Identification of QTL for agronomic traits contributed by a barley

Mediterranean landrace

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Abstract

The basis of this study is the finding that some Spanish barley landraces performed better than modern cultivars at low production sites. The objective of this study was to identify favorable QTL for interesting agronomic traits contributed by the landrace SBCC073. To achieve this objective, a population of 100 BC1F5 lines was derived from the cross between the elite cultivar Orria, with high productivity, and the Spanish landrace SBCC073, which was the best at low production trials. The population was evaluated in field trials for three years (2011, 2013, and 2014) in Zaragoza, Spain. The population was genotyped with a DArTseq[®] genotyping-by-sequencing assay. A genetic linkage map was developed using markers of four flowering time genes and 1227 SNPs of good quality. The genetic map resulted in 11 linkage groups, covering a total distance of 871.1 cM. Five QTL for grain yield were detected on 2H.1, 4H, 5H and 6H.2. SBCC073 alleles contributed to increased yield in three of them. A region, at the end of chromosome 5H, contains favorable alleles for early vigor, higher grain yield and earlier flowering, all derived from SBCC073. Orria alleles contributed to increase grain yield and simultaneously to reduce plant height on the same region of 6H.2, and to increase thousand kernel weight on chromosomes 3H and 5H.

Additional keywords: introgression, drought, breeding, genetic resource, adaptation.

Introduction

The production of high-yielding varieties with stable performance across years is a challenging task for cereal breeders working for Mediterranean environments. Partly to blame is the ample variability in timing, duration and severity of drought stress in the Mediterranean (Baum *et al.* 2003) which, ultimately, affects yield (Loss and Siddique 1994; Pswarayi *et al.* 2008).

Barley landraces are acknowledged as a valuable resource for breeding in the Mediterranean region (Nevo 1992; Ceccarelli *et al.* 1995), as they were selected in these same unfavorable environments, often grown in stressful environments with zero to limited agronomic input (Ceccarelli *et al.* 2000). For instance, landraces yielded between 25% and 61% more than modern cultivars under stress conditions, while modern varieties yielded 6–18% more than landraces under optimum conditions in Syria (Ceccarelli 1996). Besides, it is a proven fact for many crops, and indeed in barley, that the genetic variability present in old landraces has not been fully exploited in modern breeding (Fischbeck 2003).

Barley landraces, therefore, represent an important genetic resource for barley improvement, especially for biotic (Jefferies *et al.* 2003; Chen *et al.* 2013; Hofmann *et al.* 2013) and abiotic stress (Yahiaoui *et al.* 2014). Many studies have reported that barley landraces present a high level of genetic diversity for morphological traits (Ceccarelli *et al.* 1987; Lakew *et al.* 1997; Hadado *et al.* 2009), molecular markers (Demissie and Bjørnstad 1997; Russell *et al.* 2003; Yahiaoui *et al.* 2008) and agronomic traits (Yahiaoui *et al.* 2014). Nowadays, research is focusing on the valorization of this genetic resource by building and evaluating core-collections (Igartua *et al.* 1998; Bowman *et al.* 2001; Lasa *et al.* 2001; Knüpffer and van Hintum 2003). However, in the past, the introgression of this exotic

variation was a long and difficult process due to linkage drag. Molecular markers now provide a means to overcome this problem (Forster *et al.* 2000).

Spanish barley landraces reveal a wide genetic diversity, possibly due to their adaptation to diverse environmental conditions. They also are quite different from current European cultivars, which make them a potential new resource for barley breeding (Yahiaoui *et al.* 2008). In several studies, barley landraces from Spain have shown a good potential to contribute useful genes and alleles for barley breeding (Igartua *et al.* 2008; Silvar *et al.* 2010).

