



# Breeding effects on the cultivar × environment interaction of durum wheat yield



Joan Subira<sup>a</sup>, Fanny Álvaro<sup>a</sup>, Luis F. García del Moral<sup>b</sup>, Conxita Royo<sup>a,\*</sup>

<sup>a</sup>IRTA (Institute for Food and Agricultural Research and Technology), Field Crops Program, 25198 Lleida, Spain

<sup>b</sup>Departamento de Biología Vegetal, Facultad de Ciencias, Instituto de Biotecnología, Universidad de Granada, 18071 Granada, Spain

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## ABSTRACT

Understanding the effect of past durum wheat breeding activities on the cultivar × environment (C × E) interaction of yield and yield components may guide future breeding strategies. A historical series of 24 cultivars released in Italy and Spain during the 20th century was grown in 13 environments with average yields ranging between 1425 and 6670 kg ha<sup>-1</sup>. The most important environmental factors affecting the C × E interaction for yield were reference evapotranspiration before anthesis and water input during grain filling. The response of cultivars to environmental variables in terms of yield and yield components was associated to the allelic composition for the *Rht-B1* locus. Improved semi-dwarf cultivars (carrying the *Rht-B1b* allele) had the best yield performance in environments with high water input after anthesis, while tall cultivars (carrying allele *Rht-B1a*) were better adapted to environments with high evapotranspirative demand before anthesis and low water input after it. The introduction of the *Rht-B1b* allele improved the capacity of the crop to respond to water availability during grain filling by increasing the number of grains spike<sup>-1</sup> and grain weight. Yield increases due to breeding caused a loss of stability from the static viewpoint, but not from a dynamic approach based on the superiority measure ( $P_i$ ). Some semi-dwarf cultivars maintained the levels of yield stability characteristic of the old tall ones. Our results suggest that durum breeding in the 20th century enhanced the response of the crop to environmental improvements.

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## 1. Introduction

Durum wheat (*Triticum turgidum* L. var. *durum*) is a staple crop in the Mediterranean Basin, where Italy and Spain are among the main European producers (EUROSTAT, 2014). In Mediterranean countries, which represent around 75% of the world durum-wheat growing area, durum wheat is grown mainly under rain-fed conditions. In these environments, yield is generally constrained by water scarcity and heat stress during grain filling, since low and unpredictable seasonal rainfalls and high temperatures are common at the end of the crop cycle (Loss and Siddique, 1994). Moreover, the diversity of thermo-pluviometric patterns results in large spatial and temporal yield fluctuations (Anderson, 2010; De Vita et al., 2010; García del Moral et al., 2003, 2005; Royo et al., 2010). The expected advent of more adverse weather conditions for wheat production in Europe as a consequence of climate change (Trnka et al., 2014; Yang et al., 2014) will require unprecedented efforts towards the release of new cultivars, not only more productive,

but also offering improved yield stability across a range of environmental conditions.

The study of historical series formed by cultivars representative of the germplasm developed and cultivated in different periods provide useful information for understanding the agronomical and physiological mechanisms responsible for the yield changes observed over time. Such kind of studies have shown that different approaches were followed in Italy and Spain to release improved durum wheat cultivars (Royo, 2005). Italian breeding programmes, largely relying on local landraces, were conducted from the beginning of the century (Borghini, 2001; Martos et al., 2005). However, in Spain breeding efforts were discontinuous, and foreign germplasm, mainly from CIMMYT, was massively introduced in the country from the 1970s (Royo 2005; Royo et al., 2007). Although different, both approaches resulted in the modification of identical crop characteristics and genetic gains of similar magnitude, 17–20 kg ha<sup>-1</sup> y<sup>-1</sup> in Italy (De Vita et al., 2007; Royo et al., 2008), and 24 kg ha<sup>-1</sup> y<sup>-1</sup> in Spain (Royo et al., 2008). Compared with unimproved germplasm, modern Italian and Spanish cultivars have early flowering (Isidro et al., 2011), a larger harvest index, more spikes per unit area and more grains per spike (Álvarez et al., 2008b; Royo et al., 2007), while grain weight remained almost unchanged (Álvarez et al., 2008b). The introduction of dwarfing

\* Corresponding author. Tel.: +34 973 032850x1521; fax: +34 973 238301.

E-mail addresses: [joan.subira@irta.cat](mailto:joan.subira@irta.cat) (J. Subira), [fanny.alvaro@irta.cat](mailto:fanny.alvaro@irta.cat) (F. Álvaro), [lfgm@ugr.es](mailto:lfgm@ugr.es) (L.F. García del Moral), [conxita.royo@irta.es](mailto:conxita.royo@irta.es) (C. Royo).

genes during the second half of the 20th century produced the greatest advances in durum wheat breeding because they not only strongly affected plant height (Peng et al., 1999), thus, reducing plant lodging, but had also a pleiotropic effect on various agronomic traits (Elias and Manthey, 2005; Singh and Trethowan, 2007). However, the effect of dwarfing genes on the cultivar  $\times$  environment (C  $\times$  E) interaction of durum wheat has been poorly explored until now.

Different cultivars may show contrasting responses to a given environment as a consequence of the C  $\times$  E interaction, a critical issue in cultivar evaluation (Becker and León, 1988). The assessment of the relative contributions of the cultivar, the environment and the C  $\times$  E interaction to cultivar performance is essential to determine the adaptation capacity, which is the cultivar ability to reach its full potential in a specific environment in spite of the constraints imposed on the crop. Some authors have suggested that good performance under severe stress conditions and maximum yield potential in optimal environments are mutually exclusive concepts. They consider the presence in cultivars of constitutive traits for specific adaptation to limiting environments advantageous (Annicchiarico et al., 2005). Nevertheless, breeding programs of the International Maize and Wheat Improvement Center (CIMMYT) that seek wide adaptation and select genotypes at sites of high yield potential (Braun et al., 1996) have also been successful in providing yield increases in limiting environments (Araus et al., 2002; Trethowan et al., 2002).

Yield stability is a property that cultivars need in order to respond to the seasonal fluctuations characteristic of Mediterranean environments. Stability is usually defined as the unaltered performance of a cultivar between years and/or locations and may be considered from two different viewpoints: (i) the static or biological concept, which refers to the lack of response of a cultivar to any variation of the environment; and (ii) the dynamic or agronomic concept, which refers to the fact that a cultivar will respond predictably to improved growing conditions (Becker and León, 1988; Cubero and Flores, 2003). The static concept is usually linked to low-yielding cultivars (Becker and León, 1988), while the agronomic concept must be accomplished together with improved yield potential to ensure that a cultivar maintains its superiority under a wide range of environments, management practices, and biotic and abiotic stresses (Singh and Trethowan, 2007). A number of statistical methods for elucidating the information contained in a C  $\times$  E interaction data matrix have been proposed for assessing adaptation and stability (Rharabti et al., 2003).

The objectives of this study were (I) to assess the changes produced by breeding activities during the last century in the C  $\times$  E interaction for yield and yield components, (II) to identify the meteorological variables involved in the differential response of the cultivars to the environment, and (III) to ascertain the changes over time in the stability of yield and yield components.

## 2. Material and methods

### 2.1. Experimental data

Thirteen field experiments were conducted during six growing seasons, from 2000 to 2005, at three sites: Gimenez (41°40'N, 0°20'E) and Foradada (41°88'N, 0°76'E; only in 2002) in north-east Spain, and Chimeneas (37°08'N, 3°49'E) in southern Spain (Table 1). 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 at winter and spring and less evenly distributed precipitation.

