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Genes controlling barley malt quality: A QTL meta-analysis

Mahjoubeh Akbari[1], Hossein Sabouri[1*], Maryam Pasandideh[2], Fakhtak Taliei[1], and Ahmad Reza Dadras[3]

[1]Department of Plant Production, Faculty of Agriculture and Natural Resources, Gonbad Kavous University, Gonbad Kavous, Iran.
[2]BioGenTAC lnc., Technology Incubator of Agricultural Biotechnology Research Institute of Iran, North Branch (ABRII), Rasht, Iran.
[3]Olive Research Station of Tarom, Crop and Horticultural Science Research Department, , Agricultural and Natural Resources Research and Education Center, AREEO, Tarom, Iran.
*Corresponding author; hossein.sabouri@gonbad.ac.ir

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Abstract

Objective: Malt quality in barley is a complex quantitative trait governed by multiple genes and influenced by environmental factors, making genetic improvement challenging. The present study aimed to integrate QTL data from multiple independent studies through meta-analysis to identify stable, consensus genomic regions (MQTLs) controlling key malt quality traits. The ultimate goal was to provide reliable genomic targets for marker-assisted selection to accelerate breeding programs for improved barley malt quality.

Methods: A comprehensive literature search was conducted across Web of Science, Scopus, PubMed, ScienceDirect, and Google Scholar to identify all published QTL studies related to barley malt quality. A high-density consensus genetic map was constructed by integrating several well-established reference maps. The unified map incorporated multiple marker systems, including AFLP, SSR, RFLP, RAPD, SAP, DArT, EST, CAPS, STS, RGA, IFLP, and SNP markers, ensuring comprehensive genome coverage. Individual QTLs were projected onto the consensus map, and the optimal number of MQTLs per chromosome was determined using the Akaike Information Criterion, Bayesian Information Criterion (BIC), and empirical Bayesian procedures. To validate the biological relevance of the identified MQTLs, genes located within 2 Mb intervals flanking each MQTL peak position were retrieved from major genomic databases, including EnsemblPlants, GrainGenes, NCBI Gene, and BarleyMap.

Results: Through meta-analysis, the 184 individual QTLs were consolidated into 35 MQTLs distributed across all seven barley chromosomes. The most significant MQTL, designated MQTL7.2, harbored 25 overlapping QTLs and explained 68% of the phenotypic variance. MQTL6.4 contained 12 QTLs controlling alpha-amylase, diastatic power, viscosity, beta-glucan, Wort beta-glucan, and grain protein content, explaining 38% of phenotypic variance. Gene mining within MQTL intervals identified 54 unique candidate genes. Gene ontology enrichment analysis revealed significant involvement in

monoatomic anion transport, tetracycline transmembrane transport, mRNA pseudouridine synthesis, and transmembrane transporter activity. MicroRNA prediction revealed 33 unique miRNAs regulating the identified genes, with hvu-miR6192, hvu-miR6184, hvu-miR6182, hvu-miR6176, hvu-miR6189, and hvu-miR6214 targeting multiple genes.

Conclusion: The identified MQTLs exhibited substantially reduced confidence intervals compared to individual QTLs, providing more precise genomic targets for breeding applications. Eleven major MQTLs with R^2 values exceeding 20% represented high-priority genomic regions for marker-assisted selection. The Mega-MQTL7.2, explaining 68% of phenotypic variance and harboring QTLs for multiple malt quality parameters, represents a particularly valuable breeding target. These findings will facilitate marker-assisted selection strategies to accelerate genetic improvement of barley for the malting and brewing industries, ultimately contributing to the development of superior malting barley cultivars with enhanced quality characteristics.

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Introduction

Barley (*Hordeum vulgare* L.) ranks as the fourth most important cereal crop globally after wheat, rice, and maize, and serves as an excellent model for genetics and genomics research. This crop demonstrates remarkable environmental plasticity across diverse agro-ecological zones due to its extensive evolutionary adaptation (Zhou *et al*. 2009; Zhou *et al*. 2012a; Ghomi *et al*. 2021). Barley is utilized primarily for animal feed, malting, brewing, and human consumption, with its distinctive chemical composition and health-promoting dietary fibers attracting considerable attention from agriculturists and nutritionists (Farag *et al*. 2022). The malting industry represents a particularly significant economic sector, with global annual production capacity exceeding 22 million tons, over 90% of which derives from barley (Oliveira *et al*. 2012; Rani and Bhardwaj 2021). The malting process involves controlled partial germination followed by drying, during which seed cell walls are degraded and diastatic enzymes are activated to hydrolyze starch into fermentable sugars, producing malt extract essential for brewing and distilling industries (Gubatz and Shewry 2011).

Meta-analysis, proposed by Glass (1976), uses a combination of various studies to create more precise and meaningful forecasts. Extensive QTL mapping studies have generated substantial and

often overlapping datasets for various agronomic traits in crops (Goffinet and Gerber 2000). QTL meta-analysis systematically reviews and synthesizes these reported QTLs to consolidate redundant information and identify refined, high-confidence genomic regions termed 'meta-QTLs' (MQTLs), which represent consensus chromosomal intervals with enhanced statistical power and reduced confidence intervals (Arcade *et al.* 2004; Veyrieras *et al*. 2007).

The identified MQTLs have shorter confidence intervals than individual QTLs, which leads to a deeper understanding of the genetic framework of the complex traits, and subsequently, a consensus linkage map is generated that shows different QTLs using a simple scaling law (Kaur *et al.* 2023; Kumari *et al.* 2024). The MQTL approach integrates QTL data from independent mapping experiments to identify consistent chromosomal regions associated with quantitative traits such as yield and yield-related components, while simultaneously enhancing statistical power and improving precision in QTL detection (Goffinet and Gerber 2000; *Arcade et al.* 2004). Candidate genes associated with these QTLs have been proposed in several studies (Khahani *et al.* 2019; Akbari *et al.* 2022). This integrative approach combining QTL mapping with gene annotation has been successfully applied across a range of major crops, including wheat (Kumar *et al.* 2021; Saini *et al.* 2021, 2022; Tanin *et al.* 2022; Kumar *et al.* 2023), rice (Sandhu *et al.* 2021; Anilkumar *et al.* 2022; Kumari *et al.* 2023), barley (Li *et al.* 2013; Zhang *et al.* 2017; Akbari *et al.* 2022), and maize (Kaur *et al.* 2021; Makhtoum *et al.* 2021a; Makhtoum *et al.* 2021b; Sheoran *et al.* 2022; Makhtoum *et al.* 2022a; Makhtoum *et al.* 2022b; Wang *et al.* 2022; Gupta *et al.* 2023; Karnatam *et al.* 2023; Sethi *et al.* 2023)

As mentioned above, malt barley is used in the food and beverage industries. To identify and publish quality malt types, many quality traits are involved in detecting the proper barley grain (Carvalho *et al.* 2021; Farag *et al.* 2022). Using a mapping population derived from the Baudin × AC Metcalfe cross, 16 QTLs associated with seven malt quality traits were identified across four barley chromosomes, with 1 to 4 QTLs detected per trait at LOD threshold values > 3.0. Zhou *et al*. (2016) identified a major QTL in the telomeric region of chromosome 5H that pleiotropically controlled malt extract yield, soluble protein content, free amino nitrogen, and α-amylase activity, explaining 25.6-33.2% of the phenotypic variance for these traits. Additionally, four QTLs for diastatic power, three located on chromosome 1H and one on chromosome 5H, collectively accounted for 26% of the phenotypic variation. Two QTLs were also identified for the increase in α-amylase, and the 5H chromosome telomere area assigned 25.6% of the main QTL's phenotypic variations. Goddard *et al.* (2019) performed a QTL analysis and detected 12 QTLs on 4 chromosomes, 2H, 3H, 4H, and 7H, explaining 6.4 to 21.3% of the phenotypic variation for malting quality. Marquez-Cedillo *et al.* (2000)

analyzed a doubled haploid population of 140 lines, derived from the Harrington × Murex barley cross, aimed at characterizing the number, genomic positions, and effects of quantitative trait loci (QTLs) influencing malt quality. Using simple interval mapping and composite interval mapping, they integrated phenotypic data for malt quality traits, collected across eight environments, with a genetic linkage map containing 107 markers, ultimately identifying seventeen QTLs associated with seven key grain and malt quality characteristics.