Some Spanish barley landraces showed a good agronomic behavior, out-yielding elite barley varieties under low productivity conditions (Yahiaoui *et al.* 2014). Landrace derived line SBCC073 was the highest yielding line in a series of field trials, when considering only the experiments in which average yield was below 3 t ha⁻¹. The objective of this study was to identify the genomic regions (QTL) of interesting agronomic traits that may be contributed by this line, crossed to an elite barley cultivar.

Material and methods

Plant material

A barley population of one hundred BC1F5 lines was developed from the barley (SBCC073 × Orria) × Orria backcross population in the framework of the Spanish public barley breeding program, at the Aula Dei Experimental Station, Zaragoza, Spain. SBCC073 is a landrace-derived inbred line included in the Spanish Barley Core-Collection (Igartua *et al.* 1998), which out-yielded 26 cultivars in a series of field trials at low production sites across Spain (Yahiaoui *et al.* 2014). Orria [(((Api x Kristina) x M66.85) x Sigfrido's) x 79W40762] is a semi-dwarf cultivar selected in Spain from a CIMMYT nursery, which is highly productive across

most Spanish regions. This cultivar is an outstanding parent of the Spanish national barley breeding program (Igartua *et al.* 2015).

Genotyping and map construction

The BC1F5 population was genotyped using DArTseq™ (Ren *et al.* 2015), a genotyping-by-sequencing platform provided by Diversity Arrays Technology, Australia. This assay generated 2483 polymorphic SNP markers. These were filtered, according to different quality criteria: 177 SNP markers having more than 10% heterozygotes were deleted; 346 SNP markers with more than 10% missing data were removed, as well as 13 markers with over 75% of SBCC073 alleles (which were clearly outliers in the distribution of marker allele frequencies). After filtering, 1947 SNP markers were kept. Finally, co-segregating SNPs were removed, leaving a single SNP per genetic position, reducing the number of markers to 1227. This number still ensures excellent coverage for a population of this size and characteristics. Flowering time genes *VrnH1*, *PpdH1*, *PpdH2* and *VrnH3* were also placed in the map. They were assayed with perfect markers using gene-specific primers to genotype the population (Table S1). The PCR reactions were performed on a GeneAmp 2700 thermocycler (Applied Biosystems), in a final volume of 15 µl, containing 50 ng of template DNA, 1x PCR Buffer (Biotools, Madrid, Spain), 0.3 mM dNTPs, 0.15 µM of each primer and 1 U of Tth DNA Polymerase (Biotools). The amplified products were separated on agarose or acrylamide gels. DArTseq SNP markers and flowering time genes were used to construct the genetic map and perform the QTL analyses. In a first step, Joinmap 4 (van Ooijen 2006) was used to create linkage groups at LOD 7. For each linkage group, the maximum likelihood algorithm was used to estimate the best order of markers within it. In a second step, the distance between the markers within each linkage group was recalculated, based on the Kosambi's

mapping function using MSTMAP (Wu *et al.* 2008). MapChart software (Voorrips 2002) was utilized to draw the genetic map.

Field experiments

Field experiments were carried out at the El Vedado farm, in Zaragoza, Spain during three seasons (harvests of 2011, 2013 and 2014). In 2011, the population was at the BC1F4 generation, whereas BC1F5 seed was used for the other two seasons. The experimental design was a check plot, an unreplicated design in which two checks were repeated every five test plots to provide an estimate of the error variance. Individual plot comprised 4 rows, 2.5 m long, with 20 cm between rows. Two cultivars well adapted to the region, Barberousse and Cierzo, were used as checks. Sowing dates were 10 Nov 2010, 15 Nov 2012 and 11 Nov 2013, respectively. Yield, flowering time, and plant height were evaluated in 2013 and 2014. In 2011 only yield was evaluated, whereas early vigor and thousand kernel weight were assessed only in 2014.

