QTL detection for bread wheat processing quality in a nested association mapping population of semi-wild and domesticated wheat varieties

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Abstract

Background: Wheat processing quality is an important factor in evaluating overall wheat quality, and dough characteristics are important when assessing the processing quality of wheat. As a notable germplasm resource, semi-wild wheat has a key role in the study of wheat processing quality.

Results: In this study, four dough rheological characteristics were collected in four environments using a nested association mapping (NAM) population consisting of semi-wild and domesticated wheat varieties to identify quantitative trait loci (QTL) for wheat processing quality. A total of 49 QTL for wheat processing quality were detected, explaining 0.36–10.82% of the phenotypic variation. These QTL were located on all wheat chromosomes except for 2D, 3A, 3D, 6B, 6D and 7D. Compared to previous studies, 29 QTL were newly identified. Four novel QTL, QMPH-1B.4, QMPH-3B.4, QWdEm-1B.2 and QWdEm-3B.2, were stably identified in three or more environments, among which QMPH-3B.4 was a major QTL. Moreover, eight important genetic regions for wheat processing quality were identified on chromosomes 1B, 3B and 4D, which showed pleiotropy for dough characteristics. In addition, out of 49 QTL, 15 favorable alleles came from three semi-wild parents, suggesting that the QTL alleles provided by the semi-wild parent were not utilized in domesticated varieties.

Conclusions: The results show that semi-wild wheat varieties can enrich the existing wheat gene pool and provide broader variation resources for wheat genetic research.

Keywords: Wheat, Processing quality, Quantitative trait locus, Semi-wild wheat, Nested association mapping (NAM) population

Background

Bread wheat (Triticum aestivum L.) is a crucial source of protein, minerals and vitamins that feeds over 35% of the world’s population [1, 2]. Hence, improving the processing quality of wheat is an important goal in wheat breeding. Investigation of the relationship between seed storage protein alleles and processing characteristics indicates that storage proteins are the main determinant of wheat processing quality [3]. The seed storage proteins

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in wheat consist of gliadin and glutenin, which can be used to predict dough rheological properties, including the viscoelastic and mixing properties [4]. The genes coding for gliadin are located on the short arms of the chromosomes of homologous groups 1 and 6 [5]. Glutenin in the endosperm consists of high-molecular-weight (HMW-GS) and low-molecular-weight glutenin subunits (LMW-GS). HMW-GSs are encoded by Glu-1 loci that are located on the long arms of the chromosomes of homologous group 1, including Glu-A1, Glu-B1 and Glu-D1 [5]. LMW-GSs are encoded by Glu-3 loci that are located on the short arms of the chromosomes of group 1, including Glu-A3, Glu-B3 and Glu-D3 [6]. Research has indicated that both glutenin and gliadin are significantly associated with wheat processing quality by affecting the viscoelasticity and flexibility of dough [7, 8].

Most of the quality-related traits of interest in wheat breeding are characterized by polygenic inheritance, which is generally studied with quantitative trait loci (QTL) mapping [3, 9–16]. Some stable QTL for protein content were discovered on chromosomes 1A, 1D, 2B, 3A, 4A, 5A, 5D, 7A, and 7B [3, 7, 12, 15, 17, 18]. Krystkowiak et al. [7] detected one major QTL on chromosome 5D that influences starch content, wet gluten content, and zeleny sedimentation value. Stable QTL for the starch content of wheat flour were detected on chromosomes 4A and 7D [9]. In addition, QTL for wet gluten content of wheat flour were identified on chromosomes 5AS and 5AL [15].

Due to a complex interaction between proteins and other components, such as pentosans, the predictability of dough strength from chemical composition is difficult, and therefore rheological tests are required [19, 20]. The dough rheological characteristics of wheat are quantitative traits that are dependent on multiple genes and are greatly influenced by environmental conditions. Studies have reported that dough properties are influenced by the properties of storage proteins, which can be reflected by mixograph, farinograph, and extensograph parameters [13, 19, 21]. Many rheological tests have been widely used as predictors of wheat processing quality and end-use quality [3, 15, 19]. Mann et al. [3] discovered that dough rheology QTL were highly correlated across multiple environments and primarily influenced by the Glu-1 loci (Glu-B1, Glu-D1). Tsilo et al. [22] detected a major QTL cluster for dough rheological properties on chromosome 1B, which explained the large total phenotypic variation in dough development time, mixing tolerance index, dough stability and time to dough breakdown.