Cu *et al.* (2016) used a population of 320 doubled haploid lines developed from a cross between the barley cultivars *Navigator* and *Admiral*. They identified 63 QTLs associated with 10 malt quality traits across two distinct environments. Notably, three key traits, β-amylase activity, diastatic power, and apparent attenuation limit, each predominantly governed by a single major QTL, showed consistent effects in both environments. Five QTL were located for α-amylase, accounting for 4.02–15.52% of the phenotypic variance. The co-localization of QTLs on chromosomes 1HS, 4HS, 7HS, and 7HL, controlling six malting quality characteristics (α-amylase, soluble protein, Kolbach index, free amino nitrogen, wort β-glucan, and viscosity) indicated genetic linkage or pleiotropic relationships among these traits (Han *et al.* 2004). Han *et al*. (2004) identified seven QTLs controlling malting quality traits: one QTL for malt extract content, and two QTLs each for α-amylase activity, diastatic power, and β-glucan content.

Several QTL mapping studies have dissected the genetic architecture of malting quality traits in barley. Von Korff *et al*. (2008) identified eight QTLs for Wort viscosity on chromosomes 1H, 2H, 3H, 5H, and 6H (R^2 = 2-19.1%), while Wang *et al*. (2018) detected three peak viscosity QTLs on chromosomes 1H, 2H, and 5H, explaining 7.4%, 15.2%, and 8.5% of phenotypic variation, respectively. In a comprehensive mapping effort, Laidò *et al*. (2009) localized 19 QTLs for multiple malt quality traits, revealing that chromosome 1H contained QTLs for all examined traits, whereas chromosome 7H harbored none. Similarly, Kochevenko *et al.* (2018) reported 41 QTLs associated with malt quality traits alongside 57 yield-related and five seed quality QTLs, though only five malt quality QTLs exhibited major effects (R^2 > 10%), indicating predominantly polygenic inheritance of malting characteristics.

Li *et al.* (2005) evaluated three malting quality traits over two growing seasons and identified two QTLs associated with elevated grain protein content on chromosomes 2 and 7, along with a putative QTL significantly linked to malt extract percentage. Zhou *et al.* (2012c) developed a high-density genetic linkage map using 550 markers across 95 doubled haploid lines, derived from a cross between the Japanese cultivar *Mikamo Golden* and the North American malting barley cultivar, *Harrington* (MH-DHLs). They assessed seven malt quality traits, including, malt extract, total

nitrogen, soluble nitrogen, Kolbach index, diastatic power, Wort beta-glucan, and viscosity, across three distinct environments (location × year combinations). A total of 34 QTL were detected, accounting for 13.7-77.5% of the phenotypic variance. According to Emebiria *et al.* (2003), examining the grain protein as a covariate for malt extract and diastatic strength resulted in a two-fold increase in the number of QTLs for each trait, largely due to increased detection power, and the identification of new QTLs occurred in the chromosomal regions where no significant QTL had previously been present.

According to von Korff *et al.* (2008), 10 QTLs associated with grain protein content on chromosomes 1H, 2H, 4H, and 6H were identified. At five of these loci, alleles from exotic (non-adapted) barley germplasm were linked to higher protein levels. The most influential QTL, *QPro.S42-1H.b*, accounted for 7.9% of the genetic variance and increased protein content by an average of 6.7%. Szűcs *et al.* (2009) constructed a linkage map of 2383 loci, using the Oregon Wolfe Barley (OWB) population, and detected 154 QTLs related to malt quality. The largest number of QTLs (21 QTLs) were related to the grain protein content. Twenty QTLs were located for alpha-amylase activity and malt extract, 13 QTLs for the diastatic power, and only one QTL for the beta-amylase activity (at chromosome 4H). The largest number of QTLs was located on chromosome 5, and the smallest number was on chromosomes 3 and 6. Emebiri *et al.* (2003) identified seven QTLs for the grain protein concentration, which explained between 4.8% and 20.5% of the phenotypic variation. According to Walker *et al.* (2013), 32 QTLs for protein content and malt extract were identified on chromosomes 1H, 2H, 3H, 4H, and 7H in barley.

This study aimed to (i) construct a consensus genetic map for barley to refine QTL positions and identify stable genomic regions associated with malting quality, and (ii) conduct meta-QTL analysis by integrating QTLs controlling malt quality-related traits from previous mapping studies.

Materials and Methods

To conduct the QTL meta-analysis, all published studies related to QTLs controlling malt quality traits in barley (*Hordeum vulgare* L.) were systematically searched in Web of Science, Scopus, PubMed, ScienceDirect, and Google Scholar. Studies were screened using strict inclusion criteria to ensure reliability and comparability among datasets. Only articles that reported well-defined genetic linkage maps and provided QTL positions in centimorgans were included. In addition, QTLs were considered eligible for analysis only if they met two statistical thresholds: a minimum LOD score of 3.0 and a phenotypic variance explained (PVE) of at least 20%. Studies lacking essential statistical information, missing flanking markers, or using overlapping populations were excluded to avoid

redundancy and inconsistency. After applying these criteria, a final set of high-quality QTL studies was selected for integration.

Extraction of QTL parameters

For each retained study, QTL information was extracted in a standardized manner. Extracted parameters included chromosome number, peak position, confidence interval, flanking markers, LOD score, PVE, and the type and size of the mapping population. These datasets enabled the harmonization of QTL information obtained across different markers, populations, and experimental conditions. Each QTL was cataloged in preparation for projection onto a unified consensus map.

Construction of the consensus genetic map

A comprehensive consensus genetic map was constructed to serve as the reference framework for QTL projection. Two well-established barley linkage maps (Wenzel *et al*. 2006; Zhou *et al*. 2015) were used as primary references, supplemented by additional consensus maps (Wenzel *et al*. 2006; Khawani *et al*. 2016; Zhang *et al*. 2016) and 26 individual linkage maps. The unified map incorporated multiple marker systems, including AFLP, SSR, RFLP, RAPD, SAP, DArT, EST, CAPS, STS, RGA, IFLP, and SNP markers, enabling high genome coverage. Map construction and integration were carried out using BioMercator version 4.2 (Sosnowsky *et al*. 2012), which aligns markers, resolves conflict among maps, and produces a consistent chromosome-wise coordinate system suitable for cross-study QTL comparison.

QTL projection and MQTL identification

All extracted QTLs were projected onto the consensus genetic map using the QTL Projection module in BioMercator. This step standardized the positions of QTLs originating from diverse mapping studies. Meta-analysis was subsequently conducted using the approach of Veyrieras *et al*. (2007), which evaluates multiple statistical models based on Akaike Information Criterion, Bayesian Information Criterion, and the empirical Bayesian procedure to determine the optimal number of MQTLs per chromosome. For each identified MQTL, refined positions, sharply reduced confidence intervals, and consensus flanking markers were obtained. The resulting MQTLs represent stable, high-confidence genomic regions consistently associated with malt quality traits across multiple studies and environments.

Validation of MQTL regions

To confirm the functional relevance of the identified MQTLs, a gene-based validation strategy was implemented. Genes located within each MQTL interval were retrieved from major genomic databases, including EnsemblPlants, GrainGenes, NCBI Gene, and BarleyMap. Functional annotation, gene ontology, and pathway analyses were performed to determine the biological relevance of each gene. Special attention was given to genes previously implicated in malt quality, such as those involved in starch metabolism, carbohydrate degradation pathways, and enzyme activity during malting. MQTLs containing functionally meaningful and previously reported malt-related genes were considered validated. This integrative approach ensured that the MQTLs detected in the present study represent robust genomic hotspots with strong biological and functional support.

Identification of genes related to QTL

The physical locations of genes in the chromosomal regions were obtained in the 2Mb intervals on either side of the peak position for identified QTL based on the *Hordeum vulgar* reference genome (MorexV3_pseudomolecules_assembly) using Ensembl plant database (Bolser *et al.* 2016). A circus plot was drawn by TBtools software (Chen *et al.* 2023) to show the location of QTLs on the barley chromosomes.

Gene ontology enrichment analysis of identified genes

The conversion of gene identifiers of barley was performed using a gprofiler tool based on the model plant *Arabidopsis thaliana* (https://biit.cs.ut.ee/gprofiler/gost). Gene ontology enrichment analysis, including biological process, cellular component, and molecular function MF of the identified genes, was performed using the DAVID database (https://david.ncifcrf.gov/) with a p-value ≤ 0.05. The result of the functional enrichment analysis of the genes was shown using the SRplot tool (https://www.bioinformatics.com.cn/en).

Co-expression network of identified genes

Co-expression networks for the identified genes were constructed using the GeneMANIA tool (https://genemania.org/) based on *Arabidopsis thaliana* ortholog information, with a false discovery rate (FDR) threshold of <0.05 to control for multiple testing errors.

Prediction of related microRNA (miRNA) of genes

Related miRNAs of the identified genes in QTLs were identified using the psRNATarget server (Dai *et al.* 2018) based on all published miRNAs of barley. The network of miRNAs and target genes was constructed by Cytoscape software (3.9.1).

