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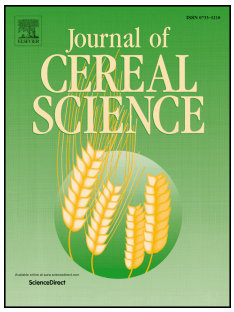

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Quantitative trait loci for sorghum grain morphology and quality traits: toward breeding for a traditional food preparation of West-Africa

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Abstract

One of the most frequently consumed sorghum food in Mali is a thick porridge, known as tô. Many grain traits contribute to its firmness and color, which are the most important qualities for consumers. These traits are related to chemical composition, physical properties, but also grain size, shape, glume adherence and color, pericarp thickness, or the presence of a testa. Quantitative trait loci for tô consistency, tô color, 16 grain traits, as well as day to flowering and grain yield, were investigated in two elite breeding populations, involved in a marker assisted selection program. A total of 51 and 71 QTLs were detected for P114 and P118, respectively. Several QTLs with high R^2 corresponded to major genes segregating in the populations such as the Z gene for pericarp thickness, the B2 and B1 genes for testa presence, the P gene for anthocyanin, and a QTL for flowering time. Many QTLs with moderate effect were detected for grain attributes associated to tô quality, without showing antagonism between grain quality and yield. The results of this study will contribute to producing new varieties combining grain productivity and grain quality favorable alleles, through the use of marker assisted selection.

Keywords: QTL; sorghum; tô; grain quality

1 Introduction

Sorghum (*Sorghum bicolor* L. Moench) is the fourth cereal in Africa in terms of total production (> 25 M tons) and the third in West Africa (> 11 M tons) where it is mainly used as human food (FAO, 2014). In West Africa, sorghum is particularly appreciated because of its good adaptation to environmental conditions. In rural areas, it is a major source of nutrients (energy, protein, vitamins and minerals) in human food. It is mainly cultivated in a family farming context to feed the family members and, possibly, generate income for family expenses through marketing of the surplus. While human consumption is based on grains, sorghum stems and leaves are also used to feed animals.

Rooney and Murty (1982) classified the sorghum-based food in eight groups according to the methods of preparation: thick porridges, thin porridges, steam cooked products, boiled sorghum, unleavened bread, leavened bread, snack food, and alcoholic and non alcoholic beverages. One of the most frequently consumed sorghum food in Africa is a thick porridge, known as tô in Mali, and as tuwo, ugali, bogobe, sankati, oka-baba or dibu in other countries. Tô is traditionally prepared using dehulled grains that are pounded into flour just before its preparation (Fliedel, 1995). After sieving, the flour is dispersed in cold water, acidified with lemon or tamarind juice or alkalinized with ashes. This mixture is then poured in boiling water and cooked while stirring constantly. Tô is consumed during the two main meals (lunch and dinner), but sometimes the remains of dinner are consumed during breakfast (Anglani, 1998; Kayode et al., 2005; Rooney and Murty, 1982). A good quality tô has a firm consistency with a good color and taste, is non sticky, and keeps its texture overnight (Fliedel, 1995). However, tô taste is generally considered as secondary because it is partly masked by the accompanying sauce (Fliedel, 1995; Trouche et al., 1999).

Several studies have explored grain quality traits contributing to a good tô consistency (Anglani, 1998; Bello et al., 1990; Cagampang and Kirleis, 1984; Chandrashekar and Kirleis,

1988; Fliedel, 1995; Perez Bouvier, 1988; Rooney and Murty, 1982; Trouche et al., 1999). The quality of the final product is influenced by both physical and biochemical properties of the grain that can play a role at various steps of the process. The first step is dehulling, which aims at eliminating most of the bran (pericarp and germ) and providing a clean and intact endosperm. It is traditionally performed manually using a mortar and pestle. Dehulling is mostly affected by some physical properties of the grain such as endosperm texture, grain hardness, pericarp thickness, and grain roundness. Hard grains have a better resistance to abrasion and allow a complete removal of brans without breaking the grains, thus the harder the grains, the better the quality of dehulling. Pericarp thickness is also important for manual dehulling which is performed on washed grain. Some additional water is added during the pounding to soften the pericarp and make easier its removal. A thick pericarp absorbs more water and is more easily detached during the dehulling than a thin pericarp (Scheuring et al., 1983). Finally, grain roundness has an impact on dehulling, as spherical grains are more uniformly dehulled because the entire grain surface is reachable during the abrasion phase. The second step of the process is the milling of dehulled grain, which aims at delivering the finest flour. The finer the flour is, the more damaged the starch granules composing the grain endosperm are, and the more soluble they are during cooking, increasing tô firmness. The efficiency of the milling step is also mainly influenced by the texture of the endosperm, a floury endosperm providing finer flour. Finally, during cooking, the last step of the process, the amylose content of the starch fraction of the endosperm is the main factor influencing the final firmness of the porridge (Bello et al., 1990; Fliedel, 1995; Kayode et al., 2005; Trouche et al., 1999).

Tô color appreciation depends on the geographical area; a good tô color ranges from white, light yellow, to light green, red or brown (Bello et al., 1990; Fliedel, 1995; Kayode et al., 2005; Trouche et al., 1999). In Mali, light colors such as white and light yellow are preferred.

Tô color is affected by the color of the flour, which in turn is affected by the presence of a pigmented testa coat and/or the presence of plant anthocyanins. A colored testa can color the flour when the testa coat is not fully removed during the dehulling. Furthermore, in humid conditions, the plant anthocyanins can spread from the glumes to grain endosperm when anthocyanins are present in glumes and glumes adhere to grains. Thus, glume adherence and glume color are also traits to be considered as possible factors influencing the color of tô.

Most of the sorghum landraces cultivated in West-Africa are well adapted to the local preparations and produce appropriate quality food. In the sixties and seventies, sorghum breeding in West Africa has mainly been focused on the improvement of productivity. However, these new varieties were not adopted by farmers-consumers because of their poor grain quality, making them not suitable for local preparations. In the eighties, the priorities in terms of breeding criteria were revised and grain quality became an important criterion in sorghum breeding. Since, sorghum breeders have attempted to combine productivity and desired grain traits in the new varieties (Chantereau et al., 1997; Fliedel, 1995; Kayode et al., 2005; Trouche et al., 1999).

Since the nineties, significant progress on knowledge of sorghum genetics has been accomplished. A number of genetic studies have been conducted on important agronomic traits using mapping populations and detection of quantitative traits loci (QTLs) (reviewed by Mace and Jordan (2011)) including grain quality traits (Boyles et al., 2017; Rami et al., 1998; Rhodes et al., 2017). An association mapping study between grain quality traits and specific genes involved in synthesis pathways of starch and grain storage proteins was also conducted (de Alencar Figueiredo et al., 2010). The sequencing of the sorghum genome (Paterson et al., 2009) permitted the large development of Single Nucleotide Polymorphism (SNP) markers and the production of high density genetic maps, enabling whole genome association mapping

116 studies (Morris et al., 2013a; Murray et al., 2009), including some on grain quality traits
117 (Boyles et al., 2017; Sukumaran et al., 2012).
118 These studies provided breeders with information regarding the genetic control of grain
119 quality traits. However, in most cases, the experimental populations that have been used were
120 disconnected from elite breeding material because of the time needed to develop them. For
121 this reason, QTLs detected in such populations have often shown to be not transferable and
122 not applicable in breeding populations. Recent marker assisted breeding methodologies such
123 as marker assisted recurrent selection (MARS) propose to integrate QTL detection and
124 breeding in the same process (Ragot et al., 2007). In such approaches, genetic markers are
125 used to identify key QTLs involved in target traits and environments, and to monitor
126 recombination in consecutive generations and pyramiding of favorable alleles through
127 crossing of progenies. The choice of the parents is in this case not guided by contrasting
128 attributes aimed at maximizing the number of detected QTLs but by parents' performance and
129 complementarity (good by good crosses) with the objective to focus on useful QTLs that are
130 segregating in the genetic material that is currently of interest to breeders.
131 In this study, we report the QTL discovery phase of such marker assisted selection program
132 aimed at jointly improving grain yield, crop adaptation and grain quality of sorghum. The
133 results obtained in this study have been used to guide the development of improved sorghum
134 varieties for West-Africa through marker-aided selection.
135

2 Materials and methods

2.1 Plant material

Two bi-parental breeding populations named P114 and P118 were used for this study. The population P114 was derived from a cross between Keninkeni and Tiandougou. P118 was derived from a cross between Lata3 and Tiandougou. Tiandougou is a caudatum line with large grain size, floury endosperm, and a thick pericarp. Keninkeni and Lata3 are guinea lines with medium grain size, vitreous endosperm, and thin pericarp.

The P114 and P118 populations were composed of 401 and 403 F_3 progenies, respectively. A single F_1 plant of each cross was selected and selfed to produce the F_2 generation. Single F_2 plants were advanced to F_3 generation in off-season using flowering initiation masks. For each F_3 individual, $F_{3:5}$ bulks of seeds were produced for the needs of phenotyping experiments, using 10 selfed F_4 plants.

2.2 Field experiments

The P114 population was evaluated in 2010 during the rainy season at the Cinzana research station (13°15′N, 5°58′E °N, 265 m ASL) from the Institut d'Economie Rurale (IER) of Mali. An unreplicated experimental design including 447 plots (401 progenies and 23 replications of the two parents) was used with the two parents regularly distributed every 10 progenies.

The P118 population was evaluated in 2011 during the rainy season at the Sotuba research station (12°39′N, 7°56′E, 381 m ASL) from IER. An augmented experimental design including 29 blocks of 16 plots was used with the two parents used as checks within each block. The 404 progenies were randomly allocated to the plots. The design was completed to 464 plots by adding supplementary replications of the parents. In both experiments, each plot included two rows of 10 plants.

For both populations, the number of days from sowing to the apparition of the first flag leaf (DTFL) was recorded. The presence of anthocyanins (ANTHO) was evaluated by visual

appreciation on plant leaves with a score from 0 to 1, where 0 was for tan (no anthocyanins) plants, 1 for plants with anthocyanins, and 0.5 for segregating families.

After harvest, panicles were dried during three weeks. For P118, glumes adherence (GLUMAD) and glumes color (GLUMCOL) were evaluated by visual observation before threshing. A three-point scale (1, 3 and 5) was used for GLUMAD. 1 represented many adherent glumes, 3 some adherent glumes and 5 no adherent glumes. A score of 1 to 4 was used for GLUMCOL with 1 being yellow, 2 red, 3 black, and 4 a mix of colors. The panicles were then threshed and grain yield (GYLD) was measured by weighing the grain harvested in each plot. The result was expressed in g/m². The grains were stored in a cold room until grain quality measurements.

2.3 Grain shape measurements

Samples were cleaned manually to remove the broken, moldy or insect-damaged kernels, straws, stones and dust. For each individual and the two parents of the population P118, 10 g of clean grain, representing 200 to 400 grains, were scattered and scanned on a flatbed photo scanner with lid removed to produce 8-bit gray scale images at 200 dpi with a dark background. A dedicated script (https://github.com/jframi/grainito) was developed as part of the ImageJ 1.46 software (Schneider et al., 2012) to detect grains on each image and analyze their shape. The grainito script loops on a series of images and successively applies i) image thresholding using one of the algorithms for automatic threshold value determination available in ImageJ, ii) watershed algorithm to separate grains that may be closely grouped together into masses, iii) particle detection based on target size and circularity of grains. An additional R script was used to detect the outliers that occurred from masses of grains that could not be accurately corrected by the watershed algorithm and correct the results accordingly.

From each image, the mean values over all grains were computed for the following parameters: major (MAJOR) and minor (MINOR) axis lengths of an ellipse fitted to each detected grain, grain roundness (GRND), computed as the ratio of the minor axis to the major axis, and grain whiteness (GWTN), computed as the mean of the grain pixel intensities. Thousand grain weight (TGW) was also computed from the number of grains detected on the image and the weight of grain placed on the scanner.

2.4 Grain quality measurements

Most chemical properties of the grain were determined by NIRS. NIRS spectral acquisitions were performed on 5 g of whole grains using quartz ring cups of 36 mm inside diameter and a monochromator Foss NIRS instrument (NIRS 6500). The reflectances from 1100 to 2500 nm at 2 nm intervals were collected. Two spectra were collected for each sample and the mean of spectra used for data analyses.

Protein content (PR), lipid content (LIP), amylose content (AMY), were predicted using the equations developed by de Alencar Figuereido et al. (2006) and pericarp thickness (PERTH) was predicted using the quantitative equation developed by Guindo et al. (2016). The predictions were validated on sub-samples of the populations using the reference methods described in de Alencar Figuereido et al. (2006) and Guindo et al. (2016). The new reference data were then included in the database and the NIRS equations were re-established and used for prediction of the whole populations. In the case of AMY, for which NIRS calibration models behave poorly (de Alencar Figueiredo et al., 2006), reference data using differential scanning calorimetry (Mestres et al., 1996) were obtained on a random subset of 200 individuals of the population P118 (AMY_Lab) in addition to the AMY variable.

The color of the testa layer (TESTA) was assessed on ten kernels. A scale from 0 to 1 was used where 0 indicated non pigmented testa, 1 pigmented testa, and 0.5 segregating families where both pigmented and non-pigmented testa were present. Based on crossing studies with

the ATx623 inbred line, which is known to have the b1b1 B2B2 genotype (Raab et al., 1984) at the B1 and B2 genes controlling the testa layer pigmentation, the genotypes of Tiandougou, Keninkeni and Lata3 lines have been determined as b1b1 B2B2, B1B1 b2b2, and B1B1 b2b2, respectively.