Several segregant biparental populations can be adopted for QTL mapping, such as backcross, F2, doubled haploid (DH), introgression lines and recombinant inbred line populations. In most previous studies, these approaches for wheat processing quality QTL mapping were utilized [9, 10, 23]. However, the linkage analysis achievable with bi-parental populations showed a narrow genetic background and was often able to detect QTL only with large intervals because of limited recombination events [24–26]. This limitation can be partially overcome by analyzing multiple related populations, such as nested association mapping (NAM) population [27, 28]. The NAM population is a composite population composed of multi-family recombinant inbred line population constructed by the hybridization of one common parent with several other parents and multi-generation continuous self-cross. Due to its wide genetic diversity and high resolution, NAM population is an ideal population for QTL analysis. Such populations have been used to identify QTL in different crops, including maize, soybean, sorghum, barley, bread wheat and durum wheat [29, 30]. However, there are few studies on QTL analysis of wheat processing quality using a NAM population [31, 32].

In previous studies, most of the material on wheat processing quality represented domesticated cultivars, and compared with wild and semi-wild varieties, their genetic diversity will decrease with domestication [33]. Through whole-genome sequencing analysis, it was determined that composite introgression from wild populations contributed to 4–32% of the bread wheat genome, which increased the genetic diversity of bread wheat [34]. Three semi-wild wheat subspecies germplasm resources unique to western China, including the Tibetan weedrace (T. aestivum ssp. tibetanum Shao) characterized by strong seed dormancy, hulled glumes and brittle spikelets, Xining rice wheat (T. petropavlovskyi Udats. et Migosch.) characterized by a long glume, and Yunnan hulled wheat, or “Tiekemai” (T. aestivum ssp. yunnanense King), named for its very hard and tough glumes that adhere to the grains [35–37]. The semi-wild wheat subspecies in China have a primitive chromosomal constitution, which is important to probe the effect of domestication on processing quality in wheat breeding [35]. Therefore, in this study, a wheat NAM population was constructed by crossing one common parent, Yanzhan 1, and four divergent parents, including three semi-wild cultivars from China and one domesticated variety from the British islands. This NAM population was used for QTL mapping for wheat processing quality, which will facilitate high-quality wheat breeding and marker-assisted selection (MAS) in wheat breeding.

Results
Phenotypic analysis of wheat processing quality
The five parents of the NAM population had different dough rheological characteristics (Fig. 1A). Among
Fig. 1 Phenotypic data of wheat processing quality of the five parents and the NAM population. **A** The four dough rheological characteristics of the five parents (a–e) and the ANOVA between five parents of four dough rheological characteristics (f–i). Labels A and B indicate significant differences at the level of $P < 0.01$, and labels a and b indicate significant differences at the level of $P < 0.05$. **B** The boxplot for four dough rheological characteristics of four RIL populations. The different color lines of black, green, yellow, red, and blue indicate the five parents of the NAM population YZ, CY, HU, YN, and YT, respectively. **C** The relationships between four dough rheological characteristics of the NAM population. YZ, Yanzhan 1; CY, Chayazheda 29; HU, Hussar; YN, Yunnanxiaomai; YT, Yutiandaomai. MIPT, midline peak time; MIPH, midline peak height; PkWd, peak width; WdEm, width at eight minutes.
them, HU (Hussar) had the best dough characteristics, while the dough characteristics of YZ (Yanzhan 1) and YN (Yunnanxiaomai) were poor. We found that the common parent YZ had a longer MlPT (midline peak time), wider PkWd (peak width) and wider WdEm (width at eight minutes) than the other parents, CY (Chayazheda 29) and YN, and had the smallest MlPH (midline peak height) compared with the other four donor parents. HU had the highest values for all dough rheological characteristics compared with the other four parents, which indicated that HU had the best dough characteristics of the individual’s studies here. CY had a longer MlPT, wider PkWd and wider WdEm than YN. YN had a wider MlPH than YZ, CY and YT but the shortest MlPT and the narrowest WdEm compared with the other four parents. Compared with YZ, CY and YN, YT (Yutiandaomai) had the longest MlPT, widest WdEm and narrowest PkWd. Observing the phenotypic data distribution of the NAM population, there was strong transgressive segregation for all dough rheological characteristics in each RIL population except for the MlPT of HU-RILs (Fig. 1B, Table S1).

