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Meta-QTL analysis of net blotch and spot blotch resistance in barley

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Abstract

Net blotch (*Pyrenophora teres*) and spot blotch (*Bipolaris sorokiniana*) are damaging foliar diseases of barley, but the quantitative trait loci (QTL) reported for resistance are scattered across mapping populations that cannot be compared directly. We meta-analysed 405 unique QTL records from 40 studies and projected the 175 with complete flanking-marker, logarithm of the odds (LOD) and phenotypic variance explained (PVE) data onto a consensus map of 29,016 markers. The Goffinet–Gerber algorithm resolved 27 meta-QTLs (mQTLs), 21 of them shared by both diseases. Meta-analysis narrowed the mean confidence interval 5.14-fold, to 11.83 cM, and raised the average LOD (9.0). Six mQTLs (MQTL1H.1, 1H.2, 4H.1, 6H.1, 6H.2 and 7H.3) met stringent criteria for QTL number, LOD and PVE. All six overlapped marker–trait associations (MTAs) from 24 genome-wide association studies, and 23 of the 27 mQTLs overlapped at least one of 757 unique MTAs. Three major mQTLs (1H.1, 6H.2 and 7H.3) span less than 12 Mb and are the most immediately useful for marker-assisted selection; the others need fine mapping. Annotation of 137 genes in seven representative regions, together with expression data from spot blotch-inoculated barley, identified 175 differentially expressed genes, including receptor-like kinase, resistance-protein-like and defence-related genes, notably in MQTL1H.1, 2H.1 and 3H.1. Candidate-gene data are still missing for three of the six major mQTLs. These regions and genes offer a prioritised resource for breeding barley with combined resistance to both diseases.

Key message

Meta-analysis of 40 studies consolidated scattered barley net blotch and spot blotch QTLs into 27 meta-QTLs, six of them major and supported by genome-wide association studies, with defence-related candidate genes.

Introduction

Barley (*Hordeum vulgare* L.) is the world's fourth most important cereal crop after wheat, rice and maize, cultivated in more than 100 countries under widely varying climates and valued as human food, livestock feed and malting raw material (Langridge 2018; Zhou 2010). Global barley production was estimated at 154.37 million metric tons in 2025–26 (USDA FAS n.d.). India produces roughly 1.86 million tonnes annually, mainly in Rajasthan, Uttar Pradesh, Madhya Pradesh and the north-eastern Gangetic plain (USDA FAS n.d.; Department of Agriculture & Farmers Welfare 2026).

Like other widely grown crops with a narrow genetic base, barley remains highly vulnerable to foliar disease. Net blotch, caused by *Pyrenophora teres*, is an increasingly damaging pathogen that occurs in two forms, net form net blotch (NFNB; *P. teres* f. *teres*) and spot form net blotch (SFNB; *P. teres* f. *maculata*) (Liu et al. 2011), while spot blotch, caused by *Bipolaris sorokiniana* (teleomorph *Cochliobolus sativus*), produces round necrotic lesions and yield losses that have been documented since at least the 1970s (Clark 1979). Depending on environmental conditions, these diseases cause yield losses of 10–40%, reaching severe levels in epidemic years (Abebe 2021), and account for a substantial share of total barley losses in major growing regions such as Australia (Murray and Brennan 2010). Because *P. teres* and *B. sorokiniana* populations are genetically diverse, resistance conferred by a single gene is rarely durable, and both pathogens exploit necrotrophic effector-triggered susceptibility mechanisms that can defeat major resistance genes (Friesen and Faris 2021; Liu et al. 2015).

Breeding for durable resistance has so far relied on quantitative trait loci (QTLs) mapped individually in dozens of biparental populations that differ in parentage, marker platform and phenotyping protocol (e.g., Bilgic et al. 2005, 2006; Bovill et al. 2010; Cakir et al. 2003, 2011; Friesen et al. 2006; Grewal et al. 2008, 2012; Gupta et al. 2010, 2011;

Lehmensiek et al. 2007; Manninen et al. 2000, 2006; Raman et al. 2003; Tamang et al. 2019; Williams et al. 1998; Wonneberger et al. 2017), so that reported intervals rarely coincide and are difficult to translate directly into breeding targets. Several major resistance and susceptibility loci have also been designated, for example *Rpt5*/*Spt1* on chromosome 6H, *Rpt4* on 7H and *Rpt6* on 5H (Liu et al. 2015, 2026).

Meta-QTL (mQTL) analysis (Goffinet and Gerber 2000; Veyrieras et al. 2007) addresses this fragmentation by projecting QTLs from independent studies onto a common consensus map and statistically clustering overlapping intervals into fewer, narrower and more robust consensus regions, an approach already used to consolidate QTL data for complex traits in other cereals (Khahani et al. 2021). In barley, meta-QTL analyses have covered abiotic stress tolerance (79 mQTLs from 337 QTLs, Li et al. 2013; 37 mQTLs, Zhang et al. 2017, as summarised by Akbari et al. 2022; 128 mQTLs from 585 QTLs, Akbari et al. 2022), grain quality (41 mQTLs from 349 QTLs, Du et al. 2024a), yield (85 mQTLs from 1,080 QTLs, Du et al. 2024b), Fusarium head blight (FHB) and deoxynivalenol (DON) accumulation (256 QTLs, Sallam et al. 2024) and multiple fungal diseases (20 meta-QTLs from 166 QTLs, including only eight net blotch and four spot blotch studies, Schweizer and Stein 2011). A recent review integrated 808 loci for net blotch and leaf scald (Liu et al. 2026). Because barley spot blotch is caused by the same pathogen as wheat spot blotch (*B. sorokiniana*), and the net blotch pathogen (*P. teres*) is a close relative of the tan spot pathogen (*Pyrenophora tritici-repentis*), we also drew on wheat studies: 19 meta-QTLs for tan spot from 104 QTLs (Liu et al. 2020) and 16 mQTLs for spot blotch from 69 QTLs (Vasistha et al. 2024). To our knowledge, however, no meta-analysis has yet been devoted to net blotch and spot blotch resistance together. Combined with *in silico* mining of the underlying physical intervals, mQTL analysis can also shortlist candidate genes for functional validation without additional field phenotyping. The present study was therefore undertaken (i) to identify consensus mQTLs for net blotch and spot blotch resistance in barley through systematic meta-analysis of published QTL studies, and (ii) to identify and functionally characterise candidate genes underlying these mQTLs using *in silico* approaches.

Materials and methods

Literature search, study selection and QTL data set

Electronic databases (PubMed, Web of Science, Google Scholar and Scopus) were searched for peer-reviewed articles published in English between 1990 and 2025, combining the terms *Hordeum vulgare*, barley, *Pyrenophora teres*, *Cochliobolus sativus* OR *Bipolaris sorokiniana*, net blotch, spot blotch, QTL, genome-wide association and resistance, with Boolean operators and truncation as appropriate to each database. Reference lists of retrieved articles and of relevant reviews were hand-searched for additional records. Studies were included if they (i) reported biparental or association-mapping populations phenotyped for net blotch and/or spot blotch resistance in barley, (ii) reported QTL or marker–trait association positions together with LOD score (or an equivalent test statistic) and percentage phenotypic variance explained (PVE), and (iii) used a marker platform for which flanking markers could in principle be located on a common consensus map. Studies were excluded when they reported disease scores without statistical QTL or association testing, when the marker data could not be resolved to named markers or positions, or when they were resistance-gene cloning or expression studies without a mapping population.

Forty studies met these criteria (Afanasenko et al. 2015; Bilgic et al. 2005, 2006; Bovill et al. 2010; Cakir et al. 2003, 2011; Carlsen et al. 2017; Dahanayaka et al. 2022; D'Souza et al. 2025; Alhashel et al. 2021; Friesen et al. 2006; Muria-Gonzalez et al. 2023; Grewal et al. 2008, 2012; Gupta et al. 2010, 2011; Haas et al. 2016; Hisano et al. 2017; Islamovic et al. 2017; König et al. 2013, 2014; Lehmensiek et al. 2007; Leng et al. 2020; Liu et al. 2015; Long et al. 2003; Ma et al. 2004; Manninen et al. 2000, 2006; O'Boyle 2009; St. Pierre et al. 2010; Abu Qamar et al. 2008; Raman

et al. 2003; Richards et al. 2024; Richter et al. 1998; Sabouri et al. 2023; Taliei et al. 2024; Tamang et al. 2019; Tyagi et al. 2008; Williams et al. 1998; Wonneberger et al. 2017), together reporting 422 QTLs on a per-study, per-trait basis. The number of QTLs, marker types and mapping method of each study are listed in Online Resource 1 (Table S1), and the population, resistance source, marker type, pathotype or isolate and inoculation stage in Table S2. Population types were doubled-haploid, recombinant inbred, F_2-derived and advanced backcross populations of 42 to 866 individuals genotyped with restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), simple sequence repeat (SSR), diversity arrays technology (DArT) and single-nucleotide polymorphism (SNP) markers. The study-selection and data-reduction workflow is shown in Fig. 1.

