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Genetic changes in durum wheat yield components and associated traits in Italian and Spanish varieties during the 20th century

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Abstract Twelve field experiments comparing 24 durum wheat varieties from three periods—old (<1945), intermediate (1950–1985) and modern (1988–2000)—were carried out in order to ascertain the advances made in durum wheat yield components and related traits in Italian and Spanish germplasm. Grain yield improvements were based on linear increases in the number of grains per m^2 and harvest index, while grain weight and biomass remained unchanged. Yield per plant increased at a rate of 0.36 and 0.44% y^{-1} and the number of grains per m^2 improved by 39% and 55% in Italian and Spanish varieties, respectively. The mean rate of increase in the number of grains per m^2 was 0.55% y^{-1}. Plants per m^2, spikes per plant and grains per spike contributed 20%, 29% and 51%, respectively, to the increase in the number of grains per m^2. The enhance of the number of grains per m^2 was due to the greater grain set in the modern varieties, since the number of spikelets per spike remained unchanged. Harvest index increased overall by 0.48% y^{-1} (0.40 and 0.53% y^{-1} in Italian and Spanish varieties, respectively). Plant height was the trait that suffered the most dramatic changes (it decreased at a rate of –0.81% y^{-1}, with little difference between the varieties of the two countries), as consequence of the presence of the *Rht-B1* dwarfing gene. Harvest index and plant height, which were the traits that most contributed to discriminating between periods, remained unchanged from 1980 to 2000. The higher rates of improvement in Spain are discussed in the context of the contrasting strategies followed to improve durum wheat yield in the two countries.

Keywords Genetic gains · Grains per unit area · Harvest index · Grain weight · Biomass · Plant height · *Rht-B1*

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Introduction

Italy and Spain are the first and second durum wheat producers in the Mediterranean basin (Royo 2005). Improvements in durum wheat yield in Italy have been mainly the result of local breeding programs that were started in 1900 by Nazareno Strampelli (Maliani 1979), while the huge rise in yield during the second half of the last century in Spain (García del Moral et al. 2005) was primarily a consequence of the introduction of CIMMYT semidwarf germplasm, which involved the gradual replacement of traditional tall cultivars by semidwarf and fertilizer-responsive varieties.

Understanding the changes in yield, yield components and associated traits through time is an essential step for improving knowledge of yield-limiting factors and informing future breeding strategies. Advances in yield during the 20th century have been widely reported in the literature for bread wheat (Austin et al. 1980; Cox et al. 1988; Perry and D'Antuono 1989; Siddique et al. 1989; Slafer and Andrade 1989; 1993; Brancourt-Hulmel et al. 2003; Shearman et al. 2005), but references to durum wheat are scarce.

Breeding contributions to wheat yield increases have been estimated in a range between 28% (Bell et al. 1995) to ca. 50% (see references in Slafer et al. 1994), the remaining 50–72% being associated with changes in agronomic practices (Araus et al. 2004). Past genetic gains in bread wheat yield have been widely associated with increased harvest index and grains per m^2 (Austin et al. 1989; Perry and D'Antuono 1989; Slafer and Andrade 1989; Reynolds et al. 1999), and decreasing plant height (Berger and Planchon 1990). These changes have been associated to the presence of the dwarfing genes *Rht-B1* and *Rht-D1*, which confer a reduced response to gibberellin (Peng et al. 1999). Actually, the response of seedlings to gibberellin is routinely used to test whether a variety contains GA-insensitive *Rht* genes or not (Gale and Gregory 1977). The higher number of grains per unit area has been the yield component most associated with yield gains in bread wheat (McCaig and Clarke 1995) and barley (Jedel and Helm 1994). Nevertheless, changes in grain weight have been null (McCaig and Clarke 1995) or even negative (Perry and D'Antuono 1989; Brancourt-Hulmel et al. 2003).

Biomass partitioning is the main physiological trait accounting for changes in bread wheat grain yield, while above-ground biomass has remained unchanged (Reynolds et al. 1999), or has increased only slightly (Austin et al. 1989; Perry and D'Antuomo 1989). However, studies with recently released varieties, both in durum (Pfeiffer et al. 2000) and bread wheat (Shearman et al. 2005), have revealed that increases in grain yield potential in the last 20 years have resulted from higher biomass.

Durum wheat has received far less attention than bread wheat and barley, and few reports on yield increases may be found in the literature. In Canada McCaig and Clarke (1995) reported yield improvements in durum wheat of about 0.81% y^{-1}, mostly based on increases in the number of kernels produced. At CIMMYT, Waddington et al. (1987) and Pfeiffer et al. (2000) reported grain yield increases based on a linear raise in the number of grains per m^2, via an augmented number of spikes per m^2 and/or grains per spike.