Results and Discussion

Construction of a consensus linkage map

In this meta-analysis, aimed at identifying MQTLs associated with malt quality in barley (*Hordeum vulgare* L.), data were compiled from multiple published studies. A total of 354 major QTLs linked to 12 key malt quality traits (Table 1), derived from diverse genetic populations, were extracted. Detailed QTL information, including mapping method, flanking markers, estimated position, 95% confidence interval (CI), LOD score, R^2 value, and other mapping parameters, was provided in Supplementary Table 1.

To integrate these QTLs onto a common genomic framework, 42 individual linkage maps along with two published high-density consensus maps (Wenzl *et al.* 2006; Zhou *et al*. 2015) were used as references. Due to limited marker overlap between original studies and existing reference maps, BioMercator v4.2 (Sosnowski *et al.* 2012) was employed to construct a unified consensus map by merging published consensus maps (Wenzl *et al.* 2006; Zhang *et al.* 2017; Khahani *et al.* 2019) with these individual maps (Table 2).

Of the 354 QTLs collected, 184 contained markers present on the consensus map and were therefore projected onto it (Figures 1-4). For the QTL projection, a 95% confidence interval was first calculated for each QTL using equations modeled for each mapping population (Darvasi and Soller 1997; Guo *et al*. 2006). These equations include those for F2 and backcross mapping populations: $CI = 530/(\text{number of lines} \times R^2)$, for RILs: $CI = 163/(\text{number of lines} \times R^2)$, and for DH populations: $CI = 287/(\text{number of lines} \times R^2)$.

QTLs were then positioned using their reported midpoints, calculated confidence intervals, original LOD scores, and R^2 values. A chromosome-wise meta-analysis was then conducted using the two-step algorithm of Veyrieras *et al.* (2007), as implemented in BioMercator v4.2. To determine the optimal number of MQTLs, representing the most likely "true" underlying QTLs, the model with the lowest Akaike information criterion was selected, as it best balances model fit and complexity relative to the original QTL data. Full descriptions of the algorithms and statistical procedures used in this software have been detailed in prior publications (Arcade *et al.* 2004; Veyrieras *et al.* 2007;

Sosnowski *et al.* 2012). All input files prepared for BioMercator v4.2, including genetic maps and QTL data for each barley chromosome, are listed in Supplementary Table 2.

Table 1. Traits used in the QTL mapping for malt quality in previous studies.

Trait	Trait components
Malt quality	Malt extract, diastatic power, α-amylase, α-amylase activity, protein content, soluble proteins, soluble proteins to total proteins ratio, grain protein content, viscosity, Wort viscosity, β-glucan, Wort β-glucan, β-glucanase activity

QTL and MQTL distribution

Among the 29 studies initially reviewed, 16 provided complete data necessary for the meta-QTL (MQTL) analysis. From these, a subset of 11 studies contributed a total of 184 QTLs, which were successfully projected onto the consensus genetic map for meta-analysis. The distribution of these QTLs across the barley genome varied by chromosome, ranging from 15 QTLs on chromosome 6H to 39 QTLs on chromosome 1H. Comprehensive details of the resulting MQTLs, including the number of underlying primary QTLs, consensus map positions, directions of allelic effect, 95% confidence intervals, and R^2 values, are summarized in the Supplementary Table 1.

In this study, 35 MQTLs were located for 184 QTLs related to malt quality. Seven MQTLs were identified on chromosome 1, 6 MQTLs on chromosomes 3 and 5, and 4 MQTLs each on chromosomes 2, 4, 6, and 7. The number of QTLs and MQTLs for each chromosome is shown in Table 3 and Supplementary Table 3. Du *et al.* (2024) identified 41 MQTLs for 349 QTLs related to barley quality traits. The number of these QTLs ranged from 19 (on chromosome 6) to 64 (on chromosome 5) (Du *et al.* 2024). In our study, the lowest number of QTLs was identified on chromosome 6, which was consistent with the results of Du *et al.* (2024).

Overlapping QTLs in MQTLs

The highest QTL overlap was observed in MQTL7.2, where 25 QTLs overlapped. Overlapping of 12 QTLs also occurred in MQTL6.4, MQTL5.3, and MQTL4.1. No overlap was observed in MQTL5.6, MQTL6.1, and MQTL6.2. Only two overlapping QTLs were observed in each of MQTL3.1, MQTL3.2, MQTL3.3, MQTL3.6, and MQTL5.1. The highest QTL overlap was observed on chromosome 1 in MQTL1.3 (11 QTLs), on chromosome 2 in MQTL2.1 (11 QTLs), on chromosome 3 in MQTL3.5 (9 QTLs), on chromosome 4 in MQTL4.1 (12 QTLs), on chromosome 5 in MQTL5.3 (12 QTLs), on chromosome 6 in MQTL6.4 (12 QTLs), and on chromosome 7 in MQTL7.2 (25 QTLs) (Supplementary Table 2). In the study by Du *et al.* (2024), the highest number of QTL overlaps was observed in MQTL1H-2 (38 QTLs), and the lowest overlap was observed in MQTL2H-7 (2 QTLs),

Table 2. QTLs associated with barley malt in this study, collected from previously published papers**.**

Reference	Marker	Population	Parents	Population Size	No. of Markers
Walker *et al*., 2013	SNP	DH	Vlamingh × Buloke	289	1536
Emebiri *et al*., 2004	AFLP, RFLP, SSR	DH	VB9524 × ND1123112	180	181
Marquez-Cedillo *et al*., 2000	AFLP	DH	Harrington × Morex	140	106
Szűcs *et al*., 2009	SNP, DArT, SSR, RFLP, STS	DH	Wolfe Dominant × Wolfe Recessive	93	2383
Wang *et al*., 2018	DArT, SSR, SNP	DH	TX9425 × Naso Nijo	150	~2500
Cu *et al*., 2016	DArT, SNP	DH	Navigator × Admiral	320	2346
Laidò *et al*., 2009	AFLP, RFLP, SSR, STS	DH	Nure × Tremois	214	104
Elía *et al*., 2010	AFLP, DArT, SSR, SCSSR, SNP	DH	Triumph × Morex	106	462
Goddard *et al*., 2019	SNP	RIL	Chevallier × NFC Tipple	188	384
Zhou *et al*., 2012	EST, SNP, RFLP	DH	Harrington × Mikamo Golden	95	550
Han *et al*., 2004	RFLP	DH	Steptoe × Morex	150	100
von Korff *et al*., 2008	SSR	BC	Scarlett × ISR42-8	301	98
Li *et al*., 2003	microsatellite markers	DH	Brenda × HS213	181	400
Kochevenko *et al*., 2018	SNP	DH	Sofiara × Victoriana	100	1782
Emebiri *et al*., 2003	AFLP, RFLP, SSR, RAPD	DH	VB9524 × ND1123112	180	270

Table 2 continued

Reference	Marker	Population	Parents	Population Size	No. of Markers
Zhou *et al*., 2016	AFLP, SSR	DH	Baudin × AC Metcalfe	178	193
Wenzl *et al*., 2006	DArT, SSR, RFLP, STS	DH, RIL	Barque73 × CPI71284-48, Clipper × Sahara, Dayton × Zhepi2, Foster × CI4196, Steptoe × Morex, TX9425 × Franklin, Yerong × Franklin	707	2935
Karakousis *et al*., 2003	AFLP, SSR, RFLP	DH	Clipper × Sahara 3771	150	211
Horsley *et al*., 2006	RFLP, SSR	F8–9, RIL	Foster × CIho 4196	250	206
Mesfin *et al*., 2003	SSR	F4–6, RIL	Fredrickson × Stander	116	143
Kleinhofs *et al*., 1993	RFLP, RAPD, SAP	DH	Steptoe × Morex	150	295
Li *et al*., 2009	DArT, AFLP, SSR	DH	TX9425 × Franklin	92	520
Li *et al*., 2003	SSR	DH	Steptoe × Morex, Igri × Franka	133	133
Graner *et al*., 1991	RFLP	DH, F_2/F_3	IGRI × FRANKA, VADA × *H. spontaneum*	206	251
Salvo-Garrido *et al*., 2001	RFLP	DH	PB1 × PB11	111	136
Ramsay *et al*., 2000	SSR	DH	Lina × *H. spontaneum* Canada Park	86	325
Fan *et al*., 2017	SSR, SNP	RILs	ZGMLEL × Schooner	190	1011
Dracatos *et al*., 2019	DArT, SNP	RIL	Pompadour × Biosaline-19	98	8610
Marcel *et al*., 2007	RFLP, AFLP, SSR	DH, RIL	Steptoe × Morex, Dom × Rec, Igri × Franka, L94 ×Vada	317	3258
Ren *et al*., 2016	SNP, SSR	DH	Huadamai 6 × Huaai 11	122	1962