Endosperm texture (ET) was determined by visual assessment on ten grains. A notation on a 1 to 5 scale developed by Maxson et al. (1971) was used where 1 corresponded to a completely vitreous endosperm and 5 to a completely floury endosperm.

Twenty grams of grains were dehulled during 5 minutes using a tangential abrasive dehulling device (Oomah et al., 1981) and the dehulled grains were weighed. The dehulling yield (DHYLD) was computed as the percentage of the weight of dehulled grains to the initial weight. The operation was replicated twice on two independent samples and the results averaged.

Tô consistency (TOCONS) was evaluated on mini-tô prepared in the food technology laboratory of Sotuba research station (IER). Dehulled grains were ground into flour using a Cyclone Sample Mill grinder. Tô was prepared based on the traditional method adapted to a small quantity of flour. Ten grams of flour were dispersed in a stainless beaker in 40 ml of water containing 4% of potash (ashes). Then the slurry was cooked on a hotplate for 10 min. After cooking, the porridge was poured into a cylinder (2 cm high and 4 cm in diameter). It was stored for about 24 hours at room temperature before testing. The upper part of the mini-tô was removed. Scoring was done by manual compression of the porridge between the thumb and forefinger by three experienced manipulators and a consensual score was then assigned to the sample with a scale rating from 1 (very consistent), 2 (consistent), 3 (soft), 4 (very soft and sticky) and 5 (very soft and very sticky). Each sample was evaluated twice and the mean value was used. The color of the tô (TOCOL) was also assessed visually on a 1 to 4 scale (1 light, 2 light brown, 3 red, 4 black).

2.5 Genotyping

DNA was extracted from a bulk of 10 F_4 plants on 382 and 400 families for P114 and P118, respectively, using the MATAB method (Risterucci et al., 2000). For P114, 200 markers were used including 76 Simple Sequence Repeat (SSR) markers and 124 SNP markers. For P118, 228 SNP markers were used. 49 SNP markers were common to the two populations. The SSR primers used in this study were described in Mace et al. (2009). The information regarding SNP markers used in this study is accessible on the SNP genotyping service web page of the Integrated Breeding Platform ("Integrated Breeding Platform," n.d.). SNP genotyping was outsourced to LGC Genomics and SSR genotyping was performed in the Grand Plateau Technique Regional de Génotypage of Montpellier (GPTR).

2.6 Statistical analysis

For both trials, an analysis of variance (ANOVA) was conducted on the replicated parents tested as block effects using a linear model. The trait values were adjusted from the block effect when it was significant. Trait correlations were computed and tested for significance at 5%.

2.7 Map construction

Marker segregations were checked for distortion to the expected ratios (3/8, 1/4, 3/8) using a Chi2 test at a significance level of 1% and 1‰. The genetic maps were built using Mapmaker (Lander et al., 1987). Linkage groups were determined using the group command with a LOD threshold of 3.0 and maximum distance of 50 cM. Loci were ordered in each group using the "order" command with the default parameters of the function. When several local orders were equally probable, the one in agreement with the expected order deduced from the physical positions of the markers was kept. The map distances for the final ordered linkage groups were computed using the Haldane mapping function.

2.8 QTL detection

The qtl R-package (Broman et al., 2003) was used for QTL analysis. The penalized likelihood model selection approach described by Manichaikul et al. (2009) was used to explore multiple QTL models and refine QTL positions in a multiple QTL framework. The *stepwiseqtl* function was used for forward/backward model selection using Haley-Knott regression, considering only additive QTL models, and with a maximum number of 8 QTLs. The main effect LOD penalty was computed for each trait from 1000 permutations of a two QTLs genome scan using the *scantwo* function with a significance level of 0.05.

The position of each QTL in the final model was refined using the *refineqtl* function. The LOD value and percentage of phenotypic variance for each QTL were estimated from a drop-one analysis comparing the full model to each sub-model with one QTL dropped. The additive effect of each QTL was estimated as half the difference between the homozygotes classes of Keninkeni/Lata3 and Tiandougou parents. A positive additive effect thus corresponds to a QTL for which the Keninkeni and Lata3 parents bring a positive effect for populations P114 and P118, respectively. Confidence intervals of all QTLs were determined using the function *lodint* with a 1 LOD support interval.

For the purpose of graphical representation of genetic maps, and to enable the comparison of QTLs positions between the two populations, all markers and QTLs of P114, were projected on P118 using the physical map as a bridge between the two maps and interpolating the genetic distances based on common markers. The same thing was done with the candidate genes reported by de Alencar Figuereido (2010) that were located on the sorghum genome. The projection was performed using the ziplinR R package (https://github.com/jframi/ziplinR). All graphical representations of maps comparisons and QTL positions were done using Spidermap software (Rami, unpublished). QTL co-localizations were determined based on the overlaps of the QTL confidence intervals.

3 Results

Table 1 summarizes the mean values of the traits measured for the parents, and the descriptive statistical parameters for their progenies: minimum (Min), maximum (Max), mean values, standard deviation (SD), and coefficient of variation (CV). Fig 1 shows the distribution of the traits for the two populations.

The two guinea parents, Keninkeni and Lata3 were not evaluated in the same experiment and could not thus be directly compared. All three parents were elite varieties of a breeding program and were therefore not expected to exhibit large differences for all traits.

Tiandougou, the common parent of the two populations, was the latest flowering with a 5 days DTFL difference as compared to Keninkeni and Lata3. It was also more productive than the two guinea parents (+ 340 $g.m^{-2}$, and + 87 $g.m^{-2}$ for GYLD as compared to Keninkeni and Lata3, respectively). In terms of grain morphology, Lata3 had slightly bigger grains than Tiandougou and Keninkeni (TGW of 23g, 22g, and 20g, respectively). The image analyses showed that Tiandougou grains were rounder than the grains of Lata3 (0.87 and 0.76 for GRND, respectively). Tiandougou had a thick pericarp (PERTH), while Keninkeni and Lata3 had a thin one and none of the three parents had a pigmented testa layer (TESTA). Tiandougou had slightly more adherent glumes than Lata3 (GLUMAD) and the glumes of Lata3 were black while the ones of Tiandougou were yellow (GLUMCOL of 1 and 3 respectively), which is related to the absence of anthocyanins (ANTHO) in the plant for the Tiandougou parent as compared to the two other parents. In terms of biochemical composition of the grain, Lata3 had a slightly higher content of amylose, lipids, and proteins than the two other parents that were similar for these traits.

For technological traits, Keninkeni and Lata3 had the same range of value for DHYLD with values superior to that of Tiandougou in both populations. The firmest tô (TOCONS) was observed with Lata3 while the two other parents had similar values of tô consistency. Lata3

had a more vitreous endosperm than Tiandougou and Keninkeni (ET value of 1.9, 2.4 and 2.5, respectively).

For each population trial, an analysis of variance was performed on the replications of the parents to test for a block effect. No significant block effect was observed except for TGW in P118 ($P<0.05$). This suggested a good homogeneity of plots in both P114 and P118. The progeny means of TGW in P118 were adjusted from the block effect.

All the traits exhibited transgressive segregations in both populations (Fig 1), except some qualitative traits for which the two parents belonged to opposite classes (ANTHO, PERTH, GLUMCOL). Transgressive segregations were particularly important for PROT, AMY, TGW, ET, and GYLD. This indicates that the guinea and caudatum parents probably differed in their allelic composition at the genes controlling most of these traits.

Pearson correlation coefficients (r) between quantitative traits are displayed in Table 2. The strongest correlation was found between PERTH and GWTN in population P118 (r=-0.84) indicating that the whiteness of the grain is mostly due to the thickness of the pericarp in this population. PERTH was also correlated to DHYLD (r=0.47 and r=0.39 in P118 and P114, respectively) indicating that a large part of dehulling yield was explained by the thickness of the pericarp and that dehulling was successful in removing the outer layers of the grain. DHYLD was positively correlated to TGW in population P114 (r=0.45) and to a lesser extent in population P118 (r=0.14). Surprisingly, DHYLD was also positively correlated to amylose content in both populations (r=0.38 and 0.32 in P114 and P118, respectively). DHYLD was positively correlated to GYLD, which could be explained by the important positive correlation between GYLD and TGW (0.53 and 0.28 in P114 and P118, respectively).

A strong positive correlation was observed between ET and TESTA in both populations (r=0.56 and 0.52 in P114 and P118, respectively). The presence of TESTA was also negatively correlated to both amylose content obtained by prediction AMY (r=-0.44 and -0.31

in P114 and P118, respectively), as well as those obtained by reference method AMY_Lab (r=-0.21 in P118) and positively correlated to TOCOL (r=0.41 and 0.30 in P114 and P118, respectively) indicating that part of the tô color was due to the presence of a pigmented testa in the grain. TOCOL was also positively correlated to ANTHO in P114 (r=0.39). Interestingly, this correlation was not found in P118, even though ANTHO was positively correlated to GLUMCOL in this population (r=0.42) and that anthocyanins in glumes are known to cause colored tô.

The grain morphology descriptors (MAJOR, MINOR, GRND and TGW) measured by image analysis on population P118 were correlated together as they were all related to the size and the shape of the grain. Grain amylose (AMY) and protein (PROT) contents were negatively correlated in both populations (r=-0.56 and -0.52 in P114 and P118, respectively) and PROT was positively correlated with lipid content (LIP) (r=0.39 and 0.46 in P114 and P118, respectively). AMY and AMY_Lab were positively correlated in P118 (r=0.62). This relatively low correlation confirmed the poor performance of NIRS to predict amylose from whole grain as previously reported by de Alencar Figuereido et al. (2006) (R^2=0.70).

The consistency of the tô was positively correlated with amylose content (r=-0.32 and -0.26 between TOCONS and AMY_Lab and AMY respectively in P118, and r=-0.11 between TOCONS and AMY in P114), taking into account that a consistent tô is represented by a low value of TOCONS. Given the negative correlation between AMY and PROT and LIP, the consistency of the tô was negatively correlated with PROT and LIP (r=0.34 and 0.20, respectively) in P118.

3.1 Linkage maps and segregation analysis

The total map distances were 1792 cM and 1346 cM and the average distance between markers 10 cM and 6 cM for P114 and P118, respectively. The longest gap with no marker

was 40 cM for both populations. The marker order was in agreement with the known positions of the markers on the genome sequence.

The segregation ratios were analyzed and compared to the Mendelian segregation ratios in F_3 generation (3/8, 1/4, 3/8) using a chi-square test. Fig 2 to 6 displayed the genetic map showing distorted markers. In P114, a total of 67 markers were significantly distorted at $P<0.01$ and 40 of the 67 were significant at $P<0.001$. In P118 a total of 51 markers showed segregation distortions at $P<0.01$, among them, 37 were significant at $P< 0.001$.

Most of the distorted markers were organized in cluster. In P114, the top of chromosome 1, from 0 to 73 cM, was strongly distorted in favor of the Keninkeni allele. The two extremities of chromosome 3 (0 to 29 cM and 136 to 175 cM) were distorted in favor of the Tiandougou allele. Several segments of chromosome 4 were also distorted in favor of the Tiandougou parent. The bottom extremity of chromosome 6 (86 to 142 cM) was distorted in favor of the Keninkeni allele, as were the top of chromosome 8 (0 to 30 cM), and the two extremities of chromosome 10 (0 to 44.9 cM and 119.6 to 168.8 cM). In P118, a segment of chromosome 2 (132 to 155 cM) was distorted in favor of Lata3 allele. Most of the chromosome 4 was distorted in favor of Tiandougou allele, as was the bottom extremity of chromosome 9 (66 to 117 cM). Finally, two segments of chromosome 6 were distorted in favor of Lata3 allele.

3.2 QTL detection

The phenotypic data collected on both populations along with genotypic data and genetic maps were used to detect QTLs using a multiple QTL model. The QTLs detected in both populations are represented on Fig 2 to 6 and summarized in Table 3. The forward/backward model selection used a main effect LOD penalty computed for each trait from 1000 permutations of a two QTLs genome scan with a significance level of 0.05. The LOD penalties ranged from 3.35 to 3.73 for P118 and from 3.47 to 3.82 for P114 (Table 3).

In P114, a total of 51 QTLs were identified for 12 traits out of the 13 traits investigated. No QTL was detected for TOCONS in the P114 population. In P118, 71 QTLs were identified for the 20 traits that were measured in this population. The number of QTLs per trait ranged from 1 (PERTH in P114 and P118, GYLD, TOCONS, TOCOL, and ANTHO in P118) to 8 (ET in P114, MAJOR, GRND, and DTFL in P118). The difference in the total number of detected QTLs and the number of QTLs per trait in the two populations can be explained by the different genetic background represented by Keninkeni and Lata3 parents and by the fact that the two populations were evaluated in two different environments.