The objective of this study was to ascertain the effects of genetic improvement during the last century in the yield components and associated traits of durum wheat in Italy and Spain, two Mediterranean countries with large durum wheat cultivation and with contrasting strategies for yield improvement during the past century. For this purpose an historical series of 24 durum wheat varieties released in different periods during the 20th century was grown in six field experiments at each of two contrasting latitudes in Spain.

Material and methods

Twenty-four durum wheat (*Triticum turgidum* L. var *durum*) varieties, 12 Italian and 12 Spanish, were selected to represent the germplasm grown in Italy and Spain during the 20th century. Based on the year of release, the varieties were assigned to three periods namely old (before 1945), intermediate (released between 1950 and 1985) and modern (released from 1988 to 2000) (Table 1). Modern varieties were chosen in Spain among the lately released by local breeding programmes, avoiding the inclusion of varieties of foreign origin (Mexican and Italian), despite being the most cultivated in the country. About 20% of the durum wheat seed certified in Italy corresponds to Simeto, the variety most used by Italian farmers.

The presence of *Rht-B1* dwarfing gene was tested in 12 seddlings of each variety following the methodology described by Gale and Gregory

Table 1 Description of the varieties used in the study

Country	Period	Variety	Year of release	GA sensitivity
Italian	Old	Balilla Falso	<1930	+
		Carlojucci	1945	+
		Razza 208	<1930	+
		Senatore Cappelli	1930	+
	Intermediate	Adamello	1985	+
		Capeiti 8	1955	+
		Creso	1974	–
		Trinakria	1970	+
	Modern	Cirillo	1992	–
		Flavio	1992	–
		Simeto	1988	–
		Zenit	1992	–
Spanish	Old	Blanco Verdeal	<1930	+
		Clarofino	<1930	+
		Pinet	<1930	+
		Rubio de Belalcázar	<1930	+
	Intermediate	Bidi 17	1950	+
		Camacho	1975	–
		Esquilache	1976	–
		Mexa	1980	–
	Modern	Ariesol	1992	–
		Astigi	1999	–
		Boabdil	2000	–
		Senadur	1995	–

(1977), and using a GA concentration of 4 ppm. All the old varieties as well as Adamello, Capeiti 8, Trinakria and Bidi 17 were sensitive to GA (Table 1), and so they are suposed to not carry the dwarfing gene *Rht-B1*.

Six field experiments were conducted from 2000 to 2005 at each of two Spanish latitudes representing contrasting environmental conditions: the Ebro Valley in the north and eastern Andalusia in the south. The southern area has a Mediterranean climate, with mild winters and hot, dry summers, while the northern area has a more continental climate, with lower temperatures in winter and spring and less evenly distributed precipitation. Details of the experimental sites are given in Table 2. Each experiment consisted of a randomized complete block design with three replications and plots of 12 m^2 (eight rows 0.15 m apart). Each plot was divided into two halves and one of them was used for destructive samplings. Experiments were planted between 17 November and 9 December in all cases. Plots were fertilized following the recommendations in each region to prevent lodging and diseases.

For yield component determination, the plants contained in 1-m-long rows were pulled out in a central row of each plot at ripening, and the number and weight of plants, spikes and grains in the sample were recorded. Harvest index was computed by dividing the grain weight by the total plant weight of the 1-m-long row sample. A sub-sample of 10 randomly selected plants was used to calculate the number

Table 2 Description of experimental sites

Site	North-Gimenells	South-Chimeneas
Coordinates	41°40′ N, 0°20′ E	37°08′ N, 3°49′ W
Altitude, m	200	684
Soil characteristics		
Classification	Mesic Calcixerolic Xerochrept	Loamy Calcixerolic Xerochrept
Texture	Fine-loamy	Silty-clay
Long-term weather data (1989–2001)		
Seasonal rainfall, mm	321	276
Average temperatures during growth cycle, °C		
Tmax	16.3	19.7
Tmean	10.6	12.9
Tmin	5.2	5.9
Sowing rate (seeds m^{-2})	400	350
Irrigation, mm	150	40[a],40[b],120[c]

Tmax, Tmean and Tmin are maximum, mean and minimum temperatures, respectively

[a], [b] and [c], years 2003, 2004 and 2005, respectively. 2000–2002 without irrigation

of spikelets per spike, grains per spike and plant height measured from the soil to the top of the spike excluding the awns. Thousand-kernel weight was determined by counting the number of grains in 10 g drawn randomly from harvested grains of each plot. Biomass at ripening was calculated from the yield and harvest index of each plot.