During the three seasons, rainfall accumulation (October to June) was quite variable: 285 and 286 mm in 2010/2011 and 2013/2014, respectively and 428 mm in 2012/2013 (Fig. 1). Autumn and spring rainfall patterns also varied notably. Autumn of 2012 was wetter than those of 2010 and 2013. On the other hand, spring of 2013 was more humid than those of 2011 and 2014, which were similar. In particular, March 2014 was remarkably drier than the same month in 2011 and 2013 (Fig. 1). Concerning temperature, first and third season winters were colder than winter of the second season. Springs (April-June) were also much warmer in the first and third seasons than in the second one (Fig. 1).

Figure 1

Phenotypic evaluation

Early vigor (EV) was scored after a visual assessment done on 06 Feb 2014. The growth aspect and densities of plants were scored from 1 (poor) to 3 (excellent). Flowering time (FT) was expressed as the number of days between January 1st and the date when 50 % of tillers had 2 cm of visible awns. Plant height (PH) was measured in cm for a single, representative plant per plot, from the ground to the base of the spike. Grain yield (GY), weight of grain after combine-harvesting, in kg ha⁻¹. To account for soil irregularities among the plots, and also to ensure crossability of the data across years, grain yield of each test plot was transformed to a percentage of the six closest check plots, i.e., the two closest flanking ones in the same tier, and the corresponding ones in the previous and the next tiers, which consisted in each case of 3 plots of cultivar Cierzo, and 3 plots of Barberousse. Thousand kernel weight (TKW) was measured as the weight in grams of 1000 clean grains sampled from the combine-harvested seed.

Data analysis

QTL analyses were performed using the procedure single trait linkage analysis (multiple environments) implemented in Genstat 16 (Payne *et al.* 2009). First, genetic predictors were constructed at 2 cM. In the first round simple interval mapping (SIM) was run. Then, QTL detected in the SIM analysis were used as cofactors to perform composite interval mapping (CIM). CIM was run iteratively until a stable solution was found for every analysis. For all traits, the Li and Ji's method, as implemented in Genstat, was used to estimate the significance threshold of the appropriate test statistic (-log₁₀P) to declare putative QTL. The minimum distance between cofactors and the minimum distance to declare an independent QTL were set at 20 and 10 cM, respectively. In the last step, the final QTL model was built. Genstat 16 was also used to perform all statistical analyses for phenotypic data. Data of the check plots was analyzed as a randomized complete block design, and used to calculate an

approximate experimental error in order to produce a least significant difference (LSD) to serve as an approximate indication of differences between test lines.

Results

Map construction

The linkage map generated with 1227 SNPs and 4 flowering time genes covered a total distance of 871.1 cM. A total of 11 linkage groups were identified (Table 1), representing 4 whole chromosomes (1H, 3H, 4H and 5H) and 3 fragmented ones (chromosome 2H in 3 groups, chromosomes 6H and 7H in 2 groups each) (Fig S1). The number of markers per chromosome ranged from 121 on 4H to 221 on 7H.

In a BC1F5 population, the expected ratio of allelic frequencies of SBCC073 and Orria should vary around a ratio 25:75. Out of 1231 markers used, 60 markers displayed significant distortion from this ratio ($P < 0.05$, with a Bonferroni correction for the number of markers), 33 markers with higher than expected SBCC073 allele frequencies, and 27 with excess of the Orria allele. The distortion was in favor of SBCC073 alleles mainly on 1H and 5H, and at the end of chromosome 3H. Most of the markers of linkage group 6H.1 were distorted in favor of the Orria allele (Table 1).

Table 1

Field trials

Descriptive statistics for agronomic traits

Over the three years of field trials, the population displayed a wide range of variation in terms of average grain yield, ranging from 1.24 t ha⁻¹ in 2014 to 5.49 t ha⁻¹ in 2013 (Table 2). Within years, 2014 presented the smallest variation whereas 2013 had the largest one. The performance of the two checks, Cierzo and Barberousse, presented the same pattern as the

population (2013>2011>2014). Cierzo out-yielded Barberousse and the average of the population in all three years. The grain yield of Barberousse was closer to the population average yield over the three years (Table 2). After grain yield correction with respect to the checks (Table3), 2011 displayed the higher percentage (103%) followed by 2013 (92%) and 2014 displayed the lowest one (68%), suggesting that the three years' agronomic conditions were quite different. In 2014, in particular, the average yields were much lower than in previous years, indicating an important effect of drought stress (Figs. 1, S2). In this year, the population also presented a much lower average than the checks, compared with the two previous years. This fact indicates that, overall, the population was less stress tolerant than the checks.