Several QTLs showed high LOD score and R^2 values corresponding to the segregation of major genes. This was the case for PERTH on chromosome 2 in position 90 (LOD value of 86.9 and 81.5 and R^2 of 64.9 and 60.8 on P114 and P118 respectively), for GWTN on the same location (LOD value of 72.5 and R^2 of 48.2 on P118), DTFL on chromosome 3 in position 74 (LOD value of 78.9 and 78.0 and R^2 of 55.7 and 48.7, on P114 and P118, respectively), TESTA on chromosome 4 in position 109 (LOD value of 40.1 and 39.3, and R^2 of 33.4 and 33.6, on P114 and P118, respectively) and on chromosome 2 in position 45 (LOD value of 24.5 and 20.8, and R^2 of 18.1 and 15.7, on P114 and P118, respectively), and ANTHO on chromosome 6 in position 102 (LOD value of 77.2 and 78.2, and R^2 of 58.0 and 59.5, on P114 and P118, respectively). The major QTL for PERTH and GWTN corresponds to the Z gene controlling mesocarp thickness (Ayyangar et al., 1934) for which map location was reported on the same locus by Boivin et al. (1999). The two major QTLs for TESTA on chromosomes 2 and 4 correspond to the B2 and B1 genes respectively. The QTL on chromosome 4 colocalizes with the Tan1 gene recently cloned by Wu et al. (2012) (Fig 2 to 6). The QTL on chromosome 2 colocalizes with the B2 gene previously mapped on chromosome 2 (Dufour et al., 1997; Rami et al., 1998) and for which a candidate gene (Sb02g006390, renamed Sobic.002G076600 in v3.1 of sorghum genome assembly) was

recently proposed by Morris et al. (2013b). The major QTL for ANTHO on chromosome 6 corresponds to the P gene already reported at the same location (Rami et al., 1998). Finally, the major QTL for DTFL on chromosome 3 has been investigated in a separate study involving the P118 population and has been shown to be involved in the fine tuning of photoperiod sensitivity (Guitton et al., 2018).

On top of chromosome 1, a QTL for TGW was detected on P114. At this locus, the Tiandougou allele conferred larger grains. This QTL was confirmed by two QTLs for MAJOR and MINOR grain axes detected at the same location in population P118 with Tiangougou allele also increasing grain size, though no QTL for TGW was located at that position for P118. Tiandougou allele was also associated in this region with higher PROT and higher GLUMAD (high value of GLUMAD correspond to low level of glume adherence). A QTL for ET was detected in the middle of chromosome 1 in both populations, associated to a QTL for DHYLD in population P118. Tiandougou allele at this locus conferred higher dehulling yield and more vitreous endosperm. Finally, one QTL for LIP was detected in the bottom part of chromosome in both populations, with Keninkeni and Lata3 conferring higher lipid content.

On chromosome 2, the major QTL for TESTA (B2 gene) was associated to a QTL for ET on both populations and a QTL for AMY on P114 and AMY_Lab on P118. At this locus, the Tiandougou allele conferred a pigmented testa, floury endosperm with lower amylose content. This association between the B2 gene and amylose content and endosperm texture is consistent with results reported previously in guinea x caudatum crosses (Rami et al., 1998). On the same chromosome, the PERTH QTL was associated to QTLs for LIP and DHYLD on both populations. At this locus, the Tiandougou allele conferred a thick pericarp, higher lipid content and a lower dehulling yield. This QTL was colocalizing with two QTLs for TGW and MINOR on population P118.

On chromosome 3, a QTL for ET was detected in P114 with no colocalization with other QTL and for which the Tiandougou allele was associated with vitreous endosperm. In both populations, QTLs for GYLD and AMY were associated with the major QTL for DTFL on the same chromosome. The Tiandougou allele conferred delayed flowering in both populations but interestingly, higher yield and amylose content in P114 but lower yield and amylose content in P118. In P114, the Tiandougou allele at this QTL was also associated to higher TGW, higher DHYLD and lower PROT.

On chromosome 4, the only QTL for TOCONS was detected in P118 and colocalized with a QTL for AMY_Lab. The Lata3 allele at this QTL conferred higher tô consistency and higher amylose content confirming the relationship between amylose content and tô consistency reported by Fliedel (1995). A QTL for DTFL was found in both populations on the same chromosome, with Tiandougou allele contributing early flowering. In P114, this QTL was colocalizing with a QTL for GYLD, TGW and DHYLD at which the Keninkeni allele provided higher yield, larger grains and higher dehulling yield. The main QTL for TESTA, corresponding to the Tan1 (B1) gene, was colocalizing with QTLs for TOCOL and ET in both populations and with QTLs for MINOR, GWTN, GLUMCOL and GWTN in P118, and ANTHO in P114. The colocalization of TOCOL with the Tan1 gene suggested than the pigmented testa had an impact on the final color of the tô, even after grain dehulling. The colocation of ET and TESTA QTLs at the two loci involved in the genetic control of pigmented testa seems to indicate a functional link between this trait and the texture of the endosperm. The colocation of Tan1 with a QTL for ANTHO in P114 and a QTL for GLUMCOL in P118 also suggested that this gene was also involved in the pigmentation at the whole plant level as reported by Wu et al. (2012). Two QTLs for AMY were also detected on chromosome 4 for P114, one with a positive effect from Keninkeni, colocalizing with the amylose extender (Ae1) gene, and the other one with a positive effect from Tiandougou.

On chromosome 5, colocalizing QTLs for AMY, ET and PROT were detected in P114, with the Tiandougou allele conferring higher amylose content, softer endosperm and lower protein content. In the same region, a QTL for MAJOR was detected for P118, at which the Tiandougou allele increased the length of the grain. A QTL for GYLD was also detected on the same chromosome in P114 with Tiandougou allele having a positive effect and QTLs for GRND and GWTN were detected in a neighboring region in P118 with Tiandougou allele having a positive effect.

On chromosome 6, QTLs for TGW, MAJOR, and MINOR were detected together in P118 with Tiandougou allele conferring a positive effect to grain size. Two QTLs for LIP were detected in both populations with a positive effect of Tiandougou allele. These QTLs were close to a QTL for ET in P114 colocalizing with a QTL for DHYLD in P118, for which the Keninkeni and Lata3 alleles conferred vitreous endosperm and higher dehulling yield. The major QTL for ANTHO on the same chromosome was associated with a QTL for TOCOL in P114 and QTLs of GLUMCOL and GWTN in P118. The Keninkeni and Lata3 alleles at this locus were both associated with high anthocyanins, colored tô for Keninkeni, colored glumes and darker grain for Lata3. The colocalization of QTLs for TOCOL, GLUMCOL, and ANTHO suggest that the pigments of the glumes can pass inside the grain when conditions are favorable and result in a colored tô.

On chromosome 7, the same colocalization of QTLs for DHYLD, DTFL, and TGW were observed for both populations. This locus was associated with a QTL for GYLD in P114 and with QTLs for GRND and MAJOR in P118. In both cases the guinea allele (Keninkeni or Lata3) was associated with higher dehulling yield, later flowering, higher yield and bigger grains. The Keninkeni allele was also associated with higher yield while the Lata3 allele contributed longer grains. These findings suggest that this locus plays a major role in the shape of the grain and consequently on grain size and grain yield.

On chromosome 8, one QTL for ET was detected at the top of the chromosome in P114, with the Tiandougou allele contributing to vitreous endosperm. Another QTL was found in P114 at the bottom of the chromosome for PROT with a positive effect of Tiandougou allele. In P118, only a small effect QTL for DTFL was detected at the bottom end of the chromosome.

On chromosome 9, a QTL for GYLD was detected in P114, with a positive effect of Tiandougou allele. This QTL colocalized with two QTLs for GRND and MAJOR in P118 for which the Tiandougou allele contributed to a rounder grain with a reduced major axis. This locus, similarly to the ones detected on chromosomes 1, 3 and 7, revealed a relation between grain morphology and grain yield.

Finally, on chromosome 10, two QTLs for GRND and MAJOR were detected in P118 with Tiandougou allele contributing to rounder grains with reduced major axis. This QTL colocalized with a QTL for AMY in P114, with Keninkeni allele having a positive effect. A QTL for LIP was detected in P114 with a large effect (R^2=17%) of the Tiandougou allele on lipid content. This QTL did not colocalize with any other trait. Two QTLs for DHYLD and ET were also detected in P114, with Tiandougou allele contributing to a more vitreous endosperm and higher dehulling yield.

4 Discussion

Ideotypes of sorghum varieties for West-African agro-ecosystems are complex constructions that need to combine adaptation for diverse and variable environments, stable productivity, quality characteristics for a large range of traditional end-uses or emerging value chains, and morphological attributes that meet farmers' preferences. Breeding such varieties is challenging as it requires measuring and assembling a large range of traits not always positively genetically correlated. Modern breeding using molecular markers provides a unique opportunity to investigate the genetic control of this large number of target traits and to monitor the process of pyramiding the favorable alleles for the genes involved in their variation. To be efficiently implemented, the use of molecular markers has to be tightly integrated into the breeding program while minimizing disruption to the breeding process. This study represents the QTL discovery phase of a marker assisted recurrent selection project that aims at combining grain productivity and grain quality.

We have analyzed two large sorghum breeding populations that were designed for this purpose using three complementary elite parents. The genotyping of the two populations provided two genetic maps with optimal marker density for QTL detection. The ordering of genetic markers was robust and consistent with their known position on the sorghum genome sequence, attesting of the quality of the genotyping data and the interest of using populations with a large number of progenies. A total of 20 traits have been measured and the trait variation in each population showed transgressive segregation in most cases. Except for the TOCONS trait in the P114 population, QTLs were detected for all measured traits. One QTL for tô consistency, which was one of our primary breeding targets, was found in population P118 and colocalized with a QTL for amylose content, confirming the role of amylose in the firmness of the tô. The fact that only one QTL was found for this trait underlines the difficulty of obtaining reliable measurements because of the complexity of the cooking process and the

subjectivity of consistency appraisal. For this reason, a good understanding of the process and of the factors that affect the quality of the final product is essential in order to focus breeding efforts on heritable components of tô quality. QTLs for grain shape parameters were reported for the first time in sorghum, thanks to an image analysis procedure that provided a rapid and reliable way to access many shape parameters at the same time.

The construction of the two genetic maps showed many highly significant segregation distortions for the molecular markers analyzed in both populations, that underlined the challenge of using real breeding populations as mapping populations. Most of the distorted markers were organized in clusters. The strongest distortions were observed on chromosomes 1, 3, 4, 6, and 8 for P114 and on chromosomes 4 and 9 for P118. A possible explanation of these high rates of segregation distortion is a selection bias that may have occurred in F_2 generation favoring one of the parental alleles. Actually, given the photoperiod sensitivity of the populations, the production of the F_3 generation was achieved in off-season in Mali from March to May 2009 using flower initiation masks. It is possible that the artificial flowering initiation process introduced a selection bias in some regions of the genome involved in the response to photoperiod. Similarly, it is also possible that F_2 plants experienced high temperatures during the flowering phase in April-May 2009 in Bamako, an issue that may have been exacerbated by the use of initiation masks. A maximum temperature of 41°C observed during 6 days and an average of 38°C were reported over this period. The presence of high temperatures during flowering has been reported to cause pollen infertility in many crop species (Bita and Gerats, 2013). Selection biases that could explain the distortions observed in both populations can also be interpreted in the light of co-localization of segregation distortions with detected QTLs. On top of chromosome 1, in the region of the most distorted zone in population P114, two QTLs were detected for TGW and PROT. The distortion observed in this region was in favor of the allele linked to smaller grains with fewer

proteins. In the bottom part of chromosome 4, highly distorted in both populations in favor of Tiandougou allele, several QTLs were detected colocalizing with the Tan1 gene controlling pigmentation of testa layer for which both Keninkeni and Lata3 had the B2 allele conferring a pigmented testa. It is possible that some progenies showing a pigmented testa may have been discarded during the population development from F_2 to F_3 generation. It is however difficult to link segregation distortions to detected QTLs, as QTL detection itself may have been affected by unbalanced genotypic classes. Distorted markers are known to affect the estimation of genetic distance between markers and the order of markers (Lorieux et al., 1995) as well as QTL detection (Xu, 2008; Zhang et al., 2010). Most of the time, segregation distortions are detrimental to QTL detection but Xu (2008) reported that it can be beneficial especially in case of purely additive QTLs.

The genetic mapping of several genes with major effect was a key result for designing the target ideotypes according to breeding objectives. Among the regions of the genomes that were significantly associated with the variation of the traits analyzed in the two populations, five corresponded to genes with major effects and important pleiotropic effects. This was the case of the gene for pericarp thickness on chromosome 2 known as the Z gene (Ayyangar et al., 1934), the two genes controlling the presence of pigmented testa layer on chromosomes 4 and 2, known as B1 and B2, respectively, the gene controlling plant anthocyanin on chromosome 6, known as P, and one gene for flowering time that has been shown to be involved in the control of the critical photoperiod trait (Guitton et al., 2018). Another major QTL for plant height (data not shown) segregating in the two populations was also located on chromosome 7 and most likely corresponded to the Dw3 gene. Interestingly, the B2 locus on chromosome 2 was found to be associated with endosperm texture and amylose content in both populations, a result already reported by Rami et al. (1998). The fact that the B1 locus that was mapped on chromosome 4 was also associated with a QTL for endosperm texture in

both populations suggested a functional link between the presence of a pigmented testa and the physical properties of the endosperm. It is possible that the presence of a pigmented testa in the peripheral layers of the grain modifies the kinetics of grain dessication and subsequently the texture of the endosperm. Morris et al. (2013b) proposed a putative bHLH transcription factor as a possible candidate for the B2 gene, based on association studies and orthology with genes known to control grain tannins in rice and Arabidopsis. There is no established link of this gene with starch biosynthesis pathway that could explain the colocalization with a QTL for amylose content. A better explanation seems to be an important linkage disequilibrium between the B2 gene and a gene involved in grain amylose content in this region. The segregation of major genes in the two populations explained a significant part of the variation of the traits, but may also have limited the power of detection for QTLs with small effects and thus reduced the prediction accuracy of the genetic value of selected progenies. The segregation of such genes with major effects in elite material is probably a consequence of the diversity of ideotypes that are considered by breeding programs. In fact, depending on the breeding objectives, these genes may either be considered as beneficial or detrimental, which may have limited the selection pressure on particular alleles for these genes. This specificity of elite sorghum germplasm of West-African breeding programs has to be taken into account for designing marker assisted breeding schemes.