Table 2 continued

Reference	Marker	Population	Parents	Population Size	No. of Markers
Varshney *et al*., 2007	SSR	DH	Igri × Franka, Steptoe × Morex, OWBRec × OWBDom, Lina × Canada Park, L94 × Vada, SusPtrit × Vada	645	775
Sato *et al*., 2009	EST, CAPS, STS, SNP, SSR	DH	Haruna Nijo × H602	93	2948
Dahleen *et al*., 2003	RFLP, SSR, AFLP, RGA	DH	Foster × ND9712 × Zhedar	75	214
Costa *et al*., 2001	RFLP, RAPD, STS, IFLP, SSR, AFLP	DH	Oregon Wolfe Barley	94	830, 725
Han *et al*., 2016	SNP	RIL	Morex × Barke	81	195
Makhtoum *et al*., 2021	SSR, ISSR, iPBS, Scot, IRAP, CAAT	RIL	Badia × Kavir	106	392
Ghaffari-Moghadam *et al*., 2019	SSR, ISSR, iPBS	F3	Badia × Comino	100	128
Gudys *et al*., 2018	SNP, SSR	RILs	Maresi × Cam/B1/CI08887//CI05761	100	819
Ellis *et al*., 2002	AFLP, SSAP, SSR	DH	Derkado × B83-12/21/5	156	241
Zhou *et al*., 2012	DArT, SSR	DH	Yuyaoxiangtian Erleng × Franklin	172	858
Ghaffari-Moghadam *et al*., 2019	SSR, ISSR, iPBS	F3	Badia × Comino	100	128
Xue *et al*., 2009	SSR, DArT	DH	CM72 × Gairdner	93	332
Xue *et al*., 2017	SSR, SNP, DArT, STS, CAPS, dCAPS	DH	Nure × Tremois	118	162
Xu *et al*., 2012	SSR, DArT	DH	TX9425 × Naso Nijo	188	626
Shavrukov *et al*., 2010	SSR, DArT, CAPS	DH	Barque-73 × CPI-71284-48	72	1180

Table 2 continued

Reference	Marker	Population	Parents	Population Size	No. of Markers
Makhtoum *et al*., 2021	SSR, ISSR, iPBS, Scot, CAAT, IRAP	RILs	Badia × Kavir	106	302
Mano and Takeda., 1997	SSR	DH	Steptoe × Morex, Harrington × TR306	149, 146	103
Liu *et al*., 2017	DArT, SSR	DH	CM72 × Gairdner	108	886
Fan *et al*., 2015	DArT, AFLP, SSR	DH	TX9425 ×Franklin	72	520
Sayed., 2011	SSR, DArT, gene-specific marker	DH	Scarlett × ISR42-8	76	371
Diab *et al*., 2004	RFLP	RILs	Tadmor × Er/Apm	167	77
Arifuzzaman *et al*., 2014	SSR, DArT	DH	Scarlett × ISR42-8	301	371
Sayed *et al*., 2012	SSR, DArT, gene-specific marker	DH	Scarlett × ISR42-8	76	371
Huang *et al*., 2018	SSR, DArT	DH	Yerong × Franklin, TX9425 ×Naso Nijo	177, 188	2500, 524
Kindu *et al*., 2014	AFLP	RILs	Prisma × Apex R	94	191
Navakode *et al*., 2009	EST, BR, GBM, GBS, RFLP, SSR, SNP	DH	OWBDOM × OWBREC	94	650
Saal *et al*., 2011	SSR	DH	ISR42-8 × Scarlett301	98	
Yang *et al*., 2004	SSR	RIL	Lewis(CI15856) × Karl(CI15487)146	146	104
Li *et al*., 2008	SSR, AFLP, DArT	DH	TX9425 × Franklin, Yerong × Franklin	92, 177	520, 524
Xue *et al*., 2010	DArT, AFLP, microsatellite markers	DH	Yerong × Franklin	156	604

Table 2 continued

Reference	Marker	Population	Parents	Population Size	No. of Markers
Zhou *et al*., 2012	SSR, DArT	DH	YuYaoXiangTian Erleng × Franklin	172	2223
Broughton *et al*., 2015	DArT, SSR	DH	Franklin × YuYaoXiangTian Erleng	126	858
Francia *et al*., 2004	SSR, RAPD, RFLP, CAPS, AFLP, STS	DH	Nure × Tremois	136	127
Skinner *et al*., 2006	SSR	DH	Dicktoo × Morex	91	94

Table 3. Number of predicted QTLs and identified MQTLs for the malting quality of barley.

Chromosome	QTL (MQTL)
1H	39 (7)
2H	22 (4)
3H	18 (6)
4H	23 (4)
5H	31 (6)
6H	15 (4)
7H	36 (4)
Total	184 (35)

MQTL5H-1 (2 QTLs), MQTL5H-5 (2 QTLs), and MQTL6H-3 (2 QTLs). Also, five QTLs did not overlap with any of the MQTLs.

Major MQTLs

Eleven MQTLs with R^2 greater than 0.20 and less than 0.40 were identified in this study. In MQTL6.4, 12 QTLs controlling traits such as alpha-amylase, diastatic power, viscosity, beta-glucan, Wort β-glucan, and grain protein content were located, which explained 38% of the phenotypic variation. MQTL5.3 explained 32% of the phenotypic variation and included 1 QTL associated with malt extract, 5 QTLs associated with α-amylase, 3 QTLs associated with β-glucanase, 2 QTLs associated with protein content, and 1 QTL associated with viscosity. MQTL4.4 explained 31% of the phenotypic variation with 10 QTLs. Also, 31% of the phenotypic variation was explained in MQTL2.2. MQTL1.6 contained 10 QTLs controlling the protein content, malt extract, and β-glucan and explained 27% of the phenotypic variation. MQTL1.3 with 11 identified QTLs explained 26% of the phenotypic variation. MQTL2.4 with 6 QTLs explained 24%, and MQTL2.1 with 11 QTLs

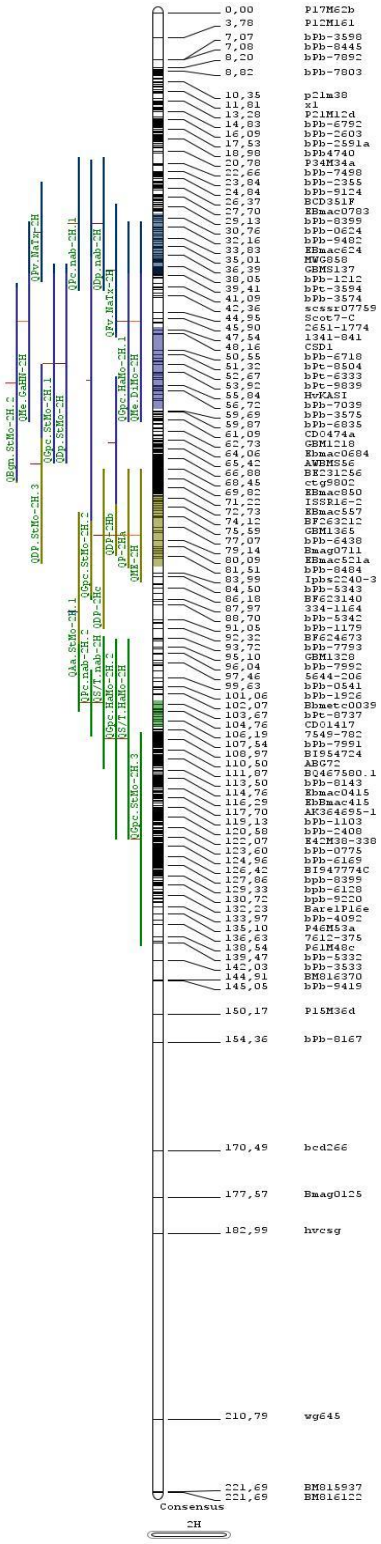

Figure 1. Genomic localization of the QTLs on chromosomes 1H and 2H for malt quality of barley in the consensus map.