Each experiment consisted of a randomized complete block design with three replicates and plots of 12 m<sup>2</sup> (8 rows 0.15 m apart) planted at a sowing rate of 400 and 350 viable seeds m<sup>-2</sup> in the north-eastern and southern experiments, respectively. Plot management was implemented to maximize yield at each location to the extent allowed by local conditions. Fertilization at seed bed and top dressing was adjusted for each experiment according to soil nutrient content and expected crop extractions in order to prevent lodging (Table 1). Weeds were chemically controlled with diclofop-methyl(methyl 2-[2,4-dichlorophenoxy] phenoxy]propanoate at 3 L ha<sup>-1</sup> and bromoxynil(3,5-dibromo-4-hydroxybenzotrile)+ioxynil (3,5-diiodino-4-hydroxybenzotrile) at 3 L ha<sup>-1</sup>. Pests were controlled with esfenvalerate[(S)- $\alpha$ -cyano-3-phenoxybenzyl(S)-2-(4-chlorophenyl)-3-methylbutyrate]+phenitrothion(O,O-dimethyl-O-[3-methyl-4-nitro-phenyl]-phosphorotioate) at 3 L ha<sup>-1</sup>. Diseases were prevented with triadimenol(1-(4-chlorophenoxy)-3,3-dimethyl-1-(1,2,4-triazol-1-yl)butan-2-ol) at 0.5 L ha<sup>-1</sup>.

Daily agro-meteorological variables were recorded in all the environments from weather stations placed at each site. For environment characterization, these data were averaged for two growing periods: from sowing to anthesis (Zadoks stage 65; Zadoks et al., 1974) and from anthesis to physiological maturity (Zadoks stage 87), using as dates of anthesis and physiological maturity the mean of all plots in each environment. The variables calculated from sowing to anthesis (SA) and from anthesis to physiological maturity (AM) were length of the period expressed as thermal time (TT, GDD growing degree-days), average daily mean, maximum and minimum temperatures ( $T_m$ ,  $T_{max}$  and  $T_{min}$ , respectively, °C), reference evapotranspiration (ETo, mm), mean daily relative air humidity (RH, %) and total water input (WI, mm) including irrigation and rainfall.

Plots were harvested mechanically at ripening and yield was expressed on a 12% grain moisture basis. From a random sample of the plants contained in a 1-m-long sample taken from a central row of each plot at ripening, the following yield components were determined: number of spikes m<sup>-2</sup>, number of grains spike<sup>-1</sup> and thousand kernel weight.

### 2.2. Plant material

Twenty-four durum wheat (*T. turgidum* L. var. *durum*) cultivars, 12 from Italy and 12 from Spain, were selected to represent the germplasm obtained in both countries during the last century (Table 2). According to their year of release, cultivars were assigned to three periods: old (mainly landraces, cultivated before 1945), intermediate (released between 1950 and 1985) and modern (released from 1988 to 2000). The intermediate group included early semi-dwarf cultivars derived from CIMMYT germplasm, while the modern group included cultivars released by local breeding programmes in both countries during the 1990s. The presence of the *Rht-B1b* dwarfing allele in the cultivars was assessed with a PCR-based marker following Ellis et al. (2002) in DNA samples obtained from young leaf tissues of single plants cultivated under greenhouse conditions. In previous studies, using the test for sensitivity to gibberellic acid conducted following Gale and Gregory (1977), the Italian cultivar 'Adamello' was classified as not carrying dwarfing genes (Isidro et al., 2011; Álvaro et al., 2008a,b,c; Royo et al., 2007), but the PCR-based marker demonstrated that it carries the dwarfing allele *Rht-B1b* (Table 2).

### 2.3. Statistical analyses

Combined analysis of variance (ANOVA), in which the cultivar and the C  $\times$  E interaction effects were partitioned into period, origin and period  $\times$  origin interaction, were performed for yield and

**Table 1**  
Localization and description of the 13 Spanish environments of the study.

Site	Gimenells (North)						Foradada (North)	Chimeneas (South)					
Coordinates	41°40'N, 0°20'E						41°88'N, 0°76'E	37°08'N, 3°49'W					
Altitude (m asl)	200						580	684					
Soil texture	Fine loamy						Fine loamy	Silty clay					
Harvest year	2000	2001	2002	2003	2004	2005	2002	2000	2001	2002	2003	2004	2005
Fertilizer (kg ha <sup>-1</sup> )													
Seed bed (N–P <sub>2</sub> O <sub>5</sub> –K <sub>2</sub> O)	106-80-80	80-150-150	80-150-150	75-75-75	75-75-75	75-75-75	60-150-60	52-52-52	52-52-52	52-52-52	45-45-45	45-45-45	45-45-45
Top dressing (N)	79	130	97	35	35	35	104	26	26	26	35	35	35
Sowing date	26 November	17 November	5 December	26 November	16 December	26 November	31 October	9 December	28 November	27 November	23 December	13 November	10 December
	1999	2000	2001	2002	2003	2004	2001	1999	2000	2001	2002	2003	2004
Experiment code	NI00	NI01	NI02	NI03	NI04	NI05	NR02	S00	S01	S02	S03	S04	S05
Environmental conditions from sowing to anthesis (SA)													
TT (GDD)	1400	1497	1241	1426	1281	1219	1458	1424	1673	1676	1590	1769	1482
T <sub>m</sub> (°C)	8.04	9.14	7.56	8.64	8.13	7.24	6.82	10.0	10.6	9.99	10.7	9.81	9.43
T <sub>max</sub> (°C)	14.3	14.9	13.3	14.7	13.6	13.2	12.2	17.7	17.6	17.4	17.5	16.9	17.8
T <sub>min</sub> (°C)	2.63	3.97	2.47	3.22	3.24	1.96	2.21	2.37	4.96	3.85	4.93	4.08	2.30
ETo (mm)	266	236	214	244	206	226	265	299	288	301	309	290	348
RH (%)	78.1	81.4	83.0	80.3	95.6	91.4	83.8	61.3	72.8	69.3	68.6	71.2	56.5
WI (rain-fall + irrigation, mm)	101 + 160	125 + 150	94.8 + 182	170 + 150	202 + 85	62.7 + 150	286 + 0	155 + 0	348 + 0	301 + 0	249 + 40	334 + 40	89.8 + 120
Environmental conditions from anthesis to maturity (AM)													
TT (GDD)	432	383	305	521	338	348	296	588	555	291	271	286	388
T <sub>m</sub> (°C)	19.5	17.3	16.7	17.6	20.0	18.8	18.2	18.4	16.6	18.1	21.3	16.2	21.1
T <sub>max</sub> (°C)	26.7	24.5	23.0	25.5	28.2	26.8	25.3	25.8	24.0	25.8	30.0	23.4	30.3
T <sub>min</sub> (°C)	12.9	10.5	10.2	10.4	12.4	11.7	10.2	10.9	9.68	10.4	12.6	10.1	12.0
ETo (mm)	177	181	155	117	140	140	153	129	139	150	118	139	182
RH (%)	70.1	70.5	65.4	78.9	87.9	85.2	59.4	56.1	57.6	51.4	45.6	66.9	38.8
WI (rain-fall + irrigation, mm)	91.1 + 0	116 + 0	87.4 + 0	62.5 + 0	6.03 + 65	52.9 + 0	63.0 + 0	68.6 + 0	48.4 + 0	20.6 + 0	0	79.8 + 0	6.00 + 0
Mean yield (kg ha <sup>-1</sup> )	3424	5241	4541	5378	6495	6670	2879	2222	2113	3131	2571	4327	1425

TT: thermal time calculated as growing degree-days; T<sub>m</sub>: mean daily temperature; T<sub>max</sub> and T<sub>min</sub>: average daily maximum and minimum daily temperatures; ETo: reference evapotranspiration computed by the Penman–FAO methodology (Allen et al., 1998); RH: average daily relative mean humidity; WI: water input (rainfall + irrigation).

yield components. For each trait the  $C \times E$  interaction was partitioned according to the AMMI model (Gauch and Zobel, 1997) and the percentage of the sum of squares explained by each interaction principal component axis (IPCA) was calculated. Factorial regression analyses were performed to identify the environmental variables with a major effect on the studied traits, thus keeping the most explanatory model for each of them. Environmental covariables corresponding to the sowing to anthesis and anthesis to maturity periods were considered for yield, number of spikes  $m^{-2}$  and number of grains spike $^{-1}$ , while for thousand kernel weight only variables from anthesis to maturity were considered.