In addition to loci with major and pleiotropic effects, many QTLs with moderate effects have been detected for most of the traits that have been analyzed. No major antagonism was detected between grain quality traits and grain yield, suggesting that it is possible to combine the favorable alleles of both categories to breed for productive varieties with satisfactory grain quality attributes. Based on QTL results, it is possible to identify what is the most favorable parental allele in each region of the genome and define one or more genotypic ideotypes that correspond to ideal patterns of recombination between the two parents with respect to the

breeding objectives. Recurrent crossing of progenies from both populations, accurately monitored by molecular markers, will facilitate the production of families with accumulated favorable alleles that can be further evaluated by breeders through conventional breeding.

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737 7 Tables

738 **Table 1. Descriptive statistics of progenies and mean values of parents.** N: number of data, Min.: minimum, Max: maximum, SD: standard

739 deviation, CV: coefficient of variation, P1: Value of Lata3 for P118 and Keninkeni for P114, P2: Value of Tiandougou

Trait		Pop.	N	Min.	Max.	Mean	S.D.	C.V.	P1	P2
AMY_Lab (%)	Amylose content (wet lab data)	P118	184	17.7	24.5	21.6	1.4	6.7	22.2	21.6
AMY (%)	Amylose content (NIRS)	P114	377	18.3	22.4	20.8	0.8	3.7	21.5	21.4
AMY (%)		P118	400	19.2	23.2	21.6	0.8	3.5	22.0	21.5
ANTHO (0 to 1 scale)	Plant anthocyan	P114	382	0.0	1.0	0.5	0.4	81.2	1.0	0.0
ANTHO (0 to 1 scale)		P118	398	0.0	1.0	0.6	0.4	69.1	1.0	0.0
DHYLD (%)	Dehulling yield	P114	379	28.3	95.0	70.8	10.5	14.9	84.1	65.4
DHYLD (%)		P118	400	53.3	90.0	79.9	4.6	5.8	85.1	73.1
DTFL (d)	Days to flowering	P114	382	52.2	75.7	64.3	5.2	8.1	65.4	70.0
DTFL (d)		P118	400	70.5	103.0	83.9	5.9	7.1	83.0	87.8
ET (1 to 5 scale)	Endosperm texture	P114	382	1.2	4.6	2.4	0.7	27.5	2.5	2.4
ET (1 to 5 scale)		P118	369	1.0	4.5	2.6	0.7	26.4	1.9	2.3
GYLD (g/ha)	Grain yield	P114	382	408.3	5746.7	3046.4	955.8	31.4	3604.5	3947.3
GYLD (g/ha)		P118	400	486.7	5363.3	2286.1	784.2	34.3	2822.8	2910.1
LIP (%)	Lipid content	P114	377	2.3	4.5	3.5	0.4	10.4	2.8	3.7
LIP (%)		P118	400	3.7	6.0	4.7	0.4	7.9	5.1	4.7
PERTH (0 to 1 scale)	Pericarp thickness	P114	377	-0.2	1.2	0.6	0.4	78.0	1.0	0.0
PERTH (0 to 1 scale)		P118	400	-0.2	1.1	0.6	0.4	75.0	1.0	0.0
PROT (%)	Protein content	P114	377	7.6	15.3	11.6	1.1	9.2	10.7	10.7
PROT (%)		P118	400	7.4	16.8	11.0	1.2	10.7	11.5	10.1
TESTA (0 to 1 scale)	Presence of testa	P114	327	0.0	1.0	0.2	0.4	143.9	0.0	0.0

TESTA (0 to 1 scale)		P118	369	0.0	1.0	0.2	0.3	164.7	0.0	0.0
TGW (g)	Thousand grains weight	P114	378	11.0	26.4	19.3	3.0	15.5	20.0	21.7
TGW (g)		P118	400	15.3	29.2	22.3	2.2	9.8	23.1	22.1
TOCOL (1 to 4 scale**)**	Tô color	P114	379	1.0	3.0	1.5	0.7	46.9	2.4	1.0
TOCOL (1 to 4 scale)		P118	400	1.0	2.0	1.0	0.2	17.8	1.0	1.1
TOCONS (1 to 5 scale)	Tô consistency	P114	379	1.0	4.0	1.9	0.8	41.6	2.2	2.1
TOCONS (1 to 5 scale)		P118	174	1.0	3.0	1.8	0.4	25.4	1.7	2.3
GLUMAD (1 to 5 scale)	Glume adherence	P118	400	1.0	5.0	4.1	1.4	34.7	4.4	4.9
GLUMCOL (1 to 4 scale)	Glume color	P118	399	1.0	3.0	1.6	0.7	44.2	3.0	1.0
GRND (0 to 1 scale)	Grain shape: roundness	P118	400	0.73	0.90	0.81	0.03	3.81	0.76	0.87
GWTN (0 to 255 scale)	Grain whiteness	P118	400	128.6	180.0	159.6	10.8	6.8	146.0	180.8
MAJOR (pixels*)	Grain shape: major axis	P118	400	22.9	28.9	25.5	1.1	4.2	26.8	25.5
MINOR (pixels*)	Grain shape: minor axis	P118	400	18.5	23.0	20.7	0.7	3.6	20.4	22.2

*1 pixel = 0.127 mm

742 **Table 2. Pearson phenotypic correlation in P114 and P118 populations.**

Trait	Pop	AMY	ANTHO	DHYLD	DTFL	ET	GYLD	LIP	PERTH	PROT	TESTA	TGW	TOCOL	TOCONS	AMY_Lab	GLUMAD	GLUMCOL	GRND	GWTN	MAJOR
ANTHO	P114	0.07																		
ANTHO	P118	0.09																		
DHYLD	P114	0.38	0.12																	
DHYLD	P118	0.33	0.11																	
DTFL	P114	0.38	-0.02	0.34																
DTFL	P118	-0.26	-0.09	0.02																
ET	P114	-0.33	-0.04	-0.24	-0.08															
ET	P118	-0.1	-0.01	-0.21	0.05															
GYLD	P114	0.4	0.03	0.34	0.29	-0.07														
GYLD	P118	0.18	0.18	0.24	-0.29	0.05														
LIP	P114	-0.13	-0.17	-0.08	0.08	-0.09	-0.1													
LIP	P118	-0.36	-0.2	-0.18	0.16	-0.24	-0.19													
PERTH	P114	0.13	0.04	0.39	-0.03	-0.21	0.01	-0.27												
PERTH	P118	0.32	0.02	0.47	0.03	-0.04	-0.05	-0.13												
PROT	P114	-0.56	-0.11	-0.1	-0.29	-0.13	-0.32	0.4	0.06											
PROT	P118	-0.52	-0.11	0.09	0.19	-0.3	-0.28	0.46	0.2											
TESTA	P114	-0.44	0.14	-0.1	0.01	0.57	0.03	-0.13	-0.22	-0.14										
TESTA	P118	-0.31	0.01	-0.14	0	0.52	0.14	-0.13	-0.11	-0.17										
TGW	P114	0.25	-0.09	0.45	0.38	-0.17	0.53	0.12	0.01	0.01	-0.06									
TGW	P118	0.05	-0.02	0.15	-0.15	0.01	0.28	0.09	-0.17	-0.07	-0.01									
TOCOL	P114	-0.14	0.39	0.18	-0.11	0.11	0.06	-0.14	0.11	-0.07	0.41	-0.06								
TOCOL	P118	-0.16	0.1	-0.07	0.01	0.25	0.03	-0.05	-0.01	-0.01	0.3	-0.02								
TOCONS	P114	-0.11	0.07	0.13	-0.05	-0.07	-0.17	0.2	0.05	0.18	-0.04	-0.09	0.13							
TOCONS	P118	-0.27	-0.13	-0.12	0.1	-0.1	-0.13	0.16	0.09	0.34	-0.04	-0.07	-0.1							
AMY_Lab	P118	0.63	0.11	0.27	-0.09	-0.12	0.16	-0.27	0.17	-0.41	-0.21	0	-0.09	-0.32						
GLUMAD	P118	0.04	-0.11	0.08	-0.07	0	0.35	-0.06	-0.03	-0.17	0.1	0.08	-0.01	-0.1	0.1					
GLUMCOL	P118	0.1	0.52	0.13	-0.13	0.04	0.22	-0.15	0.04	-0.16	0.22	0.09	0.12	0	0.1	-0.11				
GRND	P118	0.14	0.13	0.02	-0.11	0.07	0.07	-0.29	-0.17	-0.21	-0.1	-0.18	-0.06	-0.06	0.03	0.15	0.02			
GWTN	P118	-0.15	-0.14	-0.48	0.08	-0.08	-0.07	0.16	-0.84	-0.15	-0.19	0.13	-0.12	0	-0.1	-0.01	-0.25	0.16		
MAJOR	P118	-0.01	-0.19	0	-0.06	-0.15	0.18	0.27	-0.08	0.08	-0.11	0.72	-0.04	0.04	-0.02	0.11	-0.07	-0.61	0.16	
MINOR	P118	0.14	-0.08	0.02	-0.2	-0.1	0.27	0.01	-0.28	-0.12	-0.24	0.64	-0.12	-0.01	0	0.28	-0.06	0.38	0.36	0.5

743 **Table 3. QTLs detected in P118 and P114 populations.** The rows highlighted in blue
744 correspond to QTLs of the same trait co-localizing in both populations. Penal.: penality, Chr.:
745 chromosome, Conf1: lower limit of QTL confidence interval, Peak: QTL position, Conf2:
746 upper limit of QTL confidence interval, LOD: lod value at QTL position, R^2: percentage of
747 phenotypic variance explained by the QTL, add.: additivity effect.
748

	P118								P114							
Trait	**Penal.**	**Chr.**	**Conf1**	**Peak**	**Conf2**	**LOD**	**R^2**	**add**	**Penal.**	**Chr.**	**Conf1**	**Peak**	**Conf2**	**LOD**	**R^2**	**add**
AMY	* 3.46	Sb02	38.3	49.8	56.3	3.88	8.40	0.43	3.59	Sb02	37.4	42.0	45.7	13.59	11.41	0.35
	3.63	Sb02	78.3	86.3	92.3	11.20	10.97	0.32								
	3.63	Sb03	67.5	77.5	85.5	5.81	5.52	0.22	3.59	Sb03	67.9	72.3	74.7	10.33	8.50	-0.28
	* 3.46	Sb04	17.0	21.4	27.0	3.49	7.52	0.41								
***AMY_Lab**									3.59	Sb04	50.1	62.4	67.8	5.99	4.80	0.19
	3.63	Sb04	91.0	95.0	112.0	6.72	6.42	-0.22								
									3.59	Sb04	116.6	139.6	142.3	6.62	5.33	-0.22
									3.59	Sb05	0.4	48.6	77.7	4.47	3.54	-0.16
									3.59	Sb10	34.2	38.8	43.8	4.39	3.48	0.10
ANTHO									3.67	Sb04	101.3	109.6	118.3	5.73	2.70	0.09
	3.64	Sb06	100.2	102.2	104.2	78.19	59.53	0.41	3.67	Sb06	100.8	101.7	102.3	77.20	57.99	0.42
DHYLD	3.58	Sb01	91.4	98.4	106.4	6.99	5.61	-1.38								
									3.52	Sb01	154.2	159.6	174.8	4.40	3.43	2.81
	3.58	Sb02	88.3	92.3	96.3	25.06	22.39	2.93	3.52	Sb02	84.1	87.0	91.7	17.53	14.81	5.50
									3.52	Sb03	69.6	74.7	77.7	9.92	7.99	-3.96
									3.52	Sb04	85.4	90.7	96.4	7.00	5.54	3.01
	3.58	Sb04	105.0	107.4	109.0	4.65	3.68	-0.43								
	3.58	Sb06	87.2	91.2	96.2	5.95	4.75	1.19								
									3.52	Sb07	50.6	65.6	79.8	5.36	4.20	2.77
	3.58	Sb07	79.2	91.2	100.2	4.79	3.80	1.15								
									3.52	Sb10	108.5	116.1	125.7	5.58	4.38	-3.38
DTFL									3.59	Sb01	121.8	127.9	131.7	8.01	3.56	1.25
	3.69	Sb02	133.5	137.3	141.3	12.96	5.39	1.74								
	3.69	Sb03	72.5	74.5	75.5	78.01	48.71	-5.25	3.59	Sb03	73.7	74.7	74.7	78.90	55.72	-4.97
	3.69	Sb03	122.5	127.5	132.5	6.93	2.78	-1.22								
	3.69	Sb04	68.0	81.0	89.0	4.13	1.63	0.98								
									3.59	Sb04	89.6	92.4	95.6	5.14	2.24	0.98
									3.59	Sb06	18.9	37.4	77.5	3.64	1.57	-0.91
	3.69	Sb07	83.2	90.2	100.2	6.30	2.52	1.21	3.59	Sb07	64.1	83.0	95.1	4.86	2.11	0.99
	3.69	Sb08	20.5	109.5	118.5	4.59	1.82	-1.02								
	3.69	Sb10	60.0	67.5	73.5	4.45	1.76	0.89								
	3.69	Sb10	128.0	132.8	132.8	5.09	2.02	-1.01								
ET	3.57	Sb01	86.4	95.4	105.4	5.79	5.57	0.21	3.77	Sb01	66.9	83.2	179.1	5.21	3.21	0.15
	3.57	Sb02	37.3	45.2	47.3	13.64	13.79	-0.30	3.77	Sb02	42.9	46.7	54.0	16.82	11.15	-0.29
									3.77	Sb03	14.0	17.6	24.5	9.07	5.73	0.20
	3.57	Sb04	107.4	110.8	115.0	4.98	4.77	0.18	3.77	Sb04	106.0	109.6	113.2	11.03	7.05	0.21
									3.77	Sb05	17.6	32.4	37.5	7.79	4.88	-0.18
	3.57	Sb06	3.2	3.2	11.2	4.39	4.19	0.16								
									3.77	Sb06	86.7	93.4	99.9	5.52	3.41	-0.16

