Changes in Yield and Carbon Isotope Discrimination of Italian and Spanish Durum Wheat during the 20th Century

C. Royo,* V. Martos, A. Ramdani, D. Villegas, Y. Rharrabti, and L. F. García del Moral

ABSTRACT

This study evaluates the breeding of durum wheat (*Triticum turgidum* L. var. *durum*) during the 20th century with respect to yield and grain carbon isotope discrimination (Δ), and their relationship with plant height, harvest index (HI), days from sowing to anthesis, and days from anthesis to maturity. Twenty-four cultivars released before 1945 (old), between 1950 and 1985 (intermediate), and between 1988 and 2000 (modern), and previously characterized by whether dwarfing genes were present (semidwarf) or absent (tall), were selected from germplasm obtained in Italy and Spain. Experiments were conducted in six environments with average yields ranging from to 2113 to 4827 kg ha^{-1}. The total absolute genetic gain in yield across countries from before 1945 to 2000 was 20 kg ha^{-1} yr^{-1} (51% of increase), which represents a relative genetic gain of 0.61% yr^{-1}. Yield gains led to a loss of stability. The mean increase in Δ^{13}C was 6% (0.014‰ yr^{-1} or 0.09% yr^{-1}). Early heading and a long grain-filling period were correlated with high yields in the tall cultivars. Increased plant height and low Δ^{13}C values were associated with high yields for the semidwarf cultivars, while a long grain-filling period was not advantageous for semidwarf cultivars.

An understanding of changes in yield and associated traits is critical for improving the knowledge of yield-limiting factors and designing future breeding strategies. Breeding activities during the second half of the 20th century allowed the release of cultivars that responded well to new agronomic practices. For example, the introduction of dwarfing genes increased N utilization without lodging, resulting in high yields. However, Boyer (1982) has pointed out that only part of the genetic potential for yield has been realized, due partially to the poor understanding of the essential mechanisms of adaptation of the plants to unfavorable environments.

Many studies have sought to evaluate the advances made by breeding in bread wheat (*T. aestivum* L.) and other cereals (Austin et al., 1980; Cox et al., 1988, Perry and D'Antuono, 1989; Brancourt-Hulmel et al., 2003; Shearman et al., 2005), but durum wheat has been analyzed in only a few studies. Although Italy and Spain are the main durum wheat producers in the Mediterranean basin (Royo, 2005), information on the changes in yield and related traits attributed to breeding activities in the region is scarce. In Canada, McCaig and Clarke (1995) reported yield increases of 0.81% yr^{-1} from 1960 to date, while the genetic gain in durum wheat yield among CIMMYT germplasm between 1960 and 1984 is 3% yr^{-1} (Waddington et al., 1987). Past genetic gains in yield have been associated largely with decreased plant height (Berger and Planchon, 1990) combined with increased HI and grains per m^2 in bread wheat (Austin et al., 1989; Reynolds et al., 1999) as well as in durum wheat (De Vita et al., 2007; Royo et al., 2007).

Carbon isotope discrimination (Δ^{13}C) is a measure of the ^{13}C to ^{12}C ratio in plant material compared to the same ratio in the atmosphere (Farquhar and Richards, 1984). It has been used to estimate transpiration efficiency or intrinsic water use efficiency (WUE, the ratio of biomass accumulated to water transpired) of the crop, since the isotope signature is based on the integration of plant–water status over a period of time (Condon et al., 1993). When measured in plant dry matter, carbon isotope discrimination integrates transpiration efficiency, the ratio of net photosynthesis (biomass production) to water transpired, over the period during which the dry matter is assimilated (Araus et al., 2003a). Selection of low Δ^{13}C of leaf–lamina samples collected at the beginning of the stem elongation of wheat has been recommended for yield increases in environments where crop growth depends strongly on subsoil moisture stored from out-of-season rains (Condon et al., 2002; Rebetzke et al., 2002). Carbon isotope discrimination determined in seedling leaves has been used successfully to release Drysdale, a new bread wheat cultivar with improved transpiration efficiency, by the CSIRO Plant Industry (http://www.csiro.au/files/files/p2hh.pdf; verified 29 Dec. 2007) in Australia (Condon et al., 2002; Rebetzke et al., 2002).

A different approach is used when Δ^{13}C is assessed in mature grains since positive associations between yield and Δ^{13}C of grains have been reported previously for different cereal species growing under favorable environments (Condon et al., 1987; Richards, 1996; Araus et al., 1998) and from moderate water-stressed to fully irrigated Mediterranean conditions (Villegas et al., 2000; Richards et al., 2002; Royo et al., 2002; Araus et al., 2003a). Several reports on durum wheat (Villegas et al., 2000; Royo et al., 2002; Araus et al., 2003b) have highlighted

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Abbreviations: Δ^{13}C, grain carbon isotope discrimination; CIMMYT, International Maize and Wheat Improvement Center; HI, harvest index; PDB, Pee Dee belemnite.

Table 1. Experimental details.

