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Breeding effects on the genotype \times environment interaction for yield of durum wheat grown after the Green Revolution: The case of Spain[☆]

Fadia Chairi^{a,b}, Nieves Aparicio^c, Maria Dolores Serret^{a,b}, José Luis Araus^{a,b,*}

^aSection of Plant Physiology, University of Barcelona, Barcelona, Spain

^bAGROTECNIO (Center of Research in Agrotechnology), Lleida, Spain

^cInstituto de Tecnología Agraria de Castilla y León (ITACyL), Valladolid, Spain

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ABSTRACT

This study evaluates the changes caused by breeding in the genotype by environment ($G \times E$) interaction of the durum wheat varieties most widely cultivated in Spain after the Green Revolution. A set of 12 cultivars was tested in 27 environments, which are understood as the combination of different sites, years, and treatments (water regime and planting dates), representative of the durum wheat growing conditions in Spain with average grain yields (GY) ranging between 2.8 and 9.1 Mg ha⁻¹. The most important environmental factors affecting the $G \times E$ interaction for yield were the maximum and the mean temperature during the entire crop cycle. An improvement in genetic yield was observed in warm environments and under optimal water conditions that resemble those where the germplasm originated (essentially as advanced lines) before its release in Spain. Therefore, the adaptation of semi-dwarf durum in Spain has shown a tendency to specific adaptation rather than large-scale adaptation. Two different patterns of selection have been reported due the $G \times E$ interaction and changes in the ranking of genotypes: in the high yielding environments (GY > 5 Mg ha⁻¹), plants favor increased water uptake, with higher levels of transpiration and more open stomata (more negative values of carbon isotope composition, $\delta^{13}C$, and higher canopy temperature depression, CTD), whereas, in low yielding environments (GY < 5 Mg ha⁻¹) plants close their stomata and favor greater water use efficiency (less negative $\delta^{13}C$ values and lower CTD values).

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* Corresponding author at: Section of Plant Physiology, University of Barcelona, Barcelona, Spain.

E-mail address: jaraus@ub.edu. (J.L. Araus).

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1. Introduction

Durum wheat (*Triticum turgidum* L. spp. *durum*) is a crop of global significance that is cultivated on about 30–35 million hectares, and has a particular economic and cultural relevance in the Mediterranean basin where it represents a staple crop [1]. Under Mediterranean conditions, drought and its frequent association with heat are the stresses with the greatest impact on cereal yield because they usually occur together during the reproductive stages of the crop [2]. Moreover, the variability of thermo-pluviometry patterns results in large spatial and temporal yield fluctuations [3,4]. For many of the world's wheat regions, climate change modeling for the coming decades is predicting unfavorable environmental conditions and therefore the task is to not just improve genetic gain and stability, it will even be a challenge to maintain these parameters at their current levels. This is particularly urgent for durum wheat because the Mediterranean basin is a hotspot for negative predictions of climate change in terms of decreased rainfall and increased temperatures [5].

Studies addressing genetic gains in wheat yield during the last century focused on the changes through time in agronomical yield components and/or relevant physiological traits [6–10] within a wide range of environments. However, few studies have addressed the relationship between genetic gain and the pattern of adaptation in terms of examining the genotype by environment interaction ($G \times E$) [11,12]. In addition, to the best of our knowledge, there are no studies that have focused exclusively on semi-dwarf (i.e. post-Green Revolution) durum wheat genotypes. This is despite the fact that the $G \times E$ interaction is a critical factor for cultivar evaluation [13]. Indeed, it is important to understand the adaptation mechanisms of wheat cultivation and the parameters responsible for the $G \times E$ interactions in grain yield caused by the large and unpredictable seasonal and geographical fluctuations in rainfall and temperature typical of the Mediterranean drylands [3,4].

Therefore the assessment of the relative contribution of the $G \times E$ interaction is important to determine the adaptation capacity of the cultivars [11]. Nevertheless, there are two breeding strategies: selecting for wheat under stress-free conditions (aimed at wide adaptation) [14] and selecting under stress environments (specific adaptation) [15,16].

Durum wheat breeding activities in Spain started during the first half of 20th century, with local breeding programs targeting a bulk selection within landraces, as well as selecting from crosses between the Italian variety Senatore Capelli and Spanish landraces [17]. However, the huge rise in yield during the second half of the 20th century in Spain [17] was primarily a consequence of the introduction of CIMMYT semi-dwarf germplasm (the so called Green Revolution). As a consequence, most commercial cultivars grown in Spain until this day are (to a greater or lesser extent) of foreign origin, and they were primarily selected for the specific environmental conditions of these external locations [17]. However, the Spanish environments that have determined the pattern of adaptation of these semi-dwarf genotypes remain essentially unknown.

The objectives of this research were: (i) to assess the impact of breeding for yield over the last few decades within the wide range of Spain environments and (ii) to investigate their adaptation patterns.

2. Materials and methods

2.1. Plant material, growing conditions and experimental design

Twelve durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf.) Husn.) cultivars were selected to represent the germplasm grown in Spain after the Green Revolution: Mexa, Vitron, Regallo, Simeto, Gallareta, Dorondon, Burgos, Claudio, Amilcar, Avispa, Don Ricardo, and Kiko Nick (Table 1).

Twenty-seven field experiments (i.e. trials) were conducted in Spain during five consecutive crop seasons, 2013–2014 until 2017–2018, at three locations at different latitudes, and exhibiting a wide range of growing temperatures, and these were representative of the main wheat growing areas in the country. Two of the three locations are experimental stations of the Spanish “Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria” (INIA): Coria del Rio (C), Seville (37°14'N, 06°03'W, 5 m a.s.l.), and Colmenar de Oreja – Aranjuez (A), Madrid (40°04'N, 3°31'W, 590 m a.s.l.). The third station belongs to the “Instituto Tecnológico Agrario de Castilla y León” (ITACyL) in Zamadueñas (Z), Valladolid (41°41'N, 04°42'W, 700 m a.s.l.). For all of the twenty-seven trials, plots were sown in a randomized block design with three replicates (plots) per cultivar. Each plot consisted of six rows of 7.0 m length and 0.2 m apart, with a planting density of 250 seeds m^{-2} . Concerning normal planting, rainfed (RF) and supplemental irrigation (IR) conditions were imposed at Aranjuez and Zamadueñas. In the case of Coria del Rio and due to the presence of a shallow water table, caused by proximity to the Guadalquivir River, the genotypes did not experience water stress even if they grew under rainfed conditions. Late planting was also performed in Aranjuez and Zamadueñas during the last two growing seasons. Sowing took place between the end of November and the beginning of December for the normal planting at the three sites, and during the first week of February for the late plantings performed at Aranjuez and Zamadueñas (Table 2). In that last case, trials were irrigated to ensure that only temperature was the main environmental variable. During all experimental campaigns fertilizer was applied in two steps, a first basal application of 300 $kg\ ha^{-1}$ of 8–15–15 (N:P:K) in Zamadueñas and 400 $kg\ ha^{-1}$ in both Aranjuez and Coria del Rio, and then a second top dressing application of 300 $kg\ ha^{-1}$ nitric acid (NAC) in Zamadueñas and 150 $kg\ ha^{-1}$ in both Aranjuez and Coria de Rio. All trials were controlled for weeds, insect pests, and diseases by recommended chemical doses. Plants were harvested mechanically at maturity and grain yield assessed.