	P118								P114							
Trait	Penal.	Chr.	Conf1	Peak	Conf2	LOD	R^2	add	Penal.	Chr.	Conf1	Peak	Conf2	LOD	R^2	add
									3.77	Sb08	11.2	17.5	23.4	8.73	5.50	0.20
									3.77	Sb10	88.0	97.8	115.4	7.50	4.69	0.19
GYLD	3.65	Sb03	71.7	77.5	83.5	6.44	7.14	254.38	3.54	Sb03	56.6	67.9	75.7	7.20	5.79	-298.20
									3.54	Sb04	86.3	90.7	92.1	10.63	8.73	345.49
									3.54	Sb05	90.9	99.7	105.7	6.43	5.14	-288.78
									3.54	Sb07	70.4	73.7	81.1	18.20	15.65	460.80
									3.54	Sb09	39.3	51.0	64.1	4.22	3.33	-211.37
LIP	3.35	Sb01	143.4	149.4	159.4	6.69	6.56	0.11	3.63	Sb01	120.5	130.2	156.4	3.82	3.29	0.09
	3.35	Sb02	83.3	92.3	104.3	4.96	4.81	-0.10	3.63	Sb02	85.5	91.7	104.1	3.79	3.27	-0.08
	3.35	Sb06	65.2	93.2	99.2	7.59	7.48	-0.13	3.63	Sb06	75.7	80.3	83.8	8.40	7.44	-0.13
									3.63	Sb10	75.8	82.7	84.8	17.94	16.88	-0.18
PERTH	3.57	Sb02	87.3	90.3	92.3	81.51	60.87	0.45	3.47	Sb02	87.7	88.4	89.9	86.90	64.92	0.45
									3.65	Sb01	10.5	17.2	18.0	6.79	6.17	-0.41
	3.71	Sb01	57.4	66.4	71.4	7.23	7.24	-0.39								
									3.65	Sb03	57.6	69.6	74.7	6.40	5.81	0.32
									3.65	Sb03	146.1	152.0	155.5	3.77	3.37	0.19
PROT									3.65	Sb05	1.6	25.6	37.5	4.95	4.45	0.26
	3.71	Sb06	29.2	39.2	47.2	7.15	7.17	-0.44								
									3.65	Sb06	50.6	55.1	62.2	6.03	5.46	-0.37
									3.65	Sb08	101.2	116.4	117.9	7.10	6.46	0.33
	3.71	Sb09	83.0	94.0	103.0	3.93	3.86	0.25								
TESTA	3.50	Sb02	38.3	45.2	46.3	20.83	15.73	-0.16	3.82	Sb02	42.9	45.7	50.5	24.53	18.15	-0.20
	3.50	Sb04	109.0	111.0	112.0	39.35	33.60	0.24	3.82	Sb04	108.7	109.6	111.4	40.11	33.39	0.26
									3.55	Sb01	5.7	13.4	18.0	5.05	4.14	-0.96
	3.73	Sb02	83.3	100.2	105.3	4.04	3.59	-0.42								
									3.55	Sb03	69.6	72.3	76.7	10.03	8.49	-1.08
TGW									3.55	Sb04	84.6	88.4	93.6	5.29	4.35	0.79
	3.73	Sb06	63.2	73.2	84.2	4.38	3.90	-0.51								
									3.55	Sb07	64.1	68.8	72.6	20.98	19.02	1.62
	3.73	Sb07	92.2	95.2	98.2	15.93	15.17	1.02								
TOCOL	3.43	Sb04	107.0	112.0	122.0	5.66	6.31	0.06	3.69	Sb04	101.3	107.8	116.6	12.04	12.07	0.29
									3.69	Sb06	99.0	101.7	103.5	9.81	9.69	0.26
TOCONS	3.52	Sb04	21.4	26.2	30.0	3.69	9.31	-0.17								
GLUMAD	3.60	Sb01	16.4	24.4	39.4	5.56	5.35	0.38								
	3.60	Sb03	123.5	145.5	151.5	7.67	7.47	0.47								
	3.60	Sb06	38.2	48.2	59.2	6.00	5.79	-0.47								
GLUMCOL	3.51	Sb04	107.4	117.0	124.0	7.55	6.67	0.19								
	3.51	Sb06	99.2	102.2	104.2	21.73	20.91	0.63								
GRND	3.65	Sb02	1.3	6.3	9.3	4.81	2.93	-0.01								
	3.65	Sb02	140.3	143.3	150.3	11.68	7.41	-0.01								
	3.65	Sb02	161.3	170.4	170.4	3.71	2.25	0.01								
	3.65	Sb05	72.7	79.7	89.7	4.94	3.02	-0.01								
	3.65	Sb07	1.2	5.2	11.1	6.59	4.06	-0.01								
	3.65	Sb07	93.2	97.2	100.2	23.75	16.20	-0.02								
	3.65	Sb09	39.0	46.0	53.0	8.09	5.02	-0.01								
	3.65	Sb10	40.0	42.0	46.0	6.54	4.03	-0.01								
GWTN	3.67	Sb02	89.3	91.3	93.3	72.54	48.18	-10.02								
	3.67	Sb03	130.5	134.5	139.5	6.65	2.94	-2.13								
	3.67	Sb04	108.0	110.8	128.0	8.03	3.57	-2.62								
	3.67	Sb05	67.7	83.7	91.7	4.64	2.02	-1.88								
	3.67	Sb06	11.2	18.2	25.2	4.83	2.11	-1.07								
	3.67	Sb06	97.2	101.2	104.9	7.80	3.47	-2.46								

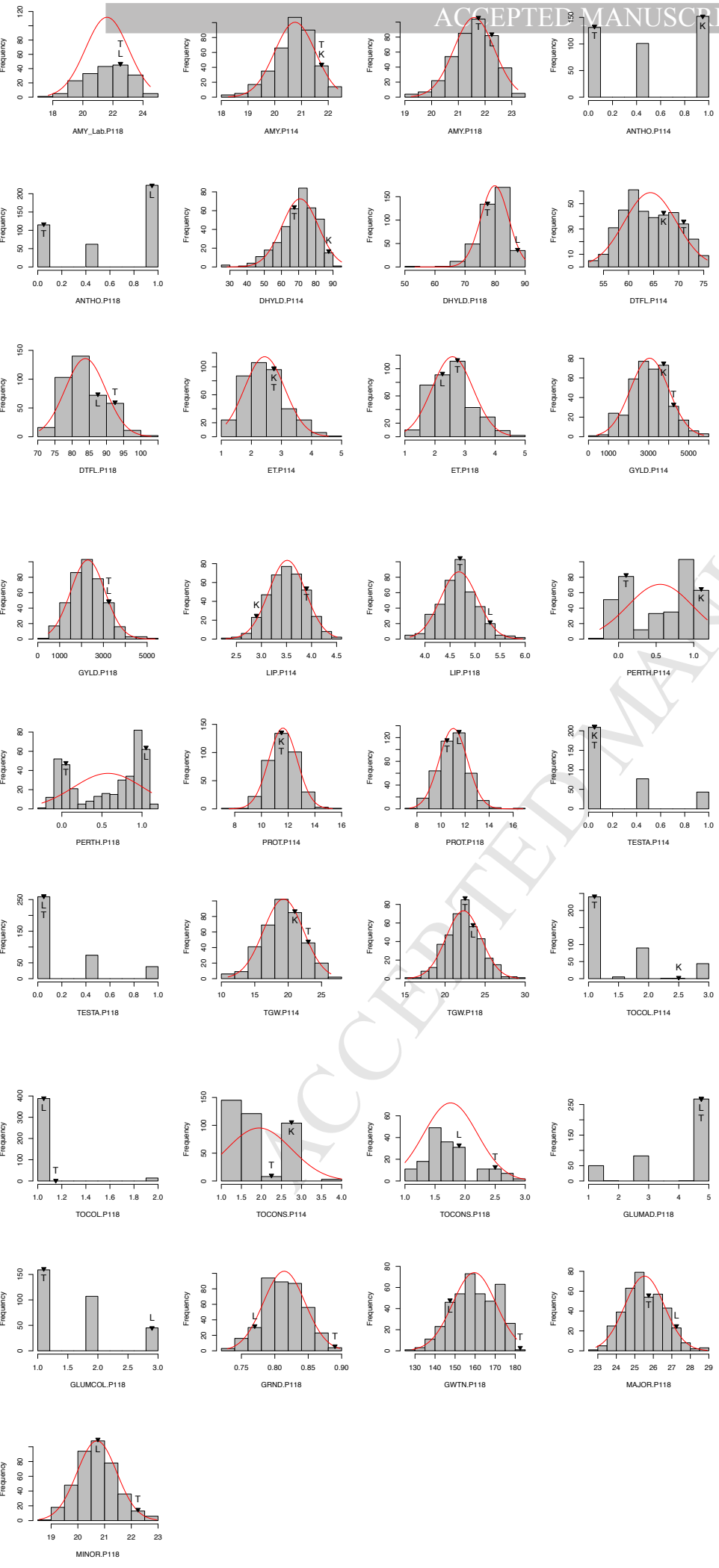
	P118								P114							
Trait	**Penal.**	**Chr.**	**Conf1**	**Peak**	**Conf2**	**LOD**	**R^2**	**add**	**Penal.**	**Chr.**	**Conf1**	**Peak**	**Conf2**	**LOD**	**R^2**	**add**
MAJOR	3.54	Sb01	10.4	15.4	21.4	8.40	4.71	-0.28								
	3.54	Sb04	65.0	71.0	84.0	9.22	5.20	-0.34								
	3.54	Sb05	4.7	8.7	19.7	6.96	3.87	-0.27								
	3.54	Sb06	57.2	68.1	73.2	4.24	2.32	-0.22								
	3.54	Sb06	92.2	96.2	100.2	6.99	3.89	-0.30								
	3.54	Sb07	92.2	95.2	98.2	33.90	22.16	0.60								
	3.54	Sb09	0.0	31.0	41.0	3.96	2.17	0.19								
	3.54	Sb10	28.0	43.0	69.0	5.38	2.96	0.22								
MINOR	3.56	Sb01	12.4	20.0	144.2	4.42	3.48	-0.16								
	3.56	Sb02	90.3	101.3	105.3	6.98	5.58	-0.21								
	3.56	Sb02	139.3	144.3	148.3	7.34	5.88	-0.23								
	3.56	Sb03	7.5	23.5	81.5	3.66	2.86	0.16								
	3.56	Sb04	108.0	110.8	112.0	9.12	7.38	-0.25								
	3.56	Sb06	68.2	73.2	82.2	6.75	5.38	-0.21								

