



Meta-QTL analysis and candidate genes identification for various abiotic stresses in maize (*Zea mays* L.) and their implications in breeding programs

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Abstract Global climate change leads to the concurrence of a number of abiotic stresses including moisture stress (drought, waterlogging), temperature stress (heat, cold), and salinity stress, which are the major factors affecting maize production. To develop abiotic stress tolerance in maize, many quantitative trait loci (QTL) have been identified, but very few of them have been utilized successfully in breeding

programs. In this context, the meta-QTL analysis of the reported QTL will enable the identification of stable/real QTL which will pave a reliable way to introgress these QTL into elite cultivars through marker-assisted selection. In this study, a total of 542 QTL were summarized from 33 published studies for tolerance to different abiotic stresses in maize to conduct meta-QTL analysis using BiomecatorV4.2.3. Among those, only 244 major QTL with more than 10% phenotypic variance were preferably utilised to carry out meta-QTL analysis. In total, 32 meta-QTL possessing 1907 candidate genes were detected for different abiotic stresses over diverse genetic and environmental backgrounds. The MQTL2.1, 5.1, 5.2, 5.6, 7.1, 9.1, and 9.2 control different stress-related traits for combined abiotic stress tolerance. The candidate genes for important transcription factor families such as ERF, MYB, bZIP, bHLH, NAC, LRR, ZF, MAPK, HSP, peroxidase, and WRKY have been detected for different stress tolerances. The identified meta-QTL are valuable for future climate-resilient maize breeding programs and functional validation of candidate genes studies, which will help to deepen our understanding of the complexity of these abiotic stresses.

Key message A total of 32 meta-QTL conferring tolerances to different abiotic stresses in maize were identified from 244 initial major QTL detected in 33 published QTL mapping studies.

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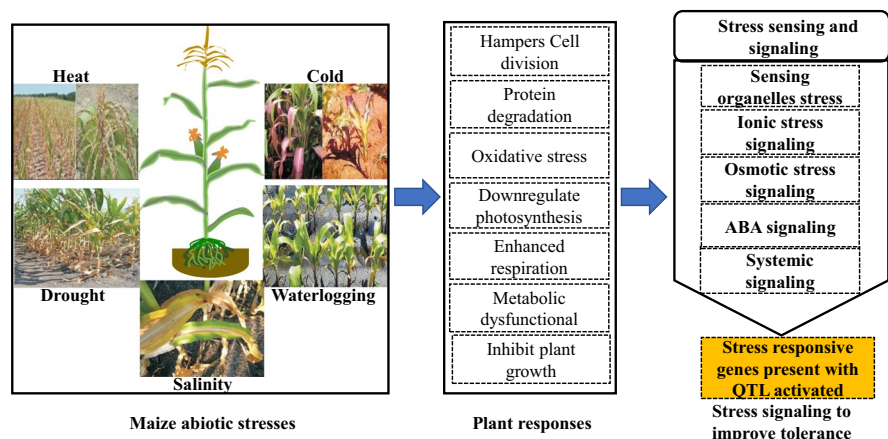
Introduction

Maize (*Zea mays* L.) also known as ‘queen of cereals’ is widely grown for food, feed, and industrial purposes to support a large portion of the world population (Sheoran et al. 2021). In recent past, it has gained importance as a source of bio-ethanol and envisaged as a potential crop to diversify the rice-based cropping system in the Indo-Gangetic plains of India (Rakshit et al. 2021). It is mainly cultivated under marginal land areas prone to rain-fed conditions imposing different kinds of biotic and abiotic stresses. Maize production largely depends on suitable climatic conditions (Gong et al. 2014), but the extreme climate-changing scenario generates several abiotic stresses like drought, heat, salinity, waterlogging, and cold stress (Krasensky and Jonak 2012; Prakash et al. 2020; Gadag et al. 2021). These abiotic stresses affect the maize growth and development processes significantly reducing global yield potential (Mittler 2006; Qin et al. 2011) (Fig. 1). To counter the negative impacts of these abiotic stresses, advancements in molecular breeding can aid in developing stress-tolerant cultivars. Various studies have been conducted to detect many quantitative trait loci (QTL) imparting tolerance for these abiotic stresses in maize (Zaidi et al. 2015; Zhao et al. 2018a; Van Inghelandt et al. 2019). The utilization of maize cultivars with desirable tolerance to these stresses is the most cost-effective approach for preventing stress damages.

The QTL analysis provides information on chromosomal regions controlling specific traits that can

be further transferred to target cultivars through marker-assisted breeding programs. Over the last few decades, QTL analyses have increased across crop species due to recent advances in genotyping platforms (Bohra et al. 2020; Kumar et al. 2021). However, a fraction of the reported QTL has been successfully utilized in marker-assisted selection (MAS) in breeding programs due to numerous factors, such as limited marker-trait association, a low number of markers used in mapping, small phenotypic variance explained, differences in the genetic backgrounds, and environmental effects (William et al. 2007; Tuberosa 2012). Many QTL have been identified for drought, waterlogging, heat, cold, and salinity tolerance in maize as reviewed by Prasanna et al. (2021). However, these QTLs have been identified from different genetic backgrounds being evaluated in diverse environments following dissimilar techniques of QTL detection, thus limiting their utility by different researchers. A meta-QTL analysis of these different experimental findings can be effective in refining the number and position of the QTL and identify stable and large effect QTL. Meta-QTL analysis enables the mapping of QTL on the same chromosome for different traits detected in different mapping populations with lower confidence intervals (CI) (Goffinet and Gerber 2000; Kaur et al. 2021). So far, meta-QTL analysis has been conducted successfully for drought tolerance in rice (Courtois et al. 2009; Khowaja et al. 2009; Khahani et al. 2021), cotton (Said et al. 2013), maize (Zhao et al. 2018a; Liu et al. 2019), and wheat (Soriano and Alvaro 2019), for abiotic stress tolerance in barley (Zhang et al. 2017),

Fig. 1 Different maize abiotic stresses (drought, waterlogging, heat, cold, and salinity) and plant responses against these stresses at molecular level in addition to the stress signalling to induce tolerance



salt tolerance in rice (Islam et al. 2019), heat and drought tolerance in wheat (Acuña-Galindo et al. 2015), leaf senescence in *Arabidopsis* (Chardon et al. 2014), flowering time in maize (Chardon et al. 2004; Wang et al. 2016a), yield-related traits in wheat, (Zhang et al. 2010), and popping traits in maize (Kaur et al. 2021). However, except for drought (Zhao et al. 2018a), meta-QTL analysis for targeting different abiotic stresses tolerance in maize has not been reported. Hence, the present study was conducted to identify the meta-QTL (MQTL) controlling different abiotic stresses tolerance in maize. The identified MQTL with refined positions and decreased CI will be valuable resources for further MAS, candidate gene mining, pathway analysis, and various other purposes like functional annotation of genes, ortho meta-QTL analysis, and linking associations with genome-wide studies.

Materials and methods

QTL database development

An exhaustive literature review was carried out from published QTL mapping studies in maize for different traits (like grain yield, flowering time, and other agronomic-based traits) that regulate abiotic stresses. From 1994 to 2019, information for 542 QTL from 33 published studies was summarized for drought (238), waterlogging (61), heat (82), cold (93), and salinity (68) tolerance in maize (Fig. 2a; Table S1). During data compilation, the QTL identified under control conditions were excluded as they were detected under normal conditions. The information related to genetic maps and various parameters of stress tolerance QTL was used in the analysis. For the meta-QTL analysis, the QTL with more than 10% or 75th percentile of phenotypic variance were used in the analysis as