During the first three years these twelve genotypes were evaluated within a set of 20 genotypes released in Spain between 1980 and 2009 [9] while in the last two years these genotypes were cultivated side by side with another twelve modern cultivars released in Spain between 1980 and 2014.

Table 1 – Set of twelve modern (semi-dwarf) durum wheat cultivars tested in this study.

| Code | Variety | Year of release | Country | Pedigree/cross name or origin |
|------|------------|-----------------|---------|--|
| 1 | Mexa | 1980 | Spain | GERARDO-VZ-469/3/JORI(SIB)//ND-61-130/LEEDS |
| 2 | Vitron | 1983 | Spain | TURCHIA-77/3/JORI-69(SIB)/(SIB)ANHINGA/(SIB)FLAMINGO |
| 3 | Regallo | 1988 | Italy | Diputación General de Aragón CIMMYT |
| 4 | Simeto | 1990 | Spain | RUFF/FLAMINGO//MEXICALI-75/3/SHEARWATER |
| 5 | Gallareta | 1994 | Spain | CIMMYT |
| 10 | Dorondon | 1998 | Spain | Genética y Gestión, S-C |
| 12 | Burgos | 1999 | Spain | SUDDEUTSCHE SAATZ |
| 13 | Claudio | 1999 | Spain | (Sel. Cimmyt × Durango) × (IS193B × Grazia) |
| 14 | Amilcar | 2001 | Italy | ZEGZAG-1/LUNDE-5//GREENSHANK-32 |
| 16 | Avispa | 2003 | Spain | Limagrain-CIMMYT |
| 18 | D Ricardo | 2008 | Spain | Agrovegetal-CIMMYT |
| 19 | Kicko Nick | 2009 | Spain | SEL.CIMMYT-35/DURANGO//ISEA-1938/GRAZIA |

2.2. Environment characterization

The growing environments were characterized on the basis of agro-climatic variables measured from sowing to physiological maturity (Zadoks stage 92) [18]. The following variables were measured: average daily minimum, mean and maximum temperature (T_{\min} , T_{mean} , T_{\max} ; °C), water input (WI,

mm, including accumulated rainfall during the crop cycle, plus irrigation when appropriate), reference evapotranspiration (ET_0 , mm) and the water deficit experienced by the crop, represented by the ratio of water input (WI) to ET_0 (WI/ ET_0). Climate data was extracted through the SiAR network of agrometeorological stations (www.eportal.mapama.gob.es/websiar).

Table 2 – Description of the 27 environments (trials) included in this study.

| Groups | Trials | T_{\min} (°C) | T_{\max} (°C) | T_{mean} (°C) | WI (mm) | ET_0 (mm) | WI/ ET_0 | GY (Mg ha ⁻¹) | GNY (kg ha ⁻¹) | $\delta^{13}\text{C}$ (‰) | CTD (°C) |
|--------|--------|--------------------|--------------------|---------------------------|------------|----------------|------------|------------------------------|-------------------------------|------------------------------|-------------|
| Coria | C2RF | 6.8 | 19.9 | 12.9 | 163.4* | 780 | 0.21 | 6.5 | 159.4 | -27.6 | 5.7 |
| Coria | C3RF | 8.5 | 19.4 | 13.5 | 351.2* | 673 | 0.52 | 5.0 | 116.0 | -27.0 | 2.7 |
| Coria | C4RF | 9.7 | 22.6 | 12.5 | 204.0* | 569 | 0.36 | 7.5 | – | – | 2.6 |
| Coria | C5RF | 6.8 | 18.0 | 12.1 | 297.8* | 669 | 0.45 | 5.6 | 123.5 | -27.5 | 4.8 |
| IR | A1IR | 3.4 | 17.7 | 10.2 | 557.7 | 634 | 0.88 | 6.7 | 121.1 | -25.8 | 4.6 |
| IR | A2IR | 3.0 | 18.0 | 9.9 | 386.0 | 726 | 0.53 | 5.1 | 125.0 | -25.8 | 6.9 |
| IR | A3IR | 3.3 | 17.3 | 9.9 | 477.1 | 632 | 0.75 | 4.5 | 135.5 | -26.2 | 2.9 |
| IR | A4IR | 7.2 | 24.3 | 11.42 | 537.2 | 804 | 0.67 | 4.9 | – | – | 2.4 |
| IR | A5IR | 2.4 | 16.0 | 8.7 | 475.8 | 726 | 0.66 | 7.4 | 183.5 | -26.2 | – |
| IR | Z1IR | 2.8 | 14.2 | 8.2 | 337.3 | 690 | 0.49 | 6.5 | 185.8 | -25.8 | 1.2 |
| IR | Z2IR | 2.4 | 14.0 | 7.9 | 387.8 | 695 | 0.56 | 7.2 | 185.6 | -25.8 | 4.9 |
| IR | Z3IR | 2.6 | 13.5 | 7.6 | 429.7 | 656 | 0.66 | 9.1 | 170.1 | -25.7 | 5.7 |
| IR | Z4IR | 2.7 | 15.5 | 8.6 | 279.0 | 633 | 0.44 | 7.0 | 176.0 | -24.9 | 3.4 |
| IR | Z5IR | 2.4 | 12.9 | 7.3 | 585.8 | 605 | 0.97 | 6.3 | 117.5 | -26.5 | – |
| Late | A4L | 8.9 | 22.0 | 15.5 | 559.6 | 559 | 1.00 | 3.7 | – | – | 12.1 |
| Late | A5L | 7.2 | 21.4 | 14.3 | 481.3 | 513 | 0.94 | 4.0 | – | – | – |
| Late | Z4L | 6.6 | 22.1 | 14.3 | 370.6 | 669 | 0.55 | 4.8 | – | – | 3.2 |
| RF | A1RF | 3.4 | 17.7 | 10.2 | 203.7 | 490 | 0.42 | 5.6 | 109.1 | -25.7 | 5 |
| RF | A2RF | 3.0 | 18.0 | 9.9 | 206.0 | 726 | 0.28 | 4.6 | 115.2 | -26.7 | 4.9 |
| RF | A3RF | 3.3 | 17.3 | 9.9 | 277.1 | 632 | 0.44 | 3.9 | 123.0 | -27.7 | 2.6 |
| RF | A4RF | 6.9 | 23.9 | 11.42 | 230.5 | 804 | 0.29 | 2.9 | – | – | 1.5 |
| RF | A5RF | 2.4 | 16.0 | 8.7 | 325.8 | 727 | 0.45 | 3.5 | 99.6 | -24.4 | – |
| RF | Z1RF | 2.8 | 14.2 | 8.2 | 212.3 | 690 | 0.31 | 3.1 | 105.5 | -24.5 | -0.6 |
| RF | Z2RF | 2.4 | 14.0 | 7.9 | 262.8 | 696 | 0.38 | 3.8 | 104.0 | -24.5 | 0.84 |
| RF | Z3RF | 2.6 | 13.5 | 7.6 | 359.7 | 673 | 0.53 | 6.6 | 105.3 | -24.5 | 1.8 |
| RF | Z4RF | 2.7 | 15.5 | 8.6 | 179.0 | 631 | 0.28 | 2.9 | 84.5 | -23.7 | 1.3 |
| RF | Z5RF | 2.2 | 13.0 | 7.2 | 476.4 | 605 | 0.79 | 6.9 | 155.8 | -26.5 | – |