Four stability indices were calculated for each trait with the whole set of data: the slope of the joint regression analysis ( $b$ ; Finlay and Wilkinson, 1963), the environmental variance ( $S^2_{xi}$ ; Roemer, 1917), the superiority measure ( $P_i$ ; Lin and Binns, 1988), and the distance of each cultivar from the origin of the axes in the AMMI biplot ( $v_i$ ; Grausgruber et al., 2000). In order to determine the changes caused by breeding activities on the stability of the studied traits, linear regression models were fitted to the relationship between the stability indices of each cultivar and its year of release. Pearson correlation coefficients were calculated between stability indices with significant changes over time. Statistical analyses were performed with Enterprise Guide v4.2 (SAS Institute, 2008), JMP V8 (SAS Institute, 2009) and GenStat v16 (VSN International, 2013) statistical software.

### 3. Results

#### 3.1. Environmental conditions

The environmental conditions from sowing to anthesis differed at northern and southern locations. Within each crop season, north-

ern environments had a shorter pre-anthesis period measured in thermal time, and showed lower mean, maximum and minimum temperatures and reference evapotranspiration, and higher relative humidity than southern ones (Table 1). From anthesis to maturity, northern environments were more humid and in general received a greater water input than southern ones, but even so environmental variables largely fluctuated between years in both the north and south. Average yield across cultivars ranged in the north from 2879  $kg\ ha^{-1}$  in Rainfed-2002 (NR02) to 6670  $kg\ ha^{-1}$  in Irrigated-2005 (NI05), and in the south from 1425  $kg\ ha^{-1}$  in 2005 (S05) to 4327 in 2004 (S04).

#### 3.2. Cultivar $\times$ environment interaction for yield

The ANOVA revealed that the effects of the environment, cultivar and  $C \times E$  interaction accounted for 76.4%, 10.4% and 9.4%, respectively, of the total variance for yield (Table 3). The mean yield of cultivars across environments ranged from 2710  $kg\ ha^{-1}$  (cv. 'Rubio de Belalcázar') to 4759  $kg\ ha^{-1}$  (cv. 'Boabdil') (Table 2). Differences between periods explained 79.9% of the variance induced by the cultivar effect, while differences between origins only explained 0.34%. Similarly, the period  $\times$  environment and the origin  $\times$  environment interactions explained 39.9% and 6.9% of the  $C \times E$  interaction, respectively (Table 3).

The first two IPCAs of the AMMI model explained 69.3% of the  $C \times E$  interaction, while IPCA3 explained an additional 11.1% (Table 3). The first IPCA, which explained 52.8% of the  $C \times E$  sum of squares, classified cultivars according to their period of release, with old and modern cultivars being clearly separated (Fig. 1A). Old cultivars were placed in the positive direction of IPCA1 and the Italian cultivar 'Senatore Cappelli' was the one with the highest value for this axis. Although intermediate cultivars did not form a sep-

**Table 2**  
Origin, year of release, presence of the *Rht-B1b* dwarfing allele determined with SSR, and yield and yield components in the 24 Italian and Spanish durum wheat cultivars of the historical series included in this study. Yield and yield components are means across 13 environments.

Period	Cultivar	Year of release	<i>Rht-B1b</i> presence	Yield $\pm$ SE ( $kg\ ha^{-1}$ )	NS $m^{-2} \pm$ SE	NGS $\pm$ SE	TKW $\pm$ SE (g)
Italian old							
	Balilla Falso	<1930	–	3680 $\pm$ 293	378 $\pm$ 28.7	26.3 $\pm$ 0.69	42.1 $\pm$ 1.02
	Razza 208	<1930	–	2942 $\pm$ 216	238 $\pm$ 15.1	28.3 $\pm$ 1.22	49.6 $\pm$ 1.22
	Senatore Cappelli	1930	–	3116 $\pm$ 236	240 $\pm$ 12.7	32.5 $\pm$ 1.18	48.0 $\pm$ 1.27
	Carlojucchi	1945	–	3450 $\pm$ 278	276 $\pm$ 16.2	32.0 $\pm$ 1.37	44.8 $\pm$ 0.91
Italian intermediate							
	Capeiti 8	1955	–	4355 $\pm$ 339	361 $\pm$ 26.9	32.2 $\pm$ 1.35	42.2 $\pm$ 0.86
	Trinakria	1970	–	3841 $\pm$ 282	312 $\pm$ 20.5	30.0 $\pm$ 0.98	41.9 $\pm$ 1.06
	Creso	1974	+	3999 $\pm$ 291	349 $\pm$ 20.6	30.1 $\pm$ 1.18	42.2 $\pm$ 1.04
	Adamello	1985	+	4306 $\pm$ 315	303 $\pm$ 17.7	33.9 $\pm$ 1.22	48.2 $\pm$ 1.32
Italian modern							
	Simeto	1988	+	4652 $\pm$ 346	312 $\pm$ 16.8	37.4 $\pm$ 1.45	49.2 $\pm$ 1.27
	Cirillo	1992	+	4454 $\pm$ 335	323 $\pm$ 20.4	36.2 $\pm$ 1.28	41.7 $\pm$ 1.02
	Flavio	1992	+	3899 $\pm$ 248	321 $\pm$ 16.8	34.8 $\pm$ 1.53	40.3 $\pm$ 1.19
	Zenit	1992	+	4268 $\pm$ 283	345 $\pm$ 20.5	32.4 $\pm$ 1.10	42.5 $\pm$ 1.14
Spanish old							
	Blanco Verdeal	<1930	–	3060 $\pm$ 264	267 $\pm$ 16.4	27.7 $\pm$ 1.18	47.9 $\pm$ 1.31
	Clarofino	<1930	–	2849 $\pm$ 212	263 $\pm$ 14.9	30.0 $\pm$ 1.03	41.7 $\pm$ 0.78
	Pinet	<1930	–	3332 $\pm$ 257	260 $\pm$ 17.3	31.8 $\pm$ 1.07	45.2 $\pm$ 1.17
	Rubio de Belalcázar	<1930	–	2710 $\pm$ 205	279 $\pm$ 19.9	29.8 $\pm$ 1.10	40.2 $\pm$ 0.87
Spanish intermediate							
	Bidi 17	1950	–	3734 $\pm$ 291	288 $\pm$ 19.0	32.2 $\pm$ 1.24	45.7 $\pm$ 1.22
	Camacho	1975	+	3973 $\pm$ 276	265 $\pm$ 16.5	36.3 $\pm$ 1.35	45.8 $\pm$ 1.28
	Esquilache	1976	+	4458 $\pm$ 326	345 $\pm$ 21.6	33.8 $\pm$ 1.30	42.8 $\pm$ 1.13
	Mexa	1980	+	3949 $\pm$ 288	342 $\pm$ 22.2	32.8 $\pm$ 1.28	43.8 $\pm$ 1.23
Spanish modern							
	Ariesol	1992	+	4380 $\pm$ 302	315 $\pm$ 18.3	35.9 $\pm$ 1.19	43.6 $\pm$ 1.21
	Senadur	1995	+	4294 $\pm$ 263	344 $\pm$ 23.7	34.9 $\pm$ 1.07	43.2 $\pm$ 1.37
	Astigi	1999	+	4617 $\pm$ 354	318 $\pm$ 18.1	42.7 $\pm$ 1.35	48.2 $\pm$ 1.07
	Boabdil	2000	+	4759 $\pm$ 324	358 $\pm$ 21.9	33.2 $\pm$ 1.16	45.2 $\pm$ 1.35

NS  $m^{-2}$ : number of spikes  $m^{-2}$ ; NGS: number of grains spike $^{-1}$ ; TKW: thousand kernel weight.