Combined ANOVA were performed with the SAS-STAT package (SAS Institute Inc 2000). Means were compared by Duncan's 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 variety release. Relative values were computed for each variety as percentage irrespective of the average value of all the varieties for a given country. Principal component analysis (PCA) was performed on the correlation matrix, calculated on the mean data across replications and years.

Results

The analyses of variance for yield components and related traits revealed that all of them, except biomass at ripening, changed significantly ($P < 0.001$) through time (data not shown). Since the period × country interaction was significant for all the traits except biomass and plants m^{-2}, the mean values of the four genotypes in each period are shown in Table 3 for the varieties of each country independently.

Changes in yield components and related traits through time have been plotted in Fig. 1, in which the significant regression lines ($P < 0.05$) fitted to these relationships have been drawn separately for Italian and Spanish sets of varieties. Absolute and relative changes (calculated as slopes of the regression equations for absolute and relative values in each case) are shown in Table 4.

Plants per unit area and yield per plant

Yield per unit area may be expressed as the product of the number of plants per unit area and the yield of each individual plant. The number of plants per m^2 increased significantly from old to modern varieties by 8.6% and 7.8% in Italian and Spanish varieties, respectively (deduced from Table 3). However, when a regression line was fitted to the relationship between plants per unit area and year

Table 3 Mean values of yield components and related traits for 24 durum wheat cultivars released in different periods in Italy and Spain and grown in 12 experiments

	NP	YP (g)	NSP	NsS	NGS	NGm^2	TKW(g)	Biomass (kg m^{-2})	Harvest index (%)	Plant height (cm)
Period of release within country of origin										
Italian										
Old	221 b	1.49 c	1.24 b	16.3 b	29.7 c	7722 c	46.4 a	10.7 b	31.2 c	112 a
Intermediate	240 a	1.73 b	1.37 a	16.2 b	31.5 b	10227 b	43.9 b	11.1 a	37.6 b	83 b
Modern	240 a	1.86 a	1.37 a	16.5 a	35.1 a	10709 a	43.9 b	10.9 ab	40.2 a	70 c
Spanish										
Old	219 b	1.38 c	1.23 c	17.4 a	29.9 c	7490 c	44.0 b	11.2 a	27.9 c	126 a
Intermediate	228 a	1.77 b	1.32 b	16.9 b	34.0 b	9934 b	44.9 a	11.0 a	37.2 b	81 b
Modern	236 a	1.93 a	1.40 a	16.2 c	36.5 a	11611 a	43.2 c	11.2 a	41.0 a	75 c
Country of origin										
Italian	234 a	1.69 a	1.32 a	16.3 b	32.1 b	9571 a	44.7 a	10.9 b	36.3 a	89 b
Spanish	228 b	1.69 a	1.32 a	16.8 a	33.5 a	9704 a	44.1 b	11.1 a	35.4 b	94 a
Latitude										
North	291 a	1.82 a	1.41 a	16.1 b	34.7 a	12481 a	48.7 a	14.9 a	36.0 a	100 a
South	171 b	1.56 b	1.24 b	17.0 a	30.9 b	6854 b	40.0 b	7.2 b	35.7 a	82 b

NP: number of plants m^{-2}, YP: yield plant^{-1}, NSP: number of spikes plant^{-1}, NGm^2: number of grains m^{-2}, TKW: thousand kernel weight, NSm^2: number of spikes m^{-2}, NsS: number of spikelets spike^{-1}, NGS: number of grains spike^{-1}

Means within columns and groups with different letters are significantly different at $P = 0.05$