Consensus map construction and QTL projection

A consensus linkage map was constructed by integrating previously published individual linkage maps and consensus maps as source maps (Online Resource 1, Table S3; marker positions in Table S4) with LPmerge (Endelman and Plomion 2014) in R. Where a publication reported more than one mapping population, or contributed separate marker sets for net blotch and spot blotch phenotyping of the same population (e.g., Afanasenko et al. 2015), each cross- or trait-specific map was treated as a separate source map. LPmerge merges maps by linear programming, minimising the deviation of the consensus marker positions from the source-map positions while keeping marker order consistent across maps. The resulting map comprised 29,016 marker loci (predominantly SNPs and SSRs) across the seven barley chromosomes.

QTLs were projected onto the consensus map in BioMercator v4.2 (Arcade et al. 2004; Sosnowski et al. 2012) by homothetic scaling of the flanking-marker positions of each source study onto the corresponding consensus interval. Of the 405 unique QTL records, 175 (43.2%) carried the flanking markers, LOD score and PVE required for projection (Online Resource 1, Table S5). The remaining 230 could not be projected because the source publication reported a single linked marker instead of a flanking interval, reported markers that could not be matched to the consensus map, or omitted the LOD or PVE values needed to weight the projected interval. These QTLs stay in the catalogue but were excluded from clustering, since projection is a prerequisite for the Goffinet–Gerber algorithm.

Meta-QTL analysis

Projected QTLs were clustered into mQTLs with the Goffinet and Gerber (2000) algorithm implemented in the MetaQTL framework (Veyrieras et al. 2007) in BioMercator v4.2. For each linkage group, one to *n* underlying-QTL models (*n* being the number of projected QTLs on that chromosome) were fitted to the projected QTL positions and confidence intervals, and the model with the lowest Akaike Information Criterion was taken as the most likely number and position of true loci. QTLs assigned to a retained model component were combined into one mQTL characterised by its peak position, confidence interval (CI), the number of contributing QTLs and the average LOD and PVE of these QTLs. Singleton clusters, in which no other QTL overlaps the interval, cannot be tested for clustering, because model selection needs at least two overlapping QTLs; these four regions were excluded from the mQTL set on statistical grounds only and are listed separately (Online Resource 1, Table S6). Physical intervals (Mb) of each mQTL correspond to the positions of its flanking markers on the barley cv. Morex reference genome (Online Resource 1, Table S7).

Prioritisation of major meta-QTLs

Because the 27 mQTLs varied widely in QTL density, statistical support and interval width, a major mQTL was defined by four criteria applied jointly: (i) QTL density, at least four contributing QTLs; (ii) statistical strength, average LOD of 10 or above; (iii) effect size, average PVE of 20% or above; and (iv) precision, a CI narrow enough to be actionable relative to the other mQTLs (assessed qualitatively together with criteria i–iii, since no accepted threshold exists for heterogeneous source data). These are prioritisation thresholds chosen for this study. All four criteria had to be satisfied simultaneously. As a sensitivity check, the median LOD and PVE of the contributing QTLs were also computed (Online Resource 1, Table S7).

Validation of meta-QTLs by genome-wide association studies

Meta-QTL intervals were cross-checked against marker–trait associations (MTAs; Online Resource 1, Table S8) compiled from 24 published genome-wide association studies (GWAS; Table S9) for net blotch (15 studies) and spot blotch (9 studies) resistance. The compiled set contained 876 records (523 net blotch, 353 spot blotch), of which 757 were unique and had a valid physical position. An MTA was counted as validating an mQTL when its physical position on the same chromosome fell within the physical interval of the mQTL. MTAs were counted once per marker, position, study and disease, so that duplicated records did not inflate counts. Because several GWAS re-analysed the same panel (the AM-2014 panel in three datasets and the Novakazi et al. (2019), overlapping panels were grouped and the number of independent panels overlapping each mQTL was recorded (Table S10). The four singleton regions were treated in the same way for comparison.

Physical anchoring, candidate-gene mining and functional annotation

Candidate genes were identified in seven representative regions: the first-listed mQTL on each chromosome (MQTL1H.1, MQTL2H.1, MQTL3H.1, MQTL4H.1, MQTL5H.1 and MQTL6H.1) and, because chromosome 7H has no MQTL7H.1 among the final 27 mQTLs, the 7H singleton region (Singleton_4). Annotated genes within the physical interval of each region were retrieved from the barley cv. Morex reference genome sequence and annotated with the Database for Annotation, Visualization and Integrated Discovery (DAVID; Sherman et al. 2022), using Gene Ontology (GO) terms (biological process, molecular function, cellular component; Online Resource 1, Table S11) and Kyoto Encyclopedia of Genes and Genomes (KEGG) pathways (Table S12). Enrichment was assessed against the whole-genome background with DAVID's Benjamini–Hochberg-adjusted $P < 0.05$ threshold. Gene identifiers (HORVU.MOREX.r2) refer to the MorexV2 assembly and annotation (Monat et al. 2019), which supersedes the bacterial artificial chromosome-based MorexV1 assembly (Mascher et al. 2017). Genes identified in this way are called putative candidate genes and not resistance genes, as no functional validation was performed. The seven regions include three of the six major mQTLs (MQTL1H.1, 4H.1 and 6H.1).

In silico differential expression

In silico differential expression of the candidate genes, and of all annotated genes within the same seven intervals, was examined with BarleyExpDB (Li et al. 2023), which compares mutant and wild-type barley under mock-inoculated and spot blotch-inoculated conditions at 12, 24 and 36 h after inoculation. Genes with an absolute fold change of 2 or more were classed as differentially expressed genes (DEGs). Because the screen was not restricted to the DAVID-annotated set, the two gene lists overlap only partly. The expression evidence derives from spot blotch inoculation and is not a test of net blotch. The functional class of each DEG was assigned from its gene description by keyword rules (Online Resource 1, Table S13).

Heterogeneity, weighting and bias

Several sources of heterogeneity among the 40 source studies were considered in interpreting the results. Within the Goffinet–Gerber framework each QTL is weighted implicitly by the width of its confidence interval, so QTLs from larger populations or denser maps contribute more precision; no additional weighting by sample size was applied. Populations differed in design (42 to 866 individuals), pathogen isolate, geographic origin and disease-scoring scale (0–9 scores, percentage leaf area affected, infection-response classes), and these differences were not modelled statistically. Marker platforms ranged from RFLP and AFLP to SNP arrays and largely explain the proportion of QTLs that could be projected. Because the literature reports only loci that were detected, small-effect loci are under-represented, and developmental covariates such as heading date and plant height, which can produce spurious co-location with resistance QTLs (Sallam et al. 2024), were rarely reported and could not be assessed.

Results

Literature search and QTL data set

The 40 studies reported 422 QTLs on a per-study, per-trait basis (Online Resource 1, Table S1), from mapping populations that differed in type, resistance source and pathotype (Table S2); after collapsing records that a study reported more than once for correlated traits, environments or growth stages, 405 unique QTL records remained, of which 175 (43.2%) carried the information required for projection onto the consensus map (Table 1, Fig. 1). The 230 non-projectable QTLs remain in the catalogue but could not enter clustering. Source QTLs were spread over all seven chromosomes (Fig. 2). Net blotch QTLs were most numerous on 6H (73), 3H (62) and 5H (52) and least numerous on 1H (22), whereas spot blotch QTLs were most numerous on 7H (32) and 3H (29) and least numerous on 6H (5). Most QTLs in both diseases had LOD scores of 2–4 (114 net blotch, 51 spot blotch), but 47 net blotch and 16 spot blotch QTLs had LOD scores above 18. The PVE classes 5–10% and 10–15% were the most frequent, and 49 net blotch and 15 spot blotch QTLs explained more than 50% of the phenotypic variance.

Table 1
Data reduction from reported to projectable QTL

Category	Number	%
Reported QTL (per-study, per-trait tally)	422	100 (of reported)
Unique QTL (within-study duplicates removed)	405	96.0 (of reported)
Projectable QTL (complete flanking-marker, LOD and PVE data)	175	43.2 (of unique)
Non-projectable QTL (incomplete marker, LOD or PVE data)	230	56.8 (of unique)

Consensus map and QTL projection

The consensus map, built from the source maps listed in Online Resource 1 (Table S3; marker positions in Table S4), comprised 29,016 markers on seven chromosomes, with genetic lengths from 212.95 cM (4H) to 450.81 cM (7H) and densities from 9.58 (7H) to 16.77 (1H) markers per cM (Table 2, Fig. 3). Marker numbers ranged from 2,065 (4H) to 6,067 (1H), and density was highest on 1H and 3H and lowest on 4H and 7H. Projected QTLs varied widely in effect size even within a chromosome; on 1H, for example, LOD ranged from 2.90 (QTL-1HL-9, net blotch) to 73.90 (Rcs6-QTL-1, seedling spot blotch resistance, $R^2 = 0.93$). Among the projected QTLs for which parameters are

tabulated (n = 162, Online Resource 1, Table S5), LOD ranged from 1.14 to 96.5 (median 4.7) and PVE from 2 to 93% (median 15%).