To evaluate the pairwise correlations between dough rheological characteristics, Pearson’s correlation was estimated using BLUP (best linear unbiased prediction) values combined over four environments (Fig. 1C). WdEm was significantly positively correlated with MlPT and PkWd but significantly negatively correlated with MlPH. PkWd was significantly positively correlated with MlPT and MlPH. The correlation between MlPT and MlPH was not significant.

The heritabilities of dough rheological characteristics in the NAM population were 42.7–84.7%, and they were differenced largely in the four RIL populations (Table S2). PkWd is a relatively important dough rheological parameter to measure wheat processing quality, and its phenotype is greatly affected by the environment (42.7–59.7%). Among them, the heritabilities of the HU-RIL and YT-RIL populations were higher, whereas those in the YN-RIL population were lower.

**QTL analysis of wheat processing quality**

A total of 49 QTL were detected on chromosomes 1A (2), 1B (17), 1D, 2A, 2B (3), 3B (11), 4A, 4B, 4D (2), 5A, 5B (3), 5D, 6A (2), 7A, and 7B (2) for wheat processing quality in four individual environments and combined QTL analysis (Fig. 2, Table S3). Ten, eighteen, eleven, and ten QTL were identified for MlPT, MlPH, PkWd and WdEm, respectively. These QTL explained 0.36–10.82% of the phenotypic variation. Thirty-four of these QTL were identified in the individual environment and the combined environment analysis. The favorable alleles of two, seven, six, ten and twenty-four QTL were provided by parents CY, YN, YT, HU and YZ, respectively (Table S4).

For MlPT, ten QTL were found on chromosomes 1A, 1B (4), 3B (2), 4B, 5A, and 7B in four environments and the combined environment analysis, explaining a range of 1.47% to 8.29% of the phenotypic variation (Fig. 2, Table S3). Six of those QTL were detected in the individual environment and combined environment analyses. One stable QTL, QMIPT-1B.2, had a favorable allele from YT and was found in two individual environments and the combined environment analysis, explaining 2.20–3.66% of the phenotypic variation. The donor parent YN contributed the best favorable allele for QMIPT-3B.1, which was stably detected in three individual environments, explaining 2.68–4.14% of the phenotypic variation. Five QTL, including QMIPT-1A, QMIPT-1B.3, QMIPT-1B.4, QMIPT-4B and QMIPT-7B, were identified in one environment and the combined environment analysis, with 4.15–8.29%, 2.80–3.28%, 3.31–4.19%, 2.74–3.11% and 1.47–4.02% of the phenotypic variation, respectively. QMIPT-1B.1, QMIPT-3B.2 and QMIPT-5A, with LOD values of 3.71–6.38, 3.08–8.03 and 2.66–4.88, respectively, were found in two environments, accounting for 2.24–5.42%, 2.07–3.70% and 1.78–1.82% of the phenotypic variation, respectively. The favorable alleles of two and three QTL of the ten QTL were provided by semi-wild parents YN and YT, respectively, while one and four QTL out of the remaining QTL were provided by domesticated parents HU and YZ, respectively (Table S4).

For MlPH, 18 QTL were identified, which were distributed on chromosomes 1B (6), 2B, 3B (5), 4D, 5B (2), 5D, 6A, and 7B in four environments and the combined environment analysis, explaining 0.36–10.82% of the phenotypic variation (Fig. 2, Table S3). Twelve of the eighteen QTL were detected in both individual environments and the combined environment analysis. The favorable alleles of two stable QTL (QMIHP-3B.3 and QMIHP-3B.4) were contributed by HU, which were identified in all four environments and the combined environment analysis, explaining 1.50–8.60% and 1.71–10.82% of the phenotypic variation, respectively. QMIHP-1B.4, a favorable allele from the common parent YZ, was stably identified in four environments, with an LOD value of 4.01–9.75 and phenotypic variation of 1.42–4.50%. QMIHP-1B.3 and QMIHP-5D, with LOD values of 5.18–10.25 and 3.21–5.99, respectively, were stably detected in the two environments and the combined environment analysis, accounting for 1.15–4.90% and 1.10–2.21% of the phenotypic variation, respectively. Eight QTL, including QMIHP-1B.5, QMIHP-1B.6, QMIHP-3B.1, QMIHP-4D, QMIHP-5B.1, QMIHP-5B.2, QMIHP-6A and QMIHP-7B, were detected in one environment and the combined environment analysis. In addition, five
QTL, **QMPH-1B.1**, **QMPH-1B.2**, **QMPH-2B**, **QMPH-3B.2**, and **QMPH-3B.5**, were identified in two environments. Three QTL with favorable alleles were detected in the three semi-wild parents CY, YN, and YT (Table S4). Compared with the other four parents, the alleles of the domesticated parent HU increased the MlPH for five QTL, while the common parent YZ decreased the MlPH for ten QTL.