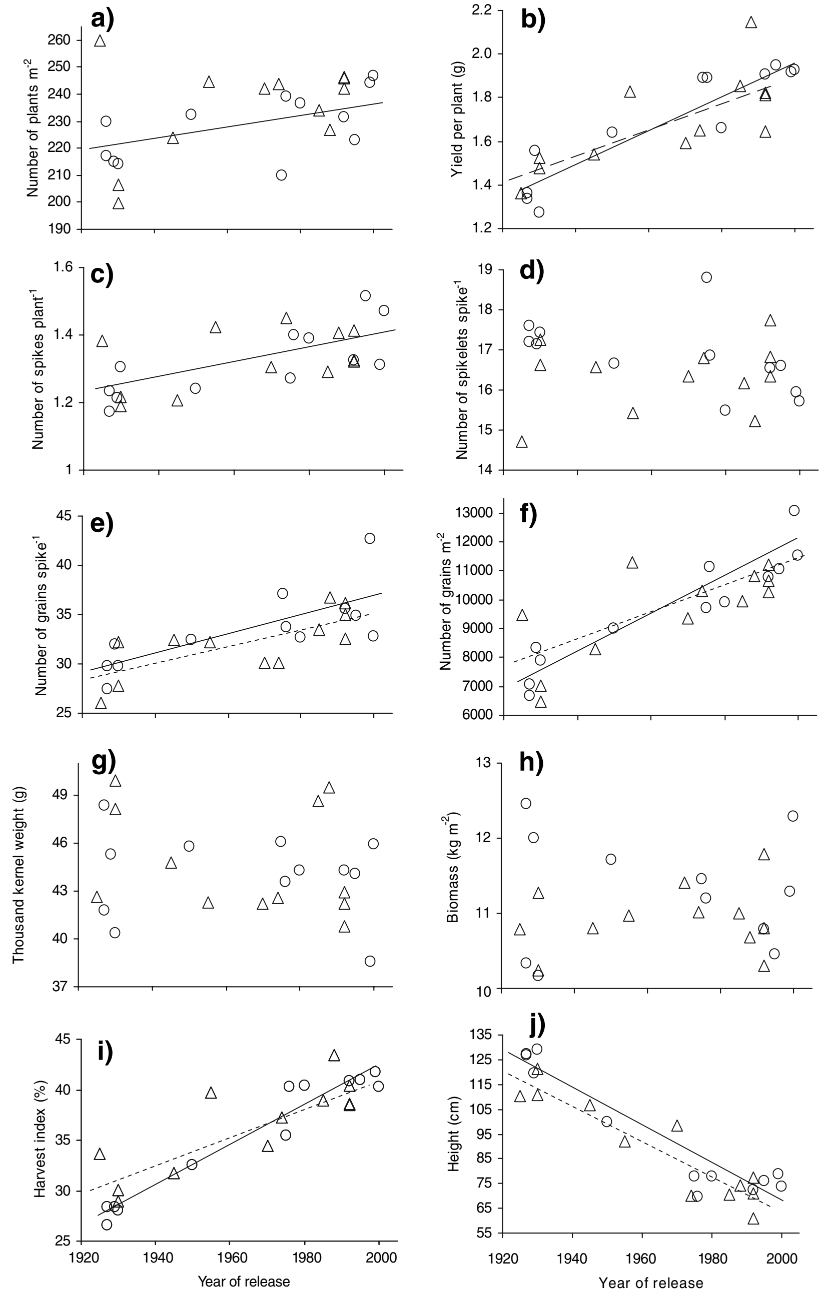

Fig. 1 Relationships between yield components and associated traits and the year of release of 12 Italian (Δ) and 12 Spanish (○) durum wheat varieties. Each point represents the mean value of one variety across 12 environments. Only significant ($P < 0.05$) linear regressions were plotted for the relationships of Italian (dotted lines) and Spanish (solid lines) varieties. R^2 values and slopes for significant equations are in Table 4

of release, the R^2 value was significant for the Spanish varieties, but not for the Italian ones (Table 4). This was probably due to the effect of the Italian old variety Balilla Falso, which had an outstanding plant density in the experiments conducted in the north, leading to an average value across experiments of 260 plants per m^2 (Fig. 1a), the highest of all varieties.

The yield per plant augmented steadily from old to intermediate germplasm (16% and 28% in Italian and Spanish varieties) and from intermediate to modern (7% and 9% in Italian and Spanish varieties, respectively). This represents a rate of 6 mg and 7 mg of grain y^{-1} or, in relative terms, 0.36 y^{-1} and 0.44% y^{-1} in Italian and Spanish varieties, respectively (Table 4, Fig. 1b).

Table 4 Absolute and relative genetic changes in yield components and related traits of Italian and Spanish durum wheat cultivars during the 20th century

Trait	Italian and Spanish (n = 24)			Italian (n = 12)			Spanish (n = 12)			Absolute changes units
	R^2	Absolute change	Relative change (% y^{-1})	R^2	Absolute change	Relative change (% y^{-1})	R^2	Absolute change	Relative change (% y^{-1})	
Plants m^{-2}	0.24*	0.26	0.11	0.18	NS	NS	0.37*	0.24	0.10	Plants m^{-2} y^{-1}
Yield $plant^{-1}$	0.70***	0.007	0.41	0.55**	0.006	0.36	0.83***	0.007	0.44	g y^{-1}
Spikes $plant^{-1}$	0.41***	0.002	0.16	0.22	NS	NS	0.58**	0.003	0.19	Spikes $plant^{-1}$ y^{-1}
Spikelets $spike^{-1}$	0.04	NS	NS	0.04	NS	NS	0.26	NS	NS	Spikelets $spike^{-1}$ y^{-1}
Grains $spike^{-1}$	0.50***	0.090	0.28	0.53**	0.089	0.27	0.53**	0.092	0.28	Grains $spike^{-1}$ y^{-1}
Grains m^{-2}	0.73***	52.6	0.55	0.58**	46.2	0.48	0.84***	57.1	0.59	Grains m^{-2} y^{-1}
Thousand kernel weight	0.04	NS	NS	0.08	NS	NS	0.02	NS	NS	g y^{-1}
Biomass	0.00	NS	NS	0.03	NS	NS	0.01	NS	NS	g m^{-2} y^{-1}
Harvest index	0.83***	0.17	0.48	0.69***	0.14	0.40	0.94***	0.19	0.53	% y^{-1}
Plant height	0.87***	−0.74	−0.81	0.87***	−0.73	−0.79	0.89***	−0.74	−0.81	cm y^{-1}