An analysis of variance for corrected yield between lines, where the residual included the genotype by environment interaction, showed significant differences between lines (Table S2).

Regarding flowering time, the range of heading dates for the population was rather wide (18 and 17 days in 2013 and 2014, respectively). The two checks flowered at similar dates, and earlier than the population average (Table 2). Plant height of the population was slightly higher than the checks, and was much taller in 2013 (64.05 cm) than in 2014 (36.12 cm), reflecting the dryness of this last season.

Table 2

Grain yield was negatively correlated with flowering time in the two years in which both traits were recorded, indicating that in both seasons earlier genotypes had higher yields. The correlation between yield and plant height was low in both years (2013 and 2014). Grain yield, on the other hand, was positively correlated with early vigor (0.67) in 2014. Flowering time had negligible correlation with plant height in both years (2013 and 2014). However, it

had a negative correlation with early vigor. No correlation was found between early vigor and plant height (Table S3, Fig S3).

QTL analyses

QTL were found for all traits. Five QTL were associated with grain yield, on linkage groups 2H.1, 4H (2x), 5H and 6H.2 (Table 3). For the QTL on 6H.2, Orria contributed the favorable allele. For three QTL, SBCC073 contributed the yield enhancing allele, with varying effect sizes. The sign of the allelic effect for the remaining yield QTL, in linkage group 2H.1, varied between environments. There were no major QTL across all environments but, at single environments, some of the QTL explained large proportions of variance, for instance 42.7% by the QTL on 6H.2 in 2013, or 32.1% by the QTL on 5H in 2014 (Table 3).

Three QTL were found for flowering time, Orria alleles contributed to delay flowering time on two of them (2H.1 and 5H). The SBCC073 allele on 3H was associated with later heading. The 2H.1 QTL, explaining 11.9 % of the phenotypic variation in 2014, is very close to *PpdH1*. A major QTL identified on 5H, explained 19-32.1% of variance in 2013 and 2014, respectively. The Orria allele at this QTL delayed flowering almost 5 days in both years (Table 3). Only one major QTL for plant height was found on 6H.2, with the SBCC073 allele increasing plant height by 11.1 cm (Table 3). This QTL explained 74.3 % of variance in 2013, whereas in 2014 it had a moderate effect. This QTL is within the same confidence interval than the grain yield QTL on the same chromosome (2.06-5.21 cM). The SBCC073 allele at this location is associated with taller plants and lower grain yield (Table 3). One QTL for early vigor was found, explaining a large percentage of variance (40%). It was located at the distal end of 5HL, near a yield QTL, with the allele from SBCC073 conferring increased plant vigor (Fig. 2, Table 3). Finally, two QTL for TKW were found on 3H and 5H in 2014 (Table 3), and in both Orria alleles contributed to increased TKW.

Figure 2

Table 3

Only one significant interaction between grain yield QTL was detected. In a combined analysis for the three seasons, there was an interaction for grain yield between the QTL on 2H.1 and the first QTL on 4H (96.61 cM). Only when the Orria allele was present at the 2H.1 QTL, there was a detectable effect for the QTL on 4H (Table 4).

Table 4

Discussion

As mentioned by Yahiaoui *et al.* (2014), some Spanish barley landraces showed good agronomic traits resulting in high-yielding under low production conditions. This potential can be used in breeding programs to increase production of elite varieties for stress-prone areas. In this study, we used a population derived from the best yielding genotypes reported in that study for good conditions (cultivar Orria) and poor conditions (landrace SBCC073), with the objective of localizing useful genomic regions that might be related to the agronomic advantage of line SBCC073 in low production trials.