	North–Lérida (cooler environments)			South–Granada (warmer environments)		
Site	**Gimenells**		**Foradada**	**Chimeneas**		
Year	2001	2002	2002	2000	2001	2002
Coordinates	41°40′ N, 0°20′ E		41°88′ N, 0°76′ E	37°08′ N, 3°49′ W		
Altitude, m	200		580	684		
Soil characteristics						
Classification	Mesic Calcixerolic Xerochrept		Xerofluvent oxiaquic	Loamy Calcixerolic Xerochrept		
Texture	Fine-loamy		Fine-loamy	Silty-clay		
PH	8.1		8.2	8.2		
P, mg kg^{-1}	16	22	7	27	32	30
K, mg kg^{-1}	127	185	174	210	221	217
Organic matter, g kg^{-1}	27	23	17	19	19	19
Average temp. during growth cycle, °C	12.6	11.2	9.8	13.8	14.3	13.7
Seasonal rainfall, mm	273	193	371	274	358	328
Agronomic practices						
Sowing density, seeds m^{-2}	400	400	400	350	350	350
Irrigation, mm	150	232	0	0	0	0
Fertilizers, Kg ha^{-1}						
N (seed bed + top dressing)	80 + 130	80 + 97	60 + 104	52 + 26	52 + 26	52 + 26
P_2O_5	150	150	150	52	52	52
K_2O	150	150	60	52	52	52
Sowing time	17 Nov. 2000	5 Dec. 2001	7 Nov. 2002	9 Dec. 1999	28 Nov. 2000	27 Nov. 2001

the usefulness of $\Delta^{13}C$ assessed on mature grains for durum wheat selection under Mediterranean conditions. Phenological differences among genotypes may affect yield and also $\Delta^{13}C$, especially in drought-prone environments.

This study analyzes the changes in yield and $\Delta^{13}C$ in mature grains attributed to breeding during the 20th century in Italy and Spain. Plant height, HI, and season length were also included in the analysis because of their strong relationship with yield and $\Delta^{13}C$. The effect of the presence of dwarfing genes on these traits and their relationships was also investigated.

MATERIALS AND METHODS

Six field experiments (hereafter referred to as environments) were performed in two different temperature regimes in Spain (Gimenells and Foradada in the Ebro Valley in the north, and Chimeneas in eastern Andalusia in the south). Sites were chosen to represent contrasting environmental conditions within Spain. The southern area has a Mediterranean climate, with mild winters and hot, dry summers. The northern area has a more continental climate, with lower temperatures in winter and spring (Table 1). Each experiment consisted of a randomized complete block design with three replications and plots of 6 m^2 (eight rows 0.15 m apart and 5 m length). Experimental details are given in Table 1. The three experiments located in the south and the one in Foradada in 2002 in the north were conducted under rainfed conditions. Experiments at Gimenells in 2001 and 2002 had supplementary irrigation.

Twenty-four durum wheat cultivars, 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 cultivars were assigned to three periods, namely old (released before 1945), intermediate (released between 1950 and 1985), and modern (released from 1988 to 2000). The presence of dwarfing genes on this germplasm was tested in a previous study (Royo et al., 2007). Based on this study cultivars were classified as semidwarf (dwarfing genes present) or tall (dwarfing genes absent) (Table 2).

The number of days from sowing to anthesis and to physiological maturity were recorded in each plot when 50% of the plants reached the stages 65 and 87 in the Zadoks scale (Zadoks et al., 1974). Harvest index was determined on a dry weight basis as the ratio between grain and plant weights of the plants contained in a 1-m-long section of the central row of each plot at ripening (stage 92 of the Zadoks scale). Plant height was measured from the soil to the top of the main spike excluding the awns on 10 randomly sampled plants per plot. Plots were mechanically harvested at ripening and grain yield was adjusted to 120 g kg^{-1} moisture level. A sample of about 2 g of matured kernels from each plot was finely ground (to pass a 0.5-mm sieve) for carbon isotope analysis. The ^{13}C to ^{12}C ratios were determined by mass spectrometry at Isotope Services Inc., Los Alamos, NM. Stable carbon isotope composition was expressed as $\delta^{13}C$ values (Farquhar et al., 1989a), where $\delta^{13}C$ (‰) $= [(R_{grain}/R_{standard})-1] \times 1000$, and R was the ^{13}C to ^{12}C ratio. Secondary standards of graphite, sucrose, and polyethylene foil calibrated against Pee Dee belemnite (PDB) carbonate were used for comparison. The accuracy of the $\delta^{13}C$ measurements was ±0.1‰. Carbon isotope discrimination was further computed as $\Delta^{13}C = (\delta_a - \delta_s)/(1+\delta_s)$, where δ_a and δ_s refer to $\delta^{13}C$ of air and plant, respectively (Farquhar et al., 1989b). On the PDB scale, free atmospheric CO_2 has a current deviation, δ_a, of approximately −8‰ (Farquhar et al., 1989a).

Combined ANOVA over latitudes, environments, countries, periods, and cultivars were performed with the SAS–STAT package (SAS Institute, 2000). Means were compared by Duncan's test at $P = 0.05$. Absolute and relative genetic gains—that is changes due exclusively to plant breeding—were computed for yield and $\Delta^{13}C$ as the slope of the linear regression between the absolute or relative value of the trait and the year of cultivar release. Relative values were computed for each cul-

Table 2. Description of the 24 Italian and Spanish cultivars used in the study.

