1 **Spanish barley landraces outperform modern cultivars at low productivity sites**

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18 With 3 tables and 2 figures, 1 supplemental figure and 4 supplemental tables

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1   **Summary**

2   Barley landraces from the western Mediterranean area have not been thoroughly exploited by modern

3   breeding. This study aims at assessing the agronomic value of a core collection of lines derived from

4   landraces of Spanish origin, and to compare them with sets of successful old and modern cultivars.

5   The agronomic performance of a set of 175 barley genotypes, comprising 159 landrace-derived lines

6   and 26 cultivars, was evaluated in a series of 10 field trials, carried out over 3 years and several

7   locations. The most relevant trait of the landraces was higher grain yield at low production sites than

8   cultivars, which may be related with better ability to fill the grain under stressful conditions. On the

9   other hand, lateness, excessive plant height and lodging were negative traits frequently found in the

10   landraces. Large genotype-by-environment interaction (GEI) for grain yield was detected, related

11   partly with differences among germplasm groups, probably indicating local adaptation. GEI was also

12   associated with the interaction of heading time and powdery mildew resistance with temperature.

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14   **Keywords:** barley, phytogenetic resources, landraces, grain yield

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1 Introduction

2 Over the 20th century, barley producers in Europe chose to substitute their landraces or primitive

3 cultivars by newly bred cultivars. New materials were readily adopted because they were specifically

4 improved for the challenges of modern agriculture and consumer demands. Old landraces were

5 gradually abandoned, and are currently kept mostly in germplasm banks.

6 Nevertheless, landraces and old cultivars persisted in some areas in Europe, probably due to a

7 combination of agronomic and socio-economic factors. A better stability of landraces compared to

8 modern cultivars under largely unpredictable environmental conditions (as in Mediterranean climates)

9 has been recurrently mentioned in plant breeding literature (van Oosterom et al., 1993, Voltas et al.,

10 1999; Lasa et al., 2001).

11 This could be the case of some Spanish landraces, which persisted under cultivation longer than in

12 other Western European regions. The best example is cultivar Albacete, a selection from a landrace

13 made around 1955, which continues to be popular in some regions of Spain due to its reliability. In the

14 semi-arid region of Aragón, it still occupied 69% of the area devoted to six-row barley in 2002 (DGA,

15 2002).

16 In general, landraces constitute one of the most valuable sources of genetic diversity. This diversity

17 has become now more accessible thanks to the advances in genomics and recombinant DNA

18 technology (Newton et al., 2010). Spanish barleys have long been known as a distinct phytogenetic

19 resource with potential to contribute favourable traits to barley breeding. The genetic singularity of the

20 Spanish barleys was described by Tolbert et al. (1979), Moralejo et al. (1994), Lasa et al. (2001), and

21 especially by Yahiaoui et al. (2008). This genetic distinctiveness may be related to the presence of

22 adaptation traits specific to Mediterranean conditions, which is worth investigating. The Spanish

23 Barley Core Collection (SBCC) was assembled as a tool to systematize the study of the genetic

24 diversity of local landraces of barley (Igartua et al., 1998).

25 So far, the Western Mediterranean barley landraces have not been widely used in modern breeding,

26 probably with the exception of the Coast types (of Spanish or North-African origin) that were

1 introduced in California by Spanish settlers in the 18th century (Florell, 1929). These landraces were

2 later one of the founding germplasm groups of current North-American barleys (Knüpffer et al, 2003).

3 The reasons for this overlook are, on one hand, the association of favourable and unfavourable traits of

4 unknown genetic control and, also, an insufficient phenotyping effort. This study is part of an effort to

5 overcome this lack of systematic phenotyping. A thorough evaluation of this collection for disease

6 resistance has been already published (Silvar et al., 2010, 2011a). The objectives of this work are to

7 describe Spanish barleys from the agronomic point of view, to assess their potential to contribute

8 favourable traits, to compare their behaviour with old and modern cultivars widely grown in Spain,

9 and to analyze the relationships of grain yield with various phenotypic and environmental traits. The

10 final purpose of this study is to spur the interest of the barley community over this valuable

11 phytogenetic resource.

12 **Material and Methods**

13 <u>Plant material</u>

14 A total of 182 genotypes were evaluated in field trials. The set comprised the following subsets: 145

15 six-row and 11 two-row Spanish inbred lines, derived from landraces after at least three generations of

16 head-to-row purification; sixteen old cultivars, widely used in Spain during the 20th century, 8 two-row

17 (Alpha, Beka, Hassan, Kym, Pallas, Union, Wisa and Zaida) and 8 six-row (Ager, Albacete, Almunia,

18 Barberousse, Dobla, Hatif de Grignon, Monlon and Pané); and, finally, ten cultivars, recently bred or

19 currently grown in Spain, used as controls of good agronomic performance (Candela, Orria, Plaisant

20 and Steptoe six-row; Gaelic, Graphic, Nevada, Seira, Tipper and Volga two-row). The first three

21 groups, six-row and two-row landrace-derived inbred lines and old cultivars, constitute the Spanish

22 Barley Core Collection (SBCC, Igartua et al., 1998).

23 <u>Field trials</u>

24 A total of 10 field trials were sown in standard dates (Table 1) in three provinces, representing relevant

25 barley growing areas of Spain (Table 1). The climatic data for the locations were provided by the

26 Spanish Meteorology State Agency (AEMET), and were gathered from stations either in the same

location of the trial (Zuera, Sádaba), or in locations within a 20 km radius (the rest). Potential evapotranspiration (ETP) was estimated based on the daily data of precipitation, maximum and minimum temperatures, using the method of Hargreaves (Hargreaves et al., 1985). Daily temperature, precipitation, ETP, and precipitation/ETP ratio were converted to monthly and seasonal (autumn, winter and spring) averages (Table 1).

Each trial occupied a large area (0.7 ha). Therefore, soil heterogeneity was a concern. To minimize its effect, the trials were subdivided in four sub-trials at each location. Each sub-trial included 44 SBCC accessions plus the 10 modern check cultivars, for a total of 54 accessions per sub-trial. One check was sown twice to fill up the last sub-trial. The allocation of genotypes to sub-trials was done in a stratified manner, keeping the original proportions of the groups (six-row lines, two-row lines, old cultivars), and also maintaining a balance of geographic origins between the four sub-sets.

The experimental design for each sub-trial was an alpha-lattice, with 3 replications. Therefore, the ten modern cultivars were replicated 12 times, 3 at each sub-trial, whereas the rest of the accessions were replicated three times. Incomplete blocks were arranged in two directions, row (k=9) and column (k=6). Each genotype was sown in 6 row plots, 6 m long, 0.2 m between rows, with a rate of 350 seeds m^{-2}. Each sub-trial had a width of 27 plots, with an alley of 1 m between tiers. The disposition of the sub-trials in the field was in quadrants, conforming a square plot of 81 m side length. Replications were nested within sub-trials.