T_{\min} , T_{\max} , and T_{mean} are average minimum, maximum and mean daily temperatures, respectively. WI, water input (rainfall + irrigation); ET_0 , potential evapotranspiration; GY, grain yield; GNY, grain nitrogen yield; CTD, canopy temperature depression; $\delta^{13}\text{C}$, the stable carbon isotope composition of mature kernels. Site code of A, C and Z correspond to location Aranjuez, Coria and Zamadueñas, respectively; numbers (1–5) correspond to the respective growing season (1, 2013–2014; 2, 2014–2015; 3, 2015–2016; 4, 2016–2017; 5, 2017–2018), and RF, IR and Late correspond to rainfed, irrigation and late planting, respectively. The effect of a shallow water table in Coria is not reflected in the WI (values with asterisks), but in the low $\delta^{13}\text{C}$ and high CTD values typical of good crop water availability [34] as well as the high $\delta^{15}\text{N}$, which suggested that the nitrogen source was not solely from chemical fertilizer (characterized by $\delta^{15}\text{N}$ values near 0‰) but strongly affected by animal and urban $\delta^{15}\text{N}$ sources [35]. Missing data is indicated by “–”. These correspond to trials where $\delta^{13}\text{C}$ and nitrogen content of grains were not measured.

2.3. Canopy temperature depression

Canopy temperature depression (CTD) was measured in the early grain filling stage (Zadocks stage 71 [18]) as $CTD = T_a - T_c$, where T_a and T_c were the air temperature and canopy temperature for each plot, respectively. The canopy temperature of each plot was measured with an infrared thermometer (PhotoTemp MX6TMTM, Raytek Corporation, Santa Cruz, CA, USA). Ambient temperature was measured simultaneously above each plot using a thermo-hygrometer (Testo 177-H1 Logger, Germany). Measurements were taken around midday on sunny days.

2.4. Stable carbon isotope signature and N content

The total N content of mature grains was analyzed using an Elemental Analyzer (Flash 1112 EA; ThermoFinnigan, Bremen, Germany) for each individual plot within the entire set of trials. The same EA coupled with an Isotope Ratio Mass Spectrometer (Delta C IRMS, ThermoFinnigan, Bremen, Germany), operating in continuous flow mode, was used to determine the stable carbon ($^{13}\text{C}/^{12}\text{C}$) isotope ratios of the same mature grains. Finely ground samples of ~1 mg and reference materials were weighed into tin capsules, sealed, and then loaded into an automatic sampler (ThermoFinnigan) before EA-IRMS analysis. Nitrogen was expressed as a concentration (g N per g DW) and atropine was used as a system check in the elemental analyses of nitrogen. The $^{13}\text{C}/^{12}\text{C}$ ratios of plant material were expressed in δ notation [19].

$$\delta^{13}\text{C} (\text{‰}) = \left[\left(\frac{^{13}\text{C} : ^{12}\text{C} \text{ sample}}{^{13}\text{C} : ^{12}\text{C} \text{ standard}} - 1 \right) \right]$$

where sample refers to plant material and standard to international secondary standards of known $^{13}\text{C}/^{12}\text{C}$ ratios (IAEA CH7 polyethylene foil, IAEA CH6 sucrose, and USGS 40 L-glutamic acid) calibrated against Vienna Pee Dee Belemnite calcium carbonate (VPDB) with an analytical precision (SD) of 0.10‰.

Measurements were conducted at the Scientific Facilities of the University of Barcelona.

Grain nitrogen yield (GNY) was calculated as follows:

$$\text{GNY} \left(\text{kg ha}^{-1} \right) = \left[\left(\text{N content} (\%) \times \text{GY} \left(\text{kg ha}^{-1} \right) \right) / 100 \right]$$

These measurements were made only in samples of 21 experiments out of a total of 27 experiments.

2.5. Statistical analysis

The response of the studied genotype (G), environment (E), and environment by genotype interaction ($G \times E$) yield was tested with ANOVA. The Additive Main effect and Multiplicative Interaction (AMMI) analysis [20] using GEA-R statistical software [21] was used to identify the best combination of genotypes and environments with respect to grain yield, and to study the effect of the $G \times E$ interaction. Biplot graphs provide visualizations for two-way data matrices and two kinds of biplots [22] are reported in this paper. The AMMI1 biplot shows the main effects, genotype and environment, and the means on the abscissa and on the ordinate show the

first principal-component axes of the interaction (IPCA1). The AMMI2 biplot shows the IPCA1 on the abscissa and the IPCA2 on the ordinate. The AMMI model was also used to evaluate the adaptability and stability of productivity.

3. Results

3.1. Environmental classification

The experiments were carried out over a large range of climatic and growing conditions. There were large differences in growing conditions, as shown not only by the variability in environmental variables during the growing cycle (temperature, water input and evapotranspiration), but also by the range of variability in crop water status traits ($\delta^{13}\text{C}$ and CTD) and grain yield (GY and GNY) (Table 2).

According to the data in Table 2, we classified the growing environments into four major groups. Group 1 “Coria” was characterized by a high mean and maximum temperature values and high availability of water thanks to the proximity of the water table. Group 2 “Late” was characterized by high mean and maximum temperature values like “Coria” and strong support irrigation but a late sowing date. Group 3 “RF” and group 4 “IR” were constituted by the rainfed and irrigated environments of the normal planting trials, respectively.

3.2. Genetic advance in grain yield within each group of environments

The analysis showed a significant progress in GY in Coria and Late (Fig. 1A, B). The genetic advance using the set of 12 genotypes was around $31 \text{ kg ha}^{-1} \text{ year}^{-1}$ in Coria and around $19 \text{ kg ha}^{-1} \text{ year}^{-1}$ in Late. A similar pattern was seen when using 23 genotypes and 13 environments from the last two seasons (Fig. S1). However, no pattern of increase was seen in the RF and IR groups when using either 12 (Fig. 1C, D) or 23 genotypes (Fig. S1).

3.3. Analysis of variance

Mean environment yields ranged between 2.88 Mg ha^{-1} (A4RF) and 9.11 Mg ha^{-1} (Z3IR) (Table 2). The combined analysis of variance (ANOVA) revealed significant environment (E), genotype (G) and $G \times E$ interaction.

Even when the analyses were performed within each of the four groups of environments, the ANOVA revealed that most of the total variation for GY within each group (calculated as the proportion of the total sum of square) was due to the effect of environments, with high values of 60.4%, 79.9%, and 72.1% in Coria, RF and IR, respectively, while in Late the values were lower (27%). The proportion of the total sum of squares due to differences among genotypes was much higher for Coria (13.7%) and Late (10.6%) than for the other two groups (2.2%, IR and 1.3%, RF) and was significant in all groups except for Late (where it was marginally significant). Also, it was different for the $G \times E$ interaction (14.1%, Coria; 20.9%, Late; 6.1, RF and 10.4%, IR) (Table 3) and the $G \times E$ interaction was significant in all groups except IR.