Cultivar	No.	Year of release	Dwarfing genes	Pedigree	Origin/Seed source†
				Italian old	
Balilla Falso	1	<1930	Absent	Not recorded	Not recorded/IDWNBP
Carlojucci	7	1945	Absent	Russello/Forlani	Not recorded/IDWNBP
Senatore Cappelli	8	1930	Absent	Jennah/Khetifa	N. Strampelli/ENSE
Razza 208	2	<1930	Absent	Not recorded	Not recorded/IDWNBP
				Italian intermediate	
Adamello	16	1985	Present	Valforte/Selezione Turca	ISC/ENSE
Capeiti 8	10	1955	Absent	Senatore Cappelli/Eiti	Stazione Granic. Sicilia/ Istituto de Germoplama di Bari, Italy
Creso	12	1974	Present	CpB14x(((Yt 54xN10xB)XCp 63 2)xTC 603)	ENEA/S.P.S.
Trinakria	11	1970	Absent	B 14/Capeiti 8	IstitutoAgronomico, Palermo/S.P.S.
				Italian modern	
Cirillo	18	1992	Present	Carlojucci/Polesine//Creso/Montanari	Miliani Genética/S.P.S.
Flavio	19	1992	Present	Latino/Cappelli	SIS
Simeto	17	1988	Present	Capeiti 8/Valnova	Stazione Granic. Sicilia/S.P.S.
Zenit	20	1992	Present	Valriccardo x Vie	S.P.S.
				Spanish old	
Blanco Verdeal	3	<1930	Absent	Not recorded	Sevilla/CRF
Clarofino	4	<1930	Absent	Not recorded	Albacete/CRF
Pinet	5	<1930	Absent	Not recorded	Valencia/CRF
Rubio de Belalcázar	6	<1930	Absent	Not recorded	Córdoba/CRF
				Spanish intermediate	
Bidi17	9	1950	Absent	Not recorded	Algeria/CRF
Camacho	13	1975	Present	Jerez 36 x Mex 246 x Lebrija…	INIA, Spain
Esquilache	14	1976	Present	Not recorded	Semillas Agrícolas S.A, Spain
Mexa	15	1980	Present	GDOVZ469/3/Jo's//61130/LSL	CIMMYT-Mexico
				Spanish modern	
Ariesol	21	1992	Present	Not recorded	Agrar Semillas, Zaragoza, Spain
Astigi	23	1999	Present	Not recorded	Complejo ASGROW Semillas, Sevilla, Spain
Boabdil	24	2000	Present	Not recorded	IRTA/Semillas Fitó, Lérida, Spain
Senadur	22	1995	Present	Not recorded	SENASA, Elorz, Spain

† IDWNBP = Italian Durum Wheat National Breeding Program; ENSE = Ente Nazionale Sementi elette, Milano, Italy; ISC = Istituo Sperimentale per la Cerealicoltura; S.P.S. = Società Produtori Sementi, Bologna, Italy; SIS = Società Italiana Sementi, Bologna, Italy; CRF = Centro de Recursos Fitogenéticos, INIA, Spain; IRTA = Institute for Food and Agricultural Research and Technology, Catalonia, Spain.

tivar as a percentage of the average value of all the cultivars for a given country. Genetic correlations were calculated for tall and semidwarf cultivars separately. Correlations were estimated from the genetic variances and covariances, following the method described by Hanson et al. (1956), as follows:

$$r_g = \sigma_{p1p2}/(\sigma^2_{p1.}\ \sigma^2_{p2})^{1/2}$$

where σ_{p1p2} is the genetic covariance component for two traits, and σ^2_{p1} and σ^2_{p2} are the respective genetic variance components.

RESULTS

Changes in Yield and Δ^{13}C

The ANOVA showed important environmental effects on both yield and Δ^{13}C (Table 3), which were higher in the north than in the south (Table 4). The environmental means for yield ranged between 2879 kg ha^{-1} (Foradada in 2002) and 4827 kg ha^{-1} (Gimenells in 2001) in the north, and between 2113 kg ha^{-1} (in 2001) and 3130 kg ha^{-1} (in 2002) in the south. The environments with the minimum (15.52‰) and maximum (16.78‰) values for Δ^{13}C coincided with those in which the minimum and maximum yields were registered in the north. In the south, Δ^{13}C means were 14.5, 15.2, and 16.1‰, while mean yields were 2228, 2113, and 3130 kg ha^{-1} in 2000, 2001, and 2002, respectively. The Italian and Spanish cultivars had similar average yields, but the former had slightly higher mean Δ^{13}C values. Italian genotypes outyielded Spanish ones in the north, while the opposite was true in the south. Italian cultivars showed more Δ^{13}C variation (from 15.0 for Balilla Falso to 16.4 for Zenit and Flavio) than Spanish cultivars (Table 5). Old Spanish cultivars were much more uniform in Δ^{13}C than were the intermediate and modern ones.

Yield and Δ^{13}C were significantly higher in intermediate and modern cultivars than in the old cultivars (Table 4). Yield and Δ^{13}C gains of modern cultivars compared with the old ones were 51 and 5.9%, respectively (Table 4). The absolute yield gain per year was 16.9 kg ha^{-1} in Italy and 23.6 kg ha^{-1} in Spain (Fig. 1). In relative terms these gains were 0.51% yr^{-1}

Table 3. Mean squares of the combined analyses of variance for grain yield, carbon isotope discrimination ($\Delta^{13}C$), harvest index (HI), plant height (PH), days from sowing to anthesis (DSA), and days from anthesis to maturity (DAM) for 24 durum wheat cultivars (Cv) released in Italy and Spain in three periods and grown on three environments (Env) at each of two latitudes (Lat).