**Table 3**

Percentage of the sum of squares (SS) in the ANOVA, AMMI and factorial regression models for the partitioning of the cultivar  $\times$  environment interaction for yield of the historical series of 24 Italian and Spanish durum wheat cultivars grown in 13 environments. ETo: reference evapotranspiration, WI: water input. SA and AM within parentheses stand for the sowing-anthesis and anthesis-maturity periods, respectively.

Source of variation	df	SS (%)	$-\log(P)$
Total	935		
ANOVA			
Environment	12	76.4	20.7
Block (environment)	26	1.00	25.2
Cultivar	23	10.4	183
Period	2	79.9	178
Origin	1	0.34	2.21
Origin $\times$ period	2	2.94	13.4
Cultivar(origin $\times$ period)	18	16.8	50.5
Cultivar $\times$ environment	276	9.41	89.9
Period $\times$ environment	24	39.9	93.1
Origin $\times$ environment	12	6.95	20.4
Origin $\times$ period $\times$ environment	24	4.48	7.99
Cultivar(origin $\times$ period) $\times$ environment	216	48.7	47.4
AMMI			
Cultivar $\times$ environment	276	9.41	89.9
IPCA1	34	52.8	109
IPCA2	32	16.5	38.7
IPCA3	30	11.1	25.0
Residuals	180	19.6	
Factorial regression			
Cultivar $\times$ environment	276	9.41	89.9
ETo <sub>(SA)</sub> $\times$ cultivar	23	18.1	46.8
WI <sub>(AM)</sub> $\times$ cultivar	23	12.1	30.8
Deviations	230	69.8	
Cultivar $\times$ environment	276	9.41	89.9
Period $\times$ environment	24	39.9	93.1
ETo <sub>(SA)</sub> $\times$ period	2	19.1	12.4
WI <sub>(AM)</sub> $\times$ period	2	15.8	10.3
Deviations	20	65.1	
Error	598	2.81	

arate cluster, 'Creso' and 'Camacho' were located in the positive direction of IPCA2, while 'Adamello', 'Esquilache' and 'Mexa' were in the negative direction. 'Adamello' and 'Mexa' were the closest to modern and old cultivars, respectively. Among the intermediate group, cultivars carrying the *Rht-B1b* allele tended to be located close to the modern cultivars, while those that did not carry it were near to the old ones. Southern environments were placed in the positive direction of IPCA2, while the irrigated northern ones were mostly in the negative direction, except North-Irrigated-2002 (NI02), which was located close to South-2004 (S04). The position of the environments within the biplot of the AMMI analysis indicates that the modern cultivars and those carrying the *Rht-B1b* allele performed better in environments South-2004 (S04) and North-Irrigated-2002 (NI02) than in the remainder.

The most explanatory model obtained by factorial regression accounted for 30.2% of the C  $\times$  E interaction sum of squares, with 16.7% of its degrees of freedom, and included two covariables: reference evapotranspiration from sowing to anthesis [ETo<sub>(SA)</sub>] and water input from anthesis to maturity [WI<sub>(AM)</sub>] (Table 3). Both covariables also explained 34.9% of the period  $\times$  environment interaction. The covariables retained in the model were depicted in the AMMI biplot according to their correlation to the first two IPCAs (Fig. 1A). Water input from anthesis to maturity was strongly and negatively correlated with IPCA1, and was positioned in the same direction as modern cultivars, while ETo<sub>(SA)</sub> was located in the positive direction of IPCA1 and IPCA2 close to five of the six southern environments, the old Spanish cultivars 'Rubio de Belalcázar' and 'Clarofino' and the old Italian cultivar 'Razza 208'.

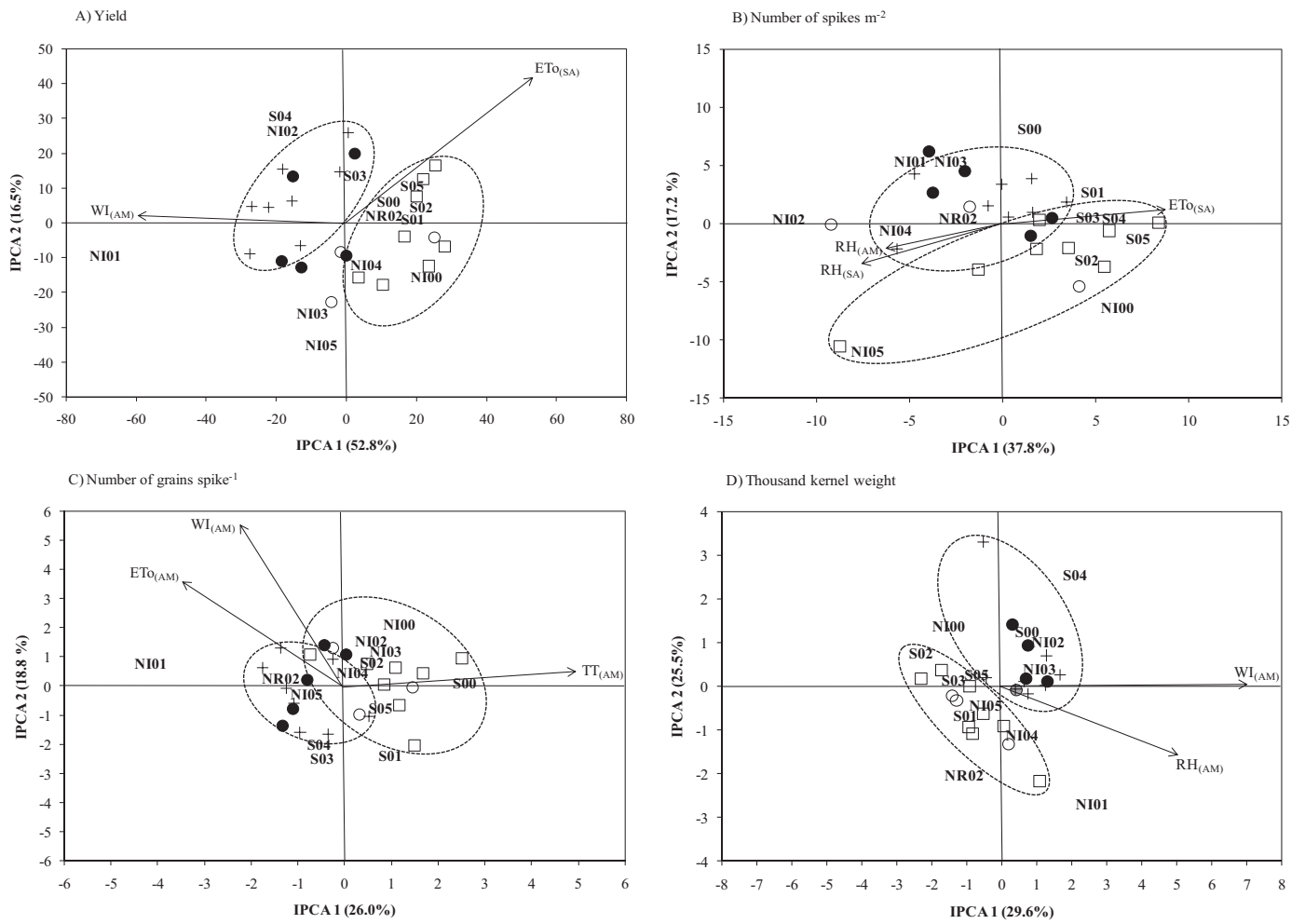
### 3.3. Cultivar $\times$ environment interaction for yield components

The ANOVA showed that the number of spikes  $m^{-2}$  was the yield component most affected by the environmental conditions, as the environment factor explained 71.3% of the total variance for this trait, while it accounted for 54.2% and 66.5% of the total variance for the number of grains spike $^{-1}$  and thousand kernel weight, respectively (Table 4). However, the number of spikes  $m^{-2}$  was also the yield component that showed the lowest C  $\times$  E interaction. Cultivar means across environments ranged between 238 and 378 for the number of spikes  $m^{-2}$ , and both values were recorded in old Italian cultivars (Table 2). On the other hand, number of grains spike $^{-1}$ , which showed the largest cultivar effect (17.7%), also had the highest C  $\times$  E interaction, which explained 16.8% of the total variance (Table 4). The number of grains spike $^{-1}$  ranged between 26.3 in 'Balilla Falso' and 42.7 in 'Astigi', and thousand kernel weight was lowest in 'Astigi' and highest in 'Simeto' (Table 2). The percentage of the sum of squares of the C  $\times$  E interaction accounted by differences between periods ranged from 14.0% for number of spikes  $m^{-2}$  to 19.3% for thousand kernel weight (Table 4), all of them lower than the 39.9% for yield, as shown in Table 3.