Table 2
Consensus genetic map statistics for the seven barley chromosomes

Chromosome	Genetic length (cM)	No. of markers	Marker density (per cM)
1H	361.73	6,067	16.77
2H	360.20	4,765	13.22
3H	262.03	4,223	16.11
4H	212.95	2,065	9.69
5H	302.70	4,028	13.30
6H	230.78	3,546	15.36
7H	450.81	4,322	9.58
Whole genome	311.60 (mean)	29,016	13.30 (mean)

Meta-QTL identification

Meta-analysis of the 175 projected QTLs gave 31 clusters, of which four were supported by a single QTL and could not be tested for clustering; they were excluded (Online Resource 1, Table S6), leaving 27 mQTLs on all seven chromosomes (Table 3, Fig. 4). Of the four excluded singleton regions, three (3H, 5H and 6H) were net blotch-associated and one (7H, Singleton_4) was spot blotch-associated. Chromosome 3H carried the most mQTLs (six), followed by 1H, 2H and 4H (four each) and 5H, 6H and 7H (three each). The number of QTLs underlying an mQTL ranged from 2 (MQTL2H.3 and MQTL4H.2) to 17 (MQTL7H.3). Average LOD scores ranged from 3.28 to 30.97 (mean 9.0) and average PVE from 5.75% to 53.4% (mean 21.1%). The CI of the mQTLs ranged from 0.40 cM (MQTL4H.2) to 36.27 cM (MQTL3H.6), with a mean of 11.83 cM, a 5.14-fold reduction relative to the source QTLs; the mean CI was reduced 9.82-fold on chromosome 4H and 5.94-fold on chromosome 7H. Mean LOD and PVE of the mQTLs (9.0; 21.1%) were close to those of the source QTLs (8.7; 21.7%), as expected for averaged values, so the gain from meta-analysis lies in interval precision and consensus and not in effect size.

Table 3
Summary of the meta-QTL (mQTL) analysis for net blotch (NB) and spot blotch (SB) resistance in barley

mQTL	Chr	No. of QTLs	Peak/CI (cM)	Physical interval (Mb)	Avg. LOD	Avg. PVE (%)	Disease	MTAs[a]
MQTL1H.1	1H	5	10.62/12.40	0.6–5.06	30.97	53.4	NB, SB	2 (1/1)
MQTL1H.2	1H	4	49.69/18.89	5.06–244.65	17.06	33.65	NB, SB	52 (8/44)
MQTL1H.3	1H	5	61.5/3.58	22.44–24.07	4.91	12.52	NB, SB	0
MQTL1H.4	1H	6	94.64/23.03	435.52–482.19	4.67	12.92	NB, SB	12 (10/2)
MQTL2H.1	2H	11	10.1/5.12	4.43–630.02	3.34	10.76	NB, SB	53 (22/31)
MQTL2H.2	2H	8	20.79/16.12	26.35–507.77	6.00	18.33	NB, SB	15 (8/7)
MQTL2H.3	2H	2	52.11/14.75	30.15–178.63	3.88	7	SB	11 (7/4)
MQTL2H.4	2H	9	75.06/11.46	26.10–545.53	6.74	13.73	NB	23 (8/15)
MQTL3H.1	3H	5	7.24/5.68	3.94–282.89	8.71	11.98	NB, SB	80 (36/44)
MQTL3H.2	3H	10	32.54/7.20	13.91–20.89	6.74	22.01	NB, SB	32 (7/25)
MQTL3H.3	3H	4	50.65/18.40	150.42–597.54	3.83	10.75	NB, SB	51 (48/3)
MQTL3H.4	3H	3	57.85/4.06	462.04–587.42	3.62	14.1	NB, SB	35 (32/3)
MQTL3H.5	3H	11	81.17/1.87	192.53–490.01	3.71	8.54	NB, SB	17 (16/1)
MQTL3H.6	3H	3	101.05/36.27	462.28–555.63	6.06	12.6	NB, SB	21 (19/2)
MQTL4H.1	4H	4	49.45/2.40	12.19–495.09	11.66	26.75	NB, SB	21 (19/2)
MQTL4H.2	4H	2	60.1/0.40	155.63–529.09	3.28	5.75	SB	13 (3/10)
MQTL4H.3	4H	7	77.45/6.63	6.37–6.75	8.68	17.64	NB, SB	0
MQTL4H.4	4H	4	104.66/20.03	569.32–571.43	9.24	22.73	NB, SB	0
MQTL5H.1	5H	5	33.75/19.96	380.93–426.57	3.73	24.26	NB, SB	3 (3/0)
MQTL5H.2	5H	16	57.45/3.56	21.02–486.313	4.62	21.94	NB, SB	18 (17/1)
MQTL5H.3	5H	3	80.24/7.27	319.65–508.61	11.90	18.13	SB	13 (12/1)
MQTL6H.1	6H	6	37.09/8.97	19.58–540.63	17.45	48.4	NB	120 (117/3)
MQTL6H.2	6H	4	45.32/6.36	22.28–33.77	30.43	46.52	NB	4 (3/1)

mQTL	Chr	No. of QTLs	Peak/CI (cM)	Physical interval (Mb)	Avg. LOD	Avg. PVE (%)	Disease	MTAs[a]
MQTL6H.3	6H	7	58.54/8.28	106.79–159.07	3.61	33.04	NB, SB	10 (10/0)
MQTL7H.2	7H	4	81.16/27.08	4.26–4.44	6.16	15.57	NB, SB	0
MQTL7H.3	7H	17	113.4/8.89	32.61–39.45	17.61	34.94	NB, SB	3 (0/3)
MQTL7H.4	7H	6	121.84/20.85	42.64–47.59	4.48	11.74	NB, SB	1 (0/1)

[a] Number of unique GWAS marker–trait associations (MTAs) whose physical position lies within the mQTL interval, with net blotch/spot blotch MTAs in parentheses. The four excluded singleton regions are given in Online Resource 1 (Table S6); flanking markers and the QTLs underlying each mQTL are in Table S7. Chr, chromosome; Avg., average; CI, confidence interval; LOD, logarithm of the odds; PVE, percentage phenotypic variance explained.

Conserved and disease-specific meta-QTLs

Twenty-one of the 27 mQTLs (77.8%) were associated with both net blotch and spot blotch, and six were disease-specific: MQTL2H.4, MQTL6H.1 and MQTL6H.2 with net blotch alone and MQTL2H.3, MQTL4H.2 and MQTL5H.3 with spot blotch alone (Table 3). The source QTLs allow this overlap to be resolved further (Online Resource 1, Table S7). In 14 of the 21 shared mQTLs, spot blotch QTLs co-clustered with SFNB QTLs only, in one with NFNB QTLs only, in four with both forms, and in two with net blotch QTLs whose form was not specified. The overlap between the two diseases therefore rests mainly on SFNB QTLs, and whether NFNB shares these regions cannot be judged from the present data. The three net blotch-specific mQTLs are of particular interest for targeted net blotch breeding, and MQTL6H.1 and MQTL6H.2 carry two of the highest average PVE values in the study. The spot blotch-specific MQTL5H.3 (average LOD 11.90) is comparable in statistical strength to several shared mQTLs despite three contributing QTLs.

Prioritisation of major meta-QTLs

Six mQTLs met all four criteria: MQTL1H.1, MQTL1H.2, MQTL4H.1, MQTL6H.1, MQTL6H.2 and MQTL7H.3 (Table 4). MQTL1H.1 had the highest average LOD (30.97) and PVE (53.4%), followed by MQTL6H.1 (48.4%) and MQTL6H.2 (46.52%) for PVE, and MQTL7H.3 integrated the largest number of QTLs (17). All six overlapped at least one GWAS-derived MTA (next section), but they differ in physical precision and in the strength of GWAS support. MQTL1H.1 (4.5 Mb), MQTL6H.2 (11.5 Mb) and MQTL7H.3 (6.8 Mb) span narrow physical intervals and are realistic near-term fine-mapping and marker-validation targets. MQTL1H.2 (~ 240 Mb), MQTL4H.1 (~ 483 Mb) and MQTL6H.1 (~ 521 Mb) span very broad intervals despite narrow genetic CIs (for example, the 2.40 cM CI of MQTL4H.1 corresponds to ~ 483 Mb), a pattern consistent with suppressed recombination in pericentromeric regions of barley chromosomes; they are promising targets for fine mapping rather than immediately deployable markers. MQTL3H.1 had more overlapping MTAs (80) than any major mQTL but did not qualify as major because its average PVE was 11.98%, which shows why the criteria were applied jointly and not on GWAS support alone.