Source of variation	df	Grain yield ($\times 10^5$)	$\Delta^{13}C$	HI	PH	DSA	DAM
Lat	1	2709.3***	84.8***	3851.9***	38741.4***	33320.4***	5503.2***
Env (Lat)	4	506.2***	36.3**	593.4***	4438.5***	23062.5***	754.2***
Block (Env × Lat)	12	11.1***	3.9***	20.8*	73.3*	7.3*	10.8
Country	1	2.0	2.6***	179.7***	2713.4***	884.1***	476.2***
Period	2	642.5***	27.6***	5124.9***	64330.2***	2042.1***	399.2***
Country × Period	2	33.2***	0.4	286.2***	1042.1***	577.7***	31.4*
Lat × Country	1	16.8**	0.2	69.0**	92.7	2.4	15.5
Lat × Period	2	161.9***	0.7*	359.6***	1.8	18.5*	56.9***
Cv (Country × Period)	18	15.6***	0.7***	106.5***	1334.0***	143.1***	49.7***
Env (Lat) × Country	4	26.1***	0.2	59.4***	65.7	2.4	17.1*
Env (Lat) × Period	8	28.5***	0.8***	172.3***	669.1***	37.6***	78.1***
Lat × Country × Period	2	14.8**	0.3	19.5	57.9	31.2***	33.9**
Env(Lat) × Country × Period	8	3.2	1.0***	13.5	82.4**	14.7***	21.1**
Lat × Cv (Country × Period)	18	9.0***	0.3	23.3**	97.3***	19.0***	18.7***
Residual	348	2.3	0.2	9.9	29.2	3.5	6.9
Total	431						

* Significant at 0.05 probability level.

** Significant at 0.01 probability level.

*** Significant at 0.001 probability level.

Table 4. Mean values of grain yield, carbon isotope discrimination ($\Delta^{13}C$), harvest index (HI), plant height (PH), days from sowing to anthesis (DSA) and days from anthesis to maturity (DAM) for the set of 24 durum wheat cultivars. Figures in parenthesis indicate the percentage of change from old to modern cultivars. Means for each trait within latitudes, countries and periods followed by the same letter are not significantly different at $P < 0.05$.

	Grain yield	$\Delta^{13}C$	HI	PH	DSA	DAM
	kg ha^{-1}	‰		cm	d	
			Latitude			
North	4074 a	16.2 a	0.31 b	96 a	167 a	40 a
South	2490 b	15.3 b	0.37 a	78 b	150 b	32 b
			Country			
Italy	3304 a	15.8 a	0.35 a	85 b	157 b	37 a
Spain	3260 a	15.6 b	0.34 b	89 a	160 a	35 b
			Period			
Old	2541 c	15.2 c	0.28 c	111 a	163 a	34 c
Intermediate	3470 b	15.8 b	0.36 b	79 b	156 b	38 a
Modern	3837 a	16.1 a	0.39 a	71 c	156 b	36 b
Gains (old to modern)	(51%)	(5.9%)	(41.9%)	(–36%)	(–4.3%)	(5.9%)
			Country–period			
Italian						
Old	2681 b	15.3 c	0.30 c	106 a	159 a	36 c
Intermediate	3544 a	15.9 b	0.37 b	79 b	155 c	39 a
Modern	3687 a	16.2 a	0.38 a	68 c	157 b	37 b
Spanish						
Old	2400 c	15.2 b	0.26 c	116 a	166 a	33 b
Intermediate	3395 b	15.8 a	0.35 b	79 b	158 b	37 a
Modern	3986 a	15.9 a	0.40 a	73 c	156 c	36 a

Table 5. Mean values across environments of grain yield and carbon isotope discrimination ($\Delta^{13}C$), harvest index (HI), plant height (PH), days from sowing to anthesis (DSA), and days from anthesis to maturity (DAM) for each durum wheat cultivar. Data are means of six environments.

Cultivar	Grain yield	$\Delta^{13}C$	HI	PH	DSA	DAM
	kg ha^{-1}	‰		cm	d	
			Italian old			
Balilla Falso	2974 a	15.0 b	0.32 a	106 b	156 b	36 b
Carlojucci	2949 a	15.5 a	0.31 a	98 c	156 b	39 a
Senatore Cappelli	2460 b	15.3 ab	0.27 b	118 a	162 a	35 b
Razza 208	2341 b	15.2 ab	0.29 b	101 c	164 a	32 c
			Italian intermediate			
Adamello	3714 a	16.0 a	0.37 a	69 c	156 a	38 a
Capeiti 8	3545 a	15.9 a	0.38 a	86 b	154 c	40 a
Creso	3716 a	16.1 a	0.37 ab	69 c	155 b	38 a
Trinakria	3201 b	15.5 b	0.35 b	93 a	155 b	39 a
			Italian modern			
Cirillo	3789 ab	16.1 b	0.36 b	70 b	158 a	37 b
Flavio	3280 c	16.4 a	0.37 b	59 c	159 a	35 b
Simeto	4009 a	15.9 b	0.41 a	76 a	154 c	40 a
Zenit	3669 b	16.4 a	0.39 a	68 b	157 b	37 b
			Spanish old			
Blanco Verdeal	2241 b	15.1 a	0.22 b	116 a	164 c	33 a
Clarofino	2359 b	15.1 a	0.28 a	115 a	167 b	32 a
Pinet	2746 a	15.3 a	0.26 a	116 a	165 c	33 a
Rubio de Belalcázar	2254 b	15.1 a	0.27 a	118 a	169 a	32 a
			Spanish intermediate			
Bidi17	2822 c	15.5 b	0.30 c	97 a	160 b	36 ab
Camacho	3418 b	16.0 a	0.35 b	76 b	163 a	35 b
Esquilache	3831 a	15.7 ab	0.38 a	66 c	156 c	38 a
Mexa	3510 b	15.9 a	0.38 a	77 b	153 d	38 a
			Spanish modern			
Ariesol	3872 b	16.0 a	0.41 a	74 b	154 b	37 a
Astigi	4045 ab	15.9 a	0.40 a	77 a	156 a	35 b
Boabdil	4198 a	15.9 a	0.39 b	72 bc	157 a	34 b
Senadur	3830 b	16.0 a	0.41 a	71 c	154 b	37 a