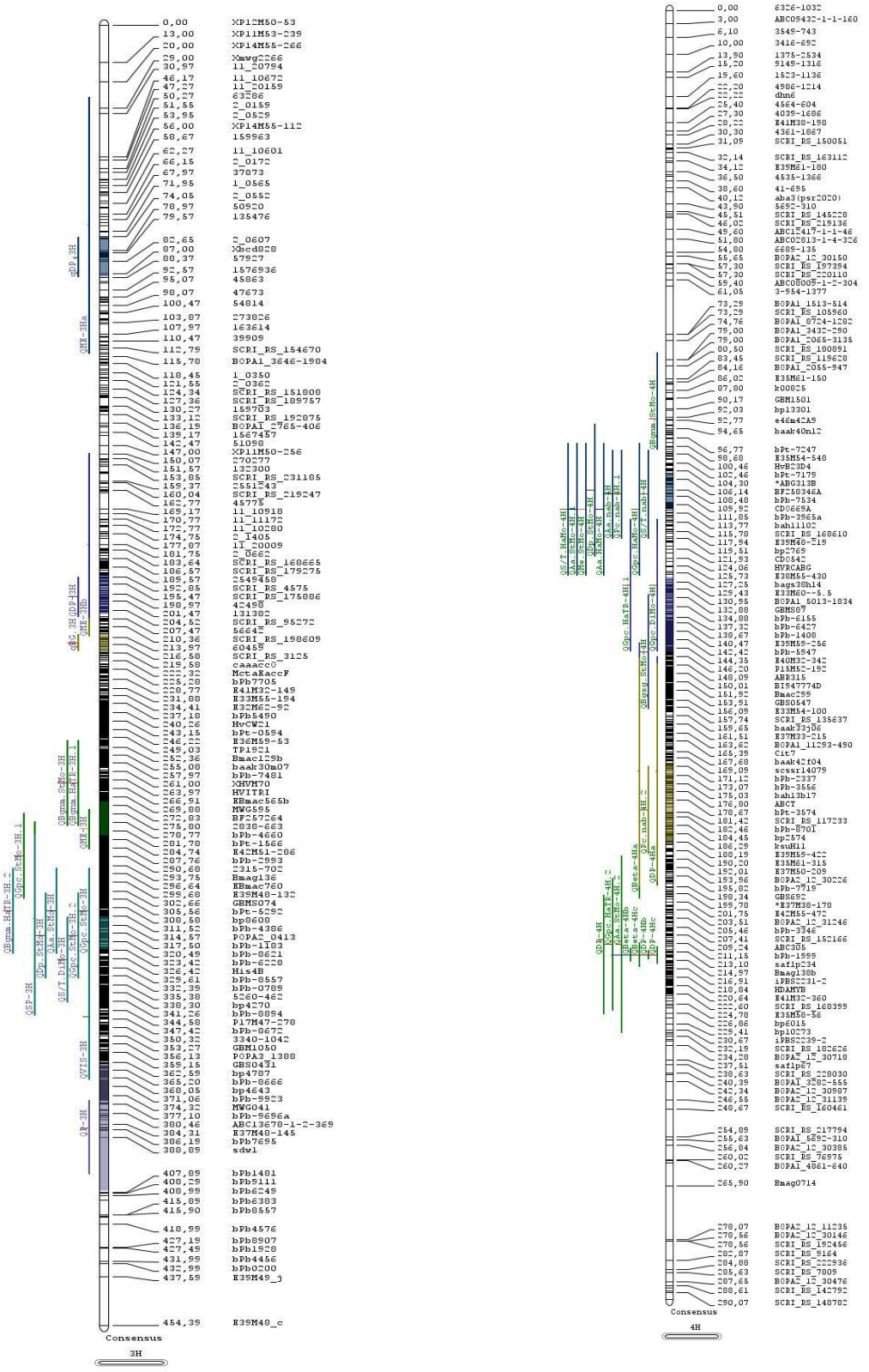

Figure 2. Genomic localization of the QTLs on chromosomes 3H and 4H for malt quality of barley in the consensus map**.**

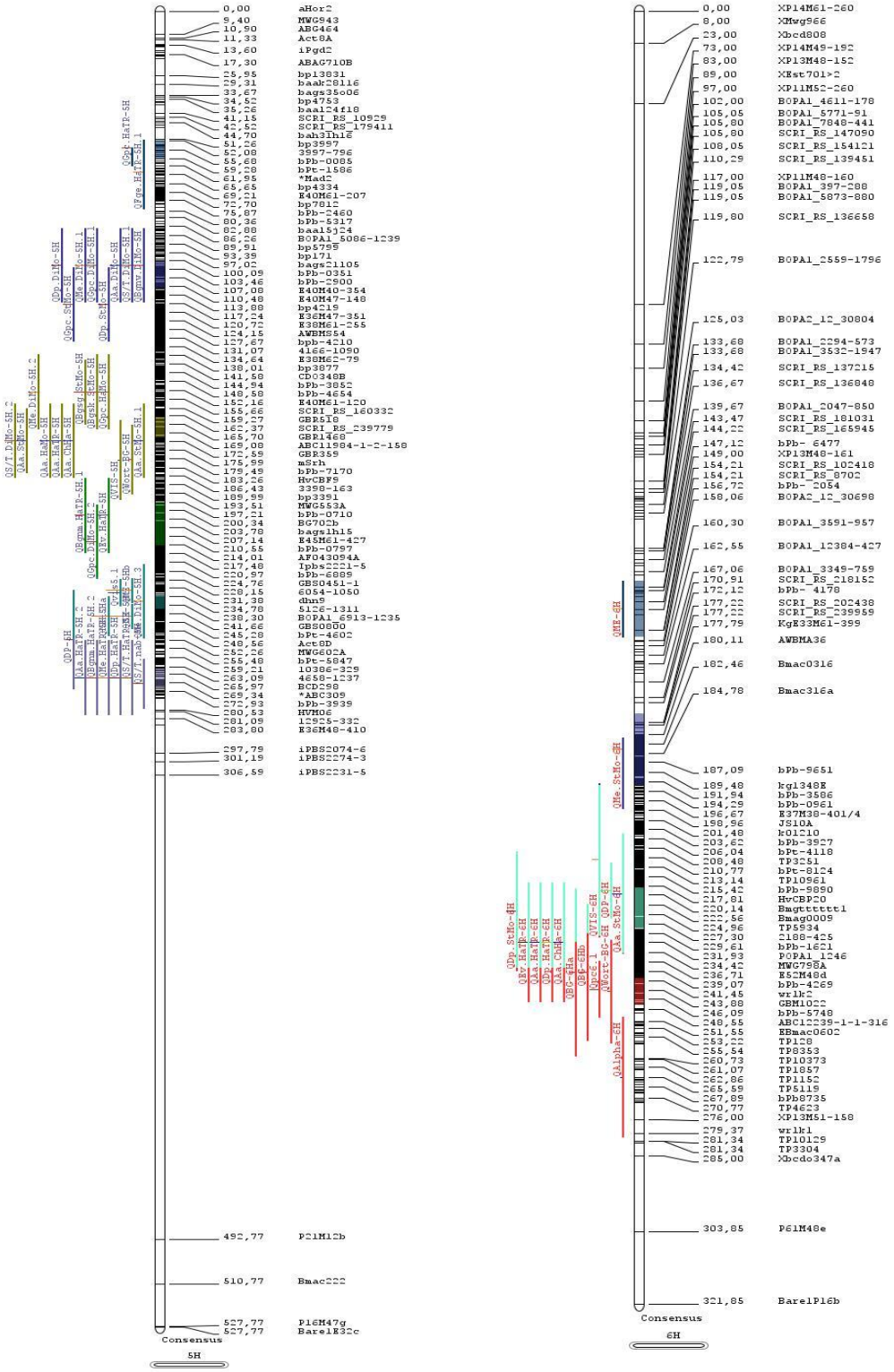

Figure 3. Genomic localization of the QTLs on chromosomes 5H and 6H for malt quality of barley in the consensus map**.**