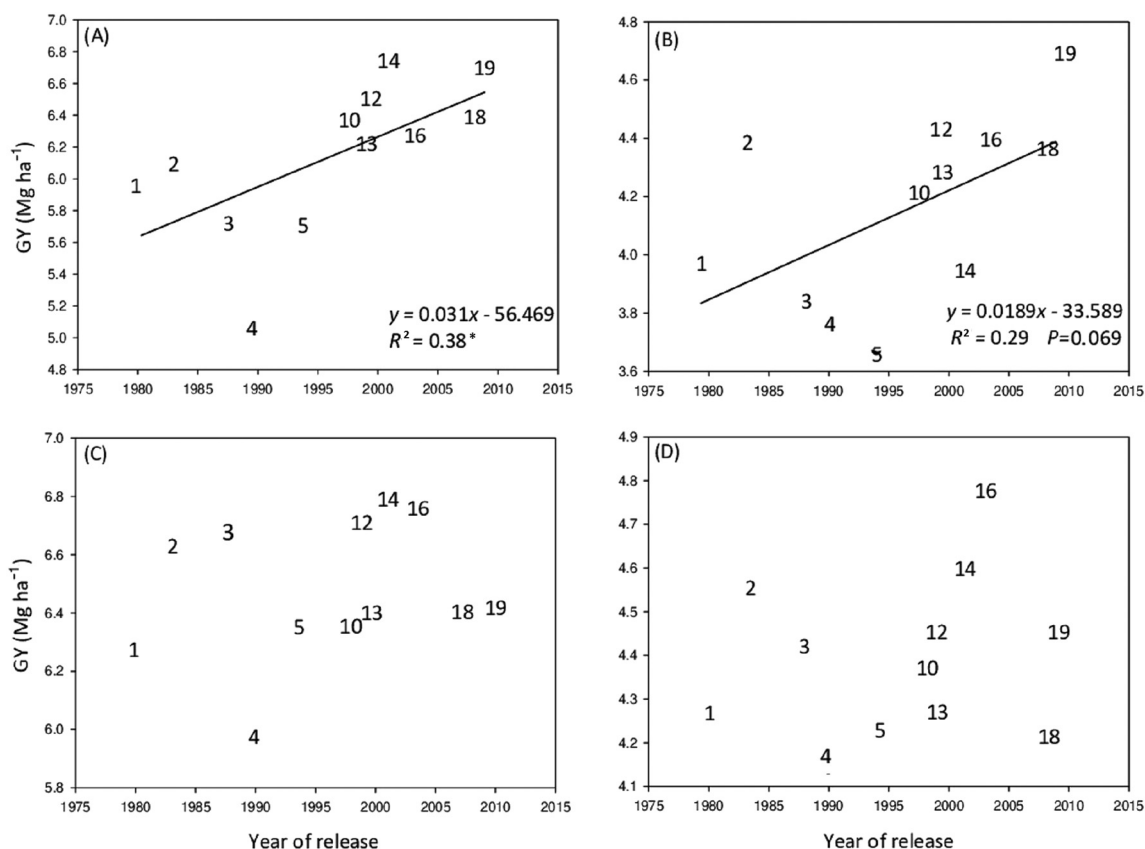


Fig. 1 – Relationship between grain yield and the year of cultivar release for each group of environments. (A) Coria; (B) Late; (C) IR; (D) RF. For each group of environments, each point represents the average GY value of a given cultivar across the environments and replicates. Numbers represent genotypes: (1) Mexa, (2) Vitron, (3) Regallo, (4) Simeto, (5) Gallareta, (10) Dorondon, (12) Burgos, (13) Claudio, (14) Amilcar, (16) Avispa, (18) D Ricardo, and (19) Kicko Nick.

The mean environment GNY ranged between 84.5 kg ha⁻¹ (A4RF) and 185.8 kg ha⁻¹ (Z1IR) (Table 2). The combined analysis of variance (ANOVA) revealed significant E and G effect and no G × E interaction was observed. The ANOVA analyzed separately for each of the four groups of environments revealed significant E effects for GNY (Table S1). The G effect was highly significant only in Coria and the G × E interaction was marginally significant in Coria and not significant in the other groups of environments (Table S1). Most of the total variation within each group was due to significant differences among environments with around 50% for Coria and IR and lower for RF (28%). The proportion of the total sum of squares due to differences among genotypes was much lower under RF (1.7%) than IR (2.4%) and in Coria (13.7%), whereas the G × E interaction was quite similar (around 12%) for the three groups.

The mean environment carbon isotope composition ($\delta^{13}\text{C}$) ranged between -27.7‰ (A3RF) and -23.7‰ (Z4R) (Table 2). The combined ANOVA revealed a significant E effect but no effect for G and G × E interaction was observed. The ANOVA for the four groups of environments separately and revealed significant E effects for $\delta^{13}\text{C}$ (Table 4). The G effect was highly significant only in Coria and no G × E interaction was observed in any group of environments. Therefore, most of the total

variation was due to significant differences among environments: 57% for Coria; 39.6% for RF and a lower value for IR (21.4%). The three groups showed similar G × E interaction values (around 12%).

3.4. AMMI analysis

G, E, and the G × E interaction effects were also studied with the AMMI model. The results showed that the decomposition of genotype-by-environment interaction through the AMMI model (Figs. 2, 3), considering the first two principal-component axes of the interaction (IPCA), captured most of the G × E interaction sum of squares (SS_{GEI}) effect for GY in the four groups of environments determined, ranging from 58% (IR) to 100% (Late). In Coria, the first, second and third IPCA explained 37%, 36%, and 26% of the variation in the SS_{GEI} , respectively. In Late, 77% of the variation in the SS_{GEI} was captured by the IPCA1 axis and a further 23% by the IPCA2 axis. Values of 37% and 32% of the variation in the SS_{GEI} were captured by IPCA1 under IR and RF, respectively, and a further 21% and 30%, respectively, were explained by the IPCA2 axis.

Fig. 2 shows the AMMI1 biplot for each environment. The abscissa shows differences in genotype and environment effects and the ordinate differences in interaction patterns.