The first three IPCAs explained 69.4%, 58.8% and 65.9% of the C  $\times$  E sum of squares for number of spikes  $m^{-2}$ , number of grains spike $^{-1}$  and thousand kernel weight, respectively (Table 5 and Fig. 1B–D). One of the two environmental covariables [ETo<sub>(SA)</sub>] retained in the factorial regression model that dissected the C  $\times$  E interaction for yield also entered the model for the number of spikes  $m^{-2}$ . Reference evapotranspiration from sowing to anthesis jointly with the average daily relative humidity from anthesis to maturity [RH<sub>(AM)</sub>] and from sowing to anthesis [RH<sub>(SA)</sub>] explained 52.8% of the C  $\times$  E sum of squares (Table 5A). These covariables were highly correlated with IPCA1 (Fig. 1B), which tended to separate the environments according to their latitude, with the exception of North-Irrigated-2000 (NI00), which was located in the positive direction of this axis, close to the southern environments due to its high ETo<sub>(SA)</sub>. The vector of ETo<sub>(SA)</sub> was close to southern environments, in accordance with their greatest ETo<sub>(SA)</sub>, as shown in Table 1. All the remaining northern environments were in the direction of RH<sub>(SA)</sub> and RH<sub>(AM)</sub>. No clear trend was observed in the behaviour of cultivars of different periods regarding these environmental covariables, because old and modern cultivars were mainly separated along IPCA2, but they showed large variability within periods. Among old cultivars, 'Balilla Falso', which was the one with the highest number of spikes  $m^{-2}$ , was close to North-Irrigated-2005 (NI05), in Fig. 1B, while 'Senatore Cappelli', which was among the cultivars with the lowest number of spikes  $m^{-2}$ , was the closest to the vector of ETo<sub>(SA)</sub>.

The C  $\times$  E interaction for the number of grains spike $^{-1}$  was mainly due to the different sensitivities of the cultivars to three post-anthesis environmental variables: thermal time [TT<sub>(AM)</sub>], water input [WI<sub>(AM)</sub>] and reference evapotranspiration [ETo<sub>(AM)</sub>]. These three variables accounted for 32.3% of the C  $\times$  E sum of squares and TT<sub>(AM)</sub> and ETo<sub>(AM)</sub> for 37.1% of the period  $\times$  environment interaction (Table 5). Modern and intermediate cultivars carrying the *Rht-B1b* allele were mainly placed in the negative direction of the IPCA1, indicating that they tended to produce more grains spike $^{-1}$  in environments with low TT<sub>(AM)</sub>, and high WI and ETo after anthesis (Fig. 1C).

The lowest thousand kernel weight corresponded to 'Astigi' and the highest to 'Simeto' (Table 2). The regression model explaining the C  $\times$  E interaction for thousand kernel weight included two environmental covariables after anthesis: water input [WI<sub>(AM)</sub>] and average daily relative humidity [RH<sub>(AM)</sub>], which jointly accounted for 24.1% of the C  $\times$  E interaction (Table 5C). The AMMI biplot (Fig. 1D) clustered old and intermediate tall cultivars apart from



**Fig. 1.** Biplot of the of the first two axes of the AMMI model for: (A) yield, (B) number of spikes m<sup>-2</sup>, (C) number of grains spike<sup>-1</sup>, and (D) thousand kernel weight. Environments are indicated in bold (NI, north irrigated; NR, north rainfed; S, south) followed by the year of the experiment. Cultivars are identified as follows for each period: (□) old, (●) intermediate cultivars carrying the *Rht-B1b* allele, (○) intermediate cultivars not carrying the *Rht-B1b* allele, and (+) modern. ET0: reference evapotranspiration; RH: average daily relative humidity; TT: thermal time; WI: water input. Subscripts SA and AM within parentheses stand for the sowing-anthesis and anthesis-maturity periods, respectively.

the modern and intermediate ones carrying the *Rht-B1b* dwarfing allele. The latter were mostly placed in the positive direction of IPCA1, which was strongly correlated with WI<sub>(AM)</sub>. Large variability existed between tall cultivars regarding their performance

in environments with high relative humidity after anthesis. The modern Spanish cultivar ‘Senadur’ was placed in the upper part of Fig. 1D, suggesting that it showed the highest C × E interaction for thousand kernel weight.

**Table 4**

Percentage of the sum of squares (SS) in the ANOVA models for the partitioning of the cultivar × environment interaction for yield components of the historical series of 24 Italian and Spanish durum wheat cultivars grown in 13 environments.

Source of variation	df	Number of spikes m <sup>-2</sup>		Number of grains spike <sup>-1</sup>		Thousand kernel weight	
		SS (%)	–log(P)	SS (%)	–log(P)	SS (%)	–log(P)
Total	935						
Environment	12	71.3	22.7	54.2	20.1	66.5	19.9
Block (environment)	26	0.65	2.41	0.78	1.77	1	11.6
Cultivar	23	9.61	88.6	17.7	111	14.8	160
Period	2	36.2	48.2	53	82.5	7.52	25.8
Origin	1	1.49	3.02	3.35	7.96	1.8	7.52
Origin × period	2	2.67	4.23	1.72	3.7	5.23	18.5
Cultivar(origin × period)	18	59.6	59.7	42	57	85.4	149
Cultivar × environment	276	10.7	28.6	16.8	36.2	12.7	66.4
Period × environment	24	14	11.9	17.9	20	19.3	36.8
Origin × environment	12	2.83	1.59	2	1.05	4.29	7.95
Origin × period × environment	24	6.52	3.21	7.58	5.59	4.74	5.42
Cultivar(origin × period) × environment	216	76.6	24.3	72.6	28.3	71.7	53.7
Error	598	7.74		10.5		5.05	

**Table 5**

Percentage of the sum of squares (SS) in the AMMI and factorial regression models for the partitioning of the cultivar  $\times$  environment interaction for yield components of the historical series of 24 Italian and Spanish durum wheat cultivars grown in 13 environments. ETo: reference evapotranspiration; RH: average daily relative humidity; TT: thermal time; WI: water input. SA and AM within parentheses stand for the sowing-anthesis and anthesis-maturity periods, respectively.