For PkWd, eleven QTL were stably detected on chromosomes 1A, 1B (4), 2B, 3B (2), 4A, 6A, and 7A,
Eight important genetic regions for wheat processing quality

In this study, eight important genetic regions were found on chromosomes 1B (4), 3B (3), and 4D (Table 1). QG-3B.1 was associated with all dough rheological characteristics, QMlPT-3B.1, QMlPH-3B.3, QPKWd-3B.1, and QWdEm-3B.1, within 4.71 Mb of physical distance. Three genetic regions, QG-1B.3, QG-3B.2, and QG-4D, influenced MlPH and WdEm. QG-1B.2, located on flank marker B500047700_51–IAAV4866, was associated with MlPT, MlPH, and PkWd. QG-3B.4, located on flank marker tpb00488b10_1365–Pu_c28580_432, influences dough rheological characteristics MlPT, MlPH, and WdEm. In addition, QG-1B.1 and QG-3B.3 were located on flank markers wsnp_Ku_rep_c70742_70379526–tplb0059c20_2221 and wsnp_Ex_c64005_62987067–wsnp_BE497740B_Ta_2_1, respectively, which influence PkWd and WdEm, and PkWd and MlPT, respectively.

Discussion

Trait correlations

Wheat processing quality is a quantitative genetic trait controlled by multiple genes and affected by the environment. The dough characteristics influenced by glutenin and gliadin are comprehensive traits that reflect wheat processing quality. In this study, a NAM population consisting of three unique semi-wild wheat cultivars of China (CY, YN, and YT), the Chinese domesticated cultivar YZ, and the British domesticated cultivar HU was...
used to identify QTL regulating wheat processing quality. The small size of a single RIL population that constitutes the NAM population leads to fewer recombination events among parents and limits the precise locations of QTL. Even the NAM population based on polymorphism between YZ and the other four parents contains a series of recombinants with broader genetic bases, more populations are required to improve the mapping resolution and increase the number of QTL detected. In this study, the genetic map was generated by using 90 K SNP array. With the rapid development of sequencing and gene-chip technologies, new generation of high-density SNP chip [38] or genome re-sequencing [39] can offer high-resolution genetic map, by which more QTL related to wheat processing quality are supposed to be identified.

Here, we found that the dough rheological characteristics were different among three semi-wild wheat varieties (YN, YT, CY) and two cultivated wheat cultivars (HU and YZ) (Fig. 1A). Therefore, the NAM population composed of the five parents was used to detect QTL of wheat processing quality. The results show that the NAM population had large variation between three semi-wild RIL populations, CY-RILs, YN-RILs, and YT-RILs (Fig. 1B).

The difference between MlPT and MlPH was not significant, but there were significant correlations between the other dough rheological characteristics (Fig. 1C). Moreover, one important genetic region, QG-3B.1, associated with all dough rheological characteristics, was detected (Table 1). In addition, in terms of the association among the four dough rheological characteristics, MlPT was significantly positively correlated with PkWd and WdEm (Fig. 1C). Specifically, PkWd and WdEm increased with increasing MlPT (verified by QG-1B.2, QG-1B.4 and QG-3B.3; Fig. 1B-C, Table 1). Although MlPT and MlPH were colocalized between two genetic regions, QG-1B.2 and QG-1B.4, the correlation between MlPT and MlPH was not significant. We suspect that this may be because MlPT is related to the protein content, while MlPH is related to the gluten strength and the ability of the dough to resist external forces. WdEm was significantly positively correlated with PkWd (verified by QG-1B.1) and significantly negatively correlated with MlPH (substantiated by QG-1B.3, QG-3B.2, and QG-4D, Fig. 1C, Table 1).