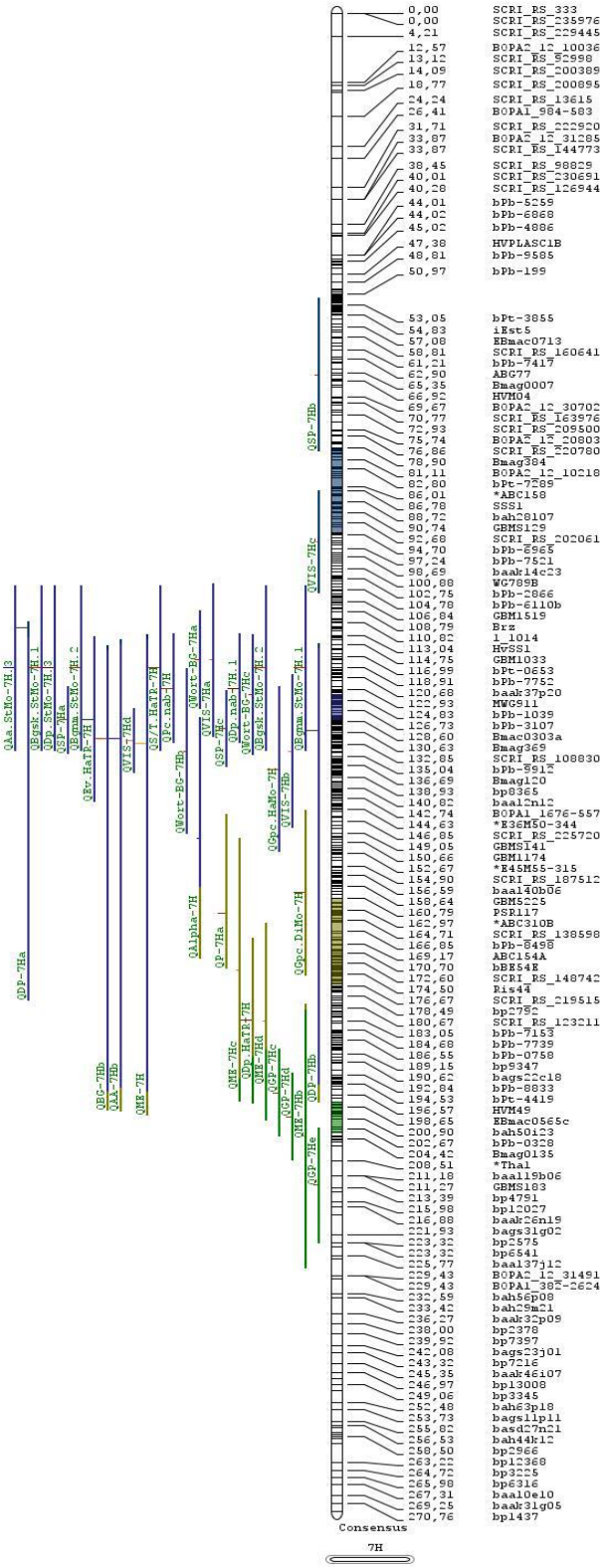

Figure 4. Genomic localization of the QTLs on chromosome 7H for malt quality of barley in the consensus map.

explained 23% of the phenotypic variation. MQTL2.3, MQTL3.4, and MQTL5.2 with 8, 5, and 8 QTLs, respectively, showed an R^2 value of 0.22. These QTLs controlled traits such as β-glucan, protein content, diastatic power, malt extract, and α-amylase (Supplementary Table 1).

Mega MQTLs related to malt quality

A total of 25 QTLs were located in MegaMQTL7.2, explaining 68% of the phenotypic variation. These MegaMQTLs included 1 QTL associated with malt extract, 4 QTLs associated with diastatic power, 4 QTLs associated with β-glucan, 4 QTLs associated with Wort β-glucan, 3 QTLs associated with viscosity, 5 QTLs associated with the protein content, and 3 QTLs associated with α-amylase. Some of these QTLs were detected in more than one MQTL. Diastatic power is the ability to hydrolyze starch into simple sugars during barley germination. Diastatic power is a key indicator of the combined activity of starch-degrading enzymes, including α-amylase, β-amylase, α-glucosidase, dextrinas, and is directly correlated with beer brewing performance and quality (Cu *et al*. 2016; Yousif and Evans 2020). Protein content is negatively correlated with malt extract and Wort β-glucan and increases the diastatic power (Yin *et al.* 2002; Sayre-Chavez *et al.* 2022). QDP-7Ha, QDp.StMo-7H.3, QDp.nab-7H.1, and QDP-7Hb are the QTLs identified for the diastatic power in this MQTL.

After MegaMQTL7.2, MegaMQTL6.3 exhibited the second-highest phenotypic variance explanation of 49%. This meta-QTL integrated 11 individual QTLs associated with five malt quality traits: diastatic power, α-amylase activity, viscosity, and β-glucan content (both grain and Wort). The co-localization of QTLs for these traits is consistent with the biochemical interdependence of barley malt quality parameters, which are collectively influenced by β-glucan levels, starch-degrading enzymes (α-amylase, β-amylase, and limit dextrinase), and total grain protein content (Yin *et al*. 2002). The structural properties of β-glucans are important in increasing the viscosity of solutions and gel formation, and their concentration, molecular weight distribution, and structure are effective in gel formation (Marconi *et al.* 2014). In general, barley malt should have low levels of β-glucan, low viscosity, and high diastatic power to be used for beer production (Kunze 2004). Two QTLs, QBG-6Ha and QBG-6Hb, which had R^2 of 0.138 and 0.172, respectively, and were detected within confidence limits of 24–66 and 28–62, were responsible for controlling β-glucan in this MegaMQTL.

MegaMQTL4.1 and MegaMQTL3.5, each with an R^2 of 0.44, are the effective MegaMQTLs identified in this study. These MegaMQTLs contained 12 and 9 QTLs, respectively. Most of the QTLs detected in these MegaMQTLs control protein-related characteristics. Soaking and germination regimes are designed to improve the quality and processing properties of malts to produce malts with high extract and soluble proteins and low viscosity. Given that barley is the main grain in malting, it

is suggested that these regimes produce malts with similar quality to the commercial barley malts (Almaguer *et al.* 2024). Malting barley not only improves processing properties, but also creates specific colors, flavors, and aromas. Different barley genotypes contribute to aroma, but flavor is most influenced by malting (Bettenhausen *et al.* 2018; Morrissy *et al.* 2023; Stewart *et al.* 2023).

Controlling the amount of modification in the grain to achieve the recommended values for each malt quality index is the goal of the maltster during the malting process. The efficiency of malt performance during the brewing process is determined by malt quality indices such as extract, soluble proteins, and viscosity (Back *et al.* 2020). Malts with lower than recommended levels of extract and soluble proteins and higher viscosity are classified as low-modified malts that perform poorly in the brewing process. Also, malts with lower viscosity and higher than recommended levels have lower quality (such as head stability and flavor stability) that ultimately affect mouthfeel (Evans and Sheehan 2002; Krebs *et al.* 2020; Lehnhardt *et al.* 2021). QVIS-3H was the only QTL identified in MegaMQTL3.5 controlling viscosity at confidence levels of 102 and 146. This QTL was located in more than one MQTL.

Physical locations of genes related to QTLs

In total, 54 unique genes were identified in the 2Mb intervals upstream and downstream of the peak position of QTLs based on the reference barley genome. The location of QTLs on the barley chromosomes is presented in Figure 5.

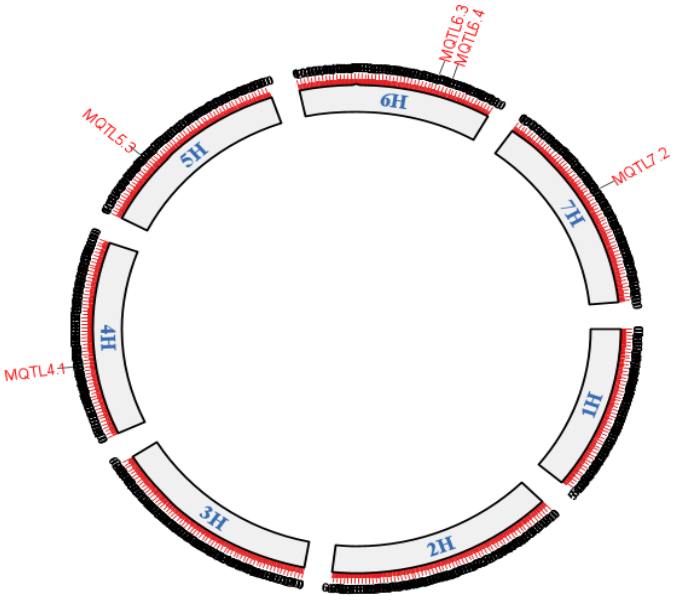

Figure 5. The location of identified QTLs on the barley chromosomes.

Gene ontology enrichment of identified genes

Gene ontology enrichment analysis illustrated that most identified genes were significantly enriched in biological processes, including monoatomic anion transport, tetracycline transmembrane transport, mRNA pseudouridine synthesis, xenobiotic transmembrane transport, and transmembrane transport (Figure 6). The results showed that significant cellular component (CC) terms were the GID (glucose-induced degradation deficient) complex and cytoplasm. In addition, significant molecular function (MF) terms, included mechanosensitive monoatomic ion channel activity, tetracycline transmembrane transporter activity, transmembrane transporter activity, and pseudouridine synthase activity (Figure 6). The KEGG pathway enrichment analysis showed that some of the identified genes were significantly enriched in the circadian rhythm pathway.