Source of variation	df	SS (%)	$-\log(P)$
<b>(A) Number of spikes <math>m^{-2}</math></b>			
Cultivar $\times$ environment	276	10.7	28.6
AMMI			
IPCA1	34	37.8	35.7
IPCA2	32	17.2	13.2
IPCA3	30	14.4	10.6
Residuals	180	30.6	
Factorial regression			
ETo <sub>(SA)</sub> $\times$ cultivar	23	29.9	31.6
RH <sub>(AM)</sub> $\times$ cultivar	23	12.7	10.6
RH <sub>(SA)</sub> $\times$ cultivar	23	10.2	7.55
Deviations	207	47.3	
Period $\times$ environment	24	14	12.3
ETo <sub>(SA)</sub> $\times$ period	2	21.8	2.66
Deviations	22	78.2	
<b>(B) Number of grains <math>spike^{-1}</math></b>			
Cultivar $\times$ environment	276	16.8	36.2
AMMI			
IPCA1	34	26	27.1
IPCA2	32	18.8	18.3
IPCA3	30	14	12.6
Residuals	180	41.2	
Factorial regression			
TT <sub>(AM)</sub> $\times$ cultivar	23	13	13.4
WI <sub>(AM)</sub> $\times$ cultivar	23	10.9	10.5
ETo <sub>(AM)</sub> $\times$ cultivar	23	8.39	6.92
Deviations	207	67.7	
Period $\times$ environment	24	17.9	20
TT <sub>(AM)</sub> $\times$ period	2	28.7	4.93
ETo <sub>(AM)</sub> $\times$ period	2	8.38	1.45
Deviations	20	62.9	
<b>(C) Thousand kernel weight</b>			
Cultivar $\times$ environment	276	12.7	66.4
AMMI			
IPCA1	34	29.6	51.5
IPCA2	32	25.6	45.2
IPCA3	30	10.7	16.4
Residuals	180	34.1	
Factorial regression			
WI <sub>(AM)</sub> $\times$ cultivar	23	15.5	29.3
RH <sub>(AM)</sub> $\times$ cultivar	23	8.58	14.1
Deviations	230	75.9	
Period $\times$ environment	24	19.3	36.8
WI <sub>(AM)</sub> $\times$ period	2	15.6	2.47
Deviations	22	84.4	

### 3.4. Trends in stability for yield and yield components

The study of the linear models fitted to the relationships between the year of release of cultivars and the yield stability indices calculated for each cultivar resulted in statistical significance for three of them (Fig. 2). The slope of the joint regression analysis ( $b$ ) and the environmental variance ( $S^2_{xi}$ ) increased at a rate of  $3.8 \times 10^{-3} y^{-1}$  and  $2.13 \times 10^{-2} y^{-1}$ , respectively (Fig. 2A and B), indicating an increase in responsiveness to the environmental conditions over time. The slope of the joint regression analysis for yield ranged between 0.68 ('Rubio de Belalcázar') and 1.27 ('Astigi'), with modern cultivars having the maximum range (from 0.89 to 1.27). A negative trend was observed for the superiority measure ( $P_i$ ;  $10^6$ ), whose rate of change was estimated as  $-3.6 \times 10^{-2} y^{-1}$  (Fig. 2C). The distance from the origin of AMMI axes ( $v_i$ ) did not show a significant linear trend for yield for the cultivars released

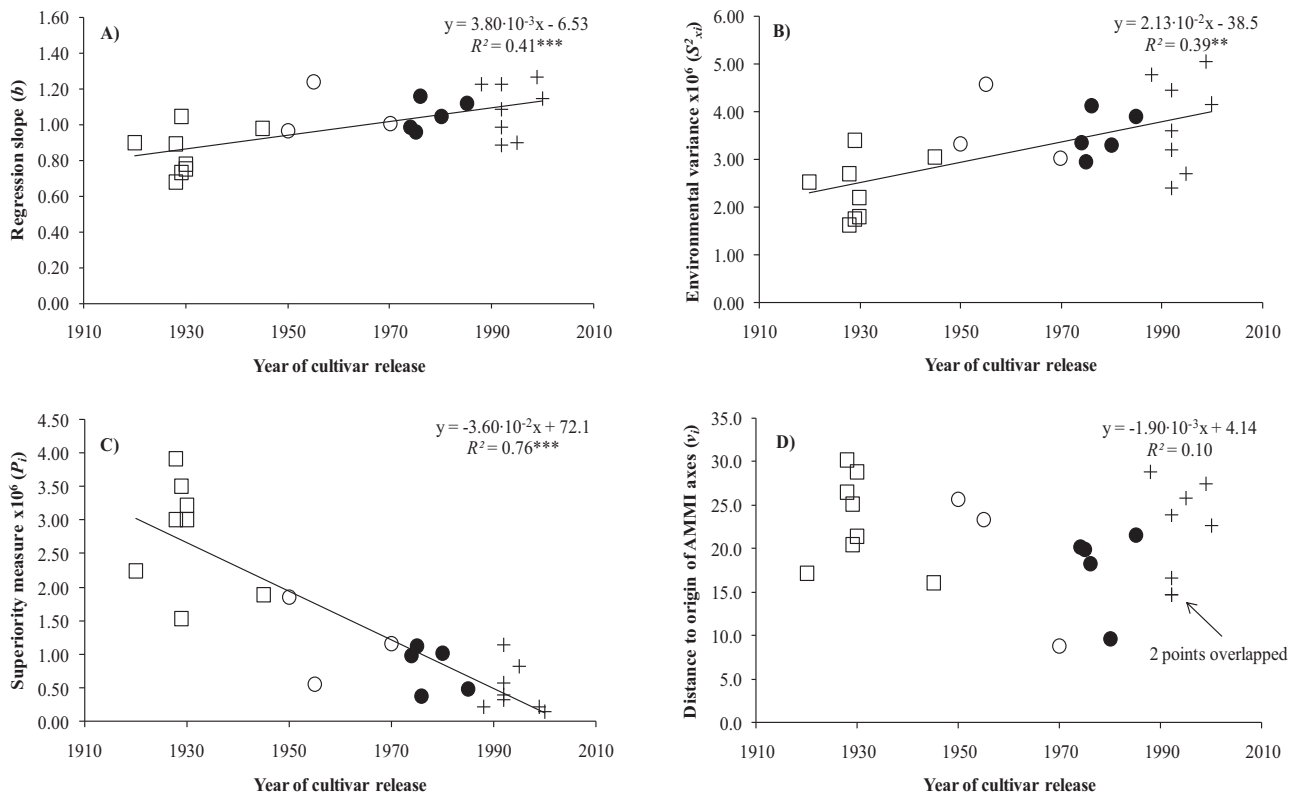
during the 20th century, although the lowest values for this index were recorded in intermediate cultivars (Fig. 2D). 'Mexa' and 'Trinakria' were the cultivars with the lowest values for  $v_i$ , suggesting that their yields had a low  $C \times E$  interaction. Strong and significant relationships existed between yield stability indices, showing a significant trend over time. For yield, the Pearson correlation coefficient between  $b$  and  $S^2_{xi}$  was  $r = 0.99$  ( $P < 0.0001$ ), between  $b$  and  $P_i$  it was  $r = -0.89$  ( $P < 0.0001$ ), and between  $S^2_{xi}$  and  $P_i$  it was  $r = -0.85$  ( $P < 0.0001$ ).

For the number of spikes  $m^{-2}$  significant changes were only observed in  $P_i$ , which decreased over years at a rate of  $-117 y^{-1}$  (Table 6). The minimum and maximum values of  $P_i$  for the number of spikes  $m^{-2}$  were recorded in two old Italian cultivars, 'Balilla Falso' ( $P_i = 1992$ ) and 'Razza 208' ( $P_i = 21265$ ), respectively. The stability indices for the number of grains  $spike^{-1}$  followed a similar trend to the ones estimated for yield (Table 6). The trend found for the slope of the joint regression analysis was of the same magnitude as that calculated for yield ( $3.1 \times 10^{-3} y^{-1}$ ), but the rates of change for  $S^2_{xi}$  ( $0.23 y^{-1}$ ) and  $P_i$  ( $-1.06 y^{-1}$ ) were lower than those estimated for yield. For the number of grains  $spike^{-1}$ , the old Italian cultivar 'Balilla Falso' showed extreme values for the three stability indices: the lowest for  $b$  (0.60) and  $S^2_{xi}$  (18.0) and the highest for  $P_i$  (164). The extremes for these indices, indicating the lowest stability for the number of grains  $spike^{-1}$ , were recorded in three modern cultivars: 'Cirillo' ( $b = 1.63$ ), 'Flavio' ( $S^2_{xi} = 81.9$ ) and 'Astigi' ( $P_i = 1.81$ ). No significant linear change was observed in the stability calculated for thousand kernel weight (Table 6).