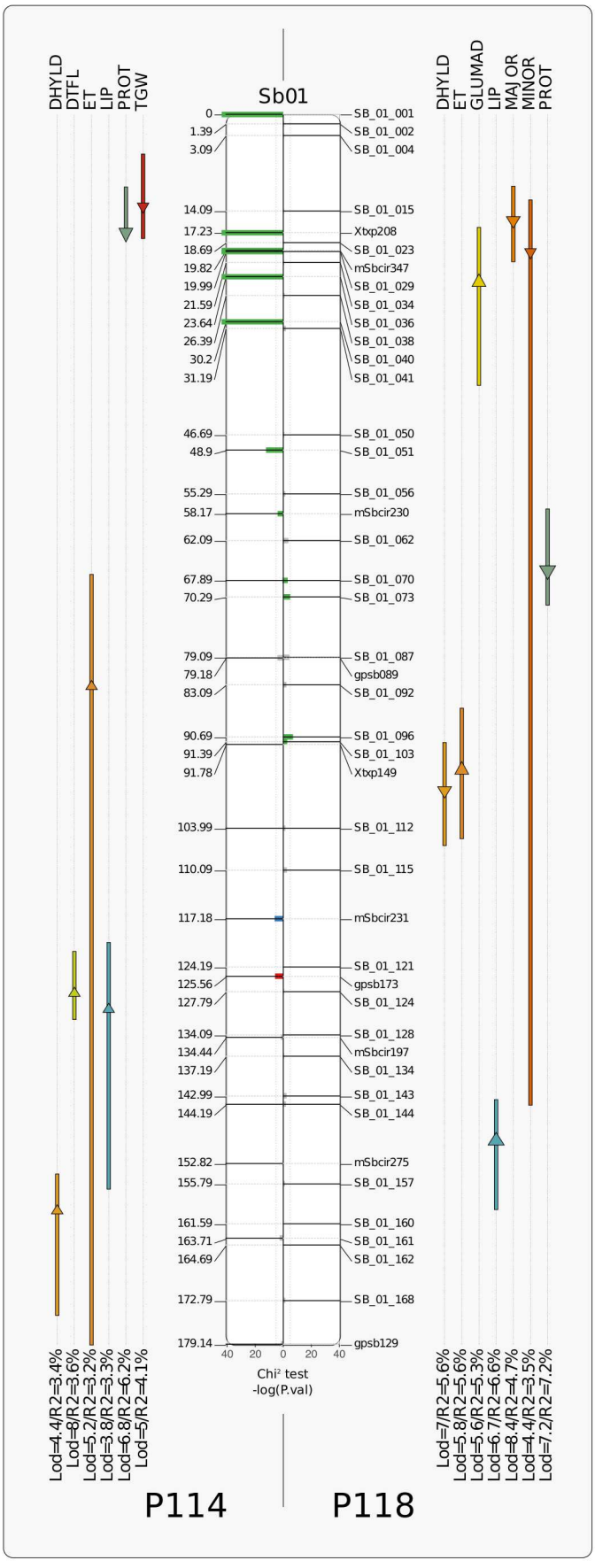
749

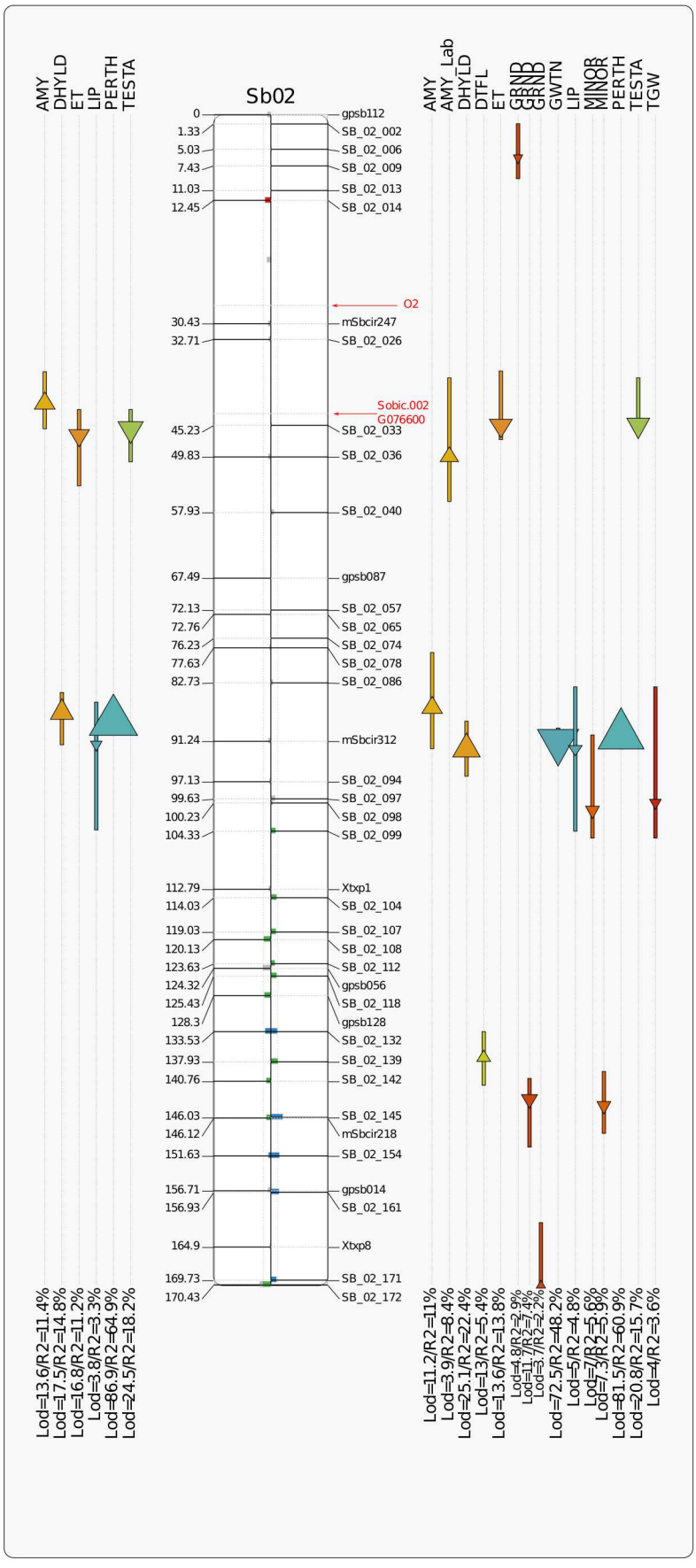
8 Figure Captions

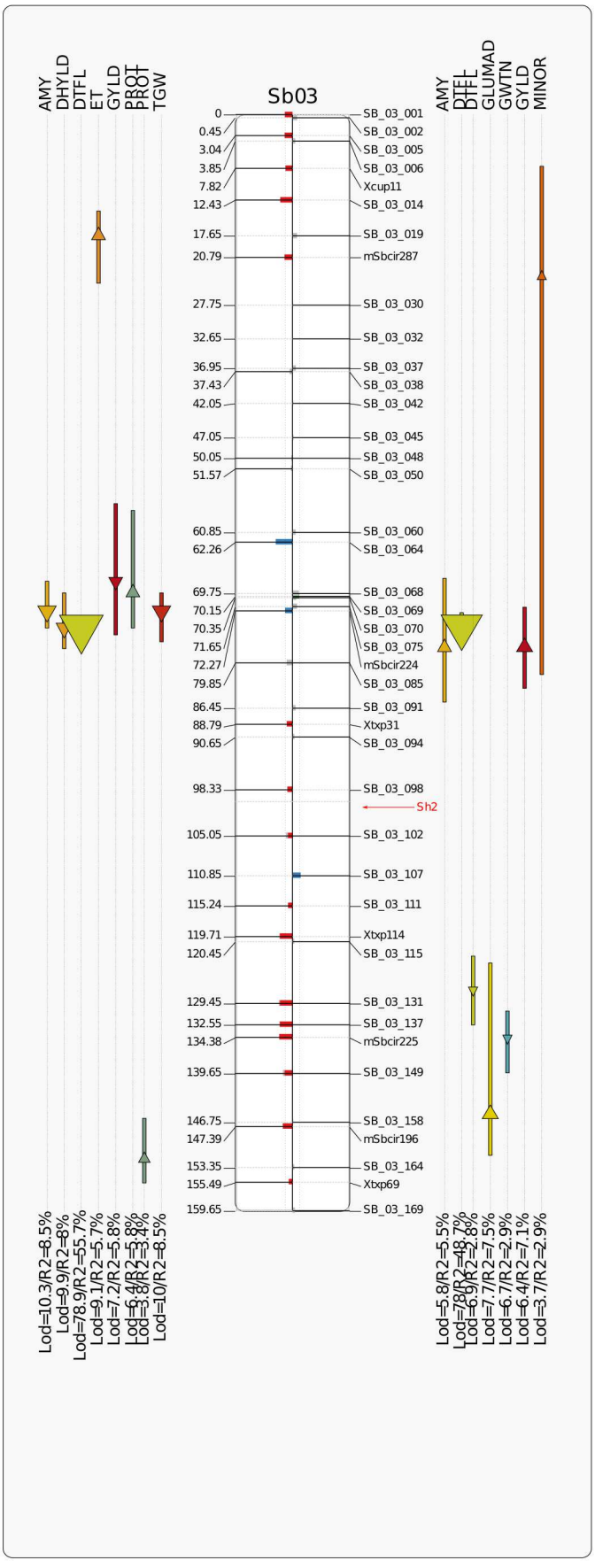
Fig 1: Distribution of the traits for the two populations P114 and P118. Laboratory amylose content (AMY_Lab); predicted amylose content (AMY); Presence of anthocyanins (ANTHO); Grain Dehulling yield (DHYLD); Date to first flag leaf (DTFL); Endosperm texture (ET); Grain yield (GYLD); Lipid content (LIP); Pericarp thickness (PERTH); Protein content (PR); Color of the testa layer (TESTA); Thousand grain weight (TGW); Color of the tô (TOCOL); Tô consistency (TOCONS); Glume adherence (GLUMAD); Glume color (GLUMCOL); Grain roundness (GRND); Grain whiteness (GWTN); Grain major axis length (MAJOR); Grain minor axis length (MINOR).

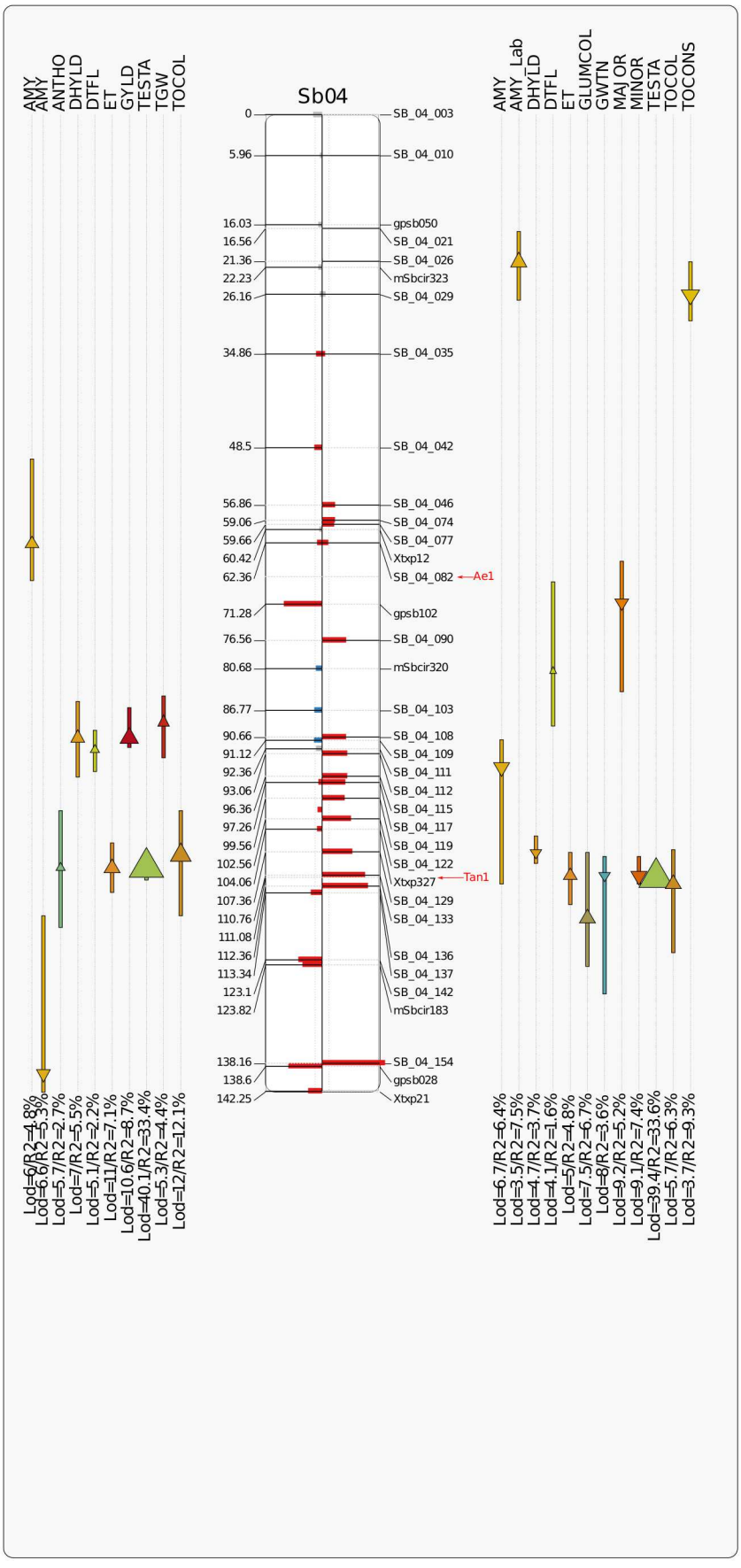
Fig 2 to 6: Genetic maps, segregation distortions and detected QTLs. Populations P114 and P118 are represented on left side and right side of chromosomes, respectively. Segregation distortions are represented in the body of each chromosome as bar plots of –log(P value) of a chi square test. Green, red, and blue bars represent segregation distortions in favor of Keninkeni or Lata3 homozygous class, Tiandougou homozygous class and heterozygous class, respectively. QTLs are represented by a triangle located at the QTL location and a rectangle representing the confidence interval. The orientation of the QTL triangles represent the sign of the additive effect of the QTL: toward top for Keninkeni and Lata3 alleles, toward bottom for Tiandougou allele. Red arrows indicate the location of known or candidate genes.