Table 3 – Analysis of variance for grain yield (GY) for twelve durum wheat genotypes grown in each of the four groups of environments as well as the combined set of environments.

| Source of variation in GY | df | SS | SS (%) | F | P-value |
|---------------------------|-----|----------|--------|-------|---------|
| Combined | | | | | |
| Total | 968 | 3099.810 | | | |
| E | 26 | 2516.154 | 81.2 | 198.0 | 0.000 |
| G | 11 | 43.307 | 1.4 | 8.056 | 0.000 |
| G × E | 286 | 219.686 | 7.1 | 1.572 | 0.000 |
| Error | 645 | 315.225 | | | |
| Coria | | | | | |
| Total | 143 | 211.01 | | | |
| E | 3 | 127.52 | 60.4 | 163.8 | 0.000 |
| G | 11 | 28.88 | 13.7 | 10.12 | 0.000 |
| G × E | 33 | 29.69 | 14.1 | 3.468 | 0.000 |
| Error | 96 | 24.91 | | | |
| Late | | | | | |
| Total | 107 | 96.817 | | | |
| E | 2 | 26.272 | 27.1 | 23.64 | 0.000 |
| G | 11 | 10.294 | 10.6 | 1.684 | 0.094 |
| G × E | 22 | 20.247 | 20.9 | 1.656 | 0.057 |
| Error | 72 | 40.004 | | | |
| IR | | | | | |
| Total | 358 | 7831.8 | | | |
| E | 9 | 740.9 | 79.9 | 165.4 | 0.000 |
| G | 11 | 11.6 | 1.3 | 2.123 | 0.019 |
| G × E | 99 | 56.3 | 6.1 | 1.144 | 0.205 |
| Error | 239 | 118.9 | | | |
| RF | | | | | |
| Total | 357 | 852.6 | | | |
| E | 9 | 614.8 | 72.1 | 124.8 | 0.000 |
| G | 11 | 18.7 | 2.2 | 3.099 | 0.001 |
| G × E | 99 | 88.6 | 10.4 | 124.8 | 0.001 |
| Error | 238 | 130.3 | | | |

The genotypes on the right side of the graph show yield levels above the average. Further, genotypes and environments lying close to the abscissa axis (IPC1 score close to 0) did not interact with each other, while positive or negative scores on the ordinate axis indicate genotypes that interacted positively with environments characterized by having a score of the same sign.

The values on the abscissa reflected the agronomical potential for environments and the general improvement status for genotypes [23]. Genotypes towards the center of the biplot had zero interaction; therefore they had a general adaptation with different mean grain yields and thus they can be considered stable with high or low performance. Indeed, the environmental variability was much higher than genotype variability in the four environments. In relation to interactions, especially in the RF and IR environments, the genotypes showed large variability. Between the genotypes in Coria and Late, where greater differences in productivity existed, the rank was higher. The highest average yield was shown by the genotypes Kicko Nick [19] and Amilcar [14] in Coria, by Kicko Nick [19] in Late, by Amilcar [14] and Avispa [16] under IR and by Avispa [16], Amilcar [14] and Vitron [2] under RF (see Table 1 for the name of genotypes). The genotypes that did not interact much with the environments in Coria were Dorondon

Table 4 – Analysis of variance for carbon isotope composition ($\delta^{13}\text{C}$) (‰) for twelve durum wheat genotypes grown in each group of environments as well as the combined set of environments.

| Source of variation ($\delta^{13}\text{C}$) (‰) | df | SS | SS (%) | F | P-value |
|---|-----|--------|--------|-------|---------|
| Combined | | | | | |
| Total | 748 | 1853.5 | | | |
| E | 20 | 878.27 | 47.4 | 25.99 | 0.000 |
| G | 11 | 15.403 | 0.83 | 0.829 | 0.611 |
| G × E | 220 | 99.516 | 5.36 | 0.268 | 1.000 |
| Error | 497 | 839.56 | | | |
| Coria | | | | | |
| Total | 107 | 18.937 | | | |
| E | 2 | 8.074 | 42.6 | 57.85 | 0.000 |
| G | 11 | 4.056 | 21.4 | 5.284 | 0.000 |
| G × E | 22 | 1.784 | 9.4 | 1.162 | 0.308 |
| Error | 72 | 5.024 | | | |
| RF | | | | | |
| Total | 318 | 1237.8 | | | |
| E | 8 | 489.5 | 39.6 | 19.60 | 0.000 |
| G | 11 | 11.7 | 0.9 | 0.340 | 0.976 |
| G × E | 88 | 57.6 | 4.7 | 0.210 | 1.000 |
| Error | 211 | 658.4 | | | |
| IR | | | | | |
| Total | 321 | 269.4 | | | |
| E | 8 | 57.7 | 21.4 | 8.873 | 0.000 |
| G | 11 | 6.4 | 2.4 | 0.720 | 0.719 |
| G × E | 88 | 32.1 | 11.9 | 0.440 | 1.000 |
| Error | 214 | 173.8 | | | |

[10] and Claudio [13]; in Late they were Vitron [2] and Dorondon [10]; under IR Vitron [2] and Mexa [1]; and under RF Dorondon [10] and Simeto [4]. In the RF environments (Fig. 2D), the genotypes Avispa [16] and Vitron [2] gave a good average yield, but their performance was very positive in the Z3 and A3 trials, while they were below the average in Z5. In Coria (Fig. 2A), the genotypes Kicko Nick [19] and Amilcar [14] differ in interaction but not in main effect; thus the genotype Amilcar [14] was comparatively favored in the most productive trial while the genotype Kicko Nick [19] was favored in the less productive trial.

The AMMI2 biplot (Fig. 3) is more informative on the G × E interaction and shows the multiplicative effects of G × E interactions contained in the first two IPCs. Genotypes and environments in the center of the graph did not show a significant interaction, while genotypes and environments lying close to the outer parts of the graph interacted positively, and if their angle was less than 90°, the genotypes possessed a specific adaptation to this environment. In the AMMI2 biplot for Coria (Fig. 3A), the genotypes Gallareta [5], Dorondon [10], Mexa [1], and Kicko Nick [19] had a positive interaction with the C2RF trial, but because Gallareta [5] had the longest vector and was the closest to this environment, it thus possessed specific adaptability to the conditions of this trial. In relation to Late (Fig. 3B), the genotypes Mexa [1] and Simeto [4] had positive interactions with the A5L trial, but Mexa [1] had a specific adaptation to this environment. For RF conditions (Fig. 3D), the genotype Burgos [12] indicated specific adaptation to the Z5RF trial.