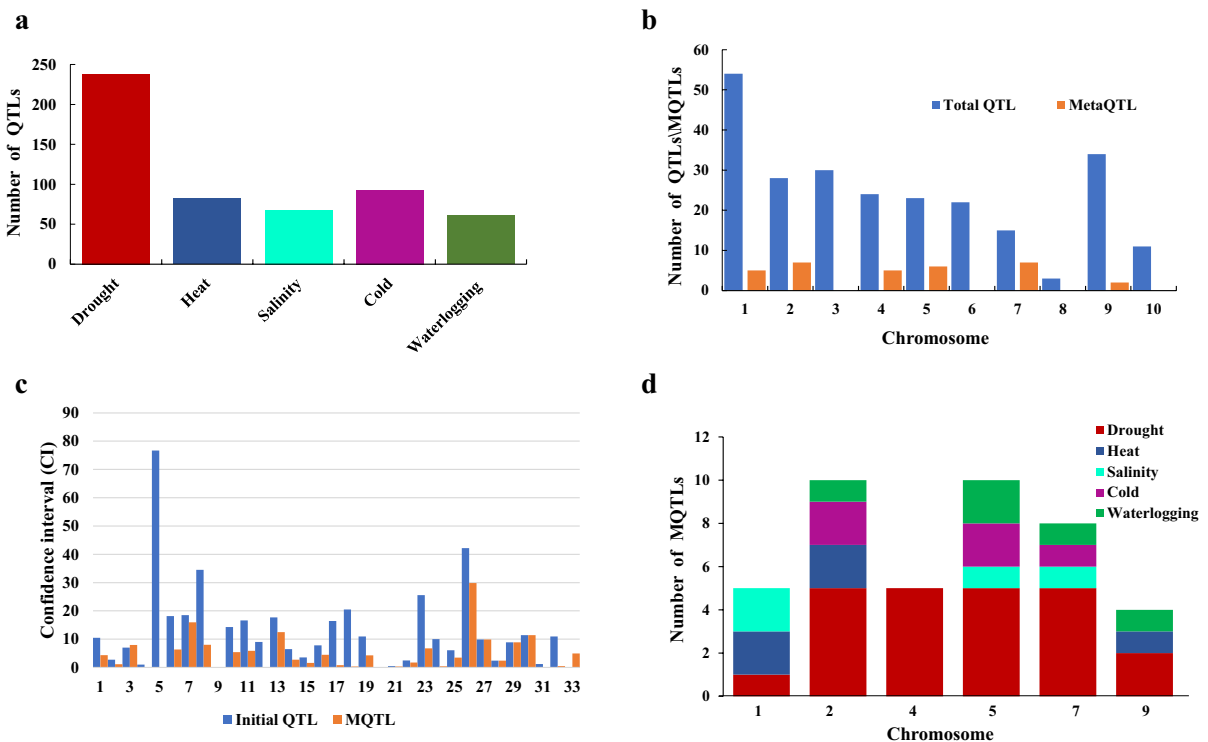


Fig. 2 **a** Summary of initial QTL for different abiotic stresses in maize used for meta-QTL analysis. **b** Chromosome wise meta-QTL detected from 244 initial QTL for abiotic stresses in maize. **c** Confidence interval (CI) of detected MQTL and

initial QTL residing within these MQTL. **d** Chromosome wise distribution of meta-QTL detected for different abiotic stresses tolerance on whole maize genome

these are potential candidates to be utilised for MAS (Collard et al. 2005; Rossi et al. 2019). For salinity and waterlogging studies, mostly minor QTL (with less than 10% phenotypic variance) have been reported; hence, for these traits, minor QTLs were also considered for the analysis. After filtering with the above criteria, a total of 244 initial QTLs were used for meta-QTL analysis. For different studies, the mapping populations size varied from 75 to 302 progenies including F_2 (12), F_3 (2), F_4 (1) backcross (BC) (1), doubled haploid (DH) (2), and recombinant inbred lines (RILs) (15) populations phenotyped at different locations and years (Table 1).

Consensus map and QTL projection

A high-resolution map, 'ISU Integrated IBM 2009', available on MaizeGDB (https://www.maizegdb.org/data_center/map) was used as a reference map to construct the consensus map as it has high marker density with different types of markers. It consists of 9073 markers with a total length of 2400.97 cM. A SNP marker-based dataset (Dell'Acqua et al. 2015) was also integrated into the reference map for the inclusion of SNP-based QTL studies as applied by Khahani et al. (2021). To conduct the meta-QTL analysis, the algorithmic-based 'MetaQTL' software was used for QTL projection in XML file format (https://www.bioinformatics.org/downloads/list.php?group_id=693). For QTL projection on the consensus map, LOD (logarithm of odd) value, phenotypic variance (R^2), QTL positions, and CI were compiled from published studies to conduct the meta-QTL analysis. For most of the studies, the QTL position was already given based on the position of the flanking marker on the consensus map. The QTL without positions were assigned positions as per the flanking markers. The QTL which lacked CI was calculated using the $530/N \times R^2$ approach for F_2 and BC, while $163/N \times R^2$ for RIL population-based studies (Darvasi and Soller 1997), where N is the size of population and R^2 is the phenotypic variance explained by each QTL.

Meta-QTL analysis

Following the generation of consensus map and QTL projection, 'BioMercator V4.2.3' was used for MQTL detection (Arcade et al. 2004; Veyrieras et al. 2007; Sosnowski et al. 2012) (<https://urgi.versailles.inra.fr>

[Tools/BioMercator-V4](#)). The meta-QTL analysis first determined the number of potential MQTL on each chromosome from different experiments based on best model values, i.e. AIC (Akaike information content), AICc (AIC correction), AIC3 (AIC 3 candidate models), BIC (Bayesian information criterion), and AWE (average weight of evidence). The QTL models with the lowest value in at least three of the five models were used to determine the number of MQTL on each chromosome (Swamy et al. 2011; Chardon et al. 2014). The physical positions within 95% CI of each MQTL were calculated, and the flanking markers for each MQTL were selected from Maize GDB database (<http://maizegdb.org/>).

Candidate gene identification

The locus lookup browser (www.maizegdb.org) was used to determine the physical position of the flanking markers. In case of flanking markers without physical position, the next closest outer marker was used to detect genomic coordinates of the MQTL. The physical lengths of the obtained MQTL were determined to retrieve candidate genes linked with abiotic stresses from the maizeGDB database. Further, the 'qTeller' tool available on maizeGDB was used for identifying genes present within the MQTL physical interval by selecting the expression datasets of B73 genome version 4 for particular stresses only (Woodhouse et al. 2021).

In silico expression analysis of identified candidate genes

The in silico expression analysis of identified candidate genes under drought, heat, cold, and salinity stress was carried out obtaining the transcriptome data for these abiotic stresses from Hoopes et al. (2019). From the publicly available abiotic stress experiment datasets, the transcriptomic data for the identified candidate genes in the current study was extracted. In previous experiments, to induce abiotic stresses such as drought, salt, and temperature stress (heat and cold), the plant roots (Opitz et al. 2014), leaves, and whole plant tissues above the ground (Makarevitch et al. 2015) were used. The data included the stress treatments as roots exposed to drought stress at 0 MPa (mega Pascal), low MPa, and very low MPa water potential for six and 24 h, above-ground whole tissue exposed to temperature stress

Table 1 Details of independent QTL mapping studies for various abiotic stress tolerance used for meta-analysis in maize

S. No	Populations number	Population type	Parents of population	Population size	Marker	QTL identified	Traits phenotyped/QTL identified per traits	Reference
Drought stress								
1	1	F ₂	DTP79 × B73	116	SSR	45	Grain yield (5), number of rows per ear (5), number of kernels per row (7), kernel weight (5), ear length (5), ear diameter (5), kernel length (2), kernel width (6), kernel thickness (5)	Nikolić et al. (2013)
2	1	F ₃	SD34 × SD35	230	RFLP	11	Grain yield (5), anthesis-silking interval (3), number of ears per plants (3)	Agrama and Moussa. (1996)
3	1	F ₄	B73 × Mo17	112	RFLP	55	Grain yield (5), 100 seeds weight (1), test weight (2), cob diameter (4), ear diameter (4), kernel rows per ear (4), row length (4), ear length (3), kernel width (3), growing degree days on anthesis (4), growing degree days on silking (3), anthesis-silking interval (4), grain moisture (6), stay green (3), plant height (3), ear height (2)	Beavis et al. (1994)
4	1	RIL	Zong3 × 87-1	187	SSR	9	Relative shoot fresh weight (5), leaf temperature difference (4)	Liu et al. (2011)
5	1	RIL	Zong 3 × 87-1	221	SSR	17	Ear length (6), kernel number per row (5), 100-kernel weight (2), kernel weight per plant (4)	Lu et al. (2006)
6	1	F ₂	Ac7643 × Ac7729/TZSRW	234	RFLP	20	Male flowering (10), female flowering (10)	Ribaut et al. (1997)
7	1	F _{2:3}	Ac7643 × Ac7729/TZSRW	211	RFLP	6	Anthesis-silking interval (6)	Vargas et al. (2006)
8	1	F _{2:3}	D5 × 7924	180	SSR	25	Anthesis-silking interval (4), grain yield (8), plant height (5), ear height (4), ear setting (4)	Zhu et al. (2011)

Table 1 (continued)

S. No	Populations number	Population type	Parents of population	Population size	Marker	QTL identified	Traits phenotyped/QTL identified per traits	Reference
9	1	F _{2:3}	DTP79×B73	105	SSR	21	Sugar concentration (1), grain yield (3), leaf abscisic acid content (1), osmotic potential (4), relative water content (1), root density (1), root dry weight (1), total biomass (1), leaf surface area (8)	Rahman et al. (2011)
10	2	F _{2:3}	Langhuang×TS141	202	SSR	16	Plant height (1), ear height (4), anthesis-silking interval (2), ear weight (4), cob weight (3), 100-kernel weight (1), ear length (1)	Zhao et al. (2018a)
11		F _{2:3}	Chang7-2×TS141	218	SSR	17	Plant height (1), ear height (4), anthesis-silking interval (1), ear weight (3), cob weight (3), 100-kernel weight (2), ear length (3)	
Waterlogging stress								
12	1	F ₂	HZ32×K12	288	SSR	25	Plant height (8), shoot dry weight (6), root length (3), root dry weight (3), total dry weight (5)	Qiu et al. (2007)
13	1	F ₂	HZ32×K12	247	SSR	10	Plant height (2), root length (1), seed dry weight (3), total dry weight (3), root dry weight (1)	Osman et al. (2013)
14	1	RIL	CAWL-46-3-1×CML311-2-1-3	211	SNP	15	Grain yield (5), root lodging (3), stem lodging (4), brace root (2), chlorophyll content (1)	Zaidi et al. (2015)
15	1	BC ₂ F ₂	HZ32×K12	180	SNP	8	Seedling height (1), shoot fresh weight (1), root fresh weight (3), root dry weight (2), root dry weight (1)	Zhang et al. (2013)
16	1	F ₂	B64×Teosinte	186	AFLP, SSR	3	Adventitious (nodal) root formation (3)	Mano et al. (2005)

