Agric. Res.* 51, 235–245.
- Royo, C., 2005. Durum wheat improvement in Spain. In: Royo, C., Nachit, M.M., Di Fonzo, N., Araus, J.L., Pfeiffer, W.H., Slafer, G.A. (Eds.), *Durum Wheat Breeding: Current Approaches and Future Strategies*. Food Products Press, New York, pp. 883–906.
- Royo, C., Álvaro, F., Martos, V., Ramdami, A., Isidro, J., Villegas, D., García del Moral, L.F., 2007. Genetic changes in durum wheat yield components and associated traits in Italy and Spain during the 20th century. *Euphytica* 155, 259–270.
- SAS Institute Inc., 2000. SAS OnlineDoc®.
- Sayre, K.D., Rajaram, S., Fischer, R.A., 1997. Yield potential progress in short bread wheats in northwest Mexico. *Crop Sci.* 37, 36–42.
- Shearman, V.J., Sylvester-Bradley, R., Scott, R.K., Foulkes, M.J., 2005. Physiological processes associated with wheat yield progress in the UK. *Crop Sci.* 45, 175–185.
- Siddique, K.H.M., Belford, R.K., Perry, M.W., Tennant, D., 1989. Growth, development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. *Aust. J. Agric. Res.* 40, 473–487.
- Slafer, G.A., Miralles, D.J., 1993. Fruiting efficiency in 3 bread wheat (*Triticum aestivum*) cultivars released at different eras—number of grains per spike and grain weight. *J. Agron. Crop Sci.* 170, 251–260.
- Slafer, G.A., Satorre, E.H., Andrade, F.H., 1994. Increases in grain yield in bread wheat from breeding and associated physiological changes. In: Slafer, G.A. (Ed.), *Genetic Improvement of Field Crops*. Marcel Dekker, Inc., New York, pp. 1–68.
- Tashiro, T., Wardlaw, I.F., 1990. The effect of high temperature at different stages of ripening on grain set, grain weight and grain dimensions in the semi-dwarf wheat ‘Banks’. *Ann. Bot.* 65, 51–61.
- Waddington, S.R., Cartwright, P.M., 1983. A quantitative scale of spike initial and pistil development in barley and wheat. *Ann. Bot.* 51, 119–130.
- Waddington, S.R., Osmanzai, M., Yoshida, M., Ranson, J.K., 1987. The yield of durum wheats released in Mexico between 1960 and 1981. *J. Agric. Sci.* 108, 469–477.
- Yu, Z.W., Van Sanford, D.A., Egli, D.B., 1988. The effect of population density on floret initiation, development and abortion in winter wheat. *Ann. Bot.* 62, 295–302.