Table 6. Mean values of grain yield, carbon isotope discrimination ($\Delta^{13}C$), harvest index (HI), plant height (PH), days from sowing to anthesis (DSA) and days from anthesis to maturity (DAM) for the durum wheat cultivars with or without dwarfing genes.

Dwarfing genes	Grain yield	$\Delta^{13}C$	HI	PH	DSA	DAM
	kg ha^{-1}	‰		cm	——— d	———
Absent (±SE)	2717 (±113)	15.3 (±0.10)	0.30 (±0.83)	106 (±2.29)	161 (±2.23)	35 (±0.62)
Present (±SE)	3760 (±165)	16.0 (±0.10)	0.38 (± 0.59)	71 (±1.29)	156 (±1.96)	37 (±0.70)
% of change between groups	38.4	4.6	30.2	–33.0	–3.1	5.7

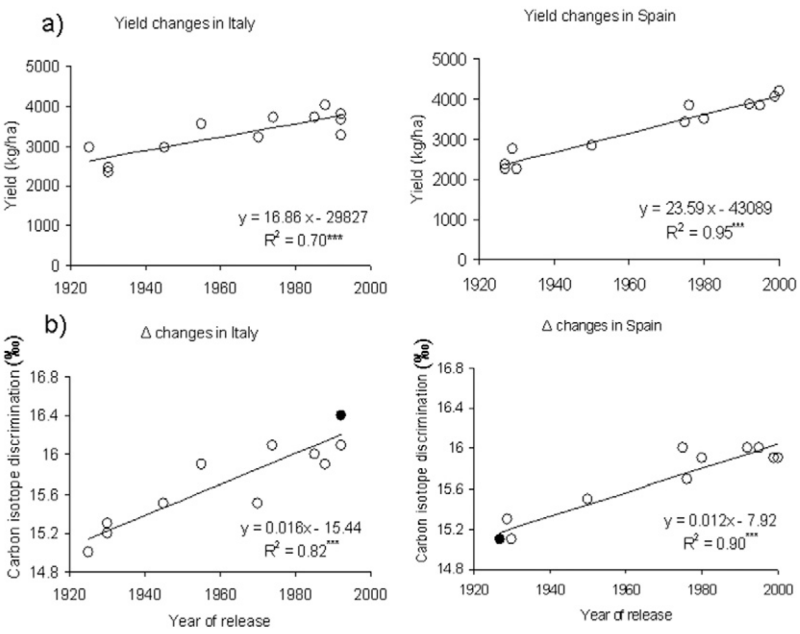

Fig. 1. Absolute changes in (a) grain yield and (b) grain carbon isotope discrimination of 12 Italian and 12 Spanish durum wheat cultivars released during the 20th century. Each point was obtained by averaging data of six environments and three blocks per environment. Solid dots indicate overlapping of two points.

in Italy and 0.72% yr^{-1} in Spain. Changes in $\Delta^{13}C$ were 0.016 ‰ yr^{-1} (equivalent to 0.10% yr^{-1}) in Italy and 0.012 ‰ yr^{-1} (equivalent 0.08% yr^{-1}) in Spain. Mean values calculated separately for cultivars carrying or not carrying dwarfing genes showed that semidwarf cultivars had 38.4% higher yield and 4.6% higher $\Delta^{13}C$ than taller cultivars (Table 6).

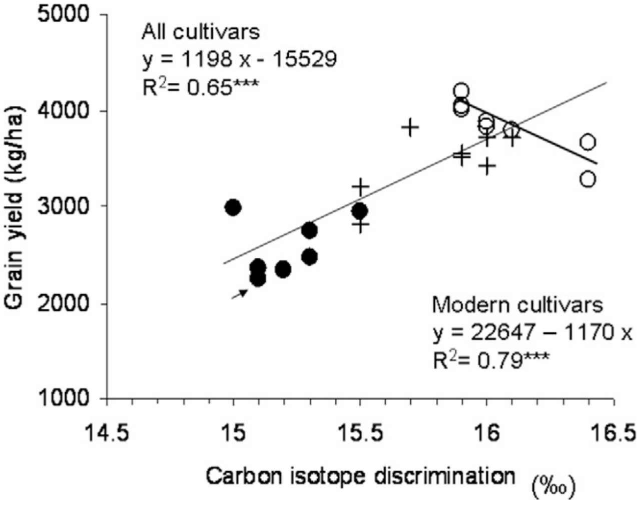

Fig. 2. Relationship between carbon isotope discrimination of kernels and grain yield for durum wheat cultivars released in Italy and Spain in three periods during the 20th century: (solid circle) old, (plus sign) intermediate, and (circle) modern. Each point was obtained by averaging data of six environments and three blocks per environment. The arrow indicates two overlapped dots.