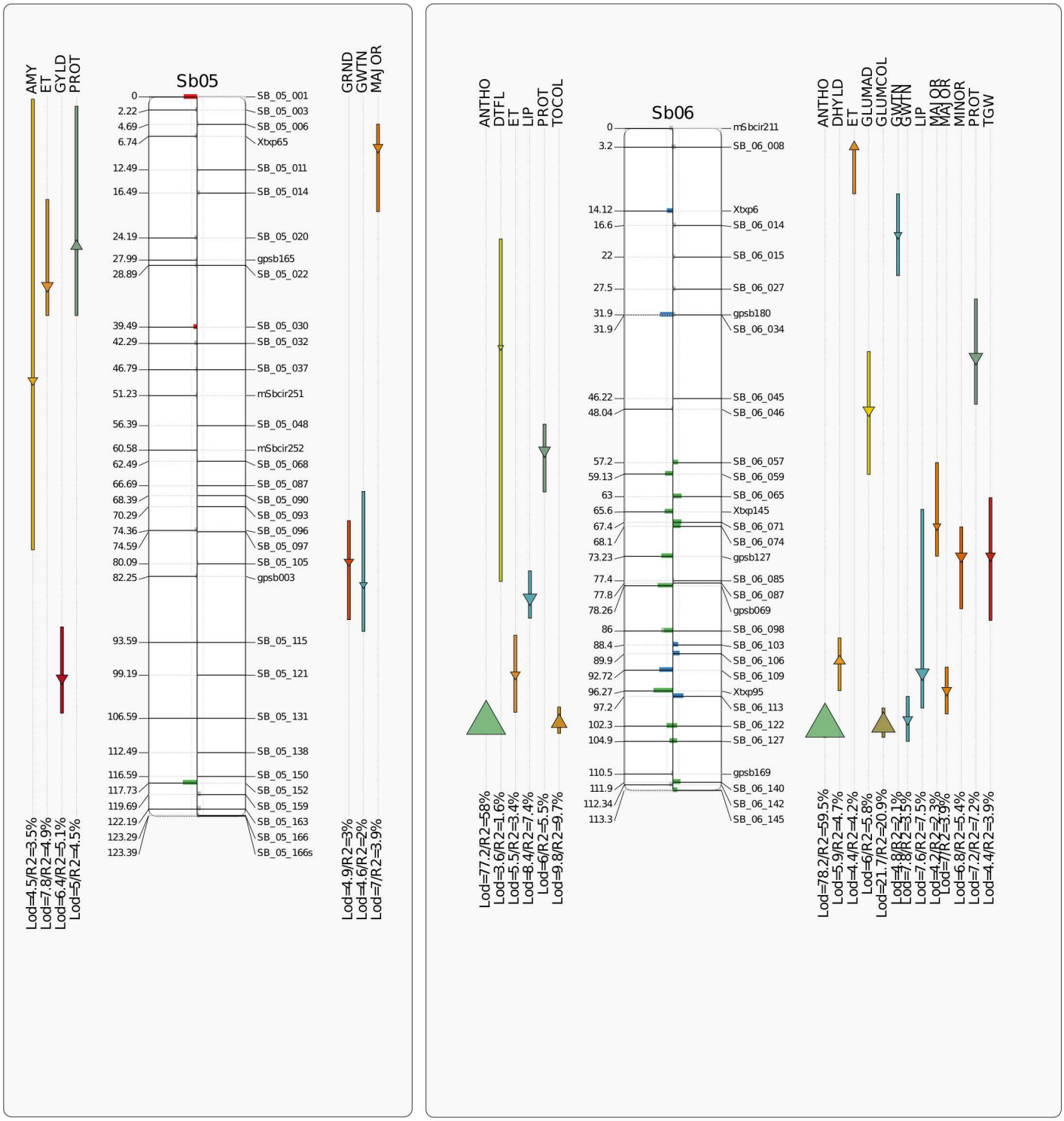


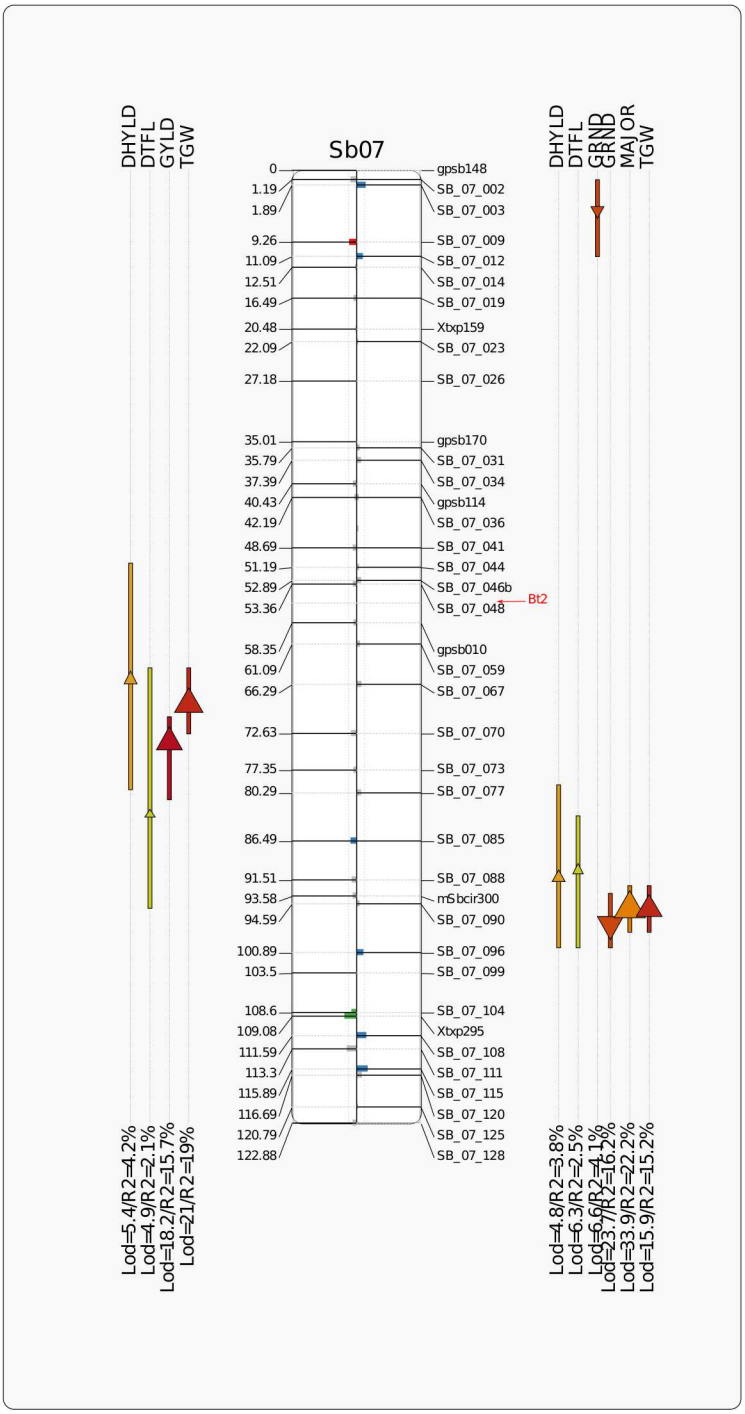

Sb01
DHYLD
DTFL
ET
LIP
PROT
TGW
DHYLD
ET
GLUMAD
LIP
MAJOR
MINOR
PROT
0 SB_01_001
1.39 SB_01_002
3.09 SB_01_004
14.09 SB_01_015
17.23 Xtxp208
18.69 SB_01_023
19.82 mSbcir347
19.99 SB_01_029
21.59 SB_01_034
23.64 SB_01_036
26.39 SB_01_038
30.2 SB_01_040
31.19 SB_01_041
46.69 SB_01_050
48.9 SB_01_051
55.29 SB_01_056
58.17 mSbcir230
62.09 SB_01_062
67.89 SB_01_070
70.29 SB_01_073
79.09 SB_01_087
79.18 gpsb089
83.09 SB_01_092
90.69 SB_01_096
91.39 SB_01_103
91.78 Xtxp149
103.99 SB_01_112
110.09 SB_01_115
117.18 mSbcir231
124.19 SB_01_121
125.56 gpsb173
127.79 SB_01_124
134.09 SB_01_128
134.44 mSbcir197
137.19 SB_01_134
142.99 SB_01_143
144.19 SB_01_144
152.82 mSbcir275
155.79 SB_01_157
161.59 SB_01_160
163.71 SB_01_161
164.69 SB_01_162
172.79 SB_01_168
179.14 gpsb129
40 20 0 20 40
Chi² test
-log(P.val)
Lod=4.4/R2=3.4%
Lod=8/R2=3.6%
Lod=5.2/R2=3.2%
Lod=3.8/R2=3.3%
Lod=6.8/R2=6.2%
Lod=5/R2=4.1%
Lod=7/R2=5.6%
Lod=5.8/R2=5.6%
Lod=5.6/R2=5.3%
Lod=6.7/R2=6.6%
Lod=8.4/R2=4.7%
Lod=4.4/R2=3.5%
Lod=7.2/R2=7.2%
P114
P118

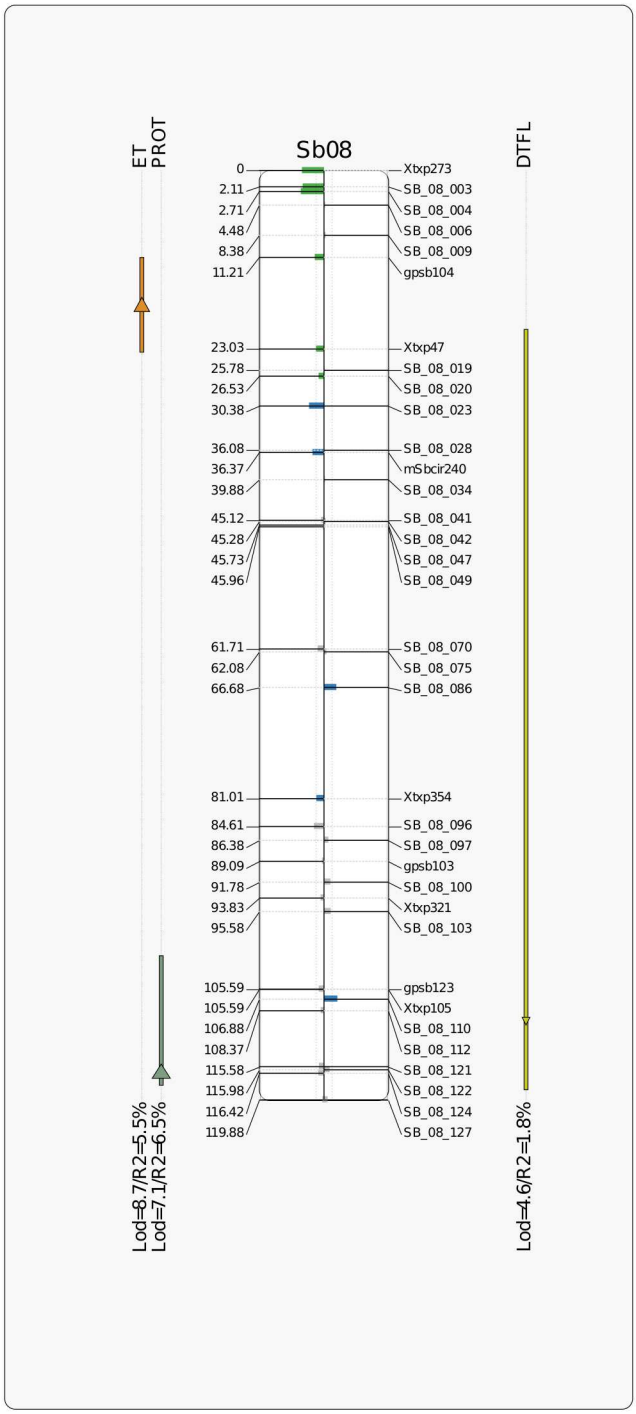

Sb02
AMY
DHYLD
ET
LIP
PERTH
TESTA
AMY
AMY_Lab
DHYLD
DTFL
ET
GRNB
GRNB
GWTN
LIP
MINOR
PERTH
TESTA
TGW
0 gpsb112
1.33 SB_02_002
5.03 SB_02_006
7.43 SB_02_009
11.03 SB_02_013
12.45 SB_02_014
O2
30.43 mSbcir247
32.71 SB_02_026
Sobic.002
G076600
45.23 SB_02_033
49.83 SB_02_036
57.93 SB_02_040
67.49 gpsb087
72.13 SB_02_057
72.76 SB_02_065
76.23 SB_02_074
77.63 SB_02_078
82.73 SB_02_086
91.24 mSbcir312
97.13 SB_02_094
99.63 SB_02_097
100.23 SB_02_098
104.33 SB_02_099
112.79 Xtxp1
114.03 SB_02_104
119.03 SB_02_107
120.13 SB_02_108
123.63 SB_02_112
124.32 gpsb056
125.43 SB_02_118
128.3 gpsb128
133.53 SB_02_132
137.93 SB_02_139
140.76 SB_02_142
146.03 SB_02_145
146.12 mSbcir218
151.63 SB_02_154
156.71 gpsb014
156.93 SB_02_161
164.9 Xtxp8
169.73 SB_02_171
170.43 SB_02_172
Lod=13.6/R2=11.4%
Lod=17.5/R2=14.8%
Lod=16.8/R2=11.2%
Lod=3.8/R2=3.3%
Lod=86.9/R2=64.9%
Lod=24.5/R2=18.2%
Lod=11.2/R2=11%
Lod=3.9/R2=8.4%
Lod=25.1/R2=22.4%
Lod=13/R2=5.4%
Lod=13.6/R2=13.8%
Lod=4.8/R2=2.9%
Lod=11.7/R2=7.4%
Lod=3.7/R2=2.2%
Lod=72.5/R2=48.2%
Lod=5/R2=4.8%
Lod=7/R2=5.6%
Lod=7.3/R2=5.9%
Lod=81.5/R2=60.9%
Lod=20.8/R2=15.7%
Lod=4/R2=3.6%