Table 1 (continued)

S. No	Populations number	Population type	Parents of population	Population size	Marker	QTL identified	Traits phenotyped/QTL identified per traits	Reference
Cold stress								
17	1	F ₂	ETH-DH7×ETH-DL3	254	SSR	45	Leaf greenness (10), operating quantum yield of PSII (6), leaf area (7), shoot dry weight (4), nitrogen content (3), carbon ratio nitrogen (4), carbon content (1), maximum quantum efficiency of PSII primary photochemistry (6), minimum fluorescence (2), maximum fluorescence (2)	Jompuk et al. (2005)
18	1	RIL	Ac7643×Ac7729	233	SSR	16	CO ₂ fixation (4), photosynthetic maximum quantum efficiency of PSII primary photochemistry (3), quantum efficiency of photosystem II (5), minimum fluorescence (1), Stomatal resistance (3)	Fracheboud et al. (2002)
19	1	RIL	B73×Mo17	243	SSR	12	Low-temperature germination rate (6), low-temperature primary root length (6)	Hu et al. (2016)
20	1	F ₂	ETH-DH7×ETH-DL3	254	SSR	18	Minimum florescence (3), maximum quantum efficiency of PSII primary photochemistry (4), carbon exchange rate (2), leaf greenness (2), operating quantum efficiency of photosystem II (2), photochemical quenching factor (1), shoot dry weight (3), trapping efficiency of PSII (1)	Fracheboud et al. (2004)
21	1	RIL	B73×MO17	302	SSR	2	Leaf colour (2)	Rodríguez et al. (2008)
Heat stress								
22	2	RIL	B73×NC350	185	SNP	15	Leaf firing (9), leaf blotching (5), tassel blasting (1)	McNellie et al. (2018)
23		RIL	B73×CML103	195	SNP	7	Leaf firing (3), leaf blotching (3), plant death (1)	

Table 1 (continued)

S. No	Populations number	Population type	Parents of population	Population size	Marker	QTL identified	Traits phenotyped/QTL identified per traits	Reference
24	6	RIL	S067×P040	107	SNP	9	Dry yield (2), adjusted dry yield (2), female flowering (1), male flowering (3), leaf scorching (1)	Frey et al. (2016)
25		RIL	S058×S070	107	SNP	9	Dry yield (2), adjusted dry yield (2), female flowering (1), male flowering (3), leaf scorching (1)	
26		RIL	L012×L017	106	SNP	9	Dry yield (2), adjusted dry yield (2), female flowering (1), male flowering (3), leaf scorching (1)	
27		RIL	L043×L023	106	SNP	9	Dry yield (2), adjusted dry yield (2), female flowering (1), male flowering (3), leaf scorching (1)	
28		RIL	S067×L012	107	SNP	9	Dry yield (2), adjusted dry yield (2), female flowering (1), male flowering (3), leaf scorching (1)	
29		RIL	S070×L023	75	SNP	9	Dry yield (2), adjusted dry yield (2), female flowering (1), male flowering (3), leaf scorching (1)	
30	6	F _{3:4}	S067×P040, S058×S070, L012×L017, L043×L023, S067×L012, S070×L023	607	SNP	6	Leaf greenness (1), plant height (1), leaf scorching (1), leaf length (2), leaf elongation rate (1)	Van Inghelandt et al. (2019)
Salinity stress								
31	1	RIL	F63×F35	161	SNP	20	Field germination rate (1), field salt tolerance rank (1), salt tolerance rank (3), tissue water content (4), shoot Na + concentration (2), shoot K + concentration (4), shoot K + / Na + ratio (5)	Cui et al. (2015)

Table 1 (continued)

S. No	Populations number	Population type	Parents of population	Population size	Marker	QTL identified	Traits phenotyped/QTL identified per traits	Reference
32	1	DH	PH6WC×PH4CV	209	SNP	41	Root length (1), shoot length (6), full length (3), root fresh weight (2), shoot fresh weight (2), full fresh weight (2), root dry weight (2), shoot dry weight (3), full dry weight (1), root length salt tolerance index (1), shoot length salt tolerance index (3), full length salt tolerance index (3), root fresh weight salt tolerance index (1), shoot fresh weight salt tolerance index (4), full fresh weight salt tolerance index (2), root dry weight salt tolerance index (1), shoot dry weight salt tolerance index (2), full dry weight salt tolerance index (2)	Luo et al. (2019)
33	1	DH	PH6WC×PH4CV	240	SNP	7	Plant height (7)	Luo et al. (2017)

Abbreviations: *RIL* recombinant inbred lines; *DH* doubled haploid; *BC* backcross; *AFLP* amplified fragment length polymorphism; *RFLP* restriction fragment length polymorphism; *SSR* simple sequence repeat; *SNP* single nucleotide polymorphism

control for cold and heat stress, and leaves exposed to salt stress at 0 mM (Milli molar) and 200 mM concentrations. The expression data of all recognized candidate genes for abiotic stresses was retrieved using maize eFP (electronic fluorescent pictograph) browser (http://bar.utoronto.ca/efp_maize) (Li et al. 2010) except for waterlogging stress as no expression data was available for waterlogged treatment. The genes with a higher number of transcripts showing positive fold-change (Log_2) were up-regulated, while the genes having a lower number of transcripts with negative fold change ($\text{Log}_2 \leq -1$) were down-regulated. A heatmap of abiotic stress-responsive genes was generated using Heatmapper software (<http://www.heatmapper.ca/>) by following the hierarchical average linkage clustering method (Babicki et al. 2016). In the study, a p value of < 0.05 and $\text{Log}_2 \geq 1$ was used as the threshold to detect significant gene expression differences.

Results

Detected MQTL for different abiotic stresses and their distribution on the maize genome

Out of the 244 initial major QTL, a total of 197 QTL (80.73%) were successfully projected on the consensus map for different abiotic stresses (drought, heat, salinity, cold, and waterlogging) in maize. Consequently, chromosome 1 has the highest (38), and chromosomes 8 and 10 have the lowest (3 and 11) number of the projected QTL. In the meta-QTL analysis; a total of 32 MQTL consisting of 118 initial QTL were detected on six chromosomes (1, 2, 4, 5, 7, and 9) representing 48.36% of the total 244 initial QTL on all ten chromosomes of the maize genome (Fig. 2b, Table 2). The data supported a significant reduction in the respective CI of detected MQTL in comparison to the CI of initial QTL (Fig. 2c, Table 2; Table S1). Hence, meta-QTL analysis efficiently reduced the number of QTL in addition to narrowing down the genomic regions controlling different abiotic stress-related traits.

Out of 32 MQTL, five MQTL were located on chromosome 1 with 54 initial QTL, while seven MQTL were detected on each chromosome 2 and 7, and five, six, and two MQTL were located on chromosomes 4, 5, and 9, respectively (Fig. 2b). Among

abiotic stresses, the MQTL for drought tolerance were detected on six chromosomes, with chromosomes 2, 4, 5, and 6 each containing five drought-tolerant MQTL, while two and one MQTL were detected on chromosomes 9 and 1, respectively. On chromosome 4, all five MQTL consisted of drought-tolerant initial QTL (Fig. 2d; Fig. 3). In total, five MQTL for heat tolerance were detected on chromosomes 1(2), 2 (2), and 9 (1), while four were detected for salinity tolerance on chromosomes 1 (2), 5 (1), and 7 (1). For cold tolerance, five MQTL were detected on chromosomes 2 and 5 with each having two and chromosome 7 having one, while for waterlogging tolerance, five MQTL were detected with one MQTL detected each on chromosomes 2, 7, and 9 and two MQTL were located on chromosome 5 (Fig. 2d; Fig. 3).