A significant positive association was found between yield and $\Delta^{13}C$ when the data from all genotypes were pooled ($R^2 = 0.65$, $P > 0.001$). However, the correlation tended to be positive for the old and intermediate cultivars, but negative for the modern set (Fig. 2). Phenotypic stability was assessed for yield and $\Delta^{13}C$. The slope of the linear regression, fitted to the relationship between cultivar yield in each experiment on the experiment mean yield, was used as a measure of yield stability according to Finlay and Wilkinson (1963). The relationship between the slopes of these regressions and the cultivar mean across environments is shown in Fig. 3. The horizontal line in Fig. 3a separates input responsive cultivars adapted to favorable environments (slope >1) and cultivars with the highest stability (slope <1). The slope values for yield ranged from 0.32 (Senatore Cappelli) to 1.70 (Astigi). All the tall cultivars except Capeiti were located in the bottom left part of Fig. 3a, corresponding to the region of low yield but high stability. Astigi, Boabdil, and Simeto were the most input-responsive cultivars. The slopes of the regression analysis for $\Delta^{13}C$ varied less than slopes for yield [0.62 (Capeiti 8)–1.34 (Ariesol)] (Fig. 3b).

The increase in the slope values for yield with the year of release (Fig. 4a) indicates that selection enhanced the potential for genotypes to respond to more productive environments. The slopes of the Italian cultivars increased significantly at a rate of 1.12% yr^{-1}, while this increase was 1.39% yr^{-1} for the Spanish cultivars (Fig. 4a). For $\Delta^{13}C$, the slopes increased at a rate of 0.6% yr^{-1} for the Italian germplasm and the slopes remained constant for Spanish cultivars (Fig. 4b).

Changes in Harvest Index, Plant Height, and Phenology

Harvest index was higher in the south and increased significantly over time in both the Italian and Spanish cultivars (Tables 3 and 4). Among the old cultivars, the Italian cultivars had greater HI than did the Spanish cultivars, and the opposite was true for the modern genotypes. Genetic variability for HI existed for all sets of cultivars (Table 5). A 36% reduction in plant height occurred between old and modern genotypes (Table 4). Plants were taller in experiments conducted in northern environments than in southern ones.

The largest changes in phenological stages occurred between old and intermediate cultivars in both countries (Table 4). The period from sowing to anthesis was longer in the Spanish cultivars than the Italian ones, but the latter had a longer grain-filling period. The period to anthesis decreased in modern Spanish cultivars and was shortest in the intermediate group of Italian cultivars. The longest grain-filling period was recorded on intermediate Italian cultivars. However, grain filling lasted 1 and 3 d more in modern Italian and Spanish cultivars, respec-

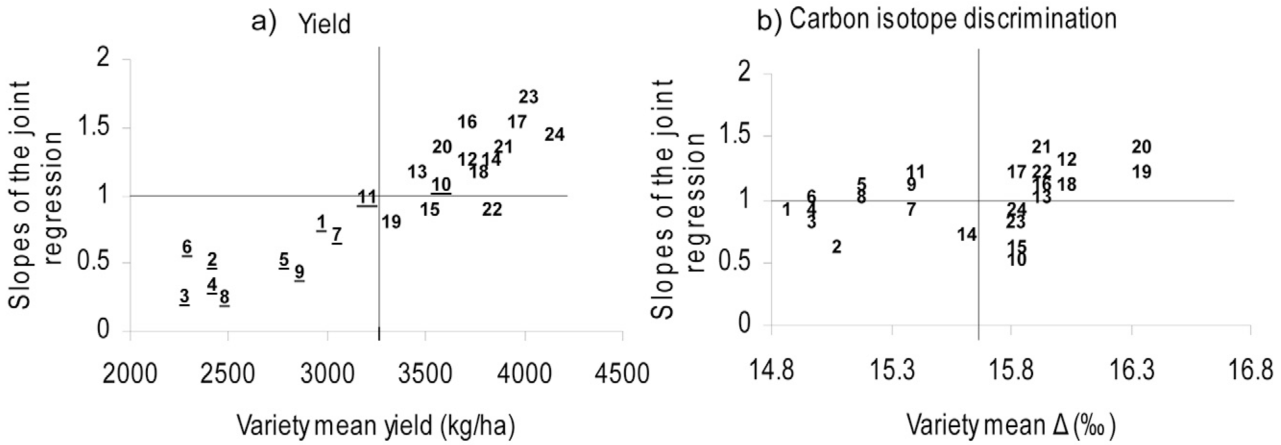

Fig. 3. Relationship between the cultivar stability determined as the slope of the joint regression and the cultivar mean for (a) yield and (b) grain carbon isotope discrimination ($\Delta^{13}C$) for the 24 durum wheat cultivars. Means for grain yield and $\Delta^{13}C$ are symbolized with vertical lines. Numbers correspond to cultivars according to Table 2 1 to 8 = old, 9 to 16 = intermediate, and 17 to 24 = modern. Underlined numbers in Fig. 3a correspond to cultivars not carrying dwarfing genes.