Although no selection pressure was applied during the construction of the population and, therefore, we did not expect to find regions with allelic frequencies departing significantly from the expected, some regions presented distorted allelic frequencies. This suggests that some selection was suffered by the population, probably in response to uncontrolled environmental traits.

In Mediterranean areas, precipitations and temperature are the main factors associated with grain yield (Yau *et al.* 1992; Royo *et al.* 2014). The present QTL study was carried out over three quite diverse cropping seasons. Overall, grain yield was relatively good in 2011

and 2013, and rather poor in 2014. From the climate data (Fig. 1), the two years of good yield had in common a high precipitation level in March. This is a crucial month for winter cereals in the region, in which overall tillering and the production of fertile tillers is determined (Garcia del Moral *et al.* 1984, 1991).

In 2014, under less favorable climatic conditions, the population yielded on average much less than the two checks (Table 2), suggesting that the recurrent parent Orria (whose alleles constitute 75% of the genome of the lines of the population overall) was more drought sensitive than the checks. This assumption was supported by the finding that there were more grain yield QTL for which the favorable allele came from SBCC073 in 2014 than in any of the other two years (2011, 2013). Apparently, the positive effects of SBCC073 were more conspicuous under low production conditions, in agreement with its purported agronomic behavior, as explained in the introduction section. Grain yield QTL detected on 5H and 6H.2, although not always significant, at least presented effects with consistent sign across very different years, and seem the most promising ones for breeding. The QTL on 4H were detected only in the year of lowest yield but, at least, do not reduce yield in the two more favorable seasons. Therefore, they do not have detrimental effects for the genotypes and may be considered as favorable alleles for stressful conditions.

The grain yield QTL on 5H is particularly interesting for its large effect, and also because it co-locates with QTL for early vigor and flowering time, with the favorable allele always contributed by SBCC073. This QTL on 5H shows an apparently constitutive effect of SBCC073 alleles with positive effect on yield across a range of levels of production. It is located at the distal end of the long arm, distal to all QTL of several agronomic traits found by Tondelli *et al.* (2014), co-locating with the region of a yield QTL reported in an association panel tested under drought (Comadran *et al.* 2008). Also, von Korff *et al.* (2008) found a grain yield QTL in

269 this region at the Tadmor × ER/Apm population tested under Mediterranean environments.
270 They reported a QTL for grain yield with qualitative marker by environment interaction.
271 Cuesta-Marcos *et al.* (2009), working in environments similar to ours, also found two QTL for
272 grain yield on 5H in a doubled haploid population, but they are both proximal to our QTL.
273 Inostroza *et al.* (2009), testing a population of introgression lines derived from wild barley,
274 found a marker x environment interaction for grain yield on 5HL in a similar position to the
275 one described in our population. In that study, the *H. spontaneum* allele at the QTL
276 decreased grain yield by 16-40%. We cannot be sure whether this is the same QTL as the one
277 found in our study, although the results do not suggest that. In another study, Naz *et al.*
278 (2012) found a QTL derived from wild barley on 5HL that, when introgressed in a drought
279 susceptible cultivar (Scarlett), increased the root volume. In a greenhouse experiment
280 carried out with the parents of this population (Boudiar 2014), root dry weight of SBCC073
281 was higher than Orria under drought and control conditions. We do not have data to prove
282 that the distal end of 5HL of SBCC073 is responsible for favorable root traits, but it is a
283 hypothesis that we look further to addressing in the future. The coincidence of a QTL for
284 grain yield and early vigor on 5HL adds interest to this hypothesis. Ceccarelli *et al.* (1991)
285 reported that early vigor is one of the traits leading to adaptation in marginal environments.
286 Early vigor has already been exploited to improve water use efficiency and yield in wheat
287 (Rebetzke *et al.* 2007; Richards *et al.* 2007). This relationship could be due to a more profuse
288 root growth, which may be due to a number of factors, among them a more efficient
289 nitrogen uptake (Pang *et al.* 2014). In wheat, a QTL associated with early germination was
290 located on the long arm of chromosome 5D (Landjeva *et al.* 2010), in a syntenuous region to
291 that found in our study. These evidences suggest that a gene(s) on the distal part of
292 chromosome 5H could underlie the relationship between early vigor and root growth. In