Traits

The traits recorded were plant height (PHT), measured at maturity, in one representative plant of each plot, as the height from the tillering node to the point of insertion of the flag leaf; heading date (HED), as the number of days from January 1st until the day when 50% of the stems of each plot displayed 2 cm protruding awns; lodging (LDG), recorded only at the trials in which it was present, following the visual scale of IPGRI (1994), with values from 1 (very low) up to 9 (very high); grain yield (YLD), as grain weight per plot in q ha^{-1}; test weight (TW), determined with a grain analyzer (Dickey-John); thousand kernel weight (TKW); yield components (only at Zuera, Zaragoza, 2003), namely, number of ears m^{-2} (SPM), number of grains by ear (KS), number of grains m^{-2} (KM), and weight of 1000 grains

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1 (TKW), from hand-harvest of a segment 1 m long of two central rows of each plot, for two

2 replications; incidence of foliar diseases (leaf rust, LR; net blotch, NB; powdery mildew, PM) at trials

3 in which the attacks were severe enough to reveal apparent genotypic differences (visual scores from

4 1-resistant to 9-susceptible on plot basis); malting quality traits, carried out at the DAMM company

5 facilities in Bell-lloc, Lleida, with samples from the FOR03 trial, which produced good grain quality.

6 The traits recorded were caliber of grains, as the percentage of grains that passed through a sieve of

7 2.2 mm (screening, SCR), the percentage of grains retained by a sieve of 2.5 mm (kernel plumpness,

8 KP); the percentage of the malt rendered soluble upon mashing in the laboratory, i.e., the solids

9 content of wort (MEX), and the percentage of protein in the grain (PRT). A complete list of trials

10 where these traits were recorded is provided in Table S1.

11 <u>Statistical analyses</u>

12 Each sub-trial was analyzed following the alpha-lattice design, using the procedure *proc mixed* of SAS

13 (1988). BLUPs for the genotypes for each trait at each sub-trial were calculated accordingly. In a

14 second analysis, the 10 check cultivars included in all sub-trials were analyzed, following a

15 randomized complete block design (RCBD), with three replications nested within the four sub-trials

16 (analyzed with *proc glm*, SAS, 1988). When the averages of the 10 checks for a particular trait were

17 significantly different between sub-trials, this was interpreted as a true difference due to uncontrolled

18 environmental conditions (possibly soil), and a correction was carried out. A factor, K, was calculated

19 dividing the general average of the field trial by the average of the sub-trial. The corrected data were

20 obtained multiplying the corresponding K value by the trait value of the genotypes included in each

21 sub-trial. This correction was actually rather light, and was preferred over the option of correcting on

22 the basis of the values of the 10 common checks, as this apparently overcorrected the data.

23 A previous diversity study based on molecular markers, revealed the occurrence of four different

24 groups of accessions, or populations, in the landrace-derived Spanish lines, based on genetic

25 differences (Yahiaoui et al., 2008). These populations were taken into account as possible sources of

26 variation for the phenotypic traits measured in this study. The four groups (numbered G1 to G4)

27 comprised 17, 9, 48 and 82 genotypes, respectively. For the purpose of this analysis, the SBCC sets of

old six-row cultivars, old two-row cultivars, and the 10 modern check cultivars were also considered as groups, G5 to G7, respectively.

Genotype was considered as a random factor, as the genotypes are a representative sample of all Spanish landrace barleys, and of cultivars widely grown in Spain. Environment, a combination of location and year for each field trial was considered fixed, because of the low number of degrees of freedom. This choice was justified because the number of field trials used was enough for an agronomic evaluation, but it is uncertain whether their frequencies are a representative sample of all possible environments in our conditions.

An AMMI analysis (Gauch, 1988, 1992) was carried out to describe the genotype-by-environment interaction (GEI) for grain yield, the main trait under study. This analysis was performed with routines *proc glm* and *proc princomp* in SAS (SAS, 1988). The number of significant terms in the AMMI model was evaluated with the method of Gollob (1968). The graphical representation of the AMMI model was enriched by plotting additional genotypic, phenotypic and environmental (climatic) variables, to study their relationship with the GEI of grain yield. A regression analysis of these variables with the genotypic principal component scores of the AMMI axes was performed. The regression coefficients were represented on the biplots, with length proportional to the coefficient of determination (percentage of variation of AMMI axes explained) of each external variable. Some of the environmental covariates were highly correlated among themselves. To reduce redundancy among them, a principal component analysis for these variables was carried out and only the most representative variables were shown in the AMMI graphical representations.

Finally, sets of external genotypic and environmental variables were introduced in the analysis of variance for grain yield by means of factorial regression (van Eeuwijk, 1995). These sets of variables were introduced as covariate for the GEI in a sequential manner as shown in Baril et al. (1995). Then, the two subsets of best covariates were combined in a single analysis, testing all their possible interactions until arriving at the most parsimonious model possible (the one that explained the largest proportion of the GEI sums of squares, using a minimum number of degrees of freedom).

1   **Results**

2   The values of trial ART02 were not included in the analysis of grain yield, because severe lodging

3   impeded a good separation of plots during harvest. The results of three six-row Spanish accessions

4   originally included in the analysis are not reported, as they turned out to be duplicates, after analysis

5   with molecular markers (Yahiaoui et al., 2008).

6   Corrections due to differences among sub-tests were necessary at eight trials for grain yield, four for

7   test weight, two for thousand kernel weight, and three for plant height. The correction factors were

8   quite low, with the most extreme values being 0.9447 and 1.0618 for plant height at SAD02 and

9   ART02, respectively, which means correction of approximately ± 6%.

10   <u>Responses of groups of genotypes</u>

11   There were noticeable differences between landraces and cultivars for all traits (Fig. 1). The analyses

12   of variance for each trait are presented in Tables 2 and S2. The genotypic differences were broken

13   down into *between* and *within* genetic groups (as defined in the M&M section). For most traits, mean

14   squares for *between groups* were larger than *within groups*, especially for plant height, lodging and

15   test weight, but also for powdery mildew resistance, grain yield, leaf rust resistance, thousand kernel

16   weight and heading time. The GEI was also broken down in the same manner. The mean squares for

17   this interaction were also larger *between* than *within* groups by trial for all traits.