## 4. Discussion

The environmental traits affecting the growth of durum wheat showed great variability across the 13 environments included in this study. This variability caused a difference of  $5245 kg ha^{-1}$  between the most- and the least-yielding experiments, which is more than four times the yield obtained in the least-yielding one. The environmental effect explained 76.4% of yield variability, a lower value than the 98% found in a previous study, in which 191 durum wheat accessions were tested at nine sites of four Mediterranean countries (Royo et al., 2010), but higher than the 57% previously reported for bread wheat (Sanchez-Garcia et al., 2012). In the present study the environmental effect accounted for 54.2–71.3% of the observed variance in yield components. These values are much higher than those found in a previous study conducted in the same country that tested a historical series of 27 bread wheat cultivars in eight environments (Sanchez-Garcia et al., 2012). These results suggest larger  $C \times E$  interaction for durum wheat than for bread wheat. However, in both studies the number of grains  $spike^{-1}$  was the yield component least affected by environmental conditions.

In spite of the great effect of environmental conditions on yield, the  $C \times E$  interaction was highly significant for this trait and explained ca. 10% of its variance. This value is within the range of those reported by previous studies conducted in wheat in the SEWANA (South of Europe, West Asia and North Africa) region (Anderson, 2010; De Vita et al., 2010; Mohammadi and Amri, 2013; Sanchez-Garcia et al., 2012). The partition in the ANOVA of the cultivar effect between periods, origins and their interactions revealed that the period of cultivar release was much more important than the origin of the cultivars for explaining the variability of yield. In addition, as shown by the ANOVA and the biplot of the AMMI model, the contribution of the period to explaining the  $C \times E$  interaction for yield was much greater than that of the origin, thus leading to the conclusion that the contrasting breeding strategies followed in Italy and Spain during the 20th century evidenced by previous studies (Martos et al., 2005; Royo et al., 2007) resulted in similar adapta-



**Fig. 2.** Relationship between the year of release of the 24 cultivars of the historical series and the stability indices calculated for grain yield: (A) slope of the joint regression analysis (b); (B) environmental variance ( $S^2_{xi}$ ); (C) superiority measure ( $P_i$ ); (D) distance from the origin of AMMI axes ( $v_i$ ). Cultivars are identified as follows for each period: (□) old; (●) intermediate cultivars carrying the *Rht-B1b* allele; (○) intermediate cultivars not carrying the *Rht-B1b* allele; and (+) modern. \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

tion patterns. This result, and the similar ones obtained for yield components, show the presence of different patterns of adaptation to environmental constraints within the set of cultivars of the historical series and justify the identification of the cultivar period but not the origin in Figs. 1 and 2.

The AMMI analysis for yield clustered apart old and modern cultivars, and assigned the intermediate ones to one or the other group according to their allelic composition for the *Rht-B1* locus. Given that the *Rht-B1b* allele was present in all modern cultivars but was absent in the old ones, clusters in the biplot separated tall and semi-dwarf cultivars, thus demonstrating that the introduction and spread of the *Rht-B1b* allele in the early 1970s (Royo and Briceño-Félix, 2011) was critical for explaining the changes observed in the adaptation of durums over time. The location of the point representing the cultivar ‘Adamello’ in the same cluster as modern and intermediate semi-dwarf cultivars in Fig. 1A suggests a common adaptation pattern, which is in agreement with the presence in this cultivar of the *Rht-B1b* allele, as detected by the PCR-marker.

The most important environmental factors affecting the C × E interaction for yield were reference evapotranspiration before anthesis [ $ETo_{(SA)}$ ] and water input after this stage [ $WI_{(AM)}$ ]. The

clustering in the biplot for yield of modern and intermediate semi-dwarf cultivars in the direction of the vector representing  $WI_{(AM)}$  indicates that they had the best yield performance in environments with high water input during grain filling, such as North-Irrigated-2002 (NI02) and South-2004 (S04). Moreover, the location of the cluster including old and intermediate tall cultivars on the opposite side and closer to the vector of  $ETo_{(SA)}$  suggested that they adapted better than semi-dwarf cultivars in terms of yield to environments with high evapotranspiration before anthesis and low  $WI$  during grain filling. It is well known that the introduction of dwarfing alleles in wheat cultivars during the 20th century reduced plant height and lodging and improved the partitioning of assimilates to the grain increasing the sink capacity of the crop (Addisu et al., 2010; Álvaro et al., 2008a; Rebetzke et al., 2012; Yousefian et al., 1992), and the harvest index (Royo et al., 2007), thus allowing the crop to take advantage of more favourable conditions in terms of nutrients and water availability, and therefore crop intensification. The results of the current study indicate that when water is available after anthesis, semi-dwarf cultivars have a greater potential than the tall ones to use it in benefit of yield increases. Within the old cultivars, ‘Senatore Cappelli’ (also known as ‘Cappelli’) showed the

**Table 6**

Relationships between the year of release of the 24 cultivars of the historical series and the stability indices calculated for yield components. Same data for yield are in Fig. 2.

Trait	Regression slope (b)		Environmental variance ( $S^2_{xi}$ )		Superiority measure ( $P_i$ )		Distance to the origin of AMMI axes ( $v_i$ )	
	Slope	$R^2$	Slope	$R^2$	Slope	$R^2$	Slope	$R^2$
Number of spikes $m^{-2}$	$1.7 \times 10^{-3}$	0.05	28	0.02	-117	0.36**	$-4.2 \times 10^{-2}$	0.16
Number of grains spike $^{-1}$	$3.1 \times 10^{-3}$	0.25*	0.23	0.18*	-1.06	0.56***	-0.01	$3 \times 10^{-3}$
Thousand kernel weight	$1.4 \times 10^{-3}$	0.1	0.2	0.15	0.19	0.05	$-3.9 \times 10^{-3}$	0.03

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .



highest score for IPCA1, which was strongly and negative correlated with  $WI_{(AM)}$ . This result indicates that this cultivar was among the ones least affected by water stress during grain filling, and that it was also the least responsive to water input during grain filling. The position of the point representing 'Senatore Cappelli' close to the vector of  $ET_{O(SA)}$  in the biplot for the number of spikes  $m^{-2}$  suggests that its adaptation pattern was related to the higher number of spikes  $m^{-2}$  in environments with high reference evapotranspiration before anthesis. Though it was the cultivar with the lowest number of spikes  $m^{-2}$  across environments, this yield component was less affected by conditions of high  $ET_{O(SA)}$  and low  $RH_{(SA)}$  and  $RH_{(AM)}$  than other old cultivars; however, it took advantage to form heavy grains when relative humidity and water input after anthesis were high, as shown by Fig. 1D. These results reveal a good performance of this cultivar in environments with high evapotranspirative demand before anthesis, and a great efficiency in the use of water during grain filling that resulted in heavy grain formation. These characteristics of adaptation of 'Senatore Cappelli' to stress environments may be behind its large contribution to durum wheat improvement in Italy, where it has been widely used as a parental line and is still present in the background of some of the most successful Italian durum wheat cultivars grown nowadays (Di Fonzo et al., 2005).

The number of spikes  $m^{-2}$  was the yield component with the highest environmental effect and the lowest  $C \times E$  interaction. Old cultivars tended to perform better in southern environments, with high  $ET_{O(SA)}$  and low  $RH_{(SA)}$  and  $RH_{(AM)}$ , than modern ones. This effect was due to their lower responsiveness to favourable conditions, as revealed by the significant decrease in the superiority measure ( $P_i$ ) over the 20th century. The number of spikes  $plant^{-1}$  was significantly improved in durum wheat by breeding activities during the last century (Royo et al., 2007), thus increasing the capacity of the crop to revert resources to additional tillers under favourable conditions.