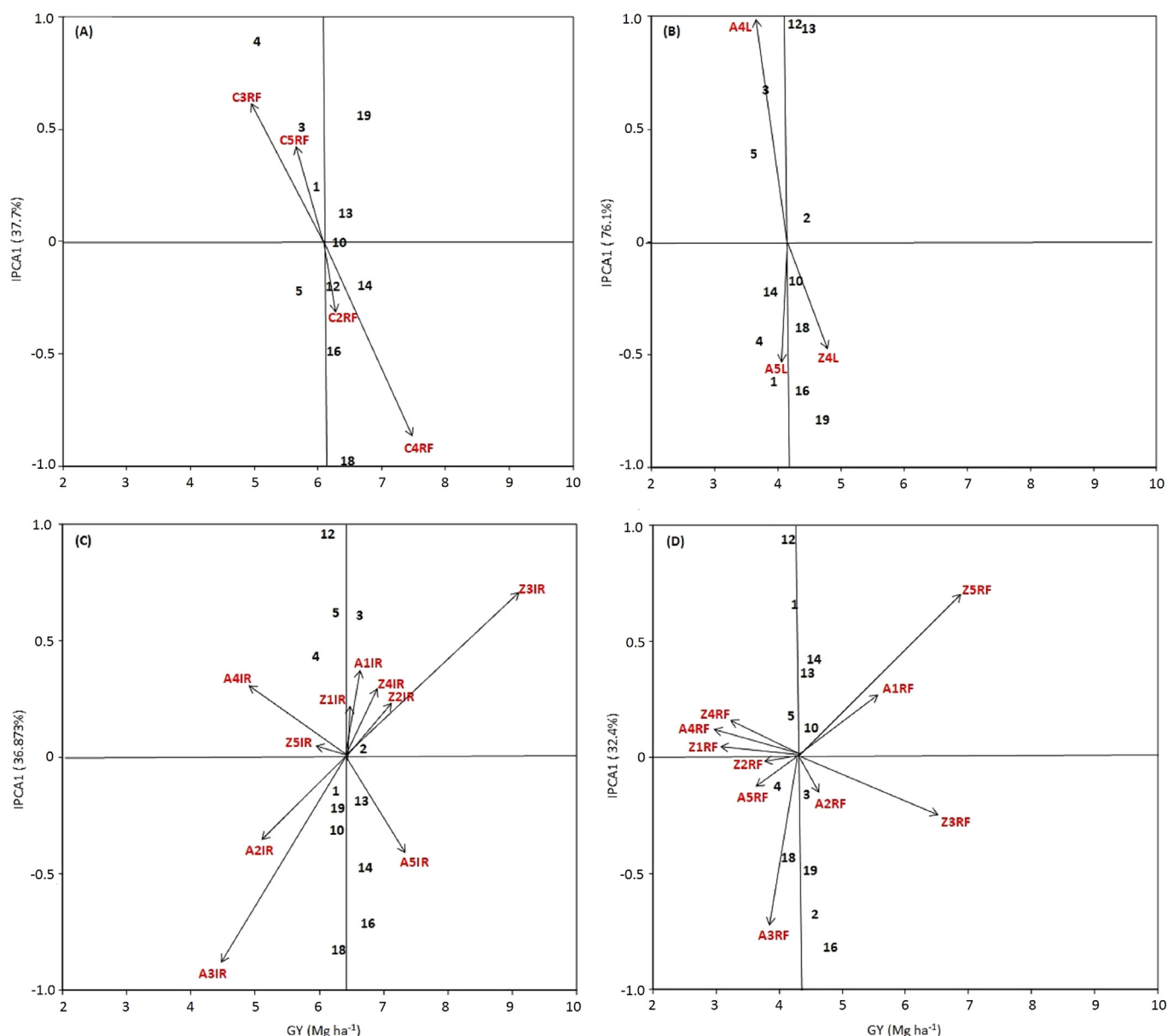


Fig. 2 – AMMI1 biplot for GY (Mg ha⁻¹) of the 12 semi-dwarf durum wheat genotypes evaluated in each group of environment. (A) Coria; (B) Late; (C) IR; (D) RF. Red codes represent environments (see Table 2). Numbers represent genotypes: * (1) Mexa, (2) Vitron, (3) Regallo, (4) Simeto, (5) Gallareta, (10) Dorondon, (12) Burgos, (13) Claudio, (14) Amilcar, (16) Avispa, (18) D Ricardo, and (19) Kicko Nick.

3.5. Climate conditions and genetic gain

To understand the relationship between genetic gain and agro-climatic parameters that form the basis of $G \times E$ interactions, correlations have been made between the coefficient of correlation of the year of cultivar release vs. GY (that is, the genetic gain for grain yield) and different climate parameters (T_{\max} , T_{\min} , and T_{mean}). Positive relationships were found for the correlation coefficient of the genetic gain for GY with T_{\max} (Fig. 4B) and T_{mean} (data not shown), while no relationships existed with T_{\min} (Fig. 4A).

3.6. Relationship between GY, $\delta^{13}\text{C}$, and CTD

Across the set of 21 environments where the $\delta^{13}\text{C}$ of mature kernels was analyzed (Table 2) the GY was negatively correlated with the correlation coefficient between the year of cultivar release and the $\delta^{13}\text{C}$ of mature kernels across the same set of environments ($R^2 = 0.25$, $P < 0.05$) (Fig. 5A) and marginally correlated with the coefficient of correlation between GY and $\delta^{13}\text{C}$ ($R^2 = 0.14$, $P = 0.08$) (Fig. 5B). Across the set of 22 environments where CTD was measured (Table 2) the GY was positively correlated with