18   Grain yield was higher overall for cultivars than for landrace-derived lines. The mode for cultivars and

19   landraces was on the same yield class, but there were only cultivars at the highest yielding class. In a

20   further step, trials were divided into two subsets according to overall productivity, with the threshold

21   around 3000 kg ha^{-1}: high productivity (YLD-H) for trials BEL02, VLD02, ART04 and SAD04, and

22   low productivity (YLD-L) for trials SAD02, FOR03, SAD03, VED03, and VLD03. At high

23   productivity trials, the cultivars yielded more than landrace lines, with most cultivars placed at the two

24   highest yielding classes, in which there were no landrace lines. At the low productivity trials, however,

25   landraces outyielded cultivars on average. Only 2 out the 25 highest yielding genotypes averaged over

26   low productivity trials were cultivars, and the first 9 were landraces. There were differences among the

8

1   landrace groups as well (Table 2), with accessions from G4 showing a clear advantage over the other

2   landrace groups at low yielding sites (Table S3). In these trials G4 and G3 actually performed on

3   average as well as the best groups of cultivars.

4   Landraces were, overall, later flowering than cultivars, with an average delay ranging from 2.3 to 5.8

5   days among trials (Table S4). Ranges of flowering dates were larger for landraces (between 17.5 and

6   26.0 days) than for cultivars (between 9.7 and 19.0 days, Table S4). The most frequent flowering date

7   for cultivars was around April 24-26, whereas for the landraces the mode was on April 28th (Fig. 1).

8   Plant height was another trait in which landrace lines and cultivars presented striking differences.

9   Most cultivars were very short, below 64 cm, whereas all landraces surpassed this height, with a mode

10   around 83 cm, with the exception of G2 lines, which were shorter (Table S4). The pattern for lodging

11   was similar to plant height, most cultivars being lodging resistant, whereas most landraces were prone

12   to lodging.

13   Regarding yield components, the number of spikes and the number of kernels per square meter were

14   larger for cultivars, though these traits were calculated only for one location. The two groups of two-

15   row materials (G2 and G6) presented higher number of spikes per area than the rest. Number of

16   kernels per spike was larger for landrace lines, but this was expected as 93% of them are six-row,

17   whereas only 46% of cultivars are six-row. Test weight was larger for cultivars than for landraces, but

18   thousand kernel weight was superior for landraces overall, particularly for groups G3 and G4, which

19   had larger values than cultivars. This was true for 7 out of the 8 trials in which this trait was

20   calculated.

21   Besides the main field trials reported here, the whole SBCC or the subset of landrace-derived

22   accessions were tested in additional locations in smaller, unreplicated plots (6 rows, 25 cm apart, 3.5

23   m long). In two of these trials there were disease attacks severe enough to reveal apparent genotypic

24   differences. One trial at the province of Gerona (north-western tip of Spain), in 2000, suffered attacks

25   of leaf rust (LR) and powdery mildew (PM), whereas one trial at Valladolid, also in 2000, had a

26   powdery mildew attack. Also, noticeable damage due to net blotch (NB) was observed in trials ART02

1 and FOR03, and due to PM at BEL02 and SAD02. There seems to be ample diversity for powdery

2 mildew and leaf rust resistance in landrace lines, and less for the reaction to net blotch (Table 2).

3 Regarding quality traits, grain size parameters (SCR, KP) for the landrace lines were comparable to

4 the results of cultivars. Differences in malt extract and grain protein were almost non-existent,

5 probably due to low replication of these measurements, and are just a rough indication of the malting

6 quality potential of the genotypes tested.

7 <u>Joint analysis for grain yield</u>

8 The analysis of variance for grain yield revealed large differences between genotypes, and also a

9 significant GEI. For both the principal effect (genotype) and the GEI, the mean squares *between*

10 *groups* were much larger than *within groups*. Furthermore, when the GEI *between groups* was broken

11 down, it was evident that the larger share of this interaction was contributed by the comparison of high

12 vs. low productivity trials (Table 3).

13 The AMMI analysis for grain yield suggested some trends in the GEI (Figs.2 and S1). The first three

14 axes were significant, explaining 48.0%, 28.0% and 15.5% of the sum of squares of the GEI,

15 respectively (Table 3). Actually, the third axis may represent mostly noise, as we could expect a

16 maximum of 81% of the GEI sums of squares due to pattern, as estimated by the method proposed by

17 Gauch (1992). Therefore, the AMMI2 model is more parsimonious, and will be kept for further

18 analyses. The trials could be classified roughly in three groups: two highly interactive groups, one

19 with trials from the province of Valladolid (VLD03, VLD02) and the other with trials from the

20 province of Lleida (BEL02, ART04), and the last group with the trials showing the least interaction,

21 four from the province of Zaragoza (SAD02, SAD03, SAD04, VED03) and one from Lleida (FOR03).

22 The first axis indicated a contrast between trials BEL02 and ART04 on one side, and VLD02 and

23 VLD03 on the other. The second axis was driven mostly by the contrast between SAD03 and FOR03

24 vs VLD02 and ART04. The separation between most cultivars (particularly those belonging to G5 and

25 G7) and the landraces indicated different GE responses. Most cultivars had negative scores on both

26 axes, whereas the landraces were distributed over the other three quadrants of the plot, although some

27 were placed close to the origin, meaning that their GEI was minimal. There were differences between

10

1 groups of landraces as well. Almost all accessions from G3 had positive scores on the first axis. The

2 accessions from the other 3 landrace groups were more scattered, but it is remarkable that, almost

3 exclusively, accessions from G4 were found in the second quadrant. Therefore, there were apparent

4 differential adaptations between cultivars and landraces, but also among landrace groups.

5 The genotypic covariate with largest positive correlations with the first axis was the reaction to

6 powdery mildew, followed by plant height, lodging, leaf rust and heading time. Test weight, on the

7 other hand, showed a strong negative correlation with the first axis. This axis also was significantly

8 (and positively) correlated with maximum temperatures and evapotranspiration in the fall. We can

9 speculate that good growing conditions during vegetative growth promoted plant development (higher

10 plant height and lodging) at VLD02 and VLD03, but also favoured the development of diseases,

11 particularly for the accessions with positive scores on the first axis, mostly landraces from all groups.

12 The landraces and cultivars with negative scores on the first axis probably combined smaller size with

13 some tolerance to diseases. The fact that no landrace had sizeable negative scores on both axes means

14 that there was no line combining reduced plant height and lodging and good tolerance to disease.

15 Actually, this may be one of the reasons of the overall superiority of modern cultivars in Spain. The

16 second component showed less strong correlations with genotypic and environmental covariates. The

17 strongest one was with plant height which, overall, appears as the main genotypic factor causing GEI

18 in this study. Test weight was the other genotypic covariate with a remarkable correlation, negative,

19 with the second axis.

20 In general, the cultivars showed relatively better performance at the higher yielding sites, except

21 VED03, whereas G3 accessions showed an opposite pattern. The cultivars, in general, did not present

22 a relatively good performance at the lowest yielding trials (SAD02, FOR93, SAD03, VLD03),

23 whereas some landraces from groups G1, G2 and G3 had better relative adaptation at these trials.