The criteria based on averages are sensitive to a few very high values. The median LOD of the contributing QTLs was below 10 in five of the six major mQTLs (only MQTL1H.2 kept a median LOD of 10 or more), and the median PVE stayed at or above 20% in five of the six (MQTL4H.1 fell to 13%; Table 4, Online Resource 1, Table S7). The high average LOD of MQTL1H.1 is driven by the two Rcs6 QTLs (LOD 57.33 and 73.90; R^2 0.88 and 0.93), which behave

like major genes. The LOD criterion should therefore be read as identifying regions with at least one very strong contributing QTL.

Table 4
The six major meta-QTLs for net blotch and spot blotch resistance in barley

mQTL	Physical interval (Mb)	Span (Mb)	No. of QTLs	Avg. LOD (median)	Avg. PVE % (median)	Flanking markers	MTAs (NB/SB); studies, independent panels
MQTL1H.1	0.6–5.06	4.5	5	30.97 (9.40)	53.4 (34.0)	SNP_11381_87/bags30b07	2 (1/1); 2 studies, 2 panels
MQTL1H.2	5.06–244.65	~ 240	4	17.06 (11.16)	33.65 (28.5)	LG14_48968303/bPb3217.1	52 (8/44); 12 studies, 11 panels
MQTL4H.1	12.19–495.09	~ 483	4	11.66 (5.00)	26.75 (13.0)	8982_26043486/XBmac906	21 (19/2); 9 studies, 9 panels
MQTL6H.1	19.58–540.63	~ 521	6	17.45 (7.95)	48.4 (46.0)	GBM1270/bPb-2969	120 (117/3); 16 studies, 14 panels
MQTL6H.2	22.28–33.77	11.5	4	30.43 (7.52)	46.52 (24.0)	11_20745/ISSR-C9	4 (3/1); 4 studies, 3 panels
MQTL7H.3	32.61–39.45	6.8	17	17.61 (7.15)	34.94 (21.0)	SCRI_RS_168638/28949631	3 (0/3); 1 study, 1 panel

Median LOD and PVE are those of the QTLs contributing to each mQTL (Online Resource 1, Table S7). MTA, GWAS marker–trait association; NB, net blotch; SB, spot blotch. Avg., average; LOD, logarithm of the odds; PVE, percentage phenotypic variance explained.

Validation of meta-QTLs by genome-wide association studies

The 24 GWAS came from panels of 94 to 3,490 genotypes analysed in 13 countries or regions (Table 5) and represent 21 independent panels (Online Resource 1, Table S8 for the 876 MTA records and Table S9 for the studies). Of the 27 mQTLs, 23 (85.2%) overlapped at least one unique MTA (range 1–120; 610 mQTL–MTA overlaps in total), and four (MQTL1H.3, MQTL4H.3, MQTL4H.4 and MQTL7H.2) overlapped none (Online Resource 1, Table S10). Twenty-one mQTLs overlapped net blotch MTAs, 21 overlapped spot blotch MTAs, and 19 overlapped both. All six major mQTLs were supported: MQTL6H.1 (120 MTAs from 16 studies and 14 panels), MQTL1H.2 (52 MTAs, 12 studies, 11 panels), MQTL4H.1 (21 MTAs, 9 studies), MQTL6H.2 (4 MTAs, 4 studies, 3 panels), MQTL7H.3 (3 MTAs, one study) and MQTL1H.1 (2 MTAs, 2 studies). MQTL3H.1 had the most overlapping MTAs from independent panels (80 MTAs, 15 panels). For the disease-specific mQTLs, MTAs of the matching disease predominated in MQTL6H.1 (117 of 120 net blotch MTAs), MQTL6H.2 (3 of 4) and MQTL4H.2 (10 of 13 spot blotch), but not in MQTL2H.3 (7 net blotch, 4 spot blotch), MQTL2H.4 (8 net blotch, 15 spot blotch) or MQTL5H.3 (12 net blotch, 1 spot blotch). The four singleton regions overlapped 8, 3, 5 and 7 MTAs, respectively. Because the physical intervals of several mQTLs span hundreds of Mb, overlap can arise by chance, and validation is most informative for the narrow intervals (MQTL6H.2 and MQTL1H.1) and for mQTLs supported by many independent panels.

Table 5
Genome-wide association studies (GWAS) contributing marker–trait associations (MTAs) used to validate the meta-QTLs

Panel (no. of genotypes)	Genotyping platform	MTAs	Model	Country	Reference
Net blotch					
298 (EEBC)	iSelect SNP (7,842 SNPs)	20	MLM	East Africa	Adhikari et al. 2019
3,490 (elite breeding lines)	BOPA1 and BOPA2 (1,536 SNPs)	59	MLM	USA	Adhikari et al. 2020
336 (AM-2014 panel)	9K iSelect (6,519 SNPs)	39	MLM	USA	Amezrou et al. 2018
336 (spring barley, AM-2014)	9K iSelect (6,519 SNPs)	74	MLM	USA	Amezrou et al. 2018
376 (Barley CAP)	BOPA (3,072 SNPs)	14	MLM	USA	Burlakoti et al. 2017
282 (Turkish wild barley)	PCR-GBS (530 SNPs)	14	CMLM, FarmCPU	Turkey	Clare et al. 2021
234 (diverse genotypes)	Illumina NextSeq 500 (2,354 SNPs)	18	MLM	Ethiopia	Daba et al. 2019
654 (barley genotypes)	DArTseq (35,049 SNPs)	38	MLM	Australia	Fowler 2018
122 (diverse genotypes)	GBS (18,525 SNPs)	12	MLM, GLM, FarmCPU	Egypt	Esmail et al. 2023
431 (European landraces)	DArTseq (10,153 SNPs)	17	GAPIT	Poland	Czembor and Czembor 2023
188 (*Ptt* isolates)	SilicoDArT (14,286 DArT, 6,662 SNPs)	38	MLM	Australia	Martin et al. 2020
449 (worldwide landraces and cultivars)	50k iSelect (33,818 SNPs)	32	CMLM	Germany	Novakazi et al. 2019
261 (HI-AM)	DArTseq (19,493 SNPs)	83	MLM	Morocco	Rehman et al. 2025
957 (World Barley Core Collection)	9K iSelect (6,525 SNPs)	46	GLM, MLM	USA	Richards et al. 2017
94 (Siberian spring barley)	50K SNP chip (27,319 SNPs)	19	GLM, MLM	Russia	Rozanova et al. 2019
Spot blotch					
94 (spring barley)	50K iSelect (44,040 SNPs)	77	GLM	Russia	Bykova et al. 2017
360 (advanced inbred lines)	BOPA1 (1,096 SNPs)	8	MEMQ	Latin America	Gutiérrez et al. 2015
336 (AM-2014 panel)	9K iSelect (6,519 SNPs)	25	MLM	India	Gyawali et al. 2018

Panel (no. of genotypes)	Genotyping platform	MTAs	Model	Country	Reference
Net blotch					
350 + 250 (DIV panel)	50k SNP chip (30,145 SNPs)	6	MLM	USA	Kunze et al. 2024
449 (VIR association panel)	50k iSelect (33,818 SNPs)	38	CMLM	Russia	Novakazi et al. 2019
340 (elite two-row spring barley)	GBS 1.0 (21,364 SNPs)	29	MLM	Australia	Roy et al. 2025
200 (spring barley)	50k SNP array (25,068 SNPs)	137	MLM, GLM, FarmCPU	Canada	Tucker et al. 2024
1,480 (barley core collection)	9k iSelect (6,244 SNPs)	20	Naïve, IBS, MDS, PCA	USA	Wang et al. 2017
3,072 (BCAP)	BOPA1 and BOPA2 (3,072 SNPs)	13	MLM	USA	Zhou and Steffenson 2013

MTA counts are those reported by each study (523 for net blotch, 353 for spot blotch). CMLM, compressed mixed linear model; GAPIT, Genome Association and Prediction Integrated Tool; GLM, general linear model; MEMQ, multi-environment multi-QTL model; MLM, mixed linear model. The AM-2014 panel (three datasets) and the Novakazi et al. (2019) panel (two datasets) were each counted as one independent panel. CAP and BCAP, Barley Coordinated Agricultural Project; BOPA, barley oligonucleotide pool assay; DArT, diversity arrays technology; FarmCPU, fixed and random model circulating probability unification; GBS, genotyping-by-sequencing; IBS, identity by state; MDS, multidimensional scaling; PCA, principal component analysis; SNP, single-nucleotide polymorphism; VIR, Vavilov Institute of Plant Genetic Resources.

Named resistance and susceptibility loci within meta-QTLs

Six mQTLs included QTLs designated in the source studies as named loci (Table 6): the Rcs6 spot blotch QTLs in MQTL1H.1, *Rpt6* in MQTL5H.1, *Rpt4* in MQTL7H.3, Rpt-type net blotch loci from chromosome 6H in MQTL6H.1 and MQTL6H.2, and the *rpt.k*/*rpt.r* loci, now designated *Spt1.K*/*Spt1.R*, in MQTL6H.3. *Rpt4* and *Rpt6* have been described as spot form net blotch loci (Liu et al. 2026), which fits their occurrence in shared mQTLs that also contain spot blotch QTLs.