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

On average, Italian and Spanish varieties had similar yields per plant, but the Italian set had more plants per unit area. Both the number of plants and the yield per plant were higher in the northern experiments.

Spike components

The number of spikes per plant increased from old to modern germplasm by 10% and 14% in Italian and Spanish varieties, respectively. However, the R^2 value of the relationship between spikes per plant and year of release was not significant for the Italian germplasm, while the relative increase in the number of spikes per plant was 0.19% y^{-1} within the Spanish set of varieties (Table 4, Fig. 1c).

The rate of genetic change in the number of spikelets per spike was not significant for either country (Table 4, Fig. 1d). However, the number of grains per spike increased from old to modern varieties by 18% and 22% in Italian and Spanish varieties, respectively (deduced from Table 3). The rate of increase was similar for both sets of germplasm (Table 4, Fig. 1e).

On average, Spanish varieties had more spikelets and grains per spike (Table 3). The number of spikes per plant and the number of grains per spike were greater in the north than in the south, but more spikelets per spike were achieved in the southern experiments.

Grains per unit area and kernel weight

The two main yield components—number of grains per unit area and individual grain weight—followed contrasting pattern of changes through time. The number of grains per unit area increased overall by 39% in Italian varieties (32% from old to intermediate and 5% from intermediate to modern) and 55% in Spanish germplasm (33% from old to intermediate and 17% from intermediate to modern varieties, respectively, deduced from Table 3). The regression equations fitted to the relationships between grains per unit area and year of release were significant for both sets of varieties, also revealing a higher slope for gains in Spanish than in Italian germplasm (Table 4, Fig. 1f).

On the other hand, thousand kernel weight decreased by 5% from old to intermediate Italian varieties, though it remained constant during the last period. The weight of grains of Spanish durum wheat increased by 2% in the first period and decreased by 4% in the second (Table 3). The R^2 of the regression equations fitted to the relationships between thousand kernel weight and year of release were not significant in any case (Table 4, Fig. 1g).

On average Italian and Spanish varieties had a similar grain number per unit area, but Italian varieties had heavier grains (Table 3). Again, both yield components were higher in the northern experiments.

Biomass production and allocation

Changes in biomass and harvest index, the two yield components in terms of biomass production and allocation, followed contrasting patterns. Biomass was not modified by breeding activities (Tables 3, 4, Fig. 1h), while harvest index (Fig. 1i) increased from old to modern germplasm by 29% and 47% in Italian and Spanish varieties, respectively. The changes between old and intermediate varieties (20% and 33% in Italian and Spanish varieties, respectively) were greater than those between intermediate and modern varieties (7% and 10%, respectively, deduced from Table 3). The global rate of change was 0.48% y^{-1}, corresponding to 0.53% y^{-1} to Spanish varieties and 0.40% y^{-1} to Italian germplasm.

Plant height

Among the traits analyzed, plant height was the one that suffered the most dramatic changes. The plant height of Italian varieties decreased on average by 37%, mostly in the period between old and intermediate varieties (–26%). In Spain the total reduction was 41%, and was also greater in the first period (–36%) than in the second (Table 3). The rate of relative genetic change was similar for both countries (Table 4, Fig. 1j).

Multivariate analysis

In order to detect the combination of variables that best explained the variability between groups of varieties, PCA was carried out including yield and the 10 yield components and related variables shown in Table 4. Given that the environment strongly affected the traits analyzed, multivariate analysis was carried out with the mean genotype values for each latitude.