24 The results of the factorial regression pointed at several genotypic and environmental covariates as

25 related to the GEI of grain yield. Actually, the mean squares of the interaction terms including some of

26 these covariates were remarkably larger (Table 3) than those derived from other partitionings of GEI

27 (AMMI and genotypic groups). The reaction to powdery mildew was the main genotypic factor related

1 to grain yield GEI, particularly when considered together with the maximum fall temperature. Heading

2 time, again in interaction with maximum fall temperature, was the second most important genotypic

3 factor, followed by lodging which in turn, did not show any significant interaction with environmental

4 covariates. Only 1.7 % of the degrees of freedom of GEI, corresponding to the interaction of the three

5 genotypic covariates with Trial, explained 38.8% of its sums of squares. Moreover, just two degrees of

6 freedom of the GEI (0.14%), corresponding to the interaction of powdery mildew resistance and

7 heading time with maximum fall temperature, explained 21.1 % of the GE sums of squares.

8 **Discussion**

9 This study aimed at the characterisation of a potentially useful genetic resource, the Spanish landraces

10 of barley, which has been scarcely used in modern plant breeding. Previous studies determined that

11 they show clear genetic differences with the germplasm used in mainstream barley breeding in Europe

12 (Yahiaoui et al., 2008) and also that they may carry adaptations to environmental conditions that may

13 be useful for other regions in a climate change scenario (Casas et al., 2011). The present study gives a

14 complete overview of the agronomic potential of Spanish landraces. The main finding of this study is

15 the identification of drastic changes of genotype order between productivity levels, revealing that

16 landraces are superior under mid-to-low production conditions. This is a relevant message for

17 European breeders, because it means that some of these landraces possess traits that may have not

18 been well captured in current cultivars. This finding is particularly interesting at this moment, in which

19 breeders are looking for sources of favourable traits to increase resilience of crops to respond to

20 climate change challenges.

21 The large differences found between landraces and cultivars were not unexpected. Variety

22 replacement over the 20th century occurred for a reason, and this study hints at several traits as the

23 possible basis underlying this replacement. From the agronomic point of view, a detrimental trait of

24 the landraces is the excessive plant height that induces lodging under mid-high yielding conditions.

25 Lower plant height and lodging in cultivars compared to landraces may have resulted from adaptation

26 to modern fertilization levels. In fact, reduced plant height has been one of the main outcomes of

27 modern breeding in winter cereals (Austin et al., 1980; Friedt, 2011). The longer growth cycle of the

landraces may be affected by the age in which they were developed. The original landraces were collected mostly in the first half of the 20th century, whereas the cultivars were bred in the second half of the century, mostly in the last quarter. Several studies have found an increase of temperatures in many regions of the world and, specifically, in Northern Spain over the second half of the past century (an average of 1.4ºC, reported by Peñuelas et al., 2002) and in Southern Spain from 1986 until 2008 (García-Mozo et al., 2010). These increases have caused, for instance, an advancement of leaves unfolding in trees of 16 days over 49 years (Peñuelas et al., 2002), and an advancement of flowering time of arboreal and herbaceous species, correlated with temperature increase (García-Mozo et al., 2010). This shift of phenological events must have affected crops as well. For instance, by advancing the occurrence of stressful situations during grain filling for winter cereals, due to earlier episodes of high temperatures. This increase of risk of high temperature stress for Southern Europe over the last century was indeed detected by the IPCC (IPCC, 2007). Therefore, an advancement of heading time in modern varieties, to avoid increasingly early terminal stress, is not surprising. A similar shortening of growth cycle due to breeding was observed for durum wheat (De Vita et al., 2007, Royo et al., 2008). On the other hand, the earliest heading time observed in landraces and cultivars was the same, suggesting that there is a minimum safety threshold to achieve heading, after the period of high risk of late frosts is over.

The landraces, in general, presented worse agronomic ability than cultivars. However, they also displayed large variability for most traits, suggesting a possible use for breeding. In this respect, one of the most important results of this study is that landraces presented better adaptation to low yielding environments. Finding as many as nine landrace-derived lines which outyielded 26 cultivars under our mid-to-low production conditions was an unexpected result of this study. These results suggest that modern breeding has not impacted Spain as it has impacted barley production in Central and Northern Europe. This phenomenon was already detected at a number of studies carried out in the Mediterranean region with different sets of local germplasm (Pswarayi et al., 2008a,b; Ceccarelli, 1994; Ceccarelli and Grando, 1989, 1996). These studies, however, focused mostly on field trials with very low production levels, around or below 1 t ha^{-1}, whereas average grain yields of our low yielding

are representative of a higher productivity level, between 1.7 and 2.4 t ha^{-1} (Table S4). It was expected that, at this level, yield potential would still be the main feature determining grain yield, as found by Rizza et al. (2004) for Southern Italy, but this was not the case. This level of production is very common on large areas of barley cultivation in Spain and in other countries with Mediterranean climates, like Spain, Algeria or Australia, which are among the main barley producers (FAOSTAT, 2013). Usually, the main limitation to realize higher yields in Mediterranean environments is limited water availability (Rizza et al., 2004) and, therefore, any superior germplasm under these conditions may carry some positive drought tolerance traits. Abundant research on drought tolerance of crops indicates that different mechanisms may be relevant at different productivity levels, (Cattivelli et al., 2008). Therefore, the best Spanish landraces represent useful resources for breeders to mine for traits useful for drought tolerance, particularly at moderate yielding levels.

The landrace lines were not homogeneous agronomically. Actually, the groups of landraces made according to their genetic diversity (Yahiaoui et al., 2008) also presented notable differences for several agronomic traits. It is remarkable that accessions from groups G3 and G4 had higher TGW than groups of cultivars, even though these two groups were significantly later heading than the cultivars and, therefore, experienced slightly worse grain filling conditions than the cultivars. This may be partially explained by a balancing effect between yield components but it also suggests the presence of stress tolerance mechanisms during grain filling in the Spanish accessions of groups G3 and G4. Kernel weight is the yield component which is most affected in winter cereals suffering terminal stress (Stone and Nicolas, 1994; Brancourt-Hulmel, 1999), particularly under Mediterranean conditions (Voltas et al., 1999), and different mechanisms to maintain adequate grain filling under stress have been proposed (Blum, 2005). Actually, improvement of grain filling under stress has been identified as one of the main outcomes of breeding in durum wheat (Alvaro et al., 2008). The potential of some Spanish landraces to enhance grain filling under stress merits further exploration.

There were significant differences between accessions for grain yield, and also a large GEI term. In both cases, a large part of both terms was due to the differences between genotypic groups, particularly landraces and cultivars, although the differences within groups were still significant.