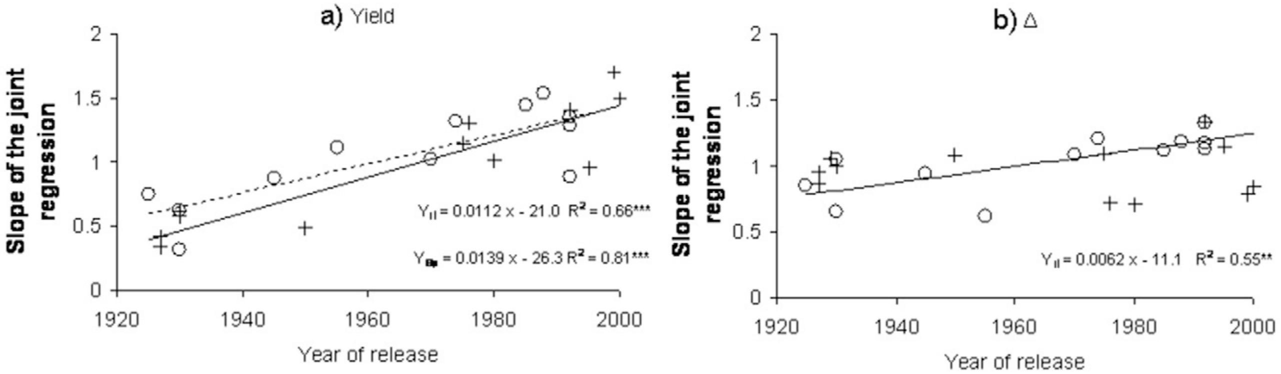

Fig. 4. Absolute changes in the slopes of the joint regressions over the year of release of 12 Italian (circle) and 12 Spanish (plus sign) durum wheat cultivars released during the 20th century. The dotted line corresponds to Spanish cultivars.

tively, than in the old ones. All old Spanish cultivars had a similar grain-filling duration (Table 5). Semidwarf cultivars were 33% shorter, had a higher HI, flowered earlier, and had a longer grain-filling period than the tall ones (Table 6).

Genetic Correlations

The relationship between traits due to pleiotropy or linkage was assessed for tall and semidwarf cultivars separately by means of genetic correlations (Table 7). A strong relationship was found between yield and $\Delta^{13}C$ in both sets of cultivars, but it was positive for tall cultivars and negative for semidwarf cultivars. The opposite was true for the genetic correlation between yield and plant height, with semidwarf cultivars having a positive relationship and tall cultivars having a negative relationship. Yield was negatively associated with the number of days to anthesis in both tall and semidwarf cultivars, but a very strong and positive relationship was found between yield and grain-filling duration in tall genotypes.

DISCUSSION

Environmental Effects

The latitude effect explained most of the variability of the traits studied. Lower temperatures in the north, compared with the south, may have been partially responsible for the longer season length and the greater plant height, $\Delta^{13}C$ values and yields obtained in the northern experiments. A previous study demonstrated that differences in the temperature regimes between the north and the south of Spain accounted for greater durum wheat yields obtained in northern environments (García del Moral et al., 2003). Higher HI obtained in the south may be associated with the shorter plants that were probably the result of warmer temperatures and water stress compared with the north.

Table 7. Genetic correlations between grain yield, carbon isotope discrimination ($\Delta^{13}C$), harvest index (HI), plant height (PH), days from sowing to anthesis (DSA) and days from anthesis to maturity (DAM) for the set of 24 durum wheat cultivars. Data above the diagonal correspond to cultivars without dwarfing genes (tall) and below the diagonal to cultivars with dwarfing genes (semidwarf, shaded data).

	Yield	$\Delta^{13}C$	HI	PH	DSA	DAM
Yield		0.89***	0.84***	−0.92***	−0.99***	0.99***
$\Delta^{13}C$	−0.99***		0.68*	−0.57	−0.58	0.74*
HI	0.57*	−0.34		−0.80**	−0.80**	0.83***
PH	0.56*	−0.54*	0.22		0.75**	−0.76**
DSA	−0.72**	0.26	−0.81***	−0.20		−0.91***
DAM	−0.45	0.12	0.28	0.24	−0.67**	

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

Genetic Improvement of Yield and Associated Traits

The total absolute genetic gain in grain yield throughout the two Mediterranean countries was 20 kg ha^{-1} yr^{-1} (51% of increase), which amounts to a relative genetic gain of 0.61% yr^{-1}. These values are similar to the genetic yield gain of 19.9 kg ha^{-1} yr^{-1} recently reported for durum wheat in Italy (De Vita et al., 2007), and values of 0.4 to 0.6% yr^{-1} reported for bread wheat (Deckerd et al., 1985; Austin et al., 1989; Perry and D'Antuono, 1989; Canevara et al., 1994). However, evaluations of genetic gains by the durum wheat breeding program of International Maize and Wheat Improvement Center (CIMMYT) reached much higher values. Pfeiffer et al. (1996) found that the gain in yield increase in durum wheat between 1967 and 1994 was 1.7% yr^{-1} and a yield increase of almost 3% yr^{-1} over the 1960 to 1984 period was reported by Waddington et al. (1987). Differences between our results and those reported by CIMMYT may be partially due to the testing environments. Yield improvements at CIMMYT were achieved under optimal environments (Worland and Snape, 2001), while our experiments were conducted in Mediterranean environments with moderate stress. The differences in yield improvements may also reflect the impact of a substantial breeding investment at international centers compared to national programs.