Table 6
Named loci among the QTLs contributing to the meta-QTLs

mQTL	Named locus (source QTL designation)	Description in the literature
MQTL1H.1	Rcs6-QTL-1, Rcs6-QTL-2	Seedling spot blotch resistance locus *Rcs6* on the short arm of 1H, the recessive allele of the dominant susceptibility gene *Scs6* (Steffenson et al. 1996; Bilgic et al. 2006; Leng et al. 2018)
MQTL5H.1	*Rpt6*	Designated spot form net blotch locus on 5H (Liu et al. 2026)
MQTL6H.1	Rpt-CIho2291, Rpt	Net blotch resistance loci from CIho 2291 (O'Boyle 2009) and Rpt-type loci from chromosome 6H (Abu Qamar et al. 2008)
MQTL6H.2	Rpt-Nomini	Net blotch resistance locus from cultivar Nomini (O'Boyle 2009)
MQTL6H.3	*rpt.k*, *rpt.r* (*Spt1.K*, *Spt1.R*)	Dominant susceptibility loci at the *Rpt5*/*Spt1* locus on 6H (Abu Qamar et al. 2008; Liu et al. 2026)
MQTL7H.3	*Rpt4*	Designated spot form net blotch resistance locus on 7H (Liu et al. 2026)

Candidate genes

Functional annotation of the seven representative regions gave 137 unique putative candidate genes (Online Resource 1, Table S11). Gene numbers per region were 27 (MQTL1H.1), 36 (MQTL2H.1), 20 (MQTL3H.1), 17 (MQTL4H.1), 6 (MQTL5H.1), 18 (MQTL6H.1) and 13 (7H singleton region). GO classification covered cellular component, molecular function and biological process (Resource 2: Fig. S1), with binding, catalytic activity, cellular process and metabolic process the most frequent categories and immune system process a small class (0.2%). Protein kinase activity was the most frequent molecular-function term (13 genes, plus five annotated with the related term kinase activity); eight genes carried the term ADP binding, which is commonly assigned to nucleotide-binding adaptor shared by APAF-1, R proteins and CED-4 (NB-ARC)-type resistance proteins, and ten carried defence-response terms (three each in MQTL1H.1 and MQTL2H.1, two in MQTL3H.1, one each in MQTL4H.1 and MQTL5H.1 and none in MQTL6H.1 or the 7H region). Oxidoreductase and monooxygenase terms (11 genes) and heme binding (6 genes) were also recurrent. KEGG enrichment was tested on the 112 genes with KEGG annotation. Ten pathways were significant at Benjamini-adjusted $P < 0.05$, led by biosynthesis of secondary metabolites (37 genes, $P = 1.22 \times 10^{-11}$), metabolic pathways (47 genes, $P = 3.38 \times 10^{-10}$) and protein processing in the endoplasmic reticulum (12 genes, $P = 6.44 \times 10^{-6}$), followed by peroxisome (6 genes, $P = 0.0035$) and glutathione metabolism (6 genes, $P = 0.0099$). The plant–pathogen interaction pathway (5 genes) was not significant ($P = 0.34$; Online Resource 1, Table S12).

Spot blotch-responsive expression of candidate regions

Differential expression within the seven regions was examined with BarleyExpDB in mutant and wild-type barley under mock and spot blotch-inoculated conditions at 12, 24 and 36 h. The screen identified 175 unique DEGs (Online Resource 1, Table S13): 33 in MQTL1H.1, 43 in MQTL2H.1, 33 in MQTL3H.1, 21 in MQTL4H.1, 8 in MQTL5H.1, 19 in MQTL6H.1 and 18 in the 7H singleton region. Because the screen covered all annotated genes in the intervals, 123 of the 175 DEGs (70.3%) were among the 137 annotated candidate genes and 52 were additional spot blotch-responsive genes. Hierarchical clustering (Resource 3: Fig. S2) separated samples first by treatment (mock versus inoculated) and then by time point, with mutant and wild-type samples of the same treatment and time point adjacent to each other; genes formed two broad reciprocal clusters, one with higher and one with lower expression in inoculated samples.

Classification of the DEGs by gene description (Table 7, Online Resource 1, Table S13) showed that 29 of 175 (16.6%) encoded resistance-protein-like proteins (8), receptor-like or Lr10-type kinases (9) or other kinases, phosphatases and U-box proteins (12), and 17 encoded defence, redox or cell-wall proteins. R-protein-like and receptor-like kinase genes were concentrated in MQTL1H.1, MQTL2H.1 and MQTL3H.1, whereas MQTL6H.1 contained none and MQTL4H.1 was dominated by defence-related and stress-protein genes such as oxalate oxidase 2 and class I heat shock proteins. This classification is annotation-based, and 103 DEGs were uncharacterised or of other function.

Table 7
Functional classes of the differentially expressed genes (DEGs) in the seven representative regions

Region	Candidate genes	DEGs	R-protein-like[a]	Receptor-like kinases[b]	Other kinases[c]	Defence, redox, cell wall	TFs[d]	Examples of DEGs
MQTL1H.1	27	33	1	4	3	6	3	Lr10-like kinases (two), RGA4-like protein, defensin Tm-AMP-D1.2-like, glutathione S-transferases
MQTL2H.1	36	43	3	2	4	3	1	RPM1, RGA3 and RGA4 proteins, receptor-like kinases, peroxidase 1-like, laccase-15-like
MQTL3H.1	20	33	3	2	2	2	0	Pik-2-like and RPM1-like proteins, Lr10-like kinase, wall-associated receptor kinase 2-like, germin-like protein 8–8
MQTL4H.1	17	21	0	0	1	4	1	Oxalate oxidase 2, class I heat shock proteins, NF-YA7-like
MQTL5H.1	6	8	1	0	1	0	0	EDS1L-like protein
MQTL6H.1	18	19	0	0	1	1	0	Class III heat shock protein; four secondary-metabolism genes
7H singleton	13	18	0	1	0	1	1	SERK2-like LRR receptor kinase, NAC domain protein 48-like, sulfiredoxin
Total	**137**	**175**	**8**	**9**	**12**	**17**	**6**	103 DEGs of other or unknown function

[a] Disease-resistance protein (RGA, RPM1, Pik-2-like) and EDS1-like genes. [b] Receptor-like, wall-associated, SERK and Lr10-type rust-resistance kinases. [c] Other protein kinases, phosphatases and U-box proteins. [d] Transcription factors and regulators. The 20 secondary-metabolism genes (cytochrome P450, synthases, transferases, reductases) are not shown as a column. Classes were assigned by keyword rules from gene descriptions (Online Resource 1, Table

S13). RGA, resistance gene analogue; RPM1, resistance to *Pseudomonas syringae* pv. *maculicola* 1; EDS1, enhanced disease susceptibility 1; LRR, leucine-rich repeat; SERK, somatic embryogenesis receptor kinase; NAC, NAM, ATAF and CUC; NF-Y, nuclear factor Y.

Discussion

This meta-analysis condensed a fragmented body of barley QTL literature into 27 mQTLs and, from these, six priority regions that combine high QTL density with strong statistical support. All six overlap GWAS-derived MTAs. Three of them, MQTL1H.1, MQTL6H.2 and MQTL7H.3, also have narrow physical intervals (4.5, 11.5 and 6.8 Mb) and are the most immediately testable for marker-assisted selection (MAS) and fine mapping. MQTL1H.2, MQTL4H.1 and MQTL6H.1 combine strong statistical and GWAS support with very broad pericentromeric intervals (~ 240, ~ 483 and ~ 521 Mb) and are better regarded as fine-mapping targets. The depth of GWAS support also differs: MQTL6H.1 and MQTL1H.2 overlap MTAs from many independent panels, whereas MQTL7H.3 and MQTL1H.1 overlap only three and two MTAs from one and two studies.

Among earlier barley meta-QTL studies on disease resistance, the closest is that of Schweizer and Stein (2011). They identified 20 meta-QTLs from 166 QTLs of 28 studies (6,986-marker map) covering six pathogens, eight of them (40%) hot spots for several diseases. Only eight net blotch and four spot blotch studies contributed, and their meta-QTLs were derived from the midpoints of at least three overlapping QTLs, without LOD or PVE weighting. Here, 21 of 27 mQTLs (77.8%) are shared between net blotch and spot blotch. The higher share probably reflects our restriction to two related foliar pathogens, whereas their hot spots spanned six pathogens with different lifestyles. Liu et al. (2026) integrated 808 loci for net form net blotch, spot form net blotch (SFNB) and leaf scald on the Morex V3 assembly and delineated 94 QTL-rich clusters and 42 multi-disease regions, but did not cover spot blotch caused by *B. sorokiniana*. They also reported that only 33% of SFNB QTLs were detected in more than one study, which underlines the value of the consensus approach applied here. The FHB and DON meta-analysis of Sallam et al. (2024), based on 256 QTLs (including 96 FHB and 57 DON QTLs and agro-morphological traits) placed on a consensus map, found that only three FHB and five DON QTLs combined large effect, cross-environment consistency and independence from heading date and plant height. This supports stringent, multi-criterion prioritisation and shows that these covariates should be examined before any major mQTL is used in MAS.