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Cultivars, in general, presented plant height, heading time and lodging susceptibility better suited to modern cultivation The results of the factorial regression also indicated a large relevance of powdery mildew resistance in the determination of grain yield GEI. This was also visible in Fig. 2, in which the reaction to powdery mildew and leaf rust seem to be driving the spread of the genotypes over the first axis. Brancourt-Hulmel (1999) found that heading time, lodging and powdery mildew resistance were the main genotypic features that drove GEI in winter wheat trials in France, the same traits we have found for barley in Spain in this study. Most likely, all these traits had some relevance in the process of the substitution of modern cultivars for landraces in Spain.

The genotypic groups showed some specific features that can be used for their focused use in breeding. Group G1 was constituted by a clearly differentiated set of accessions. They had the longest growth cycle and were the tallest genotypes. Though no direct measures of biomass were made, it was evident that they produced larger biomass than the rest. It is possible that the original landraces were grown to be used as fodder, and thus may be interesting material for bioenergy uses. The accessions from G3 and G4 come from different parts of Spain (Yahiaoui et al., 2008). G3 comes from colder regions of the inland plateau, whereas G4 comes from warmer lowlands of the Southern part of the country, the coastal Mediterranean regions and the Ebro valley. The first axis of the AMMI analysis is a contrast between locations that are representative of these two areas: Valladolid (VLD02, VLD03) is in the centre of the Northern plateau, and Lleida (BEL02, ART04) is in the centre of the Ebro valley. Therefore, there was good agreement between the origin of the accessions and their position in the AMMI biplot (Fig. 2). All but one of the accessions from G3 had positive loadings in axis 1, same as VLD02 and VLD03. G4 accessions were actually more spread over the first axis, but many were on the same (negative) side as ART04 and BEL02.

Among all groups of genotypes studied, the best accessions from group G4 offer the highest potential to contribute favourable traits for grain yield and disease resistance. These lines, though later heading than cultivars, were the earliest landrace group and also showed the best scores for leaf rust and powdery mildew resistance among the landraces. Nevertheless, they should be introduced with care into breeding programs, to reduce their plant height and susceptibility to lodging. For this purpose,

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introgression through backcross is advised. Also, care should be taken to ascertain the agronomic effects of possible adaptation syndromes that have been selected for in the landraces over time, affecting at the genes of the vernalization and photoperiod pathways (Casao et al., 2011a, b). Ongoing work using genome wide association mapping, and linkage mapping approaches with biparental populations derived from the best Spanish lines (Hofmann et al., 2013; Silvar et al, 2011b; Ponce-Molina et al., 2012) is already producing useful information on markers linked to economically important traits that can be used to facilitate targeted trait introgression with marker –assisted selection.

Acknowledgments

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Table1. Geographic coordinates, climatic characteristics, sowing date of the field trials.

Location	Coordinates	Altitude (m)	Harvest year	Trial code	Sowing date	Mean T (ºC)			Min T (ºC)			Max T (ºC)			Rainfall (mm)				ETP[4]			Ratio[5]		
						A[1]	W[2]	S[3]	A	W	S	A	W	S	A	W	S	Total	A	W	S	A	W	S
Artesa de Segre (Lleida)	41º53'N 01º02'E	320	2002	ART02	31/10/2001	7.10	7.13	16.13	1.40	0.70	8.63	12.77	13.57	23.57	100	67	202	369	130	154	435	0.77	0.44	0.46
			2004	ART04	18/12/2003	9.30	5.67	16.00	4.97	0.20	9.30	13.67	11.77	22.67	130	126	167	423	113	133	410	1.15	0.94	0.41
Bell-lloc d'Urgell (Lleida)	41º38'N 00º47'E	210	2002	BEL02	07/11/2001	8.33	7.97	16.83	3.43	2.60	9.43	13.13	13.37	24.23	82	54	152	289	127	147	442	0.65	0.37	0.34
Foradada (Lleida)	41º52'N 1º00'E	455	2003	FOR03	07/11/2002	9.80	5.83	18.07	4.43	-0.63	10.30	15.13	12.33	25.80	165	178	35	378	133	147	467	1.24	1.21	0.07
Macotera (Salamanca)	40º49'N 05º17'E	892	2002	VLD02	08/11/2001	8.97	9.07	15.97	3.07	3.67	8.73	15.10	14.47	23.17	111	107	137	354	140	154	431	0.79	0.69	0.32
			2003	VLD03	11/11/2002	11.73	6.33	14.70	6.83	-3.40	5.17	16.57	16.50	23.60	199	169	72	440	137	142	419	1.46	1.19	0.17
Sádaba (Zaragoza)	42º16'N 01º16'E	440	2002	SAD02	28/11/2001	8.93	8.57	16.20	2.97	2.97	9.13	14.87	14.07	23.20	66	59	162	287	136	149	421	0.49	0.39	0.38
			2003	SAD03	27/11/2002	11.17	6.73	17.37	6.43	1.63	10.37	15.87	11.83	24.33	147	189	77	413	128	133	437	1.15	1.43	0.18
			2004	SAD04	23/12/2003	9.33	6.00	15.50	4.93	0.93	8.70	13.77	11.03	22.23	159	116	129	404	114	126	409	1.40	0.91	0.32
Zuera (Zaragoza)	41º52'N 00º39'E	298	2003	VED03	08/11/2003	11.07	7.13	18.10	6.53	2.17	11.33	15.60	12.07	24.80	138	127	106	371	125	134	439	1.10	0.95	0.24

2
3   1 Autumn; 2 Winter; 3 Spring; 4 ETP: total evapotranspiration calculated according to the method of Hargreaves; 5*Ratio*: rainfall divided by the ETP
       Source: National Institute of Meteorology

Table 2. Separation of means among the genotypic groups for all traits (see description in text). Numbers followed by the same letter in each column are not significantly different according to an LSD (P<0.05).