Many MQTL contained initial QTL for combined abiotic stress tolerance. The MQTL2.1 has combined initial QTL for drought, heat, cold, and waterlogging, while MQTL5.1 has initial QTL for drought, cold, salinity, and waterlogging tolerance. The MQTL5.2 has initial QTL for drought and waterlogging tolerance and MQTL5.6 contained drought and cold tolerance initial QTL. MQTL7.1 consists of salinity and cold tolerance QTL. The MQTL9.1 contained drought and waterlogging tolerance QTL, while MQTL9.2 contains drought and heat tolerance initial QTL. The MQTL were formed from one major initial QTL (on chromosomes 1, 2, and 7) to a maximum of 15 major initial QTLs (on chromosome 2). Among identified MQTL, one MQTL, i.e. MQTL9.2, was formed with initial QTL from five different populations. Two MQTL, i.e. MQTL2.1 and 5.1, and one MQTL, i.e. MQTL5.6, were formed with initial QTL from four and three different populations, respectively. The MQTL formed from different populations appeared to be unique as these genomic regions are found across different genetic backgrounds making it more reliable for breeding programs. The meta-QTL analysis also reduced the CI of QTL from the original 19.08 cM on average to 4.94 cM for each MQTL. MQTL9.2 has the lowest CI of 0.02 cM (8.10–8.12 cM) on chromosome 9.

Candidate genes identified for different abiotic stresses

Based on the physical positions of the 32 MQTL, a total of 1907 candidate genes were identified for

Table 2 Detected MQTL and their attributes for different abiotic stresses distributed on six chromosomes of maize

S. No	MQTL	Position (cM)	Flanking marker	Physical position (Mb)	Number of initial QTL	Number of populations	Initial QTL of abiotic stress	Initial QTL involved	Average R ²	CI (95%)	Number of candidate genes
1	MQTL1.1	39.81	e2f19-gpm33c	11.47–12.18	3	2	Drought	EW, CW, KW	14.79	4.35	19
2	MQTL1.2	45.96	magi2762-rpe1	12.97–14.62	2	1	Heat	LF, LB	11.395	1.15	47
3	MQTL1.3	62.25	IDPB71-bnlg1884	19.97–23.56	1	1	Heat	LF	15.54	7.95	101
4	MQTL1.4	78.71	gpm748b-magi73926	30.78–32.54	2	1	Salinity	SDWI, SLI	18.18	0.09	42
5	MQTL1.5	79.97	magi73926-adt5	32.54–32.87	15	1	Salinity	RDW, FFWI, SFWI, FDWI, RDWI, FFW, RFWI, RFW, SL, SFW, FL, FDW, RLI, SDW, RL	32.92	0.06	9
6	MQTL2.1	10.56	PZE-102004688-PZA-002264005	2.5–3.1	7	4	Drought, cold, heat, waterlogging	CER, ES, ASI (2), MF, FF, CC	11.15	6.36	41
7	MQTL2.2	44.89	PZE-102028305-PZE-102031753	13.30–14.80	2	1	Heat	Grain yield (2)	10.5	15.98	54
8	MQTL2.3	114.44	gpm292b-IDP3814	42.36–48.33	4	1	Cold	qøPSII, Fv/Fm, (2), SPAD	10	8.01	128
9	MQTL2.4	214.2	gpm365a/IDP4832-umc34	225.58–226.19	7	1	Drought	ASI (2), GY, GDD, KWd, SG, GM	14	0.04	15
10	MQTL2.5	252.91	umc134b-bnlg1018	41.21–42.11	2	2	Drought	EL (2)	9.59	5.44	20
11	MQTL2.6	311.87	csu1080b-mmc041	135.67–145.61	2	2	Drought	KNR, KWd	14.52	5.86	88
12	MQTL2.7	365.98	umc1108-bcd926b	187.78–189.51	1	1	Drought	MF	15.1	0.15	41
13	MQTL4.1	97.76	magi28182-IDP8269	36.91–47.22	2	1	Drought	GY (2)	14.96	12.52	196
14	MQTL4.2	123.42	umc2287-phm5665.26	232.43–236.65	4	2	Drought	EH (3), ASI	13.2	2.76	83
15	MQTL4.3	132.53	gpm439-IDP3905	162.72–171.80	4	2	Drought	EH (4)	12.37	1.59	221
16	MQTL4.4	150.37	bnlg1189-IDP7911	174.01–178.69	3	1	Drought	EW, KW, CW	12.02	4.5	136
17	MQTL4.5	188.29	IDP3840-IDP8280	202.21 – 202.40	3	1	Drought	KW, ASI, EL	12.8	0.82	7
18	MQTL5.1	74.69	PZE-105072321-PZE-105074139	77.12–81.00	7	4	Drought, salinity, cold and waterlogging	SH, RFW, SFW, KNR, LA, PH (2)	7.72	0.34	65
19	MQTL5.2	130.88	PZE105152300-PZE105155892	203.45–205.33	3	2	Drought and waterlogging	RDW, SDW, KW	7.46	4.31	47
20	MQTL5.3	233.9	umc43-bnl6.10	42.32–49.86	5	1	Drought	ED, KR, GM, CD, GY	12.6	0.04	0
21	MQTL5.4	246.41	umc1-umc1355	59.74–61.02	2	1	Cold	GR, PRL	10.7	0.35	31
22	MQTL5.5	258.82	ufg60-nmp58	70.79–74.94	2	1	Cold	EPP, GY	11.65	1.77	92
23	MTL5.6	465.43	r273b-phi085	203.60–205.29	3	3	Drought and cold	GY, SDW, EW	13.15	6.77	41

Table 2 (continued)

S. No	MQTL	Position (cM)	Flanking marker	Physical position (Mb)	Number of initial QTL	Number of populations	Initial QTL of abiotic stress	Initial QTL involved	Average R ²	CI (95%)	Number of candidate genes
24	MQTL7.1	68.12	pze-107079722- pze-107079997	134.25–134.91	3	2	Cold and salinity	RFW, FFW, SDW	5.45	0.39	17
25	MQTL7.2	88.86	gpm620c-IDP7339	85.28–94.87	2	2	Drought	ASI, EH	10.91	3.51	84
26	MQTL7.3	152.9	IDP8661-IDP8677	152.81–157.31	2	1	Waterlogging	BR, Slod	5.6	29.87	93
27	MQTL7.4	192.17	magi89825-gpm270b	165.28–165.50	1	1	Drought	EH	10.91	9.9	10
28	MQTL7.5	378.58	asg32-ufg17	157.31–158.49	1	1	Drought	KW	10.61	2.4	29
29	MQTL7.6	491.76	umc245-npi433	168.13–168.94	1	1	Drought	KW	10.61	8.9	27
30	MQTL7.7	519.59	phi069-cto938d	170.58–172.77	1	1	Drought	KL	32.08	11.42	78
31	MQTL9.1	8.1	IDP4980-umc109	3.31–4.00	11	2	Drought and water-logging	EH, EL, KRL, KWd, GDDS, GDDA, PH, GY, RDW, KR, KW	14.98	0.02	12
32	MQTL9.2	87.08	IDP6008-IDP665	110.26–113.07	10	5	Drought and heat	LA (2), EL (2), LF, EW (2), CW (2), ES	14.27	0.48	33

ASI Anthesis-silking interval, CC chlorophyll content, CER carbon exchange rate, CD cob diameter, CW cob weight, ED ear diameter, EH ear height, EL ear length, ENP number of ears per plants, ES ear setting, EW ear weight, FDWI full dry weight salt tolerance index, FF female flowering, FL full length, FDW full dry weight, FFW full fresh weight, FFWI full fresh weight salt tolerance index, Fv/Fm maximum quantum efficiency of PSII primary photochemistry, GDDA growing degree days on anthesis, GDDS growing degree days on silking, GM grain moisture, GR germination rate, GY grain yield, KR kernel row, KRL kernel row length, KW kernel weight, KNR kernel number per row, KWd kernel width, LA leaf area, LF leaf firing, LB leaf blotching, MF leaf flowering, PH plant height, PRL primary root length, qPSII operating quantum yield of PSII, RL root length, RLI root length salt tolerance index, RDW root dry weight, RDWI root dry weight salt tolerance index, RFW root fresh weight, RFWI root fresh weight salt tolerance index, SFWI shoot fresh weight salt tolerance index, SH seedling height, SFW shoot fresh weight, SDW shoot dry weight, SDWI shoot dry weight salt tolerance index, SL shoot length, SLI shoot length salt tolerance index, Slod stem lodging, SPAD leaf greenness