wheat breeding, early seedling growth vigor is getting a considerable attention due to its role in improving wheat performance. Researchers are currently breeding for this characteristic using indirect traits, such as width of seedling leaves (Zhang *et al.* 2015) or seedling root growth (Atkinson *et al.* 2015). In the latter study, two QTL of root seedling traits co-localized with QTL for grain yield and N uptake. Interestingly, George *et al.* (2014) identified a QTL for rhizosheath weight in a barley population, in the same region as our grain yield QTL on 5HL. An alternative hypothesis compatible with the pattern of traits related with this QTL is differential response to frost damage. No direct evaluation of frost damage was done and, therefore, this hypothesis cannot be discarded. It is unlikely that frost had much effect in 2013 (absolute minimum temperature of -5.0°C). In 2011, the absolute minimum temperature was -8.8°C, but no QTL effects were detected in that year. In 2014, the years in which QTL for grain yield and early vigor were detected concurrently, the absolute minimum temperature of -6.9°C, occurred just 12 days after sowing, and may have affected seedling emergence.

Two QTL for grain yield were found on 4H, with the SBCC073 alleles conferring higher yield. Grain yield QTL on that chromosome were found in linkage mapping populations (Marquez-Cedillo *et al.* 2001; Baum *et al.* 2003) and in an association panel (Locatelli *et al.* 2013). QTL for several grain yield components were also found in 4H under Mediterranean conditions (Tondelli *et al.* 2014). Although the position of those QTL is not very precise, they do not seem to coincide with ours.

The grain yield QTL found on linkage group 2H.1 presented qualitative interaction depending on the year (Fig. 2). It is located distal to well-known earliness gene EAM6, but it falls within the confidence interval. Mansour *et al.* (2014) found a grain yield QTL at a similar position in another population which also had Orria as one of the parents, whereas Francia

et al. (2011) found a large effect of EAM6 on grain yield. In these two studies, as in our case, the QTL also exhibited a strong cross-over interaction between locations. In other association studies, a grain yield QTL has also been reported in that position (Comadran *et al.* 2011; Locatelli *et al.* 2013).

In general, grain yield presented a clear negative correlation with flowering date on the two years with available data. Earliness has been repeatedly associated with higher yields in Mediterranean environments (Ceccarelli *et al.* 1998, Francia *et al.* 2011, Varshney *et al.* 2012, Tondelli *et al.* 2014). The apparent relationship of early vigour with grain yield observed in this population bodes well with prior hypothesis linking fast early development with grain yield. The discussion about the duration of growth phases of winter cereals to optimize yield in Mediterranean environments has been going on for a long time (Ceccarelli *et al.* 1991, Slafer *et al.* 2001). In this respect, rather similar hypotheses were recently put forward for wheat (Miralles and Slafer 2007) and barley (Francia *et al.* 2011), proposing fast early development ensued by relatively longer duration phase between jointing and (early) flowering as the best combination to attain high grain yields in Mediterranean conditions. Three QTL for flowering time were found on 2H.1, 3H and 5H. The QTL located on 5H is in the same region as the QTL of grain yield, and also coincides with a QTL reported in a mapping population (Borràs-Gelonch *et al.* 2010). Orria alleles on 2H.1 and 5H contributed to later flowering time. The works by Cuesta-Marcos *et al.* (2008a,b) and Tondelli *et al.* (2014) detected many QTL for flowering time under similar conditions to ours but, surprisingly, we have found no QTL in common with them for this trait, with the exception of a small QTL found on apparently the same region of 3H, only in autumn sowings (Cuesta-Marcos *et al.* 2008b). The well-known long photoperiod response gene *PpdH1* falls within the confidence interval for the 2H.1 QTL. The Orria allele, which carries the recessive allele at