Comparison with previous studies
In this study, 49 QTL for wheat processing quality were identified, 29 of which were unique to this study compared with previous studies, and four novel QTL (QMlPT-1B.4, QMlPH-3B.4, QWdEm-1B.2 and QWdEm-3B.2) were stably identified in three or more environments (Fig. 2, Tables 2, S3). For MlPT, five of ten QTL were previously reported. QMlPT-1A, with a favorable allele in HU, was mapped close to the gene Glu-A1, whose effect was consistent with the longer MlPT of Hussar (Figs. 1A, 2, Table S3) [40]. Similar genetic regions of two QTL, QMlPT-1B.3 and QMlPT-1B.4, which had favorable alleles from the common parent YZ, were reported by Tsilo et al. [22] (Fig. 2, Table S3). QMlPT-3B.1 was previously reported by Liu et al. [11] to be located at a similar genetic region on chromosome 3B. QMlPT-7B was identified close to the Psy-B1 gene, which indicates that Psy-B1 is not only associated with the synthesis of carotenoids, but might affect the wheat processing quality [41].

Eighteen QTL for MlPH were identified, five of which were previously reported (Fig. 2, Table S3). QMlPH-1B.1 was detected in two environments and was located near two genes, Gli-B1 and Glu-B3. QMlPH-1B.5 was located near gene Glu-B1 [42]. Three QTL, QMlPH-3B.2, QMlPH-3B.3, and QMlPH-6A, were detected at a similar genetic region by Carter et al. [43], Liu et al. [11], and Li et al. [23], respectively. Among the five QTL that were reported in previous studies, the allele of QMlPH-3B.3 was provided by HU with higher MlPH, and favorable alleles of the other QTL were detected in YZ with lower MlPH, indicating that YZ may have a recessive allelic variation gene that affects gluten strength (Fig. 1A, Table S3).

Regarding PkWd, eleven QTL were detected, six of which were reported by previous studies (Fig. 2, Table S3). Two QTL, QPkWd-1B.1 and QPkWd-4A, at similar genetic regions were reported by Li et al. [23, 44]. QPkWd-1B.3 was mapped close to the gene Glu-B1 [42]. Two QTL, QPkWd-2B and QPkWd-3B.1, were previously detected in three or more environments (Fig. 2, Table S3). The difference between MlPT and MlPH was not significant, but there were significant correlations between the other dough rheological characteristics (Fig. 1C).

Table 2 Four novel QTL that were stably identified in three or more environments

| QTL       | Environment | Position | Flank markers of peak                  | LOD     | PVE (%)  |
|-----------|-------------|----------|---------------------------------------|---------|----------|
| QMlPT-1B.4| E1/E2/E3/E4 | 44       | tplb0048b10_1365 Ku_c28580_432         | 4.0129–9.7453 | 1.4168–4.503 |
| QMlPT-3B.4| E1/E2/E3/E4/BLUP | 63       | wsnp_Ku_c29102_39008953 wsnp_Ex_c64005_62986957 | 6.365–32.0377 | 1.711–10.8244 |
| QWdEm-1B.2| E1/E2/E3/BLUP | 38       | Tdurum_contig20299_368 BobWhite_c48550_198 | 4.6957–5.7802 | 0.5107–2.4201 |
| QWdEm-3B.2| E1/E2/E3    | 63       | wsnp_Ku_c29102_39008953 wsnp_Ex_c64005_62986957 | 6.1816–20.4799 | 2.5958–9.7032 |

*QMlPT Midline Peak Time, MlPH Midline Peak Height, PkWd Peak Width, WdEm Width at Eight minutes. E1 2016 Dezhou, E2 2016 Tai’an, E3 2016 Heze, E4 2017 Tai’an, BLUP Best Linear Unbiased Prediction*
reported by Liu et al. [11] in a similar genetic region. In addition, QPkWd-7A was located at a similar genetic region in a previous study by Zhang et al. [15].