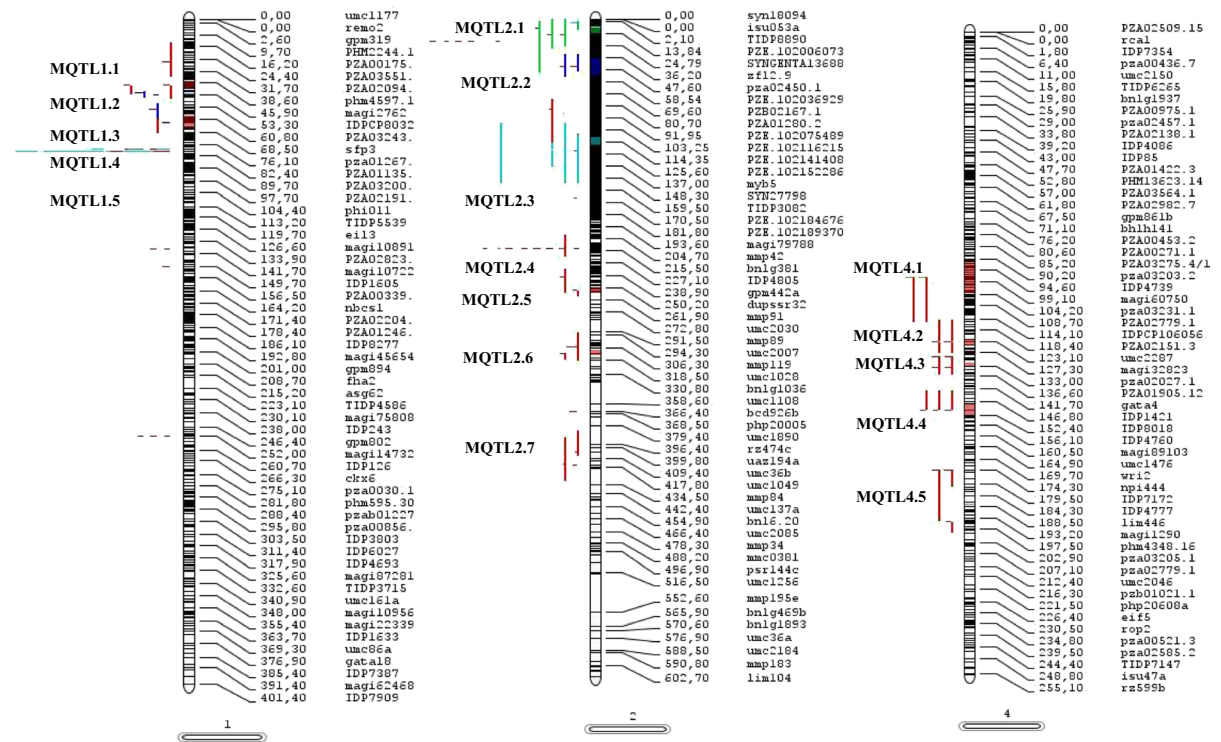


Fig. 3 Graphical representation of 32 MQTL distributed on six chromosomes of maize for different abiotic stresses {drought (red), waterlogging (green), heat (blue), cold (pink), and salinity (sea green)}

different abiotic stresses (Table S2). The number of candidate genes positioned within a MQTL ranged from 7 (MQTL7.4) to 221 (MQTL4.3). No candidate genes were detected within the small CI of MQTL5.3. Furthermore, > 100 candidate genes were present in five regions, viz. MQTL 1.3 (101), 2.3 (128), 4.1 (196), 4.3 (221), 4.4 (136), and ≤ 15 candidate genes were present in other five regions, viz. MQTL 1.5 (9), 2.4 (15), 4.5 (7), 7.4 (10), and 9.1 (12). The identified MQTL, viz. 1.1, 2.1, 2.4, 4.4, 4.5 9.1, and 9.2, with a large number of initial QTL for drought tolerance possessed 19, 41, 15, 136, 7, 12, and 33 candidate genes, respectively. A total of 93 candidate genes for waterlogging tolerance were within 29.87 cM of the CI for MQTL7.3. The MQTL for heat tolerance such as MQTL1.2, 1.3, 2.1, and 2.2, contained 47, 101, 41, and 54 candidate genes, respectively. A total of 128 and 31 candidate genes have been reported in MQTL2.3 and 5.4, respectively, containing initial QTL for cold tolerance. Two important MQTL, i.e. MQTL1.5 and 1.4, for salinity tolerance possessed 9 and 42 candidate genes, respectively. The identified

candidate genes encode for important transcription factor (TF) family proteins against abiotic stress tolerance. It supports the significance of each MQTL identified in this study, which has been elaborately discussed in discussion section.

Expression analysis of identified candidate genes responsive to abiotic stresses in maize

Out of 1907, a total of 77 candidate genes, i.e. well characterised by Hoopes et al. (2019) and encoding for stress-responsive genes, were used to analyse their differential expression patterns (Fig. 4; Table S3). The analysis showed that a total of 40 and 43 genes were up-regulated under drought stress at low MPa and very low MPa for 6-h treatment, while 31 and 29 genes were down-regulated. Similarly, 39 and 36 genes were up-regulated under drought stress at low MPa and very low MPa for 24-h treatment, as 32 and 33 genes were down-regulated. For cold and heat stress, 28 and 13 genes were up-regulated, and 45 and 56 genes were down-regulated, respectively. For salinity stress, a total

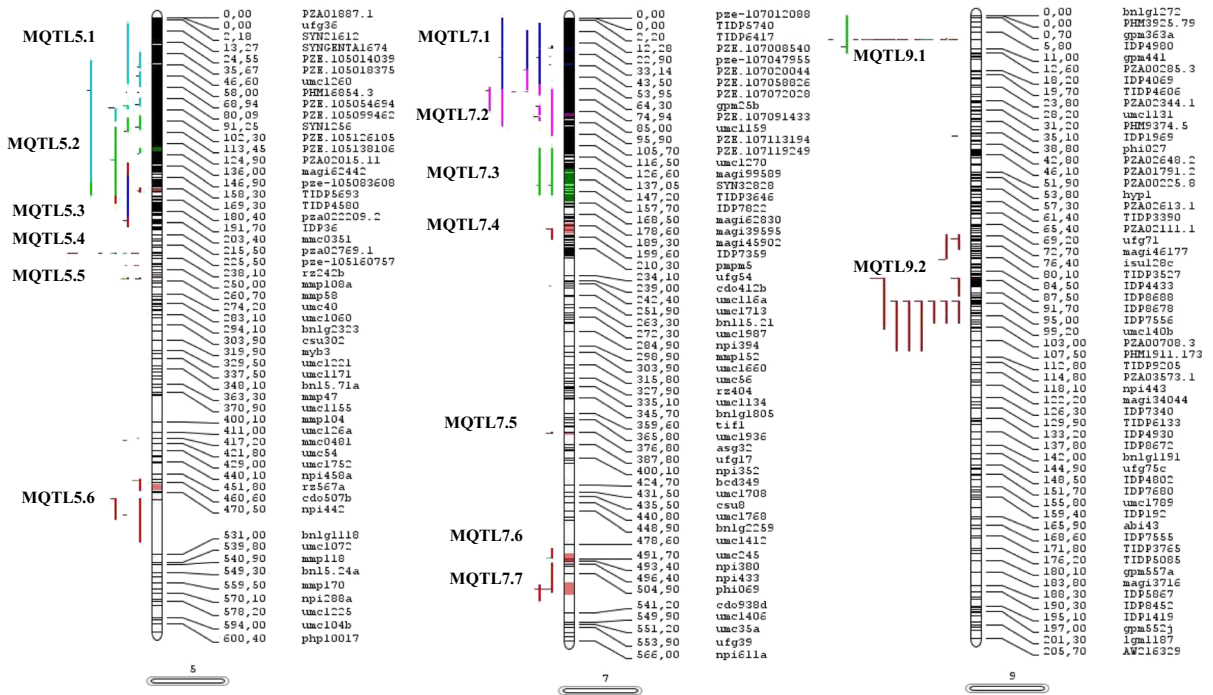


Fig. 3 (continued)