Sb03
AMY
DHYLD
DTFL
ET
GYLD
PROT
TGW
0 SB_03_001
0.45 SB_03_002
3.04 SB_03_005
3.85 SB_03_006
7.82 Xcup11
12.43 SB_03_014
17.65 SB_03_019
20.79 mSbcir287
27.75 SB_03_030
32.65 SB_03_032
36.95 SB_03_037
37.43 SB_03_038
42.05 SB_03_042
47.05 SB_03_045
50.05 SB_03_048
51.57 SB_03_050
60.85 SB_03_060
62.26 SB_03_064
69.75 SB_03_068
70.15 SB_03_069
70.35 SB_03_070
71.65 SB_03_075
72.27 mSbcir224
79.85 SB_03_085
86.45 SB_03_091
88.79 Xtxp31
90.65 SB_03_094
98.33 SB_03_098
Sh2
105.05 SB_03_102
110.85 SB_03_107
115.24 SB_03_111
119.71 Xtxp114
120.45 SB_03_115
129.45 SB_03_131
132.55 SB_03_137
134.38 mSbcir225
139.65 SB_03_149
146.75 SB_03_158
147.39 mSbcir196
153.35 SB_03_164
155.49 Xtxp69
159.65 SB_03_169
Lod=10.3/R2=8.5%
Lod=9.9/R2=8%
Lod=78.9/R2=55.7%
Lod=9.1/R2=5.7%
Lod=7.2/R2=5.8%
Lod=5.4/R2=3.8%
Lod=3.8/R2=3.4%
Lod=10/R2=8.5%
AMY
DTFL
GLUMAD
GWTN
GYLD
MINOR
Lod=5.8/R2=5.5%
Lod=7.8/R2=48.7%
Lod=6.9/R2=2.8%
Lod=7.7/R2=7.5%
Lod=6.7/R2=2.9%
Lod=6.4/R2=7.1%
Lod=3.7/R2=2.9%


Sb04
AMY
AMY
ANTHO
DHYLD
DTFL
ET
GYLD
TESTA
TGW
TOCOL
0 SB_04_003
5.96 SB_04_010
16.03 gpsb050
16.56 SB_04_021
21.36 SB_04_026
22.23 mSbcir323
26.16 SB_04_029
34.86 SB_04_035
48.5 SB_04_042
56.86 SB_04_046
59.06 SB_04_074
59.66 SB_04_077
60.42 Xtxp12
62.36 SB_04_082
Ae1
71.28 gpsb102
76.56 SB_04_090
80.68 mSbcir320
86.77 SB_04_103
90.66 SB_04_108
91.12 SB_04_109
92.36 SB_04_111
93.06 SB_04_112
96.36 SB_04_115
97.26 SB_04_117
99.56 SB_04_119
102.56 SB_04_122
104.06 Xtxp327
Tan1
107.36 SB_04_129
110.76 SB_04_133
111.08
112.36 SB_04_136
113.34 SB_04_137
123.1 SB_04_142
123.82 mSbcir183
138.16 SB_04_154
138.6 gpsb028
142.25 Xtxp21
Lod=6/R2=4.8%
Lod=6.6/R2=5.3%
Lod=5.7/R2=2.7%
Lod=7/R2=5.5%
Lod=5.1/R2=2.2%
Lod=11/R2=7.1%
Lod=10.6/R2=8.7%
Lod=40.1/R2=33.4%
Lod=5.3/R2=4.4%
Lod=12/R2=12.1%
AMY
AMY_Lab
DHYLD
DTFL
ET
GLUMCOL
GWTN
MAJOR
MINOR
TESTA
TOCOL
TOCONS
Lod=6.7/R2=6.4%
Lod=3.5/R2=7.5%
Lod=4.7/R2=3.7%
Lod=4.1/R2=1.6%
Lod=5/R2=4.8%
Lod=7.5/R2=6.7%
Lod=8/R2=3.6%
Lod=9.2/R2=5.2%
Lod=9.1/R2=7.4%
Lod=39.4/R2=33.6%
Lod=5.7/R2=6.3%
Lod=3.7/R2=9.3%


Sb05
AMY
ET
GYLD
PROT
GRND
GWTN
MAJ OR
0 SB_05_001
2.22 SB_05_003
4.69 SB_05_006
6.74 Xtxp65
12.49 SB_05_011
16.49 SB_05_014
24.19 SB_05_020
27.99 gpsb165
28.89 SB_05_022
39.49 SB_05_030
42.29 SB_05_032
46.79 SB_05_037
51.23 mSbcir251
56.39 SB_05_048
60.58 mSbcir252
62.49 SB_05_068
66.69 SB_05_087
68.39 SB_05_090
70.29 SB_05_093
74.36 SB_05_096
74.59 SB_05_097
80.09 SB_05_105
82.25 gpsb003
93.59 SB_05_115
99.19 SB_05_121
106.59 SB_05_131
112.49 SB_05_138
116.59 SB_05_150
117.73 SB_05_152
119.69 SB_05_159
122.19 SB_05_163
123.29 SB_05_166
123.39 SB_05_166s
Lod=4.5/R2=3.5%
Lod=7.8/R2=4.9%
Lod=6.4/R2=5.1%
Lod=5/R2=4.5%
Lod=4.9/R2=3%
Lod=4.6/R2=2%
Lod=7/R2=3.9%
Sb06
ANTHO
DTFL
ET
LIP
PROT
TOCOL
0 mSbcir211
3.2 SB_06_008
14.12 Xtxp6
16.6 SB_06_014
22 SB_06_015
27.5 SB_06_027
31.9 gpsb180
31.9 SB_06_034
46.22 SB_06_045
48.04 SB_06_046
57.2 SB_06_057
59.13 SB_06_059
63 SB_06_065
65.6 Xtxp145
67.4 SB_06_071
68.1 SB_06_074
73.23 gpsb127
77.4 SB_06_085
77.8 SB_06_087
78.26 gpsb069
86 SB_06_098
88.4 SB_06_103
89.9 SB_06_106
92.72 SB_06_109
96.27 Xtxp95
97.2 SB_06_113
102.3 SB_06_122
104.9 SB_06_127
110.5 gpsb169
111.9 SB_06_140
112.34 SB_06_142
113.3 SB_06_145
Lod=77.2/R2=58%
Lod=3.6/R2=1.6%
Lod=5.5/R2=3.4%
Lod=8.4/R2=7.4%
Lod=6/R2=5.5%
Lod=9.8/R2=9.7%
ANTHO
DHYLD
ET
GLUMAD
GLUMCOL
GWTN
LIP
MAJOR
MINOR
PROT
TGW
Lod=78.2/R2=59.5%
Lod=5.9/R2=4.7%
Lod=4.4/R2=4.2%
Lod=6/R2=5.8%
Lod=21.7/R2=20.9%
Lod=4.8/R2=2.1%
Lod=7.8/R2=3.5%
Lod=7.6/R2=7.5%
Lod=4.2/R2=3.3%
Lod=7/R2=3.9%
Lod=6.8/R2=5.4%
Lod=7.2/R2=7.2%
Lod=4.4/R2=3.9%


Sb07
DHYLD
DTFL
GYLD
TGW
0 gpsb148
1.19 SB_07_002
1.89 SB_07_003
9.26 SB_07_009
11.09 SB_07_012
12.51 SB_07_014
16.49 SB_07_019
20.48 Xtxp159
22.09 SB_07_023
27.18 SB_07_026
35.01 gpsb170
35.79 SB_07_031
37.39 SB_07_034
40.43 gpsb114
42.19 SB_07_036
48.69 SB_07_041
51.19 SB_07_044
52.89 SB_07_046b
53.36 SB_07_048
Bt2
58.35 gpsb010
61.09 SB_07_059
66.29 SB_07_067
72.63 SB_07_070
77.35 SB_07_073
80.29 SB_07_077
86.49 SB_07_085
91.51 SB_07_088
93.58 mSbcir300
94.59 SB_07_090
100.89 SB_07_096
103.5 SB_07_099
108.6 SB_07_104
109.08 Xtxp295
111.59 SB_07_108
113.3 SB_07_111
115.89 SB_07_115
116.69 SB_07_120
120.79 SB_07_125
122.88 SB_07_128
Lod=5.4/R2=4.2%
Lod=4.9/R2=2.1%
Lod=18.2/R2=15.7%
Lod=21/R2=19%
DHYLD
DTFL
GRND
MAJOR
TGW
Lod=4.8/R2=3.8%
Lod=6.3/R2=2.5%
Lod=6.6/R2=4.1%
Lod=23.7/R2=16.2%
Lod=33.9/R2=22.2%
Lod=15.9/R2=15.2%


Sb08
ET
PROT
DTFL
0 Xtxp273
2.11 SB_08_003
2.71 SB_08_004
4.48 SB_08_006
8.38 SB_08_009
11.21 gpsb104
23.03 Xtxp47
25.78 SB_08_019
26.53 SB_08_020
30.38 SB_08_023
36.08 SB_08_028
36.37 mSbcir240
39.88 SB_08_034
45.12 SB_08_041
45.28 SB_08_042
45.73 SB_08_047
45.96 SB_08_049
61.71 SB_08_070
62.08 SB_08_075
66.68 SB_08_086
81.01 Xtxp354
84.61 SB_08_096
86.38 SB_08_097
89.09 gpsb103
91.78 SB_08_100
93.83 Xtxp321
95.58 SB_08_103
105.59 gpsb123
105.59 Xtxp105
106.88 SB_08_110
108.37 SB_08_112
115.58 SB_08_121
115.98 SB_08_122
116.42 SB_08_124
119.88 SB_08_127
Lod=8.7/R2=5.5%
Lod=7.1/R2=6.5%
Lod=4.6/R2=1.8%

Sb09
GYLD
GRND
MAJOR
PROT
0 SB_09_003
5.5 SB_09_009
10.2 SB_09_012
12.9 SB_09_014
19.96 SB_09_017
24.8 SB_09_019
30.6 SB_09_021
35.2 SB_09_024
37.03 Xtxp67
42.6 SB_09_030
44.6 SB_09_033
46.59 SB_09_036
47.1 SB_09_037
49.5 SB_09_044
53.3 SB_09_055
60.89 SB_09_062
62.7 SB_09_080
65.74 SB_09_085
66.1 SB_09_086
69.6 SB_09_091
78.24 SB_09_097
80 SB_09_098
84.8 SB_09_101
88.3 SB_09_105
90.7 SB_09_107
97.1 SB_09_114
99.92 SB_09_117
103 SB_09_122
106.7 SB_09_127
109.42 SB_09_133
109.8 SB_09_134
111.8 SB_09_138
115.1 SB_09_141
117.5 SB_09_145
Lod=4.2/R2=3.3%
Lod=8.1/R2=5%
Lod=4/R2=2.2%
Lod=3.9/R2=3.9%

Sb10
AMY
DHYLD
ET
LIP
BTFL
GRND
MAJOR
0 SB_10_001
3.1 SB_10_004
5.01 SB_10_005
9.34 mSbcir331 Wx
11.7 SB_10_012
SssI
23.9 SB_10_021
25.27 SB_10_022
31.3 SB_10_030
38.8 SB_10_033
39.86 gpsb091
41.6 SB_10_038
44.4 SB_10_041
46.4 SB_10_043
55.87 SB_10_052
60.6 SB_10_055
64.5 SB_10_058
67.5 SB_10_062
67.5 Xtxp217
68 SB_10_064
70.4 SB_10_072
71.74 Xtxp130
73.5 SB_10_079
76.4 SB_10_083
80.76 SB_10_088
83.1 SB_10_091
85.3 SB_10_095
88.1 SB_10_098
94.1 SB_10_103
96.1 SB_10_104
101.7 SB_10_108
102.72 SB_10_109
110.5 SB_10_116
117.9 SB_10_121
126.5 SB_10_131
132.31 SB_10_137
132.8 SB_10_138
133.12 gpsb145
Lod=4.4/R2=3.5%
Lod=5.6/R2=4.4%
Lod=7.5/R2=4.7%
Lod=17.9/R2=16.9%
Lod=4.4/R2=1.8%
Lod=5.1/R2=2%
Lod=6.5/R2=4%
Lod=5.4/R2=3%

- A QTL detection conducted in breeders' populations as part of a marker-assisted selection program
- Major genes with large effect still segregates in breeding population derived from elite material
- There is no major antagonism to jointly improve grain yield and grain quality in West-African sorghum germplasm