Groups	HDN (days)		PHT (cm)		LDG (score)		YLD (q/ha^{-1})		YLD_L (q/ha^{-1})		YLD_H (q/ha^{-1})	
1	122.9	A	85.4	A	4.0	B	23.27	D	18.86	B	28.8	E
2	118.5	B	73.7	C	3.6	BC	24.01	D	18.90	B	30.4	DE
3	118.8	B	81.4	B	5.5	A	25.96	C	21.63	A	31.4	D
4	116.9	C	80.8	B	5.5	A	27.08	BC	22.08	A	33.3	C
5	112.5	E	63.0	D	1.4	D	26.75	C	18.97	B	36.5	B
6	114.2	D	74.1	C	3.0	C	28.27	B	21.59	A	36.6	B
7	114.7	D	59.8	E	1.1	D	29.90	A	21.84	A	40.0	A

Groups	TW (kg. hl^{-1})		TKW (g)		SPM (number)		KNM (number)		KS (number)		LR (score)	
1	65.5	D	35.8	D	213	C	6844	A	32.4	A	7.4	AB
2	69.3	B	38.5	C	340	A	6297	A	18.7	D	8.1	A
3	62.7	F	42.6	A	246	C	6506	A	26.3	B	8.2	A
4	63.6	E	42.6	A	259	BC	7043	A	27.8	AB	6.2	B
5	72.1	A	38.7	C	374	A	7236	A	19.1	CD		
6	67.0	C	41.0	B	259	BC	7558	A	28.5	AB		
7	69.3	B	39.1	C	323	AB	7759	A	24.6	BC		

Groups	NB (score)		PM (score)		SCR (%)		KP (%)		MEX (%)		PRT (%)	
1	5.7	BCD	4.6	B	8.0	A	53.4	C	76.5	A	11.3	AB
2	4.9	E	4.5	B	3.9	B	66.4	BC	78.2	A	12.0	A
3	5.9	AB	5.9	A	3.4	B	73.2	AB	73.2	A	10.9	AB
4	5.8	BC	4.2	B	3.7	B	70.6	AB	72.3	A	11.9	A
5	5.2	DE	2.9	C	2.0	B	81.5	A	79.9	A	11.8	A
6	6.3	A	3.9	B	2.6	B	77.1	AB	77.5	A	10.5	B
7	5.3	CDE	2.5	C	8.0	A	53.4	C	76.5		11.3	AB

Table 3. Joint analysis for grain yield, showing three different partitions of the genotype-by-environment factor: genotypic groups (see text), AMMI and factorial regression with genotypic and environmental covariates.

Source	df	SS	MS	F	
Trial	8	264928	33116	4088.4	**
Genotype	181	29322	162	20.0	**
Between groups	6	11248	1868	230.6	**
Within groups	175	18074	104	12.8	**
Genotype x Environment	1448	62942	44	5.4	**
Genotypic groups					
GE between groups	48	21667	451	55.7	**
GE bet. groups, high productivity	18	10102	561	76.1	**
GE bet. groups, low productivity	24	4747	198	24.4	**
GE bet. groups, high *vs*. low	6	6818	1136	140.2	**
GE within groups	1400	41275	29	3.6	**
GE with. groups, high productivity	525	21150	40	4.9	**
GE with. groups, low productivity	700	13150	19	2.3	**
GE with. groups, high *vs*. low	175	6975	40	4.9	**
AMMI					
AMMI1	188	30205	161	19.8	**
AMMI2	186	17594	95	11.6	**
AMMI3	184	9751	53	6.5	**
AMMI3 residual	890	5392	6	0.7	
Factorial regression					
PM*Trial	8	10978	1372	168.9	**
PM*Max T autumn	1	8049	8049	990.8	**
Deviation	7	2928	418	51.5	**
HDN*Trial	8	6903	863	106.2	**
HDN* Max T autumn	1	5204	5204	640.6	**
Deviation	7	1700	243	29.9	**
LDG*Trial	8	6539	817	100.6	**
Residual	1424	38522	27	3.3	**
Error	3276		8		