The result illustrated that the most significant biological process of the genes was monoatomic anion transport. The onion transporters are involved in signaling pathways leading to the adaptation of cells to environmental stresses (De Angeli *et al.* 2007). It was demonstrated that the regulation of the anion channels leads to regulating the pollen tube growth in plants, and it could be effective in quality traits (Stavert *et al.* 2020; Amo *et al.* 2024). The most significant molecular function was mechanosensitive ion channel activity. Mechanosensitive ion channels provide a molecular mechanism for transducing mechanical stimuli into intracellular signals (Basu *et al.* 2020; Kaur *et al.* 2020).

Co-expression network of genes

The result showed that some genes, including *AT1G13310, AT5G14020*, *MSL10, MSL9, MSL1, MSL2, MSL3, AT4G01600, AT4G40100, AT1G28200, AT5G13200, GEM*, *VAD1, AT1G34150, AT3G0695, AT1G71240, AT2G21720, AT3G18350, AT1G48840*, and *AT5G35400* were coexpressed with the identified genes (Figure 7). Some coexpressed genes appear as key players having a vital role in growth and quality traits, cell division and transport, and stress tolerance mechanisms. It was demonstrated that *AT1G13310* was involved in potassium transport, cell division, and cell death in plants (Huang *et al.* 2019). However, some mechanosensitive genes were coexpressed with the identified genes (Figure 7). Plant mechanosensitive channels participate in osmoregulation, maintenance of plastid shape, pollen tube growth, stomatal closure, and stress tolerance mechanisms (Basu *et al.* 2020; Kaur *et al.* 2020). However, *At1g28200* plays an important role in various abiotic and biotic stresses (Jiang *et al.* 2008). Therefore, the identified genes in a complex network with other co-expressed genes can be effective in the growth and development of barley.

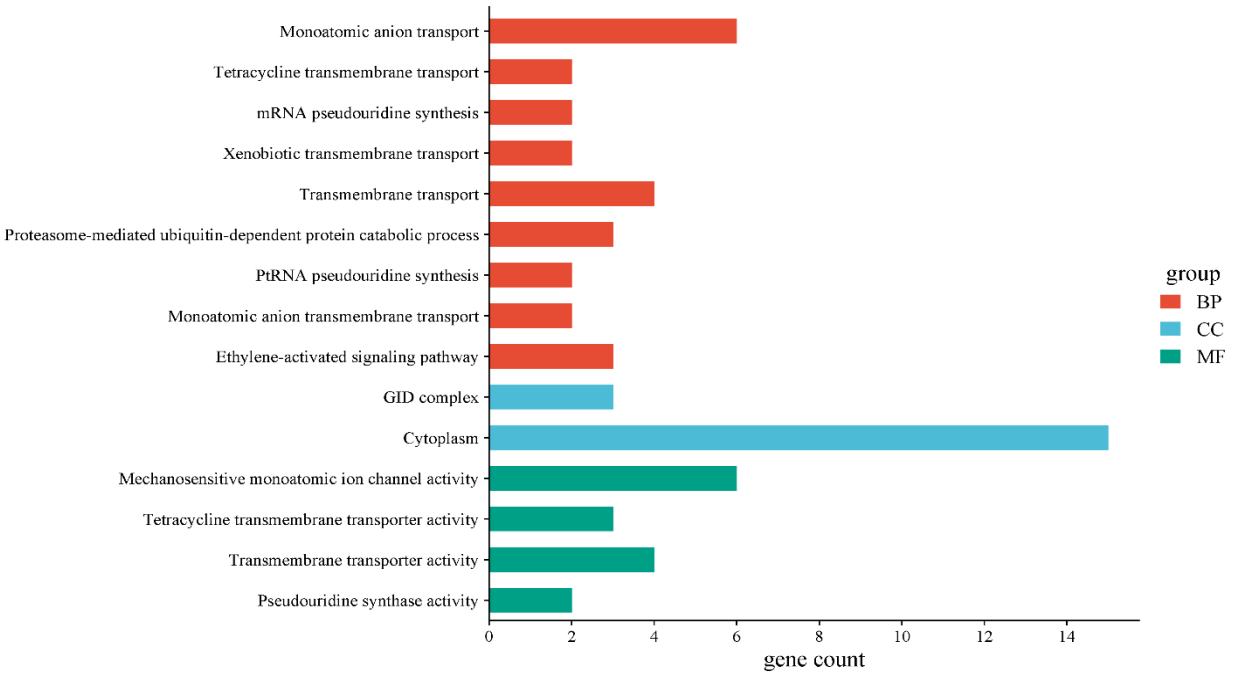

Figure 6. Bar plot of gene ontology enrichment for the identified genes with a p-value of < 0.05.

Prediction of regulatory microRNA of identified genes

The result demonstrated that the 33 unique miRNAs regulated the identified genes in barley via inhibition and translational mechanisms. Some of these miRNAs, such as hvu-miR6192, hvu-miR6184, hvu-miR6182, hvu-miR6176, hvu-miR6189, and hvu-miR6214, regulated more than one target gene (Figure 8).

The result showed that the hvu-miR6192 has six target genes in barley. Some of these genes were important in quality traits and stress tolerance in plants. For example, the *6HG0598100* (*AT3G15470*) participates in grain-quality-related traits like grain width of rice (Roy *et al.* 2024). *6HG0597730* (*AT5G08330*) was one of the target genes of hvu-miR6192. *AT5G08330* is a member of the TCP (TEOSINTE BRANCHED1/CYCLOIDEA/PROLIFERATING CELL FACTOR) family of proteins that are involved in plant biology and immunity against infectious diseases (Park *et al.* 2023). It is shown that the hvu-miR6192 has various target genes in barley and could be an important regulator of genes that were related to stress tolerance (Sabouri *et al.* 2024). However, the hvu-miR6182 regulates the defense-related target genes in barley under stress conditions (Jarošová *et al.* 2020). It was reported that the hvu-miR6184 regulates the important transcription factors that are pivotal regulators in growth, development, and responses to environmental stresses (Feng *et al.* 2024). In addition, the hvu-miR6189 is involved in the regulation of transcription factors. This suggests that

these miRNAs play an important role in plant growth and development, such as root growth and the development of leaf polarity (Li *et al.* 2022).

The results illustrated that the identified genes related to QLTs were involved in the transport and stress tolerance mechanisms of the cell. These genes were co-expressed with important genes that are related to the growth and quality traits of barley. They were regulated by important miRNAs that regulate various target genes related to important mechanisms. Therefore, the findings of this study could be helpful to improve the quality characteristics of the barley plant.