Several of our regions consolidate known loci. MQTL6H.1 and MQTL6H.2 include Rpt-type net blotch loci from 6H (Table 6) and coincide with the 6H hotspot for major-effect net blotch resistance in biparental studies (Abu Qamar et al. 2008; Liu et al. 2015; Richards et al. 2024). MQTL7H.3 integrates 17 QTLs, including *Rpt4*, and MQTL1H.1 and MQTL1H.2 lie on chromosome 1H, where QTLs for both diseases have repeatedly been reported (Bilgic et al. 2006; Tamang et al. 2019). Their added value is the combined support across studies. A formal classification of all 27 mQTLs as novel or known would require re-projecting earlier meta-QTLs onto the present physical map.

The overlap between the two diseases is consistent with shared necrotrophic effector-triggered susceptibility mechanisms and overlapping host defence pathways in *P. teres* and *B. sorokiniana* (Friesen and Faris 2021; Liu et al. 2015), and with the polygenic nature of durable, horizontal resistance to necrotrophs (Nelson 1978). It should nevertheless be read with caution. The overlap rests mainly on spot blotch QTLs co-clustering with SFNB QTLs, and literature-derived evidence cannot separate a shared mechanism from (i) correlated phenotyping of the two diseases within a study, (ii) physically linked but functionally independent loci within the same interval, or (iii) broad intervals (several hundred Mb, Table 3) that mechanically raise the chance of apparent co-location. The GWAS evidence adds a further caution: the MTAs overlapping the disease-specific MQTL2H.3, MQTL2H.4 and MQTL5H.3 were mostly from the other disease. Fine mapping and disease-specific challenge of near-isogenic lines at the major

mQTLs are needed to test whether the two diseases share resistance genes. For breeders, the pattern suggests that resistance to both diseases could be pyramided through a limited number of shared target regions.

Barley meta-QTL studies on other traits provide a second benchmark. The 6 QTLs per mQTL found here (171 QTLs) lie within the range of the abiotic stress (4, Li et al. 2013; 4.6, Akbari et al. 2022; see also Zhang et al. 2017), grain quality (9, Du et al. 2024a) and yield (13, Du et al. 2024b) studies, which rested on larger data sets of 337–1,080 QTLs. GWAS support (85.2%) exceeded that of the grain quality (25 of 41, 61%) and yield (68 of 85, 80%) mQTLs (Du et al. 2024a, b), and overlap between traits was far greater (77.8% of mQTLs shared by two diseases, against 22.8% of abiotic stress mQTLs with overlapping CIs; Li et al. 2013). Major regions are proportionally more frequent here (6 of 27, 22%) than the mega-mQTLs of Akbari et al. (2022) (three of 128, 2.3%, each explaining more than 30% of the phenotypic variation) or their other major mQTLs with R^2 above 20% (eight of 128, 6.3%). The 52 mQTLs listed in their Table 3 had R^2 of 1–55% (mean 13.4%, calculated from that table), lower than our mean PVE of 21.1%. Our mean CI of 11.83 cM (a 5.14-fold reduction) is wider than the 1.66 and 2.76 cM of the grain quality and yield mQTLs (about 9-fold and 7.86-fold reductions; Du et al. 2024a, b). This may reflect the wide CIs of many source disease QTLs and our lower projection rate (43.2%, against 50.3% for 585 of 1,162 QTLs in Akbari et al. 2022). The physical CIs of the 52 abiotic stress mQTLs listed by Akbari et al. (2022) spanned only 0.85–35.5 Mb (median 9.7 Mb, calculated from their Table 3), far narrower than our median of 125 Mb (Table 3), which underlines the need to refine the boundaries of our broad mQTLs.

Because barley spot blotch is caused by the same pathogen as wheat spot blotch, and the tan spot pathogen (*P. tritici-repentis*) is a close relative of *P. teres*, wheat meta-QTL studies on these two diseases offer a useful comparison. Tan spot yielded 19 meta-QTLs from 104 QTLs (5.5 per meta-QTL), with PVE of 6.0–27.4%, LOD of 3.9–17.0 and CI of 0.8–14.8 cM (mean 5.0 cM, calculated from Table 2 of Liu et al. 2020). Spot blotch yielded 16 mQTLs from 69 QTLs (4.3 per mQTL), with mean PVE of 13.5%, mean LOD of 5.3 and mean CI of 16.5 cM, a 4.6-fold reduction (Vasistha et al. 2024). The barley ranges (PVE 5.75–53.4%, LOD 3.28–30.97, CI 0.40–36.27 cM) are similar, with higher means (LOD 9.0, PVE 21.1%). These are driven largely by major-effect QTLs such as the two *Rcs6* QTLs in MQTL1H.1 (Table 4), and they are close to the averages of the source barley QTLs (LOD 8.7; PVE 21.7%), so the main gain of the barley meta-analysis lies in interval precision and consensus. The share of major regions (6 of 27, 22%) is close to that of wheat spot blotch (4 of 16, 25%; Vasistha et al. 2024) and tan spot (3 of 19, 16%; Liu et al. 2020), although our thresholds (average LOD of 10 or above and PVE of 20% or above) are higher, reflecting the wider spread of values in the barley data. Our GWAS overlap (85.2%) lies within the 38.7–90.5% reported for wheat meta-QTL studies (reviewed in Vasistha et al. 2024, where 12 of 16 mQTLs were validated) and exceeds the 7 of 19 tan spot meta-QTLs (36.8%) that co-located with QTLs from association studies (Liu et al. 2020). Tan spot meta-QTLs likewise showed wide physical intervals despite narrow CIs (for example 65.7–262.1 Mb for MQTL-2A.2, CI 2.6 cM) and co-localised with the known effector-sensitivity genes *Tsc1*, *Tsc2* and *Tsn1*, much as several barley mQTLs contain named loci (Table 6). Finally, our projection rate of 43.2% lies within the 44.0–75.2% reported for other wheat disease meta-analyses (Jan et al. 2021; Kumar et al. 2023; Saini et al. 2022) and slightly above the 36.8% (84 of 228 QTLs) of wheat spot blotch, and our PVE, LOD and CI ranges resemble those of wheat meta-QTLs for three rusts (Pal et al. 2022) and multiple disease resistance (Saini et al. 2022).

The candidate-gene profile is functionally diverse and not dominated by a single mechanism (Resource 2: Fig. S1). MQTL1H.1, the region with the highest average LOD and PVE, carried genes annotated with defence responses to fungi, several *Lr10*-type rust-resistance and receptor-like kinases, an RGA4-like resistance protein and glutathione S-transferases. Receptor-like kinases are primary sensors of pathogen-associated molecular patterns (Goff and Ramonell 2007), and their strong presence in MQTL1H.1, MQTL2H.1 and MQTL3H.1 is consistent with, but no proof

of, pattern-triggered immunity contributing to the quantitative resistance captured by these mQTLs. R-protein-like genes (RGA3, RGA4, RPM1, Pik-2-like, EDS1L-like) were among the DEGs in four regions, and transcription factors (MADS-box, NAC, NF-Y, zinc-finger) in four, in line with the role of transcription factor families such as WRKY and NAC in defence signalling (Eulgem and Somssich 2007; Chen et al. 2023). This echoes the barley findings of Schweizer and Stein (2011), who found receptor-like kinases, class III peroxidases and vesicle-transport genes, but not nucleotide-binding leucine-rich repeat (NB-LRR) genes, over-represented in powdery mildew meta-QTLs, together with up-regulated secretion and cell-wall genes (phenylalanine ammonia-lyase and class III peroxidases). The receptor-like kinase, peroxidase and laccase genes among our DEGs (Table 7) are compatible with this pattern, although no over-representation test was performed here. In wheat, nucleotide-binding site (NBS) and/or leucine-rich repeat (LRR)-like proteins dominated the candidate genes of 16 of the 19 tan spot meta-QTLs (Liu et al. 2020), and 411 of 516 candidate genes in wheat spot blotch were linked to biotic stress (Vasistha et al. 2024). The scale of our candidate-gene set (137 annotated genes and 175 DEGs, 123 shared) is comparable to earlier barley meta-QTL studies, which reported 67 abiotic stress-responsive candidate genes (Li et al. 2013), 2,593 genes in 52 mQTLs of which 191 were expression-responsive (Akbari et al. 2022) and 17 barley orthologs of rice and maize yield genes (Du et al. 2024b). MQTL6H.1, one of the highest-effect mQTLs, differed from the other regions. It had no defence-response GO terms and no R-protein-like or receptor-like kinase DEGs, and its annotated genes were mostly metabolic, histone and other functions. Its resistance effect may therefore be mediated by mechanisms other than classical receptor genes, or by genes outside the annotated interval. All genes are described as putative or expression-associated candidates, since no knockout, overexpression or allelism test was performed.