Regarding WdEm, four of ten QTL were detected in previous studies (Fig. 2, Table S3). Three QTL, QWdEm-1B.1, QWdEm-1D, and QWdEm-3B.1, were reported from similar genetic regions on chromosomes 1B, 1D, and 3B, respectively [11, 23, 44]. In addition, QWdEm-2A was previously reported at a similar genetic region [11, 45, 46].

**Application potential of semi-wild cultivars in breeding good-quality wheat**

Four novel QTL, QMlPH-1B.4, QMlPH-3B.4, QWdEm-1B.2, and QWdEm-3B.2, were stably detected (Table 2). One novel and major QTL, QMlPH-3B.4, was detected in all four environments and the combined QTL analysis, and its favorable allele came from the good-quality parent HU. Domesticated parent HU had the longest MlPT, highest MlPH, and widest PkWd and WdEm among the parents (Fig. 1A). QMlPH-3B.4 could be utilized for quality improvement of YZ by increasing MlPT, MlPH, PkWd, and WdEm. We generally think that QTL detected in multiple environments should also be detectable when using BLUP values. QMlPH-1B.4 was detected in four environments except for BLUP. This may be because the BLUP value only considers the contribution of genetic factors to the phenotype. Therefore, we think that environmental effects may explain why that QTL was not detected under BLUP. In summary, to achieve good-quality wheat production, breeding wheat varieties that contain high-quality genotypes is paramount, but a suitable planting environment is also necessary [47].

Forty-nine QTL were identified in this study, of which 23 were identified in one environment and combined QTL analysis. Among the 23 QTL, five, eight, eight and two QTL were for MlPT, MlPH, PkWd, and WdEm, respectively (Table S3). For PkWd, 73% of QTL were detected in one environment and combined QTL analysis, which could be because PkWd is highly influenced by the environment. This phenomenon can be verified by the heritability of PkWd, which has the lowest heritability among the four dough rheological characteristics (Tables S2). Among the 49 QTL, we found that favorable alleles of 17 QTL located on chromosome 1B were provided by YZ, CY, YN, and YT, while favorable alleles of nine QTL located on chromosome 3B were detected in domesticated parents HU and YZ (Table S3). Four Chinese cultivars have poor dough characteristics compared with the British domesticated cultivar HU (Fig. 1A). This phenomenon suggests that there may be genes on chromosome 3B of HU that affect wheat processing quality.

The existing gene pool of cultivated wheat is relatively narrow because it is composed of current and historical wheat cultivars lacking allelic variation from landraces and wild species [23, 33]. HMW-GS plays an important role in influencing dough processing quality and extensive studies have attempted to explore novel alleles of HMW-GS from wheat wild species as well as their potential application in breeding [48–50]. Recently, Talini et al. showed that *Triticum urartu*, a wild diploid wheat, present a series of new types of HMW-GS with improved flour quality than the cultivated materials [48]. The wheat relatives of *Aegilops umbellulata* and *Aegilops searsii* were also shown to have novel HMW-GS alleles different from common wheat which can be important resources for improving wheat processing quality [49, 50]. However, more genetic variations affecting process quality other than HMW-GS loci are still encouraged to be explored from wheat wild species and its relatives [48, 51].

The latest research shows that from the perspective of the whole genome level, Tibetan semi-wild wheat has been de-domesticated from local landraces, and its genome is rich in variation [52]. Therefore, as a valuable resource to broaden the genetic diversity of wheat breeding, Chinese semi-wild cultivars can be used for genetic research of wheat processing quality, especially the release of the semi-wild wheat reference genome (Tibetan semi-wild wheat) [52]. The favorable alleles of 31% of the QTL for wheat processing quality were provided by three semi-wild parents, which may be because semi-wild wheat contains alleles that are not utilized by existing cultivated wheat varieties [36, 53] (Table S4). Hence, semi-wild wheat varieties can enrich the existing wheat gene pool, provide broader resources for wheat genetic research, and help in investigating the effect of domestication on the processing quality of wheat.

**Conclusions**

A wheat NAM population consisting of semi-wild and domesticated wheat varieties was used to detect QTL for wheat processing quality. A total of 49 QTL were identified, of which four novel QTL were stably identified in three or more environments. In addition, 15 of 49 QTL favorable alleles were provided by three semi-wild parents, which indicated that semi-wild wheat contains unique genetic material that was not used in domesticated varieties. Therefore, semi-wild wheat can be used as a genetic resource to enrich the existing wheat gene pool and provide more abundant variation for genetic research on wheat processing quality. In addition, the release of whole genome data of semi-wild wheat (Tibetan semi-wild wheat) [52] provides genomic information for further discovery of excellent alleles in...
ssemi-wild wheat and highlights the significance of studying the role of semi-wild wheat in evolution.