The first two axes of the PCA shown in Fig. 2 accounted for ca. 80% of the total variance (axis 1, 56%; axis 2, 24%), indicating that most of the information contained in the data could be

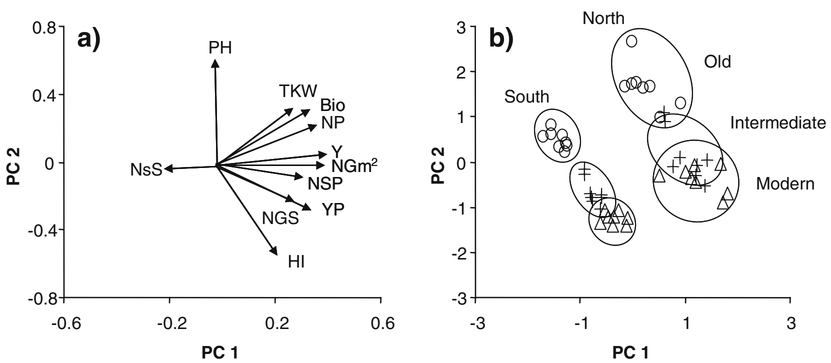

Fig. 2 Principal component analysis two-dimensional graph. In (**a**) the eigenvalues of the correlation matrix are symbolized as vectors representing yield, yield components and associated traits. PH: plant height, TKW: thousand kernel weight, Bio: biomass, NP: number of plants m^{-2}, Y: grain yield, NGm^2 number of grains m^{-2}, NSP number of spikes $plant^{-1}$, NGS: number of grains $spike^{-1}$, YP: yield $plant^{-1}$, HI: harvest index, NsS: number of spikelets $spike^{-1}$. In (**b**), points are plotted on the plane determined by the first two axes for old (○), intermediate (+) and modern (Δ) sets of varieties

summarized by projecting the points on the plane determined by the first two axes. The eigenvectors of the various components are represented in Fig. 2a. The length of each vector's projection on an axis is proportional to its contribution to the principal components of that axis, reflecting the extent to which each variable weights the two components. Principal component 1 is related to most of the variables included in the analysis in a positive direction, and to the number of spikelets per spike in a negative direction. Plant height has no effect on PC1. Grain yield, number of grains per m^2, plants per m^2, biomass and yield per plant have a similar weight on axis 1. Thus, it may be assumed that the first axis represents grain yield and associated traits, while low number of spikelets per spike. Increases in PC2 are related to increases in plant height and decreases in harvest index.

Figure 2b shows the genotype points plotted on the plane determined by the first two axes. The points are grouped in six clusters related to latitude (north and south) and period of release (old, intermediate and modern). The first axis discriminates against latitudes, while the second one differentiates between periods of release.

The number of grains per unit area was the trait most related to yield (Fig. 3a), explaining 88% of yield variations between varieties released in different periods. Harvest index was also strongly and positively associated with grain yield (Fig. 3b) and with the number of grains per m^2 (Fig. 3c), but it was negatively related to plant height.

Discussion

In this study we tried to understand the causes of yield improvement by assessing the changes suffered by the components of some numerical and physiological identities involving yield as a dependent variable.

When yield is considered as the product of plants per unit area and yield per plant, our results demonstrate that yield per plant increased at a rate close to four times the rate of increase in plant density (0.41 vs. 0.11% y^{-1} respectively), the latter component being only significant within the Spanish set of varieties. The improvement in the number of plants per unit area, albeit modest, could be attributed to a greater plant survival of modern varieties in the conditions of our experiments. The rate of yield per plant improvement was 22% higher in Spanish than in Italian varieties, which is in agreement with the early breeding work done in Italy from the beginning of the 20th century (Maliani 1979), which was not

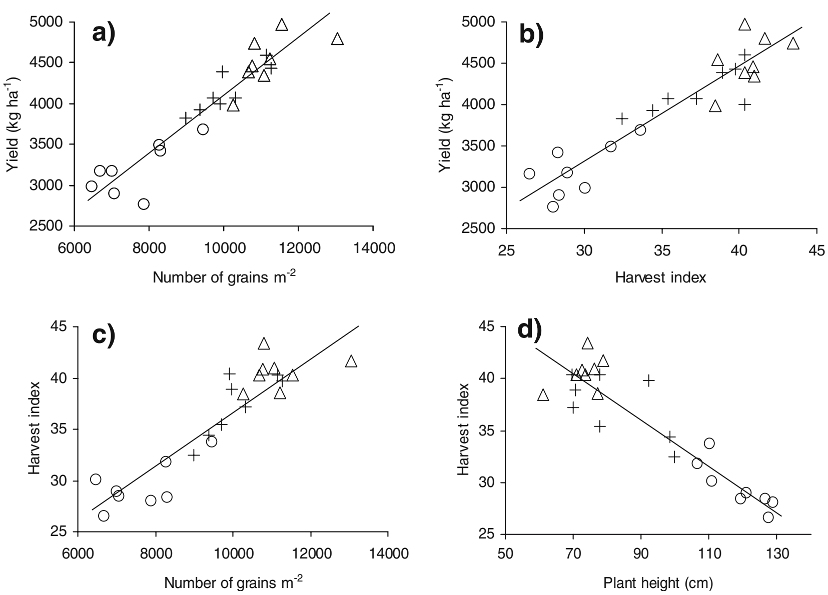

Fig. 3 Relationships between yield and (**a**) number of grains per m^2, (**b**) harvest index, and between harvest index and (**c**) number of grains per m^2 and (**d**) plant height. Points represent variety means for old (○), intermediate (+) and modern (Δ) sets of varieties

the case in Spain. This assumption is supported by the 8% greater yield per plant of old Italian varieties compared to old Spanish varieties.