The expression evidence supports the spot blotch side of the candidate-gene set. In the heatmap, treatment and time point structured the samples more than genotype, so the mutant versus wild-type contrast contributes little to the pattern. The 175 DEGs are therefore a hypothesis-generating shortlist of spot blotch-responsive genes within the intervals, not confirmation of any gene's role in resistance to either disease. No comparable net blotch resource was available, and only one public dataset was used.

Several practical applications follow. For MAS, the flanking markers of the major mQTLs (Table 4), particularly the narrow, GWAS-supported MQTL6H.2, MQTL7H.3 and MQTL1H.1, are immediately testable diagnostic marker candidates, whereas the broad-interval mQTLs need fine mapping first; all should be checked for confounding with heading date and plant height. For gene pyramiding, the high proportion of shared mQTLs suggests that a small number of introgression targets could combine net blotch and spot blotch resistance, subject to the caveats above. For genomic selection, the 27 mQTLs and their flanking markers can weight prediction models or define marker sets enriched for blotch resistance (Iwata and Jannink 2011; Nielsen et al. 2016). For parental selection, landrace collections, which harbour net blotch resistance alleles absent from modern elite germplasm (D'Souza et al. 2025), can be screened for favourable alleles at the major mQTLs. In target environments such as north-eastern India, the shortlisted genes provide starting points for allele mining and functional validation, for example by clustered regularly interspaced short palindromic repeats (CRISPR)-based knockout or transgenic overexpression.

This study has limitations inherent to literature-based meta-analysis. Source studies differed in population size, marker density, isolates and scoring method in ways that could not be corrected, and only 175 of 405 QTLs (43.2%) carried the information needed for projection. Average LOD and PVE are sensitive to a few very high values from major-gene QTLs, and LOD values from different statistics are not strictly comparable. The physical intervals of several mQTLs are very broad because of low recombination near centromeres, which reduces the specificity of GWAS overlap and gene retrieval. GWAS support depends on the panels available to date, and the absence of overlapping MTAs in four mQTLs does not indicate that they are spurious. Candidate-gene and expression profiling

covered seven representative regions and three of the six major mQTLs (MQTL1H.1, MQTL4H.1 and MQTL6H.1), so MQTL1H.2, MQTL6H.2 and MQTL7H.3 still lack candidate-gene and expression data. Extending the analysis to them, with domain-level classification of resistance-gene families, is the most important next step. Gene classes were assigned from annotations and not from domain analysis, the expression evidence is specific to spot blotch and drawn from one database, and no candidate gene has been validated functionally. Publication bias towards detected loci cannot be corrected without raw data.

Conclusions

Meta-analysis of 40 studies resolved 27 mQTLs for barley net blotch and spot blotch resistance and identified six major regions for prioritisation. All six overlap independent GWAS associations, and three of them (MQTL1H.1, MQTL6H.2 and MQTL7H.3) have physical intervals below 12 Mb that make them realistic near-term targets for marker development and fine mapping, whereas MQTL1H.2, MQTL4H.1 and MQTL6H.1 need fine mapping first. Most mQTLs (21 of 27) were shared between the two diseases, largely through spot blotch and spot form net blotch QTLs, pointing to overlapping genomic control alongside a smaller set of disease-specific regions. Annotation of 137 genes in seven representative regions and expression screening identified 175 spot blotch-responsive genes, including receptor-like kinase, R-protein-like and defence-related genes, but this resource covers only three of the six major mQTLs. Extending it to the remaining three, testing shared versus disease-specific effects by fine mapping, and functional validation of shortlisted genes are the next steps towards resistant cultivars.

Declarations

Author contribution statement

B.L. and T.A. contributed equally to this work. N.K.V. conceived and designed the study. B.L. and T.A. performed the literature search, consensus map construction, meta-QTL analysis and candidate-gene mining under the supervision of N.K.V. B.L., T.A. and N.K.V. analysed the data and wrote the first draft. All authors read and approved the final manuscript.

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Data availability. The QTL, marker–trait association, candidate-gene and expression data compiled and analysed in this study are provided in Online Resource 1.

Code availability. No custom code was used. Analyses were run with publicly available software (LPmerge in R, BioMercator v4.2, DAVID and BarleyExpDB).

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Figures

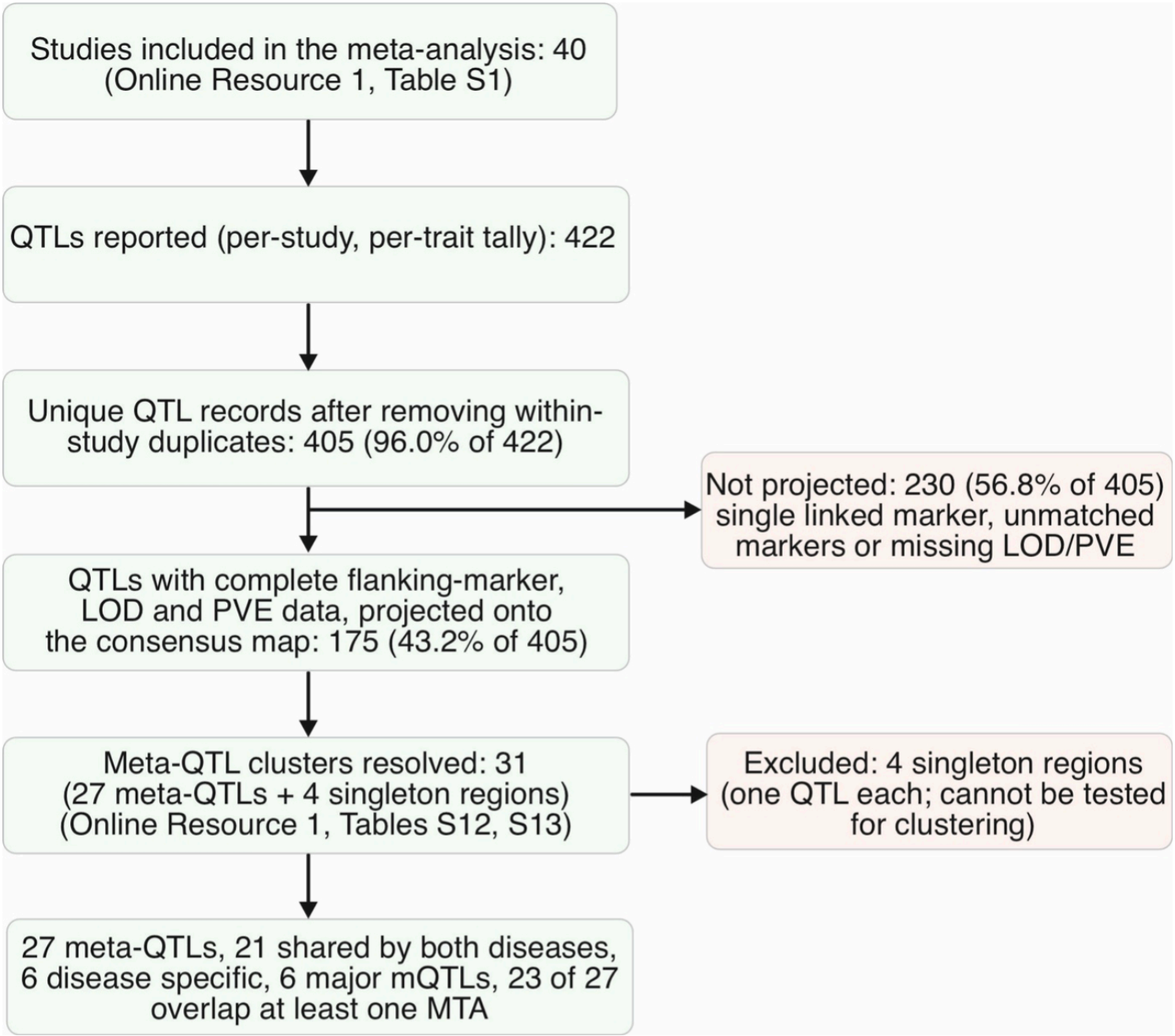


Figure 1

Study-selection and data-reduction flow diagram for the meta-analysis. PVE, phenotypic variance explained; MTA, marker–trait association