**Methods**

**Plant material and experimental design**

Previously, a wheat NAM population consisting of thirty-four RIL populations was constructed with Yanzhan 1 (YZ, *T. aestivum* L.) from Henan Province of the Huanghuai region, China as the common parent. All of the RIL populations (nine and ten generations of self-pollination) were derived using a single seed descent method. Here, to detect potential genetic alleles regulating wheat processing quality from broader genetic background, we selected four RIL populations for the NAM based QTL identification. Three of four divergent parents were semi-wild cultivars in China, including Yunnanxiaomai (YN, *T. aestivum* ssp. *yunnanense* King) from Yunnan Province [36], Yutiaodaimaoyi (YT, *T. petropavlovskyi* Udats. et Migusch.) from Sinkiang, and Cayazheda 29 (CY, *T. aestivum* ssp. *tibetanum* Shao) from Tibet [37, 52]. The other divergent parent was the British dwarf cultivar Hussar (HU), which is a good-quality cultivar [54]. The hybridizations of YZ with YN, YT, CY, and HU ultimately yielded 98, 93, 82, and 97 lines, respectively.

The NAM population along with the five parents were planted in De’zhou (E1, 116.39°E, 37.38°N), Tai’an (E2, 117.17°E, 36.17°N) and He’ze (E3, 115.50°E, 35.57°N) in Shandong Province during 2015–2016. The materials were planted again in Tai’an (E4) during 2016–2017. In each environment, each plot comprised two rows with a 2.0 m row length, 0.25 m row spacing, and 50 seeds per row. Two replicates were performed under each environment. All fields were managed in accordance with standard local practices.

**Traits investigated**

The plants in each plot were harvested to evaluate the wheat processing quality. The moisture (%) and protein (%) of grain and flour of the NAM population and greater than 2.0 in at least one RIL population when the LOD score was greater than 2.5 in the NAM population and greater than 2.0 in at least one RIL population. Previously, a wheat NAM population consisting of thirty-four RIL populations was constructed with Yanzhan 1 (YZ, *T. aestivum* L.) from Henan Province of the Huanghuai region, China as the common parent. All of the RIL populations (nine and ten generations of self-pollination) were derived using a single seed descent method. Here, to detect potential genetic alleles regulating wheat processing quality from broader genetic background, we selected four RIL populations for the NAM based QTL identification. Three of four divergent parents were semi-wild cultivars in China, including Yunnanxiaomai (YN, *T. aestivum* ssp. *yunnanense* King) from Yunnan Province [36], Yutiaodaimaoyi (YT, *T. petropavlovskyi* Udats. et Migusch.) from Sinkiang, and Cayazheda 29 (CY, *T. aestivum* ssp. *tibetanum* Shao) from Tibet [37, 52]. The other divergent parent was the British dwarf cultivar Hussar (HU), which is a good-quality cultivar [54]. The hybridizations of YZ with YN, YT, CY, and HU ultimately yielded 98, 93, 82, and 97 lines, respectively.

The NAM population along with the five parents were planted in De’zhou (E1, 116.39°E, 37.38°N), Tai’an (E2, 117.17°E, 36.17°N) and He’ze (E3, 115.50°E, 35.57°N) in Shandong Province during 2015–2016. The materials were planted again in Tai’an (E4) during 2016–2017. In each environment, each plot comprised two rows with a 2.0 m row length, 0.25 m row spacing, and 50 seeds per row. Two replicates were performed under each environment. All fields were managed in accordance with standard local practices.