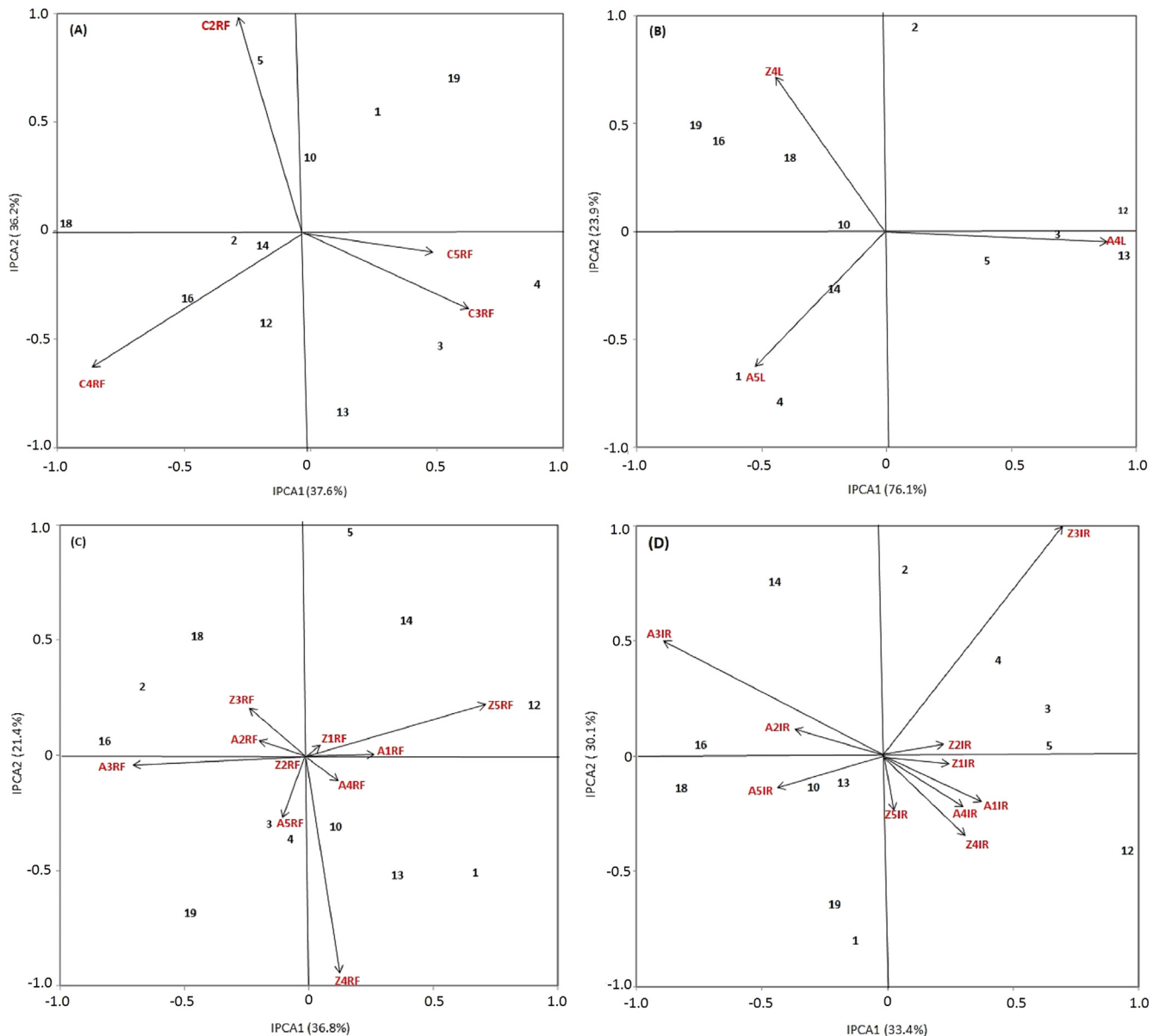


Fig. 3 – AMMI2 biplot for GY (Mg ha^{-1}) of the 12 semi-dwarf durum wheat genotypes evaluated in each group of environments. (A) Coria; (B) Late; (C) IR; (D) RF. Red codes represent environments (see Table 2). Numbers represent genotypes: (1) Mexa, (2) Vitron, (3) Regallo, (4) Simeto, (5) Gallareta, (10) Dorondon, (12) Burgos, (13) Claudio, (14) Amilcar, (16) Avispa, (18) D Ricardo, and (19) Kicko Nick.

the correlation coefficient between GY and CTD ($R^2 = 0.20$, $P < 0.05$) (Fig. 6).

4. Discussion

The environmental parameters affecting the growth of durum wheat showed large variability across the 27 environments included in this study. This variability caused a difference of 6.2 Mg ha^{-1} between the highest and the lowest yielding environments, which represents a range of more than three times the yield obtained in the lowest yielding environment. The environmental effect explained around 81% of the yield

variability, which is in the range of that reported in previous studies in durum wheat (76.4% [11] and 98% [24]) and in bread wheat (57% [12]). Our results revealed the existence of different adaptation patterns among the 12 semi-dwarf genotypes included in this work, as 7.1% of the total yield variance was explained by the different sensitivities of the varieties to the environmental conditions, namely the $G \times E$ interaction. In our study, significant genetic gain for durum wheat in Spain was mostly observed in the warmer environments with optimum conditions in terms of water availability. This result and the AMMI analysis suggest that breeding efforts after the Green Revolution for yield increases in Spain focused on adaptation to specific environments. The earliest

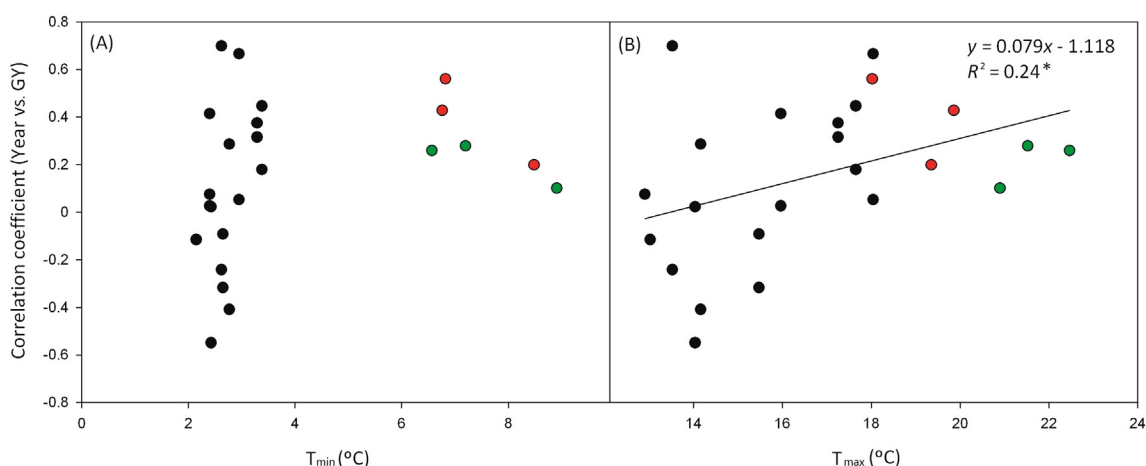


Fig. 4 – Relationship between correlation coefficient of GY vs. year of cultivar release and (A) average minimum temperature (T_{min}) and (B) average maximum temperature (T_{max}) for each environment. Each point represents the average temperature within a trial during the growing period (X-axis), and the correlation coefficient across the twelve genotypes (Y-axis) for each environment (combination between location, year and treatment). The red points correspond to Coria and the green ones to Late.

released cultivars were the lowest yielding varieties in the warmest (but well irrigated) growing conditions (Coria and Late) but not in the cooler environments (environments with low T_{max} and T_{mean} ; either rainfed or irrigated). Conversely, the most modern cultivars performed the best in the warmest sites there were no clear differences with regard to the oldest cultivars in the cooler environments. Nevertheless, because of the wide range of environments considered, the magnitude of the environment effect was much higher than that of the genotype effect. Therefore, the yield performance of the cultivars was highly influenced by environment.

Apparently, breeding in Spain has produced little progress in low yielding environments and the less warm environments (RF and IR) typical of the inland (i.e. cooler) areas of

Spain [9]. However, the yield improvement is not a complete measure of progress achieved by breeding programs, because breeding for stress conditions, for example, has focused on stability rather than yield potential. Variability in water supply and temperatures, and the related $G \times E$ interactions are the main causes for the slow breeding progress in stressed environments [25]. As a result, many farmers in marginal environments have not benefited from major crop research successes [26]. Mediterranean environments are typically stressful due to drought and associated high temperatures, particularly during the later crop stages, [27]. In the same context, De Vita et al. [3] concluded that the breeding strategies adopted during recent decades have contributed to reducing $G \times E$ and selecting genotypes with better stability

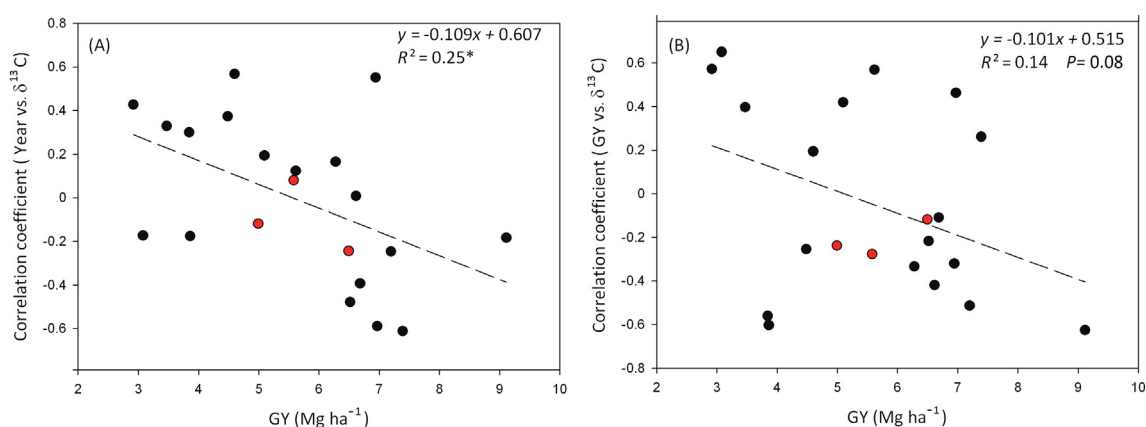


Fig. 5 – Relationship between the average GY within each environment and (A) the correlation coefficient of the year of cultivar release vs. $\delta^{13}C$ within each of the environments and (B) the correlation coefficient of the GY vs. $\delta^{13}C$ within each of the environments (B). Each point represents the average GY value of twelve cultivars (X-axis) and the correlation coefficient across the twelve genotypes (Y-axis) for each environment (combination between location, year and treatment). The red points correspond to Coria.