**: Significant at level $P < 0.01$

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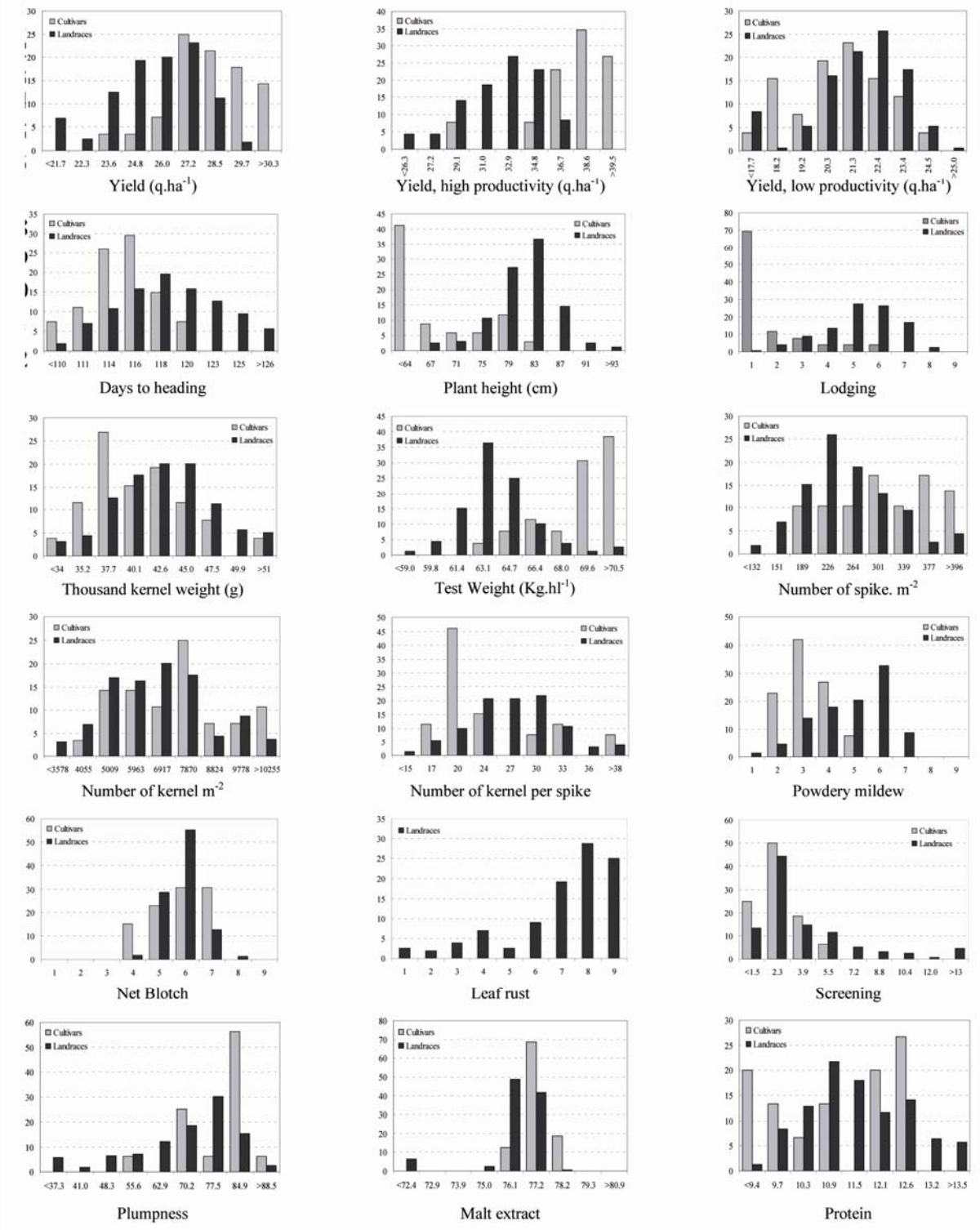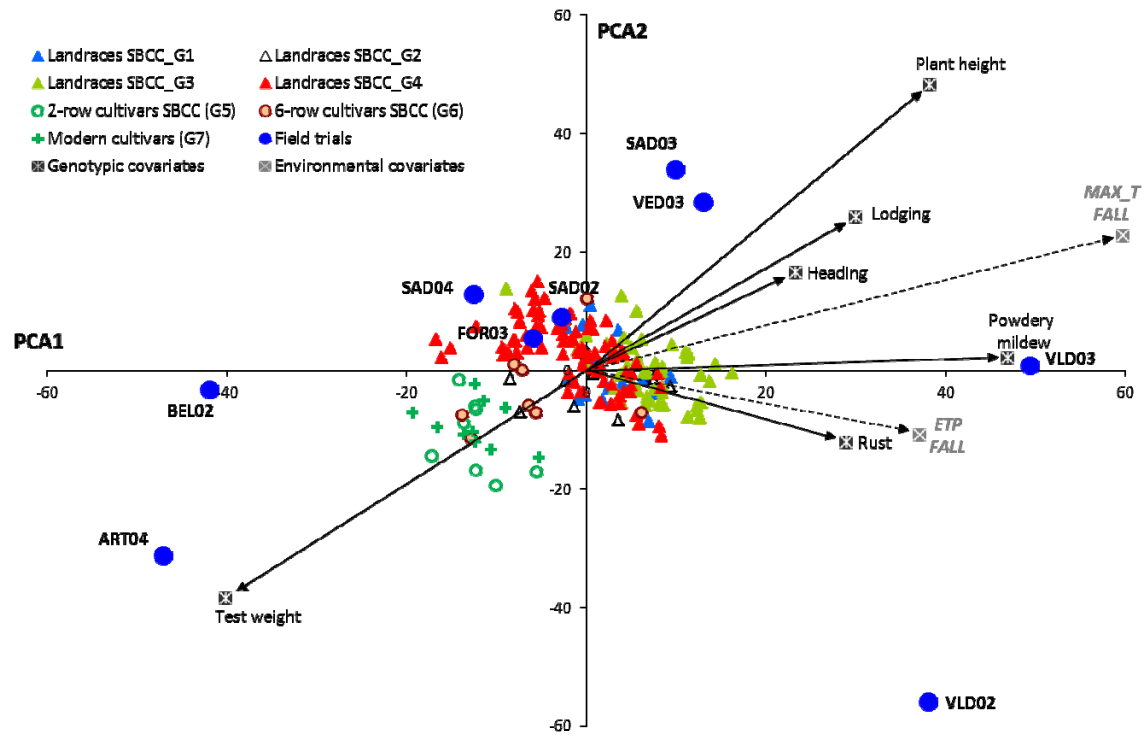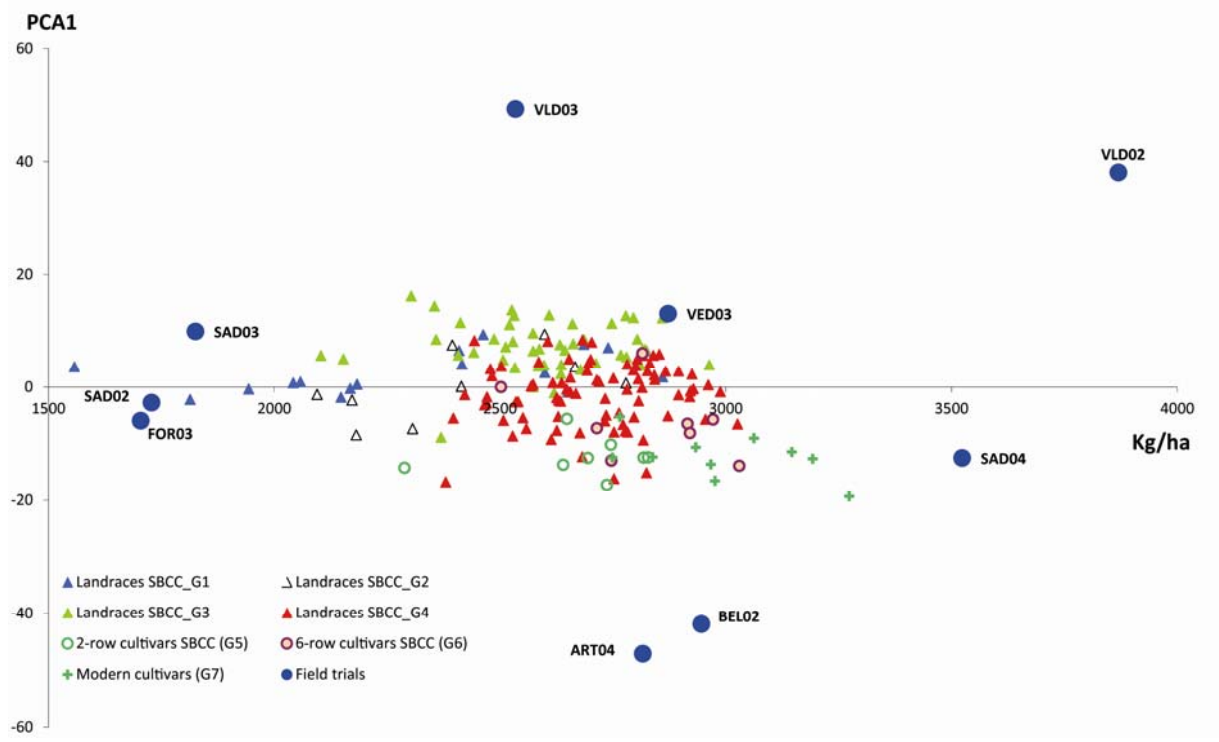
Supplemental Table 1. Traits recorded at each field trial.