An integrated high-density linkage map (containing 2009 SNP markers) published previously was used in this study [57], and the procedure was as follows: first, the redundant markers of the 90,000 SNP array were processed through the “BIN” function of IciMapping V4.1. Second, the remaining markers were divided into different linkage groups through the “MAP” function of IciMapping V4.1 [56]. Third, based on the Kosambi mapping function, we constructed four individual maps of the RILs. Finally, four individual maps were combined with Join Map V4.0 (https://www.kyazma.nl/index.php/JoinMap/). The averaged value for each line in each environment was used to conduct individual environment QTL analysis, and BLUP values across four environments for each line were used for combined QTL analysis. QTL detection for wheat processing quality was performed by joint inclusive composite interval mapping (JICIM) in IciMapping V4.1 software [56]. Using this method, the walking step was set as 1.0 cM, and a stepwise regression probability of 0.001 was used to identify QTL. A QTL was identified when the LOD score was greater than 2.5 in the NAM population and greater than 2.0 in at least one RIL population. In this study, QTL clusters affecting quality-related traits (MIPT, MIPH, PKWD, and WDEM) were defined with the prefix “QG”.

**Statistical analysis of phenotypic data**

The best linear unbiased prediction (BLUP) for each line of wheat processing quality was counted across environments using the “lmer” function implemented in the R package lme4 (https://cran.r-project.org/web/packages/lme4/index.html). Each BLUP was used to calculate the pairwise correlations for phenotypic data using the “rcorr” function implemented in the R package Hmisc. Boxplots for phenotypic data were obtained from the BLUP value using Origin Pro V9.1 software (https://www-originlab.com/). Analysis of variance (ANOVA) for the five parents in wheat processing quality was calculated by Statistics Program for Social Sciences V20 software. Furthermore, the heritabilities were calculated through the AOV function of IciMapping V4.1 software using the formula $h^2 = V_G / (V_G + V_{GEI} + V_e / r)$, where $V_G$, $V_{GEI}$ and $V_e$ are the variances of $G$ (genotypes), $GEI$ (genotype × environment interactions) and the error, respectively; $e$ is the number of environments; and $r$ is the number of replications [56].

$$V = \text{variance; } G = \text{genotype; } GEI = \text{genotype} \times \text{environment interactions; } e = \text{error; } r = \text{number of replications; } V_{GEI} \text{ and } V_e = \text{error; } r = \text{number of replications}.$$
Abbreviations
NAM: Nested association mapping; QTL: Quantitative trait loci; RIL: Recombinant inbred lines; HMW-GS: High-molecular-weight glutenin subunits; LMW-GS: Low-molecular-weight glutenin subunits; MAS: Marker-assisted selection; AACC: American Association of Cereal Chemists; BLUP: Best linear unbiased prediction; ANOVA: Analysis of variance; JICM: Joint inclusive composite interval mapping; QG: QTL cluster; Add: Additive effects; MlPT: Midline peak time; MlPH: Midline peak height; PkWd: Peak width; WdEm: Width at eight minutes; YZ: Yanzhan 1; HU: Hussiar; YN: Yunnanxiaomai; YT: Yutiandaomai; CY: Chayazheda 29.

Supplementary Information
The online version contains supplementary material available at https://doi.org/10.1186/s12870-022-03523-x.

Additional file 1: Table S1. Phenotype data of five parents in four environments and of the NAM population in individual environments and combined environments.

Additional file 2: Table S2. ANOVA analysis of quality-related traits for the NAM population.

Additional file 3: Table S3. The QTL mapping results for four dough rheological characteristics in the individual environment analysis and combined environment analysis.

Additional file 4: Table S4. The number of QTL with favorable alleles contributed by five different parents.

Acknowledgements
We thank to Prof. XYK and JZJ for the RIL populations materials.

Authors’ contributions
YGB and FSB conceived and designed the research. JMH performed the analysis, interpreted the results and drafted the manuscript. GLX, GXZ and XM grew plants, interpreted the results and drafted the manuscript. GLX, GXZ and XM grew plants, carried out the work of material planting management. All authors read and approved the final version of the manuscript.

Funding
The cost of microarray as well as other materials was founded by the National Key Research and Development Program (2016YFD0100102-2), and the labor cost was founded by the Project of Shandong Province Higher Educational Science and Technology Program (J16LF06). The funding body had no role in the design of the study and collection, analysis, and interpretation of data and in writing the manuscript.

Availability of data and materials
The SNP array data used in this study was submitted to OMIX (https://mgdc.cnccb.ac.cn/omix/), and could be accessed using accession ID OMIX001002.

Declarations
Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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Received: 14 August 2020 Accepted: 9 March 2022

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