Of the three components of yield per plant, only two were responsible for yield increases: the number of spikes per plant (which increased by 10% and 14% in Italian and Spanish varieties, respectively) and the number of grains per spike (which increased by 18% and 22% in Italian and Spanish germplasm, respectively), given that kernel weight decreased by 5% and 2% in Italian and Spanish varieties, respectively. Perry and D'Antuono (1989) found increases of 10% in the number of spikes per m^2 and decreases of about 15% in grain weight in Australian spring bread wheat varieties between 1860 and 1982. Austin et al. (1980) reported increases of 14% in the number of spikes per m^2 in winter bread wheat between 1830 and 1986. In both studies, the percentage of increase in spikes per m^2 was similar to the increases in the number of spikes per plant found in this research. However, the contribution of the number of grains per spike to yield increases was greater than that of the number of spikes per plant, since relative genetic gains in this last component were not significant for the Italian varieties and were 0.19% y^{-1} for the Spanish varieties, while the rates of improvement of the number of grains per spike were 0.27 and 0.28% y^{-1} in Italian and Spanish varieties, respectively. The cause of such increases in the number of grains per spike was not the increase in the number of spikelets per spike, which remained practically unchanged over time, but the higher grain set in the modern varieties. This increased grain number could be attributed to a higher number of fertile florets per spikelet in the modern varieties compared to the old ones, as a consequence of a higher assimilate partitioning to the spike during the preflowering critical period (Miralles et al. 2002). Moreover, the phenological adaptation manifested by the reduction of the cycle length until anthesis reported in a previous study, may have contributed to the yield rise in modern cultivars (Miralles et al. 2002).

Overall improvements in plant density (0.11% y^{-1}), spikes per plant (0.16% y^{-1}) and grains per spike (0.28% y^{-1}) contributed to the huge increase observed in the number of grains per unit area, which was surprisingly the sum (0.55% y^{-1}) of the partial genetic gains in the three yield components. Total increases in the number of grains per m^2 were 39% and 55% in Italian and Spanish varieties, respectively. These values are similar to the 37% increases reported in Great Britain by Austin et al. (1989) and the 51% increases reported in Australia by Perry and D'Antuono (1989) for bread wheat. Our results indicate that increases in the number of grains per unit area in durum wheat during the 20th century in Italian and Spanish germplasm were due, to improvements in the number of grains per spike, number of spikes per plant and plants per unit area, with relative contributions of 51, 29 and 20%, respectively.

Crop biomass at ripening remained unchanged over time, in germplasm from both countries, which suggests that the selection of yield *per se* did not lead to varieties with greater total biomass. Consequently, in terms of biomass production and allocation, increases in grain yield were due to changes in photosynthates partitioning within the plant, that is, to improvements in harvest index in association with decreases in plant height. Harvest index of Italian and Spanish varieties considered together increased at a rate of 0.48% y^{-1}, which was slightly lower than the increase in the number of grains per unit area, and slightly higher than the improvement in yield per plant. The relative change in harvest index was greater in Spanish (0.53% y^{-1}) than in Italian (0.40% y^{-1}) germplasm, which is in agreement with the greater rate of change of the yield per plant within Spanish varieties. However, in germplasm from both countries increases in harvest index were much higher between old and intermediate varieties than between intermediate and modern varieties. Figure 1i shows that the harvest index remained unchanged from 1980 to 2000. This seems to be a general tendency, since it has been reported that at CIMMYT, where dwarfing genes were introduced more than two decades before they were in Spain, the harvest index of durum wheat declined from the early to mid-1970s and advances in biomass production were largely partitioned into straw (Pfeiffer et al. 2000). The huge increase in harvest index until the 1980s was due to the introduction of semidwarf CIMMYT-derived varieties in Spain, as suggested by the presence of *Rht-B1* gene in all intermediate and modern Spanish varieties except Bidi 17, an Algerian introduction. A relationship between plant height and sensitivity to GA was observed in all Italian varieties except Adamello (Table 1, Fig. 1j). The short plant height of this variety may suggest the presence of dwarfing genes not conferring insensitivity to GA. Adamello likely carries *Rht8*, a dwarfing gene from the Japanese variety Akagomughi, that was introduced in the Italian genetic pool by Nazareno Strampelli in 1912 (Borghi 2001). In fact, among the traits studied, plant height was the attribute that suffered the most dramatic changes over time, since it decreased at a rate of –0.81% y^{-1}, with little differences between Italian and Spanish varieties. Moreover, reductions in plant height were greater in the first period than in the second period in germplasm from both countries, since plant height did not change in the varieties developed after 1975 (Fig. 1j), when dwarfing genes had been already incorporated. Numerous studies comparing old and modern varieties have demonstrated that increased partitioning of biomass to spike growth seems to be a pleiotropic effect of dwarfing genes (Abbate et al. 1995). Actually, the introduction of semidwarf cultivars with *Rht* genes in wheat is considered to be one of the causes of major advances in plant breeding during the 20th century (Rajaram 2001).