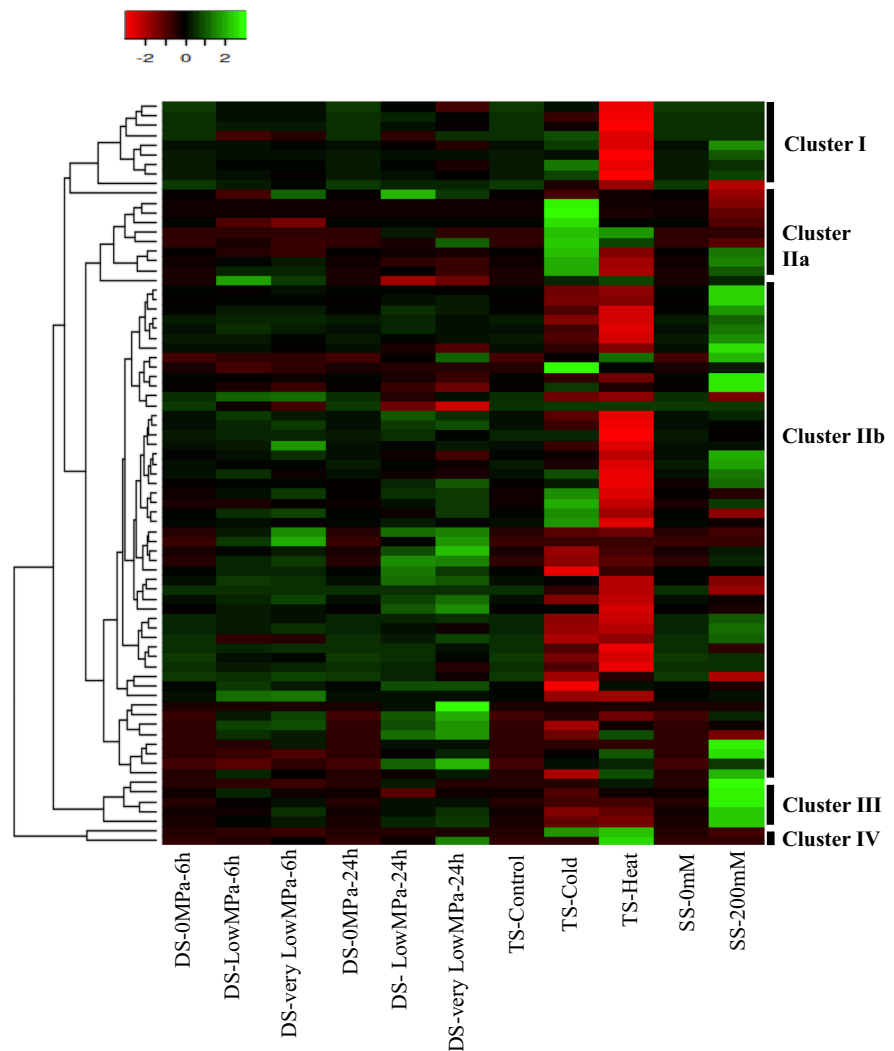
of 42 and 23 genes were up- and down-regulated, respectively. Hierarchical average linkage clustering of all these abiotic stress-responsive genes led to the identification of four clusters possessing distinct differential expressed genes (Fig. 4). Cluster I contained 10 genes among which four genes were up-regulated for cold and salinity stress, while all genes were down-regulated for heat stress. Cluster II was subdivided into two sub-clusters as IIa and IIb harbouring a total of 60 genes. Among which 35, 37, 33, and 31 genes were up-regulated under all drought stress treatments, while 23, 10, and 33 genes were up-regulated under cold, heat, and salt stress conditions. Cluster III possessed five genes which were mostly up-regulated under drought and salt stress except for Zm00001d003483 that was down-regulated under drought stress treatments. Cluster IV confined only two genes into which one gene Zm00001d049756 was up-regulated under drought, cold, and heat stress conditions, while another gene Zm00001d005766 was down-regulated under all stress conditions except heat (Fig. 4; Table S3). Moreover, a few common differentially expressed genes under all abiotic stressed conditions were also identified and showed

similar expression patterns under different stresses. For example, Zm00001d052069, Zm00001d004768, and Zm00001d017693 were up-regulated under all conditions, while genes Zm00001d049678, Zm00001d051569, Zm00001d015213, Zm00001d020013, and Zm00001d028348 were down-regulated. A few genes also showed inverse differential regulation between different stress conditions.

Discussion

Abiotic stresses are genetically complex quantitative traits as they are controlled by numerous minor genes and are highly influenced by environmental conditions (Witcombe et al. 2008). In the current study, the meta-QTL analysis for abiotic stresses (drought, heat, cold, salinity, and waterlogging) in maize detected a total of 32 MQTL located on six chromosomes (i.e. 1, 2, 4, 5, 7, and 9). From the 244 compiled QTL, 197 were projected on the consensus map using the Gaussian mixture model (Veyrieras et al. 2007), but only 118 were a part of the detected MQTL. Additionally, despite higher phenotypic variance, certain

Fig. 4 Heatmap of differentially expressed abiotic stress (drought, cold, heat, and salinity) responsive candidate genes in maize. Expression profiles of up- and down-regulated genes are presented with gradient green and red boxes, respectively. Treatment abbreviations: DS, drought stress; TS, temperature stress; SS, salt stress. Black boxes indicate missing values. The scale bar is shown at the top and log₂ value (treatment /control) was used to express fold change in gene expression



QTL were not assigned to the MQTL region due to the use of different reference maps in consensus map construction, marker type, and population heterogeneity.

Moisture stress tolerance in maize

Drought (low moisture) stress tolerance in maize

Drought is one of the major constraints in maize production as it causes nearly 30–90% yield loss and severely affects the flowering and grain filling stage (Pandit et al. 2018; Sah et al. 2020). Numerous QTL mapping studies have been undertaken in maize for drought stress (Beavis et al. 1994; Agrama and Moussa 1996; Vargas et al. 2006; Rahman et al. 2011;

Zhu et al. 2011; Zhao et al. 2018a). However, all the studies depict variable results due to diverse mapping population types and sizes used in the study, different segregation patterns in certain genetic backgrounds, and environmental conditions (Welcker et al. 2007; Farfan et al. 2015; Huo et al. 2016). Hence, the meta-QTL analysis of a total of 238 initial QTL for drought traits compiled from 11 experimental studies helped to identify the real and stable QTL for drought stress tolerance.

Two MQTL for drought tolerance, MQTL9.1 and 9.2, consisted of ten and nine initial QTL for different traits from four different studies (Beavis et al. 1994; Zhu et al. 2011; Nikolić et al. 2013; Zhao et al. 2018a). The MQTL2.4 included seven QTL for drought tolerance from a single study (Beavis

et al. 1994) with three being agronomic-based traits, while three QTL were directly used to measure drought tolerance, i.e. ASI (anthesis-silking interval), GDD (growing degree days) and stay green. Five initial drought tolerance QTL from a single study (Beavis et al. 1994) formed MQTL5.3. In the MQTL1.1, 2.1, 4.4, and 4.5, each has three initial QTL for drought tolerance-related traits such as cob weight, ear weight, kernel weight, ASI, and ear setting. Many MQTL, viz. MQTL2.5, 2.6, 4.1, 5.6, and 7.2, has two initial drought tolerance QTL mostly for agronomic traits from different studies (Vargas et al. 2006; Zhu et al. 2011; Nikolić et al. 2013; Zhao et al. 2018a). The agronomic-based traits such as plant height, ear height, ear length, ear diameter, kernel width, kernel number, and ASI have been widely utilised for QTL mapping and understanding the drought-tolerant molecular mechanisms as these traits are directly correlated with yield (Lebreton et al. 1995; Welcker et al. 2007; Fu et al. 2008; Wang and Zhang 2008; Li et al. 2009; Nikolić et al. 2013). Among these traits, grain yield and ASI are directly relevant to evaluating maize drought tolerance ability (Hao et al. 2008; Lu et al. 2010; Jia et al. 2020). Female (silk) growth is severely affected under drought stress in combination with an increase in GDD in comparison to male (tassel) so detecting the MQTL for growing degree units is highly relevant to observe its effect on ASI that subsequently affects grain yield (Beavis et al. 1994; Araus et al. 2012).

In the current study, MQTL5.3 possess no candidate gene as being low CI or may be the region is not well characterised functionally. The genes encoding for putative MYB (myeloblastosis) DNA-binding domain superfamily protein were reported in MQTL4.3, 4.4, 5.1, and 7.2. Earlier studies suggested that MYB TF regulate stomatal opening, defence mechanism, and ABA (abscisic acid)-signalling in maize and wheat under drought stress (Zhao et al. 2018b). Hence, further characterisation of these genes could validate their link to drought adaptation in maize. The ERF (ethylene responsive factor) genes were reported in MQTL2.1, 2.7, and 4.3. It has been observed that maize proteins encoded by ERF TF regulate a multitude of transcriptional programs to potentially contribute to multiple stress responses (Zhou et al. 2012). Many genes have been observed for glycosyltransferase

and glycosyl hydrolase family proteins in MQTL2.6, 2.7, 4.1, 4.2, 4.3, and 5.1, which could play role in response to different biotic and abiotic stresses as also reported in Arabidopsis, rice, and maize (Bray 2004; Opassiri et al. 2006; Kepler and Showalter 2010; Xin et al. 2018). Several LRR (leucine-rich repeat) receptor-like kinase family protein-encoding genes have been detected in several MQTL regions, viz. MQTL1.1, 2.1, 2.4, 4.2, 4.3, 5.1, 7.2, and 7.6, which could play important roles in signal transduction and drought response (Perruc et al. 2004; Alam et al. 2010). Besides, induction of peroxidase is a common feature under all the stress treatments (Kapoor and Sveenivasan 1988), and four genes encoding for peroxidase were reported from MQTL1.1, 4.2, 5.2, and 5.6 which may be involved in the stress response. Several genes in MQTL1.1, 2.6, 2.7, 4.1, 4.3, 4.4, 5.2, 7.2, 7.6, and 9.2 have been reported encoding for ZF (zinc finger) (such as C2H2, C3HC4-type RING finger) family protein. Genes encoding for different ZF proteins have been found to improve drought tolerance in various plant species such as maize (Shan et al. 2013), rice (Jan et al. 2013), and Arabidopsis (Luo et al. 2012; Zhang et al. 2016a; Wang et al. 2016b).