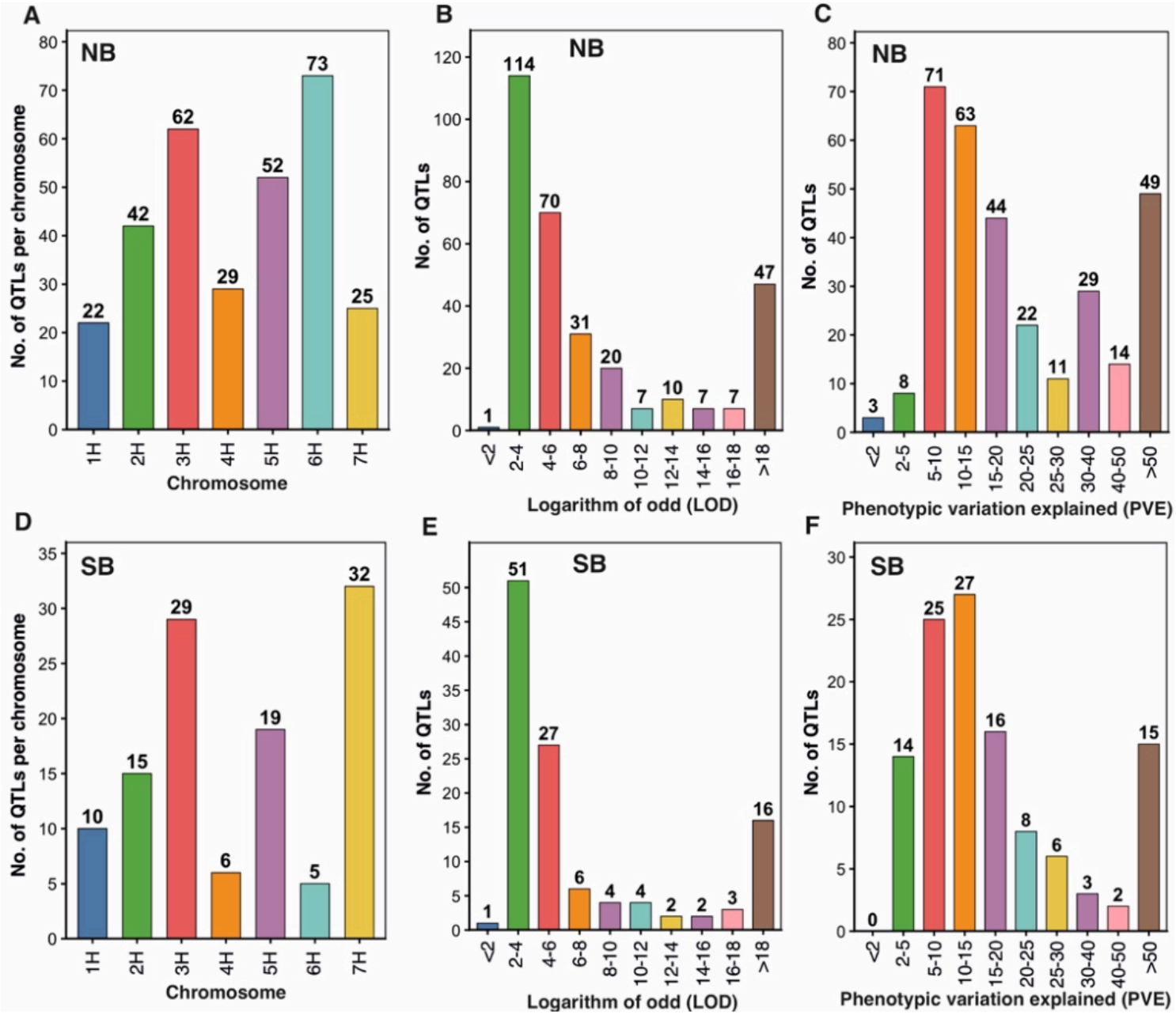


Figure 2

Distribution of the literature-derived QTLs for net blotch (NB, panels A–C) and spot blotch (SB, panels D–F) resistance in barley by chromosome (A, D), LOD score (B, E) and percentage phenotypic variance explained (PVE; C, F)

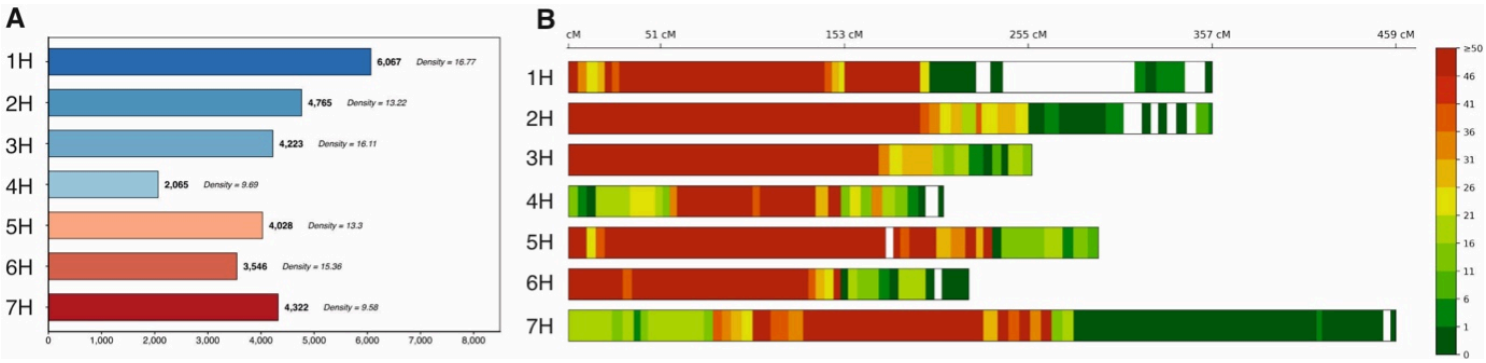


Figure 3

The barley consensus map. **A** Total marker count and density per chromosome. **B**Marker density along each chromosome (colour scale: markers per cM, dark red highest, dark green and white lowest)

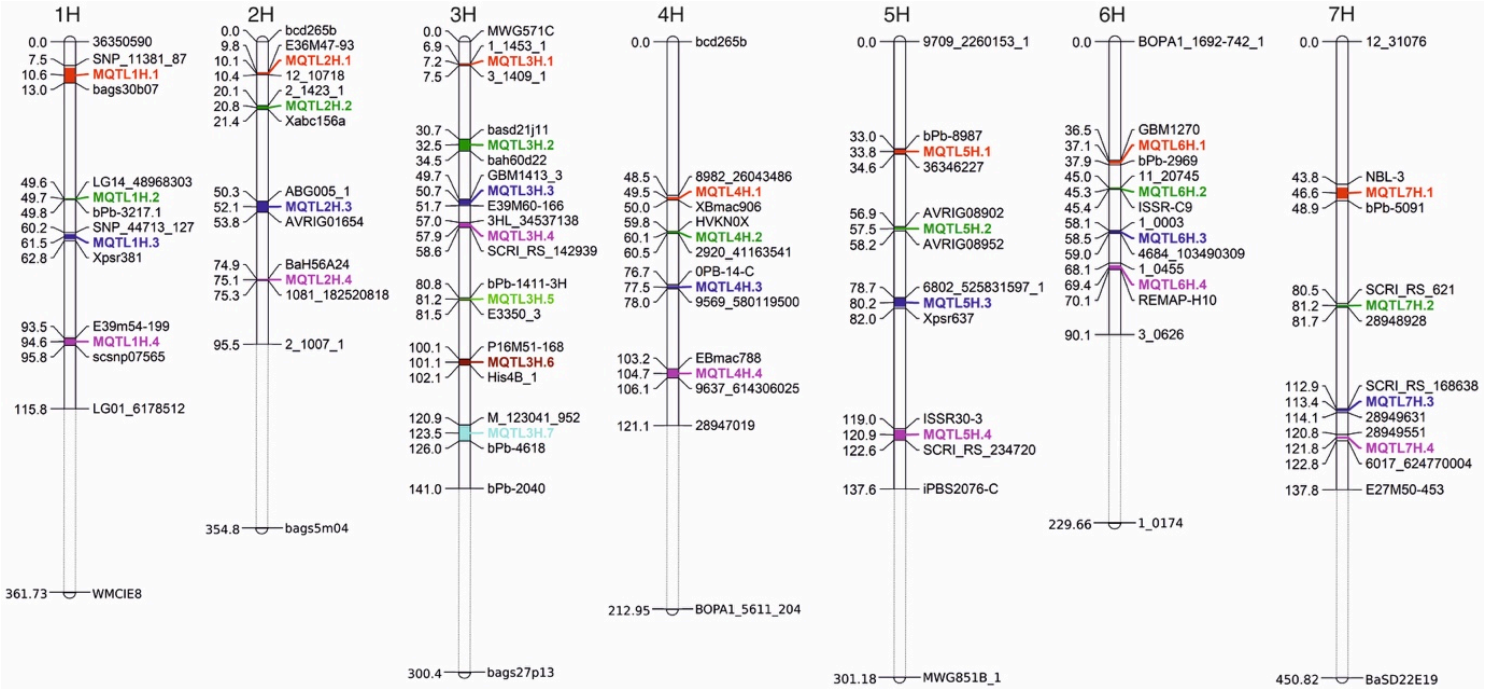


Figure 4

Consensus linkage map of the seven barley chromosomes with the positions of the 27 meta-QTLs relative to their flanking markers. MQTL3H.7, MQTL5H.4, MQTL6H.4 and MQTL7H.1 in the figure denote the four excluded singleton regions; they are not among the 27 mQTLs

Supplementary Files

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