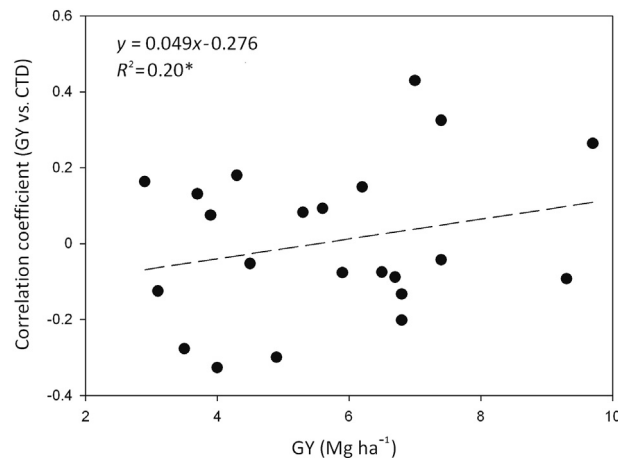


Fig. 6 – Relationship between the average GY within each environment and the correlation coefficient of GY vs. CTD within each of the environments. Each point represents the average GY value of twelve cultivars (X-axis) and the correlation coefficient across the twelve genotypes (Y-axis) for each environment (combination of location, year and treatment).

across a wide range of locations and years. As a consequence, modern genotypes outperform the old ones in all test environments with a strong adaptability to improved fertility.

The current study showed that the post-Green Revolution genotypes in Spain were better adapted to warmer environments (high T_{\max} and high T_{mean}), which agrees with a study done previously in a set of 20 semi-dwarf durum wheat genotypes in Spain [9]. This highlights the influence that the selection environment has on adaptation. In fact, 80% of the total production of durum wheat in the country is concentrated in Andalusia, which is the warmest region of Spain and most of the durum wheat varieties grown in Spain after the Green Revolution have strong Italian and CIMMYT-derived genetic backgrounds. The main breeding site for CIMMYT, and the place where the Green Revolution was developed, is in Ciudad Obregon (NW Mexico) where high temperatures during the growing season are common and plants are grown under well-irrigated conditions. In the case of cultivars derived from Italian germplasm, the material has been selected in South Italy where climatic conditions are comparable to Andalusia.

The importance of the selection environment has led some breeders to follow the strategy of conducting selection in the target environments [28]. When the number of different target environments is large so as to select for suitable genes for each specific target environment, breeders eventually share early segregating populations (F_2) with other breeders or even with farmers [29]. The establishment of separate programs is, no doubt, expensive, but it should yield greater genetic gains. The selection of genotypes exhibiting repeatable $G \times E$ patterns across a large region (i.e. representing what is known as a mega-environment), is less expensive due to the economy-of-scale component, but this may also produce reduced genetic gain within a given area [30]. As observed in this study, Spain's target environments showed wide differences, which included contrasting conditions, as can be deduced from the broad yield range (a difference of more than 6 Mg ha^{-1} between the extreme environments). Where such contrasting

environmental conditions exist, the response of genotypes (yield traits or other traits) is different. In fact, the change in the sign of the correlation coefficients across the set of the twelve cultivars, of the relationship between the average GY within each environment against the correlation coefficient of the relationship between release year vs. $\delta^{13}\text{C}$, from negative in the high yielding environments ($\text{GY} > 5 \text{ Mg ha}^{-1}$) to positive in the low yielding environments ($\text{GY} < 5 \text{ Mg ha}^{-1}$) (Fig. 5A), confirms the existence of different responses of the genotypes. Likewise, the change in the sign of the correlation coefficient between GY vs. $\delta^{13}\text{C}$ from the most- to the least-yielding environments (Fig. 5B) revealed two different response patterns. In the low yielding environments, the advantage is given to cultivars exhibiting a clearer trend towards a survival strategy, with a higher water use efficiency (WUE, understood as the ratio of net assimilation versus transpiration) as inferred by a higher $\delta^{13}\text{C}$ in mature kernels and a positive phenotypic relationship between GY vs. $\delta^{13}\text{C}$ [31,32]. By contrast, under optimum conditions, cultivars exhibiting a drought avoidance response, with a higher water use (in spite of a lower WUE), as inferred by a lower $\delta^{13}\text{C}$ in mature kernels and a negative relationship between GY vs. $\delta^{13}\text{C}$ [15,31,32] were the best performers. In fact, the effective use of water (EUW), which implies maximal soil moisture capture for transpiration and also involves reduced non-stomatal transpiration and minimal water loss by soil evaporation, and not the WUE, has been the target for crop yield improvement, even under drought [32]. The first reaction of virtually most of the plants to severe drought is the closure of their stomata to prevent water loss via transpiration, which leads to a decrease in canopy temperature depression and an increase in the WUE [32]. However, for the high-yielding environments, the more productive cultivars are able to use more water than others and would have more open stomata and therefore higher canopy temperature depression and lower $\delta^{13}\text{C}$ in plant matter [16,31,32]. In fact, the genetic advances by CIMMYT for bread wheat, for example, seems related to lower $\delta^{13}\text{C}$ and higher CTD [33],

which agrees with a higher EUW conferring better performance to cultivars selected under warm albeit well-watered conditions.

5. Conclusions

Breeding in Spain has made genetic progress in warmer environments with optimum conditions (optimum water input) environments that resemble those from where the original germplasm (mostly advanced lines) was selected. Nevertheless, current breeding is driving adaptation patterns more towards specific adaptation. Two different patterns of selection have been reported due the $G \times E$ interaction and changes in the ranking of genotypes: in the high-yielding environments ($GY\ 5\ Mg\ ha^{-1}$), plants favor increased water uptake, with high levels of transpiration and more open stomata (negative value of $\delta^{13}C$ and higher CTD), whereas, in low yielding environments ($GY\ 5\ Mg\ ha^{-1}$) plants close stomata and favor greater WUE (positive value of $\delta^{13}C$ and lower value of CTD).

Supplementary data for this article can be found online at <https://doi.org/10.1016/j.cj.2020.01.005>.

Author contribution

N.A., M.D.S. and J.L.A. conceived and designed the experiment. N.A. managed and directed the wheat trials at the experimental section of Zamadueñas (Valladolid, Spain). F.C. and M.D.S. run the stable isotopes analysis. F.C. did the statistical analysis and wrote the draft paper under the supervision of J.L.A. and M.D.S. N.A. run the additional statistical analyses of the revised manuscript.

Declaration of competing interest

There is no any conflict of interest.

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