Three MYBs, two ERFs, two bZIP (basic leucine zipper), one glycosyl hydrolase, two Glycosyltransferase family, three CBTA (calmodulin-binding transcription activator), two LRR, and three ZF encoding genes have been up-regulated for drought stress. While two MYB, two bHLH (basic helix loop helix), one WRKY, two ZF, three LRR, one 40S ribosomal unit, one UBX domain, two WD-40, one auxin response factor, one cytokinin-O-glycosyltransferase, and two peroxidase encoding genes have been down-regulated. Similarly, in previous studies (Zhang et al. 2014; Yan et al. 2014; Bianchi et al. 2015; Shi et al. 2018; Zenda et al. 2019), several genes including MYBs, bZIPs, bHLH, WRKY, and other TFs were also identified suggesting their involvement in drought adaptation responses. Three up-regulated and two down-regulated MYBs were identified in foxtail millet (*Setaria italica*) (Shi et al. 2018). Likewise, Yan et al. (2014) associated WRKY TFs as an important element in drought stress. Hence, the identified candidate genes in the current study could be important contributors to drought stress tolerance in maize.

Waterlogging (high moisture) stress tolerance in maize

Waterlogging is another serious abiotic stress that has a significant impact on maize growth and yield potential, causing 15–80% reduction in yield (Li et al. 2011; Prasanna and Rao 2014). In maize, the second leaf stage (V2) to the seventh leaf stage (V7), i.e. the early seedling stage, is more vulnerable to waterlogging stress (Liu et al. 2010). Mostly minor QTL have been identified for waterlogging tolerance in maize except for a few major QTL (Qiu et al. 2007; Zaidi et al. 2015). The meta-QTL analysis was carried out by compiling the data of 61 initial QTL from five published QTL mapping studies targeting waterlogging stress.

Three initial QTL for root and shoot fresh weight and seedling height from a single study formed MQTL5.1 (Zhang et al. 2013), while in MQTL5.2 and 7.3, each has two initial QTL for shoot dry weight, root dry weight, brace root, and stem lodging mapped from two studies (Zhang et al. 2013; Zaidi et al. 2015). The MQTL2.1 and 9.1 each possessed one initial QTL for chlorophyll content and root dry weight from already published studies of Zhang et al. (2013) and Zaidi et al. (2015). For waterlogging tolerance, grain yield is the most favoured trait directly used for selection, while the other secondary traits such as a number of brace roots, chlorophyll content, root and shoot biomass, root and stem lodging, plant and ear height, adventitious root and aerenchyma formation, and leaf injury are used as indirect selection indices in maize (Zaidi et al. 2015; Reneau et al. 2020). Hence, the MQTL identification for these traits could enhance waterlogging tolerance via their marker-assisted introgression into elite varieties.

A TF gene for the ERF family (Zm00001d001907) was revealed from MQTL2.1 which could be associated with waterlogging tolerance as also detected by Yao (2021) in maize line ‘Suwan-2’ for waterlogging tolerance. Further characterisation can find the role of this gene in controlling flooding responses and anaerobic tolerance in several plant species as stated by Licausi et al. (2010) and Gibbs et al. (2015). In MQTL5.2, a gene has been reported for MAPK (mitogen-activated protein kinase) (Zm00001d017693), which is considered as a central regulator of primary signalling, cascades like reactive oxygen species (ROS), and suppresses the action of gibberellin to hinder elongation under submergence (Singh and Sinha 2016). Two

genes in MQTL5.1 and 7.3 (Zm00001d015181 and Zm00001d021490) have been identified encoding for α/β -hydrolases superfamily protein which were induced under flooding and salinity stress. A gene has been reported for auxin-responsive protein in MQTL5.1 (Zm00001d015228) that could play an important role in integrating hormonal and environmental signals at different growth and developmental phases, inhibiting H₂O₂ accumulation, and chlorophyll reduction under abiotic stress in addition to up-regulating stress-responsive genes (Ren and Gray 2015; Guo et al. 2018). Two genes, i.e. Zm00001d017704 and Zm00001d021537, have been reported in MQTL5.2 and 7.3 for MYB family protein that is known to be positively involved in abiotic stress tolerance in plants (Dubos et al. 2010; Arora et al. 2018; Hoeren et al. 1998; Yang et al. 2012). In MQTL5.2, a gene (Zm00001d017712) for WRKY TF was detected that is involved in regulating suberin biosynthesis in outer roots during radial oxygen-loss barrier formation under waterlogging (Liu et al. 2012). In the current study, the *in silico* expression analysis of candidate genes responsible for waterlogging tolerance was not carried out due to the non-availability of its transcriptomic datasets. But Du et al. (2014) performed the expression analysis of maize AP2/ERF genes under waterlogged stress and demonstrated their important role under waterlogged stress which was also detected in this study.

Temperature stress tolerance in maize

Heat (high temperature) tolerance in maize

Heat stress significantly hampers maize yield by affecting photosynthetic efficiency, kernel abortion, and storage starch reduction (Cantarero et al. 1999; Edreira and Otegui 2013). Being a highly variable stress to measure its effects, carrying out QTL mapping studies for heat stress is really challenging task in maize (Jodage et al. 2017; Lizaso et al. 2018). The meta-QTL analysis carried out included 82 heat tolerance QTL compiled from nine experiments to identify the most stable and consistent MQTL.

The MQTL1.2 was formed from two initial heat tolerance QTL for leaf firing and leaf blotching traits, while MQTL1.3 and 9.2 have two initial heat tolerance QTL for leaf firing only from two different populations of a single study (McNellie et al. 2018). In another two MQTL, i.e. MQTL2.1 and 2.2, each contained two previously identified QTL for male and female flowering and grain yield (Frey et al. 2016). In

heat stress, the foliar and tassel traits are yield components and were affected by leaf firing, leaf blotching, and tassel blast phenotypes (Chen et al. 2012, 2017; Zaidi et al. 2016). The identification of major QTL for these secondary traits will be reliable targets for heat stress tolerance in maize.

One gene, i.e. Zm00001d002501, was reported in MQTL2.2 and encodes for a heat shock protein (HSP) whose function is known to impart heat stress tolerance (Bita and Gerats 2013). Two genes Zm00001d046921 and Zm00001d046922 from MQTL9.2 were found to be linked to F-box domain proteins. These genes could be responsible for protein protection and processing under stressed conditions (Yong et al. 2019). Several genes were annotated as 'hypothetical protein' or 'expressed protein', which may be novel candidate genes for heat stress tolerance that needs testing to assign a particular function in future experiments. In this study, 13 genes were up-regulated including two MYB, three ERF, one bZIP, one HSP40, one glycosyl hydrolase superfamily protein, one glycosyltransferase-related family protein, and two CBTA receptors, while the remaining were down-regulated in response to heat stress. Similarly, previous studies have also reported the response of major TF genes under heat-stressed conditions (Zhang et al. 2012; Qian et al. 2019; Gao et al. 2021).

Cold (low temperature) stress tolerance in maize

Maize being a cold-sensitive crop needs a relatively higher temperature threshold (25–28 °C) for its germination and vegetative growth (Holá et al. 2003; Rodríguez et al. 2014). A few studies have been carried out for QTL mapping of cold tolerance related traits in maize (Fracheboud et al. 2002; Jompuk et al. 2005; Rodríguez et al. 2008; Hu et al. 2016). In the current study, 93 QTL identified from five QTL mapping studies have been compiled to carry out a meta-QTL analysis.

Four initial QTL for cold tolerance formed MQTL2.3 (Jompuk et al. 2005), while two initial QTL controlling germination rate and primary root length at low temperature formed MQTL5.4 (Hu et al. 2016). In addition, MQTL2.1, 5.1, 5.6, and 7.1, each has one initial QTL for cold tolerance from two different studies (Fracheboud et al. 2004; Jompuk et al. 2005). Four candidate genes (Zm00001d017693, Zm00001d015181, Zm00001d014726, and Zm00001d017707) encoding for fatty acid hydroxylase

have been reported in MQTL5.1, 5.4, and 5.6 which could play putative roles in low-temperature tolerance (Palta et al. 1993). One gene (Zm00001d0177120) has been identified for the WRKY superfamily in MQTL5.6 and a few others for the MYB family (Zm00001d015226, Zm00001d017704, and Zm00001d014701) in MQTL5.1, 5.2, 5.4, and 5.6, respectively. It has been observed that WRKY proteins control the pathogen defence and senescence processes under cold stress in Arabidopsis (Eulgem et al. 2000), while MYB TF is involved in the regulation of secondary metabolism and other developmental processes (Stracke et al. 2001). However, the auxin-related gene (Zm00001d015243) was also found in MQTL5.1, which is reported to affect senescence induction as a response to severe cold stress (Kratsch and Wise 2000). The expression gene analysis identified 28 up-regulated genes for cold stress belonging to major TF families as MYB, ERF, glycosyl hydrolase superfamily protein, glycosyltransferase-related family protein, CBTA, LRR, ZF, and peroxidase. At the same time, 45 down-regulated genes were related to different families (four MYB, two NAC (NAM, ATAF, and CUC), one bZIP, one ERF, two bHLH, four glycosyltransferase-related family proteins, three CBTA, five LRR, five ZF, and one brassinosteroid synthesis). The role of each of these TF families has been well demonstrated under stress conditions (Li et al. 2015; Zhou et al. 2021). As the genetic regulation of cold stress tolerance is poorly understood, the study of cold-responsive MQTL and candidate genes residing within it could help to further understand the cold tolerance pathway in maize.