Of the 51% of total yield increase during the period under study, 36% was gained from old to intermediate cultivars and only 15% from intermediate to modern ones. This result suggests that recent genetic gains have been more difficult to achieve than they were in the past, when the introduction of dwarfing genes dramatically raised the yield potential (Rajaram, 2001; Reynolds et al., 1996; Donmez et al., 2001). However, this effect was much more noticeable in the Italian cultivars than in the Spanish cultivars. The yield increase between old and intermediate cultivars was 32% in Italy and 41% in Spain, whereas from intermediate to modern cultivars the increase was much lower, but still higher in Spain (4 and 17% in Italy and Spain, respectively).

The stability analysis for yield showed that the ability of durum wheat cultivars to respond to favorable environments (determined through the slopes of the joint regression models), increased significantly over time. Modern cultivars were better adapted to productive environments, but they lost yield stability. This loss of yield stability over time was more pronounced among Spanish than Italian cultivars (Fig. 4a).

Changes in Δ^{13}C of mature grains through time, despite being lower than 6% in both countries, could be a consequence of a greater contribution to grain filling of nonstructural carbohydrates accumulated before anthesis in modern cultivars when compared with the old ones. Unpublished results of our group, with the same set of cultivars used in this study, indicate that the translocation of assimilates accumulated in preanthesis accounted for 25, 27, and 33% of grain weight in old, intermediate, and modern cultivars, respectively.

The results demonstrated that high HI and short duration to anthesis were favorable traits for achieving high yields under Mediterranean conditions. Though they attained similar yields, Italian and Spanish cultivars differed significantly in other traits. The greatest differences in HI and season length between Italian and Spanish germplasm arose from old cultivars, which in Italy probably resulted from breeding programs started at the beginning of the 20th century (Maliani, 1979). By contrast, the limited tradition of durum wheat breeding in Spain before 1970 led to a reliance on foreign germplasm. The substantial increase in yield observed in the Spanish cultivars released in the intermediate period compared to the old one was a direct consequence of the introduction of semidwarf cultivars developed at CIMMYT during the 1970s.

The results indicate that durum wheat yield improvements in Spain and Italy have been associated with a decrease in the number of days from sowing to anthesis and a slight increase in the grain-filling duration. However, the total season length remained unaltered, as has been pointed out for Italian durum wheat by Pecetti and Annicchiarico (1998). Earliness in reaching anthesis of modern cultivars allowed them to avoid unfavorable conditions during the most sensitive phases of kernel growth (Royo et al., 2006). The introduction of dwarfing genes accounted for a large part of the yield increases. This was probably due to the pleiotropic effect of dwarfing genes on plant traits affecting yield formation, such as biomass partitioning to the growing spikes (Youssefian et al., 1992; Borner et al., 1993).

Effect of Dwarfing Genes on Phenology, Harvest Index, Yield, and Δ^{13}C

When all cultivars were considered together, and within the group of tall cultivars, a strong positive association between yield and Δ^{13}C was observed (Fig. 2). It has been suggested that positive relationships between Δ^{13}C and yield are attained when cereals are grown under favorable conditions, while negative relationships have been found in very poor environments (Araus et al., 2002). Moreover, a positive relationship between Δ^{13}C and yield may appear when the differential ability of the genotypes for taking up available water is the main determinant of yield gaps (Richards, 1996) or when constitutive or stress-adaptive traits allow the crop to escape or resist drought stress (Araus et al., 2002). This latter case seems to apply to tall cultivars in which the early heading were the most productive. A long grain-filling duration was a positive trait in tall cultivars, since it led to high HI and yield. The negative associations between plant height and yield, HI and Δ^{13}C indicate that, among the tall cultivars, the tallest ones had the lowest Δ^{13}C values and the lowest productivity.

The scenario differed sharply for the modern group of cultivars in which negative and significant phenotypic ($r = -0.89$, $P < 0.001$) and genetic ($r_g = -0.99$, $P < 0.001$) correlations between yield and Δ^{13}C were found. This indicates that cultivars with high yield had low Δ^{13}C. Negative relationships between yield and Δ^{13}C in young leaves have been extensively reported in the literature for environments in which the water available is exhausted during the crop cycle (Condon et al., 2002; Richards et al., 2002). Our study demonstrated that within the semidwarf group of cultivars the most productive were the tallest, earliest to anthesis, with low Δ^{13}C values and with superior HI.

CONCLUSIONS

Grain yield, plant height, and HI were the traits most affected by durum wheat breeding in Italy and Spain during the 20th century, while Δ^{13}C and season length were slightly modified. The incorporation of dwarfing genes led to greater yields due to the response of improved cultivars to favorable environments. High HI and early flowering are traits associated with high durum wheat yield under Mediterranean conditions. The change in the trend of the relationship between yield and $\Delta^{13}C$ in modern cultivars, when compared with the old and intermediate, may indicate that differences may exist between these groups regarding their ability for taking up available water, but this assumption needs further investigation.

Early heading and a long grain-filling period were positively correlated with yield within tall cultivars, while increased plant height was a negative trait. Among the semidwarf cultivars, low $\Delta^{13}C$ conferred an adaptive advantage that resulted in greater yields. However, unlike plant height, a long grain-filling period was not advantageous among the semidwarf cultivars.

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