Trial	Plant height	Heading date	Lodging score	Grain yield	Test weight	Thousand kernel weight	Yield components	Malting quality traits	Leaf rust	Net blotch	Powdery mildew
ART02	x	x		x	x	x				x	
BEL02		x	x	x	x	x					x
SAD02	x			x							x
VLD02	x	x		x	x	x					
FOR03		x	x	x	x	x			x	x	
VLD03	x	x	x	x	x	x					
SAD03	x			x	x						
VED03	x	x	x	x	x	x	x				
ART04		x		x	x	x					
SAD04				x	x	x					
GER00									*		
VAL00											*

1 Supplemental Table 2. Means and standard deviations of traits measured at each trial, split for landraces and cultivars.
2

Trial	Groups	HED		PHT		LDG		YLD		TW		TKW		NBL		PML	
		Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd
ART02	Landraces	121.4	5.2	84.7	6.5	-	-	20.9	3.2	62.4	2.9	39.8	5.1	3.5	0.9	-	-
	Cultivars	119.1	4.0	74.0	10.1	-	-	27.8	2.7	69.4	3.5	40.0	4.9	3.3	1.2	-	-
														-	-	-	-
BEL02	Landraces	112.1	4.7	-	-	6.5	1.3	28.5	5.0	63.5	3.0	39.8	5.0	-	-	3.9	1.6
	Cultivars	106.3	4.6	-	-	1.7	1.8	35.2	4.4	68.7	3.5	37.9	4.9	-	-	3.1	1.4
														-	-	-	-
SAD02	Landraces	-	-	61.8	5.0	-	-	17.0	2.8	-	-	-	-	-	-	3.1	0.9
	Cultivars	-	-	50.1	7.3	-	-	18.9	2.4	-	-	-	-	-	-	3.0	0.8
														-	-	-	-
VLD02	Landraces	124.0	5.1	89.5	6.7	-	-	38.4	5.9	65.6	3.0	46.2	3.7	-	-	-	-
	Cultivars	119.2	3.2	70.8	12.4	-	-	40.8	4.8	71.1	3.5	44.4	3.3	-	-	-	-
														-	-	-	-
FOR03	Landraces	116.8	3.5	-	-	5.2	2.7	16.7	2.3	63.6	2.6	37.9	3.6	8.1	0.8	-	-
	Cultivars	114.1	2.6	-	-	2.0	1.8	19.2	2.5	69.3	3.3	36.9	3.7	7.9	1.1	-	-
														-	-	-	-
VLD03	Landraces	123.4	6.2	92.3	11.4	5.2	2.5	25.8	4.0	65.6	2.3	44.0	5.0	-	-	-	-
	Cultivars	117.6	4.4	67.0	14.1	1.3	1.2	22.5	3.1	69.3	2.4	40.3	5.3	-	-	-	-
														-	-	-	-
SAD03	Landraces	-	-	76.2	6.1	-	-	18.6	3.3	62.9	2.5	-	-	-	-	-	-
	Cultivars	-	-	61.9	8.3	-	-	16.1	3.3	68.0	2.8	-	-	-	-	-	-
														-	-	-	-
VED03	Landraces	113.2	4.4	81.8	6.7	4.0	2.0	28.9	3.6	64.8	3.0	45.1	5.1	-	-	-	-
	Cultivars	109.5	3.5	67.6	11.5	2.0	2.0	27.7	3.3	69.4	3.5	40.3	5.2	-	-	-	-
														-	-	-	-
ART04	Landraces	120.0	4.0	-	-	-	-	26.5	3.1	63.5	3.2	39.6	4.3	-	-	-	-
	Cultivars	116.6	2.5	-	-	-	-	38.4	5.6	70.6	4.4	38.4	4.2	-	-	-	-
														-	-	-	-
SAD04	Landraces	-	-	-	-	-	-	34.9	4.5	63.0	3.4	40.6	4.9	-	-	-	-
	Cultivars	-	-	-	-	-	-	37.1	4.8	69.3	3.5	38.3	5.2	-	-	-	-

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4

	df	HDN	PHT	LDG	TW	TKW	SPM	KNM	KS	PM	NB	LR	SCR	KP	MEX	PRT
Environment (E)	6	10528	53551	414	451	2870				619	57 43					
Genotype (G)	181	360	1047	41	176	229				10	3					
between groups	6	2868	19626	677	3733	2294	81506	8054221	584	127	13	44	68	1350	181	7.9
within groups	175	274	410	19	54	158	8865	7249772	64	6	3	3	9	180	82	1.2
GxE		13	99	10	8	14				3	1					
between groups		52	639	28	39	62				10	3					
within groups		11	80	9	7	13				3	1					
Error		3	21	3	4	4				2	1					

1

Supplemental Table 4. Lists of the 25 best genotypes, according to grain yield over 9 trials (column "grain yield overall"), and over high productivity trials (column "grain yield – high") and low productivity trials (column "grain yield – low").

Ranking	Grain yield overall	Grain yield -high	Grain yield - low
1	Orria (G7)	Orria (G7)	73 (G4)
2	Graphic (G7)	Graphic (G7)	81 (G4)
3	Steptoe (G7)	Steptoe (G7)	16 (G4)
4	Candela (G7)	Gaelic (G7)	27 (G3)
5	Barberousse (G6)	Barberousse (G6)	91 (G4)
6	91 (G4)	Candela (G7)	38 (G4)
7	42 (G4)	Nevada (G7)	18 (G4)
8	Gaelic(G7)	Volga (G7)	75 (G4)
9	Monlón (G6)	Zaida (G5)	42 (G4)
10	Nevada (G7)	Kym (G5)	Orria (G7)
11	27 (G3)	Dobla (G6)	106 (G1)
12	81 (G4)	Ager (G6)	76 (G4)
13	18 (G4)	Alpha (G5)	39 (G4)
14	Volga (G7)	Monlón (G6)	31 (G3)
15	125 (G4)	Hassan (G5)	79 (G3)
16	73 (G4)	Tipper (G7)	51 (G3)
17	98 (G4)	91 (G4)	49 (G4)
18	Pané (G6)	Pané (G6)	14 (G4)
19	16 (G4)	145 (G4)	92 (G4)
20	Ager (G6)	Seira (G7)	109 (G4)
21	38 (G4)	42 (G4)	Steptoe (G7)
22	10 (G4)	98 (G4)	146 (G3)
23	14 (G4)	116 (G4)	11 (G3)
24	52 (G4)	4 (G1)	25 (G4)
25	4 (G1)	125 (G4)	125 (G4)

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1   Figure legends

2

3   Fig. 1: Distribution of variables measured or recorded at a series of field trials for a collection of

4   Spanish barley landraces, compared with a set of barley cultivars (see test for detailed description). The

5   classes represent either 0.5 standard deviations for the continuous quantitative traits or a unit for the

6   discreet traits

7   Fig. 2: Plot of the first two principal components of the AMMI analysis of grain yield for a series of

8   Spanish barley landrace-derived lines and cultivars, grown in Spain in nine field trials. Genotypic and

9   environmental covariates have been added to the plot, with vector lengths proportional to their

10   correlation with the AMMI axes

11   Supplemental Fig. 1: Plot of the first principal component of the AMMI analysis of grain yield for a

12   series of Spanish barley landrace-derived lines and cultivars, grown in Spain in nine field trials, versus

13   the average yield of genotypes and trials.