Among yield components the number of grains  $spike^{-1}$  had the largest genetic control but the largest  $C \times E$  interaction. It was also the one most affected by the period of cultivar release, and therefore the yield component most related to changes in crop adaptability over time. Previous studies identified the number of grains  $spike^{-1}$  as the most important yield component for raising the number of grains per unit area and yield in durum wheat during the last century (De Vita et al., 2007; Royo et al., 2007). Though the number of grains  $spike^{-1}$  is determined by different events during crop development, only post-anthesis variables explained the observed  $C \times E$  interaction for this trait, thus showing the importance of floret abortion and grain setting for durum wheat yield determination in Mediterranean environments, as pointed out by previous studies (Álvarez et al., 2008c; Ferrante et al., 2010; Isidro et al., 2011). Modern and semi-dwarf cultivars of the intermediate period tended to produce more grains per spike than tall ones in environments with higher  $WI_{(AM)}$  and  $ET_{O(AM)}$ . The observed improvement in the yield responsiveness was also mainly related to the changes in the performance of this yield component under favourable environments, as the stability indices for this trait showed a similar trend over periods to that estimated for yield. This is in agreement with the reported increase in the number of fertile florets per spike at anthesis that occurred as a pleiotropic effect of the *Rht-B1b* dwarfing allele (Álvarez et al., 2008b). Therefore, cultivars carrying this allele demonstrated a greater capacity to respond to favourable conditions for grain setting around and after anthesis and to produce more grains per spike. However, in terms of number of grains  $spike^{-1}$ , cultivars not carrying the dwarfing allele performed better than the semi-dwarf ones in environments with a long grain filling period expressed in thermal units. This difference in the adaptation pattern may be explained by the reduction of time to anthesis that resulted from breeding activities in durum wheat during the

last century (Isidro et al., 2011; Motzo and Giunta, 2007; Royo et al., 2008), which would favour old cultivars in environments with longer grain filling periods.

The adaptation of modern and semi-dwarf cultivars of the intermediate period to environments with high  $WI_{(AM)}$  was also expressed for thousand kernel weight. Although it has been reported that grain weight remained unchanged in durum wheat cultivars grown in different periods during the 20th century (Royo et al., 2007), semi-dwarf cultivars responded positively to water input during grain filling using it to raise the weight of their grains. This result can be explained by the observed increase in potential grain weight (Álvarez et al., 2008a), and grain filling duration (Royo et al., 2008) of modern durum cultivars in comparison with the old ones, and the improvement of the sink capacity caused by the introduction of dwarfing genes, which augmented the constraint to grain filling due to the source of assimilates (Álvarez et al., 2008c; Maydup et al., 2012; Sanchez-Bragado et al., 2014). In consequence, as semi-dwarf cultivars are more source-limited than tall ones and have a longer grain filling period, they could take advantage of favourable water input conditions after anthesis for the production of heavier grains.

The significant changes over time observed for three of the four stability indices calculated for yield are in agreement with the results of the AMMI analysis and indicate that breeding efforts during the last century resulted in an improvement in the response of the crop to high-input environments. The lower values of the regression slope ( $b$ ) and  $S^2_{xi}$  obtained for old cultivars in comparison with the modern ones indicate that the yield of the former hardly changed regardless of any variation in the mean yield of the environment, thus revealing that they are more stable than modern cultivars when yield stability is considered from the static point of view. This concept is usually associated with poor yields (Becker and León, 1988), as was the case of old cultivars, and is therefore undesirable for breeding purposes. However, a wide range for  $b$  and  $S^2_{xi}$  was observed in modern cultivars, thus indicating that the yield of some of them ('Flavio' and 'Senadur') was as stable as that of some old cultivars, while others ('Astigi', 'Simeto' and 'Cirillo') showed a large response to environmental changes. On the other hand, the low values of the superiority measure of Lin and Bins ( $P_i$ ) of modern cultivars indicate a short mean square distance between the performance of the cultivar and the maximum response observed across environments. Both results show a proportional increase in the performance of modern cultivars in response to the enhancement of the environmental conditions and, therefore, a trend towards a general adaptation and greater stability if this is considered a 'dynamic' concept (Becker and León, 1988). In consequence, as has been reported by previous studies conducted in Italy and Spain (De Vita and Maggio, 2006; De Vita et al., 2010; Royo et al., 2008) and involving yield data of 21 countries (Calderini and Slafer, 1998), modern cultivars not only out-yield their predecessors in relatively poor environments but also respond considerably better to environmental improvements.

Though no significant trend was observed for yield in the distance from the origin of the AMMI axes ( $v_i$ ), intermediate cultivars tended to have the lowest value for this index. Among them, 'Mexa' and 'Trinakria' were the intermediate cultivars closest to the origin of the AMMI axes, thus indicating the similitude between their yield in each environment and the environmental yield, and therefore a wide adaptation to the environment. The two cultivars have a very different origin but played an important role in durum wheat cultivation and breeding in Spain and Italy, respectively. 'Mexa' is a semi-dwarf cultivar obtained by CIMMYT as a selection from the Mexican cultivar 'Mexicali C75', which was released in 1975 and has been widely cultivated around the world (Huerta-Espino et al., 2011), thanks to its broad adaptation. 'Trinakria' is a tall cultivar from a cross of 'Capeiti 8' that has been extensively used in the

development of new Italian cultivars since its release (De Vita et al., 2010).

The only stability index that was significant for the number of spikes  $m^{-2}$  was the superiority measure ( $P_i$ ), which strongly decreased from old to modern cultivars, suggesting a better performance of the latter in terms of spike number. The old Italian cultivar 'Balilla Falso' had the lowest value for this index, in agreement with this cultivar having the largest number of spikes  $m^{-2}$  across environments. This cultivar also had the lowest  $b$  and  $S^2_{xi}$  values and the highest  $P_i$  value for the number of grains spike $^{-1}$ , and was the cultivar with the lowest number of grains spike $^{-1}$  across environments, thus indicating a low grain number in all environments, and very negligible response to improvements in the environmental conditions. On the other hand, 'Cirillo', 'Flavio' and 'Astigi' responded to better environments by increasing their number of grains spike $^{-1}$ .

No change over time was observed in the stability of grain weight, which is in agreement with the lack of increases in grain weight as a consequence of the introduction of improved cultivars during the 20th century (Royo et al., 2007).

## 5. Conclusions

The results of this study have shown that the different breeding strategies followed in Italy and Spain during the last century resulted in analogous adaptation and stability models in terms of yield and yield components. Though the improved cultivars in the two countries had different origins, among the ones analysed herein, those released after 1970 had the common presence of the *Rht-B1b* dwarfing allele, which explained the similarities in the adaptation pattern of cultivars from the two countries and is essential for understanding the changes over time in the  $C \times E$  interaction of Mediterranean durum wheat cultivars.

Our results showed that cultivars carrying the *Rht-B1b* allele used the water available during grain filling more efficiently than the old tall ones, and this benefited the yield components formed after anthesis, i.e. number of grains spike $^{-1}$  and grain weight. The earlier flowering time of modern cultivars and their longer grain filling period, revealed by previous studies (Royo et al., 2008), are probably related to their better water use during grain filling. Although the number of grains spike $^{-1}$  had the highest genetic control of the three yield components, it also showed the largest  $C \times E$  interaction and therefore the greatest response to environmental conditions.

Yield increases of modern cultivars have caused a loss of stability from the static viewpoint, but not from a dynamic viewpoint based on the superiority measure ( $P_i$ ). The current study demonstrated that breeding activities conducted in Spain and Italy during the 20th century were successful not only in improving the durum wheat yield, but also in maintaining in some improved cultivars the levels of yield stability characteristic of the old cultivars.

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