this gene, is associated with later heading. This same QTL was detected in the Orria × Plaisant population, showing QTL x environment interaction (Mansour *et al.* 2014). It was also detected in a wide cross population between SBCC145 and Beatrix (Ponce-Molina *et al.* 2012).

Many QTL for plant height have been reported at all 7 barley chromosomes (Backes *et al.* 1995; Sameri *et al.* 2006). The use of semi-dwarf genes has greatly improved barley yield with controlled plant height being used to reduce yield loss arising from lodging and to increase the harvest index (Bezant *et al.* 1996; Chloupek *et al.* 2006). One of the problems involved in the use of landraces for breeding, which is also true for the Spanish ones, is excessive plant height (Yahiaoui *et al.* 2014). Only one QTL increasing plant height derived from SBCC073 alleles was found on 6H.2, but with a very large effect. It is near the position of the grain yield QTL with both favorable alleles contributed by Orria, although it is not possible to know whether this is due to linkage or pleiotropy. Mansour *et al.* (2014) also found a QTL for plant height on the same region of 6H, also with the Orria allele reducing plant height. Markers from this region would be useful in breeding to select simultaneously for both traits. This finding contributes greatly to fulfill our objective for the focused introgression of favorable landrace traits in the background of Orria.

Future work with this population will address the combination of all favorable alleles in a single genotype, with the help of marker assisted selection (MAS). BC1F5 Lines with the highest number of favorable alleles have been selected and crosses to achieve an optimum genotype, with optimized grain yield, and keeping a maximum of other good agronomic traits of parent Orria, have been planned.

It is also possible that other Mediterranean landraces carry the same plant height allele at chromosome 6H and, therefore, it may be of general use to introgress landrace material in current cultivars.

Conclusion

The objective of this study was to detect the QTL responsible for good performance of landrace line SBCC073 under low yielding conditions, possibly related to drought stress, and to locate QTL for undesirable traits, common to barley landraces, like excessive plant height and low thousand grain weight. This objective was achieved, as several grain yield QTL were found, some of them particularly effective under low yield conditions (year 2014), in which the Orria background showed poor adaptation. These QTL, together with the plant height, thousand kernel weight and flowering time QTL, will allow a targeted introgression of SBCC073 favorable traits (and, possibly, from other landraces) into Orria background through backcross marker assisted selection.

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Table 1. Number of markers, length of each linkage group (cM) and number of markers with distorted frequencies (at $P=0.05$) of the SBCC073 x Orria genetic map.

Linkage group	Number Markers	Length (cM)	Markers with distorted frequencies
1H	132	144.3	14 (SBCC073) [†]
2H.1	121	105.8	0
2H.2	71	52.1	0
2H.3	10	16.8	0
3H	205	144.7	5 (SBCC073)
4H	121	109.8	4 (Orria)
5H	188	169.7	10 (SBCC073)
6H.1	28	12.3	20 (Orria)
6H.2	134	44.1	2 (Orria)
7H.1	63	39.1	1 (Orria)
7H.2	158	138.2	4 (SBCC073)
Total	1231	871.1	60

[†]between brackets, allele with higher than expected frequency

Table 2. Descriptive statistics (mean, minimum, maximum, LSD) for agronomic traits measured in the SBCC073 x Orria population and checks over three years.