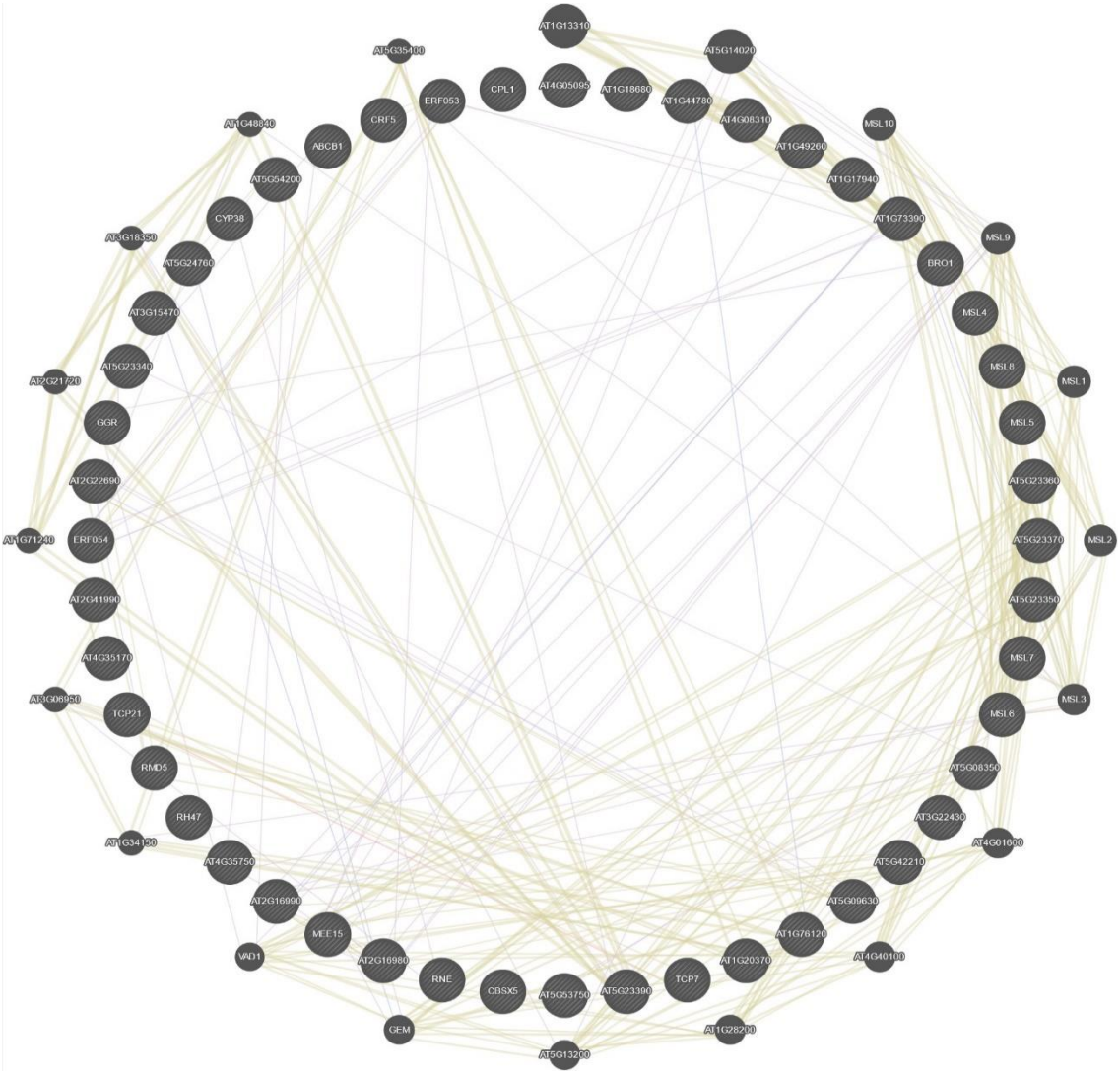

Figure 7. Co-expression network of candidate genes identified in barley meta-QTL regions, constructed using *Arabidopsis thaliana* orthologs with a false discovery rate (FDR) threshold of < 0.05.

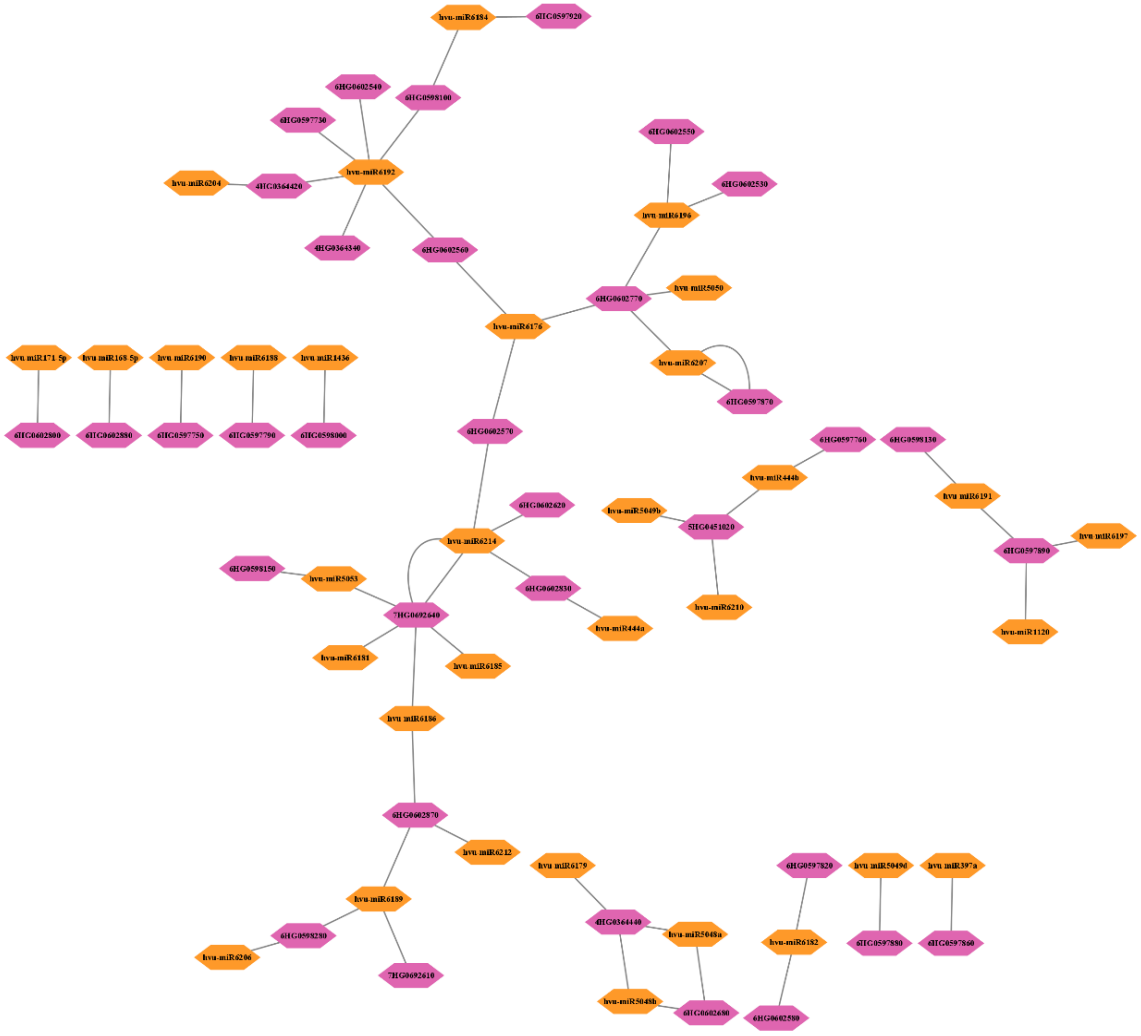

Figure 8. Regulatory microRNA network targeting candidate genes in barley malt quality meta-QTLs. Interactions were predicted via psRNATarget analysis.

Conclusion

This comprehensive meta-QTL analysis successfully integrated 184 individual QTLs from 11 contributing mapping studies (selected from 16 studies with complete data), consolidating them into 35 high-confidence MQTLs distributed across all seven barley chromosomes. The meta-analysis approach substantially refined genomic regions associated with malt quality traits, with MQTL confidence intervals considerably reduced compared to original QTLs, thereby providing more precise targets for marker-assisted selection in barley breeding programs.

The identification of MegaMQTL7.2, harboring 25 overlapping QTLs and explaining 68% of phenotypic variance for multiple malt quality characteristics, including diastatic power, β-glucan

content, viscosity, protein content, malt extract, and α-amylase activity, represents a genomic hotspot of exceptional breeding value. MegaMQTL6.3, explaining 49% of phenotypic variance and integrating 11 QTLs for diastatic power, α-amylase activity, viscosity, and β-glucan content, represents another significant breeding target. These mega-MQTLs, along with eleven major MQTLs exhibiting R^2 values exceeding 20%, constitute priority genomic regions for developing superior malting barley cultivars through marker-assisted selection and genomic selection strategies.

Gene mining within MQTL intervals identified 54 unique candidate genes significantly enriched in critical biological processes, including monoatomic anion transport, transmembrane transport, and mRNA pseudouridine synthesis. The co-expression network analysis revealed functional relationships between candidate genes and key regulatory pathways controlling mechanosensitive ion channel activity, stress tolerance, and quality trait determination. Furthermore, the identification of 33 unique miRNAs, particularly hvu-miR6192, hvu-miR6184, hvu-miR6182, hvu-miR6176, hvu-miR6189, and hvu-miR6214, which regulate multiple target genes, provides insights into post-transcriptional regulatory mechanisms governing malt quality traits.

The 11 major MQTLs identified in this study, particularly MQTL6.4 (R^2=38%), MQTL5.3 (R^2=32%), MQTL4.4 (R^2=31%), and MQTL2.2 (R^2=31%), offer immediate practical applications for marker-assisted breeding. These genomic regions control economically important traits such as α-amylase activity, diastatic power, β-glucan content, grain protein content, malt extract, and wort viscosity—all critical determinants of malting and brewing quality as defined by the ideal commercial malt criteria of American Malting Barley Association (2014).

The integration of QTL meta-analysis with functional genomics approaches employed in this study provides a robust framework for accelerating genetic improvement of barley malt quality. The identified MQTLs, candidate genes, and regulatory miRNAs represent valuable genomic resources that will facilitate the development of molecular markers for marker-assisted selection, enable targeted gene editing approaches, and support genomic selection strategies in modern barley breeding programs. Ultimately, these findings will contribute to the development of superior malting barley cultivars with enhanced quality characteristics tailored to meet the evolving demands of the global malting and brewing industries.

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Conflict of Interest

The authors declare that they have no known competing interests with any individuals or organizations concerning the subject of this article.

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