Salinity stress tolerance in maize

Salinity causes nearly 51.43 and 53.18% decrease in dry weight and leaf area of maize, respectively (Hussein et al. 2007). In maize, germination and plant stand establishment are the most vulnerable stages to salinity stress. Several QTLs have been identified for salinity stress in maize (Cui et al. 2015; Luo et al. 2017, 2019). For the meta-QTL analysis, a total of three QTL mapping studies reporting 68 QTL were utilized to detect the MQTL for salinity stress tolerance.

The MQTL1.5 was formed from 15 initial QTL controlling various morphological traits under salt stress from a single study (Luo et al. 2019), while in MQTL1.4, 5.1, and 7.1, each has two initial QTL for shoot dry weight salt tolerance index, shoot length, plant height, root fresh weight, and plant fresh weight. As maize is more sensitive to

salt stress at the early seedling stage (Farooq et al. 2015; Luo et al. 2017; Sun et al. 2018), the QTL for biomass-related traits with high heritability and directly correlated to early vigour are important to include in maize salt tolerance breeding programs (Khan et al. 2003; Giaveno et al. 2007; Yu et al. 2018; Sandhu et al. 2020). Several genes have been identified for salt tolerance in maize (Zhang et al. 2019). Three genes (Zm00001d028347, Zm00001d028348, Zm00001d028349) have been identified for peroxidase in MQTL1.4 which could be involved in the antioxidant defence pathway (Xie et al. 2018; Luan et al. 2020). The genes for LRR protein have also been identified in MQTL5.1 which could be directly involved in stress defence and root growth (Kwon et al. 2015; Guo et al. 2018). A gene (Zm00001d015176) for protein PGR has been revealed from MQTL5.1, and hormones like ABA and cytokinin play an active role in the development of tolerance to salinity stress (Farooq et al. 2015). A gene (Zm00001d028372) for bZIP has been detected in MQTL1.4 that is induced under salt stress conditions in previous studies (Li et al. 2017) that suggests it is generally involved in response to several stresses. The genes encoding for protein kinase were identified in MQTL1.5 and 7.1 and could play an important role in salt tolerance (Zhang et al. 2016b). Identification of an MYB DNA-binding protein (Zm00001d015226) in MQTL5.1 suggests a critical role of this TF family in salinity response. One gene (Zm00001d015181) in MQTL5.1 was found for the α/β -hydrolase which can enhance salt tolerance of plants by regulating osmotic balance, increasing ROS scavenging capacity, and protecting membrane integrity and photosynthesis rate (Liu et al. 2014). Under salinity stress, major TF families such as MYB, ERF, bZIP, glycosyltransferase-related family protein, CBTA, LRR, HSP 40, brassinosteroid synthesis, α/β -hydrolases, and two ZF proteins were up-regulated, while four MYB, two NAC, one bZIP, one ERF, one bHLH, two CBTA, three LRR, and four ZF proteins were down-regulated. Xie et al. (2018) also reported that TFs such as NAC, ERF, MYB, bZIP, bHLH, and ZF protein showed differential expression under salt stress in maize. It suggests that the identified TFs in the current study could play a central role in regulating salt-responsive networks in maize.

Meta-QTL for combined abiotic stress tolerance in maize

Crop productivity will be further exacerbated due to the negative impacts of increased temperature and greenhouse gases (IPCC 2014). With climate change, maize is prone to multiple abiotic stresses such as drought, heat, salinity, cold, and waterlogging during its lifespan. Due to erratic rainfall in the same season, rainfed maize during the wet season experiences both drought and waterlogging stress. Crops activate a specific type of stress response when exposed to different stresses concurrently (Rizhsky et al. 2004). The effects of these combined stresses vary with the nature of interactions between the stresses (Choudhary et al. 2016; Rafique et al. 2020) such as drought and heat stress conditions simultaneously, further aggravating yield loss (Shanmugavadeivel et al. 2019). Therefore, to understand the mechanism of combined stresses, it is very crucial to characterize the germplasm for combined stress tolerance traits.

Among the identified MQTL, MQTL2.1, and 5.1, each has seven initial QTL for drought, heat, cold, waterlogging, and salinity tolerance traits from four different studies. The MQTL5.2 has three initial QTL for drought and waterlogging tolerance, while MQTL5.6 contained three initial drought and cold tolerance QTL. The MQTL7.1 was formed from salinity and cold tolerance QTL. Likewise, MQTL9.1 contained 11 initial QTL for drought and waterlogging tolerance from two studies, while the MQTL9.2 has 10 drought and heat tolerance QTL from five different experimental studies. For different stresses, genes encoding for various families (AP2/ERF, MYB, bZIP, bHLH, GRAS, WRKY, NAC, ZF, MAPK, and HSP) involved in regulating several cellular, molecular, and biochemical functions were identified (Lu et al. 2012; Shikha et al. 2017) (Table S2). Genes Zm00001d017677 and Zm00001d017724 in MQTL5.2 and 5.6 have been reported encoding for bHLH71 TF and HLH DNA-binding domain-containing protein, respectively. The bHLH TF protein is known to be responsive to salt, heat, water-deficient, and cold stress (Seo et al. 2011). Genes encoding for MYB family TF have been identified in MQTL5.1 and 9.2. In previous studies, it has been reported that MYB TF is up-regulated when plants were subjected to both drought and heat stress, simultaneously (Rizhsky et al. 2004). One gene, i.e. Zm00001d017678, was identified from MQTL5.2 and is putative RING-H2 finger

protein ATL53. The genes encoding for the RING finger protein are mainly induced under heat and cold stress conditions, and its overexpression during these stresses could increase the acquired thermo-tolerance (Lim et al. 2013). Moreover, in the current study, many common differentially expressed genes were found belonging to MYB, WRKY, bZIP, bHLH, ERFs, NACs, ARF, HLH, and F-box proteins under abiotic stress treatments (drought, heat, cold, and salinity). Few genes showed inverse differential regulation between different stress conditions. Some genes showed similar expression patterns under different stresses. For example, Zm00001d052069 (MYB), Zm00001d004768 (glycosyl hydrolase superfamily protein), and Zm00001d017693 (MAPK) genes were up-regulated under all conditions, while Zm00001d049678 (NAC), Zm00001d051569 (bHLH), Zm00001d015213 (LRR), Zm00001d020013 (ZF), and Zm00001d028348 (peroxidase) were down-regulated. Various genes showed a similar pattern under drought and salinity stress as drought stress also causes osmotic imbalances in the plant tissues (Huang et al. 2012); hence, a similar molecular adaptation has evolved under different stresses. This indicates that the regulation of these TFs plays an important role in imparting tolerance under different stress conditions. Further, the functional validation, characterization, and annotation of these candidate genes will be valuable to increase our understanding of the complex underpinning of different types of stress tolerances in plants. These genes will prove noteworthy to carry out further intensive research efforts to strengthen climate-resilient maize breeding programs.

Conclusion

As climate change has become more of a reality, so meeting maize production demand will be further challenged in the future under various biotic and abiotic stresses. Hence, it is important to enhance our understanding of the genomic regions imparting abiotic stresses tolerance. The meta-QTL analysis revealed a total of 32 MQTL for different abiotic stresses on six chromosomes. For moisture stress tolerance, a total of 20 MQTL contained initial QTL for drought tolerance, while five MQTL comprised initial QTL for waterlogging tolerance. For temperature stress tolerance, five MQTL were detected for heat tolerance traits, while nine MQTL

regions regulate cold tolerance. Three MQTL were detected for salinity stress tolerance. Simultaneous targeting of MQTL2.1, 5.1, 5.2, 5.6, 7.1, 9.1, and 9.2 can be helpful for improving combined abiotic stress tolerance as they control different stress-related traits. The identified MQTL provide breeders the genomic regions to target for introgression via marker-assisted breeding programs. The detailed omics study and validation of identified putative candidate genes through genome editing tools and gene expression analysis may help to improve the abiotic stress tolerance in maize. However, the effectiveness and accuracy of confidence interval reduction/refinement for detecting candidate genes are still unexplored. In addition, the crossing over in different genetic backgrounds can break the linkage between target QTL and markers. Hence, it requires constant validation for identified MQTL to utilise them effectively in breeding programs. The marker-assisted introgression, cloning, and functional characterization of identified MQTL in this study could significantly strengthen the breeding efforts for developing climate-resilient maize cultivars.

Author contribution Seema Sheoran: Data compilation and analysis, interpretation of results, manuscript drafting. Mamta Gupta: Data formatting and analysis. Shweta Kumari: Meta-QTL analysis. Sandeep Kumar: QTL studies data compilation and candidate genes description identification. Sujay Rakshit: Planning, interpretation and editing of manuscript. All the authors reviewed the manuscript.

Data availability All data generated or analysed during this study are included in supplementary files (Table S1, S2, and S3).

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication All authors give consent for the publication.

Competing interests The authors declare no competing interests.

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