Traits	Population				Checks		LSD
	Years	Mean	Min	Max	Cierzo	Barberousse	
GY† (t ha ⁻¹)	2011	3.96	2.50	6.91	4.15 a	3.60 b	0.38
	2013	5.49	2.16	8.58	6.56 a	5.39 b	0.46
	2014	1.24	0.16	2.41	2.12 a	1.56 b	0.21
GY (% of checks)	2011	102.8	66.2	162.9			
	2013	92.0	37.4	140.6			
	2014	68.1	9.2	144.5			
FT (days)	2013	120	108	125	107 b	108 a	0.93
	2014	111	105	121	106 a	104 b	0.64
PH (cm)	2013	64.1	51	83	57.28 a	59.76 a	2.57
	2014	36.1	22	49	35.24 a	36.24 a	2.23
EV	2014	1.76	1	3	2.61 b	2.90 a	0.25
TKW (g)	2014	36.7	27	44	33.48 a	27.71 b	1.02

†GY : grain yield, FT: flowering time, PH: plant height, EV: early vigor, TKW: thousand kernel weight. LSD was calculated at 5 % level. Check means followed by the same letter are not significantly different, at 5 % (population not included).

Table 3. QTL for agronomic traits detected by composite interval mapping in SBCC073 × Orria population during three years.

Traits	Closest SNP	Chr.	Position	Confidence interval	-log 10 (P)	Additive effect†			% Explained variance			QTL*Year
						2011	2013	2014	2011	2013	2014	
Grain yield	3260084	2H.1	60.69	52.18 - 70.44	4.19	6.20 *	-1.38	-9.73*	11.4	0.5	9.2	*
	3263178	4H	44.70	43.50 - 46.04	4.22	-4.33	-3.42	-14.56*	5.6	2.9	20.6	*
	3257648	4H	96.61	87.55 - 101.85	7.21	-2.12	-0.14	-12.42*	1.3	0.0	15.0	*
	3258987	5H	169.65	166.79 - 169.65	11.34	1.24	-7.10*	-18.16*	0.5	12.5	32.1	*
	3258547	6H.2	1.55	0.51 - 5.72	5.86	3.67	13.13*	2.87	4.0	42.7	0.8	*
Flowering time	3255272	2H.1	27.41	22.85 - 38.71	4.59		0.16	1.49*		0.1	11.9	*
	3259503	3H	56.75	55.11 - 60.50	3.90		-2.80*	-1.34*		25.0	9.7	*
	3257463	5H	164.96	163.08 - 169.65	12.43		2.44*	2.44*		19.0	32.1	ns
Plant height	3262819	6H.2	3.62	2.06 - 5.21	8.60		-5.56*	-1.08		74.3	4.8	*
Early vigor	3258022	5H	166.79	162.68 - 169.65	9.47			-0.5			40.1	
Thousand kernel weight	3259820	3H	43.29	36.95 - 47.56	6.86			2.07			35.9	
	3257369	5H	122.53	112.1 -132.8	4.56			1.68			23.6	

†Substitution of the SBCC073 allele by the Orria allele.

Table 4. Significant interactions ($P < 0.05$) between QTL detected for corrected yield (%).

3256587 (2H.1)	257648 (4H)	Yield, average 3 seasons
SBCC073	SBCC073	92.8 b
SBCC073	Orria	93.7 b
Orria	SBCC073	106.6 a
Orria	Orria	84.9 b

Numbers followed by the same letters are not significantly different

Figure Legends

Figure 1. Monthly average temperature and cumulative precipitations at the Zuera meteorological station, close to the location of the experiment (El Vedado, Zaragoza) during the three cropping seasons studied.

Figure 2. Representation of QTL found in (SBCC073 x Orria) x Orria population on graphical chromosomes. QTL confidence intervals are shown to the right of the chromosomes. Blue bars, SBCC073 alleles produce an increase of the trait. Pink bars, Orria alleles produce an increase of the trait. YLD, FT, PH, EV and TKW correspond, respectively to yield as percentage of checks, flowering time, plant height, early vigor and thousand kernel weight. The codes of the QTL are associated with years when a qualitative interaction was observed.