Our study provides evidence that the most dramatic increases in yield in Italian and Spanish durum wheat in the past were due to increases in the number of grains per m^2 and harvest index, both traits being highly correlated, while grain weight and biomass remained unchanged. Harvest index improvements were positively associated with plant height reductions, as has been pointed out in other species (Calderini et al. 1995; Brancourt-Hulmel et al. 2003). Future improvements in grain yield through breeding may require a boost in biomass production, with harvest index being maintained (Austin et al. 1980; Hay 1995; Fischer 1996) or further increases in harvest index. Some studies have shown increased biomass to be associated with yield increases in durum wheat (Waddington et al. 1987; Villegas et al. 2001). However, variability for the rate and duration of biomass production and leaf growth has not been demonstrated in durum wheat (Villegas et al. 2001; Royo et al. 2004). On the other hand, the difference between actual harvest index and the theoretical limit of 60% fixed by Austin et al. (1980) is greater in durum wheat than in bread wheat, suggesting that there is still room for further improvements. In our experiments about 40% of the biomass was partitioned into grain in modern varieties, the highest values determined in optimal environments being around 50% (Monneveux et al. 2005). Further harvest index increases in Mediterranean conditions seem unlikely to be achieved without improvements in water use efficiency that would probably also have a positive effect on grain weight. Therefore, the identification of QTL associated with water use efficiency and their incorporation in the new developed varieties is essential in order to further raise durum wheat yield under Mediterranean conditions.

Principal component was used for the graphic interpretation of the changes occurring in yield components over time and the influence on them of the environment in which they were assessed. The results of the north and south experiments showed the same pattern of changes in yield components and associated traits, the main difference being the greater values achieved by most traits in the north than in the south, and the greater number of spikelets per spike in the south. The colder and wetter environment of northern Spain allowed genotypes to better express their yield potential, as has been pointed out in an ontogenic study about grain yield formation (García del Moral et al. 2003). Moreover, the points representing varieties in Fig. 2b were more grouped in the south than in the north, where they were more dispersed. This indicates that the more favorable weather conditions of the northern environment also maximized phenotypic differences between varieties. The greater number of spikelets per spike in the south could be a consequence of a greater competition between developing spikes in the north, where spike density was almost double that in the south. Harvest index was the most stable component since it did not change with the environment, as a consequence of its high genetic control (Bhatt 1976). Principal component analysis also revealed that the traits that most contributed to discrimination between periods were harvest index and plant height, as old genotypes were located at the upper part of Fig. 2b, in the direction of the plant height eigenvector, while modern genotypes were at the bottom-right of the same figure, in the direction of harvest index.

Italian and Spanish genotypes did not differ greatly in yield components. The Spanish varieties used in this study exceeded the Italian ones by 1% in the number of spikelets per spike, 4% in the number of grains per spike, 4% in the number of grains per unit area, 2% in biomass, 1% in kernel weight and 6% in plant height, while the Italian ones had 3% more plants per unit area and a harvest index 2% higher than the Spanish. The different magnitude of the genetic improvement in yield components in Italian and Spanish varieties may be a consequence of the contrasting breeding strategies used by the two countries to improve grain yield during the 20th century. The importance of durum wheat in Italian agriculture and pasta consumption led breeding efforts to be started in the early 20th century (Maliani 1979). On the other hand, durum wheat breeding was not a traditional activity in Spain because barley and bread wheat were the most cultivated cereals. In fact, a recent paper with the same genotypes as those used in the present study demonstrated that old, intermediate and modern Italian varieties were genetically close, while old Spanish varieties clustered apart from the intermediate and modern varieties (Martos et al. 2005). The durum wheat varieties most cultivated in Spain in the second half of the 20th century were derived from CIMMYT germplasm, and were therefore not constructed incorporating the genetic background of old varieties. This may explain why old Italian varieties had a higher harvest index, shorter plants and more grains per unit area and yield per plant than the Spanish ones, and also why the rate of improvement of these traits was higher in Spanish than in Italian germplasm.

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