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Research Article

A meta-analysis of low temperature tolerance QTL in maize

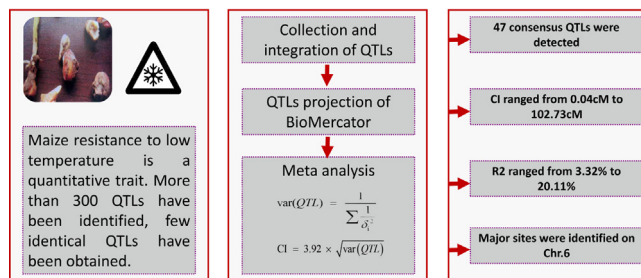
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GRAPHICAL ABSTRACT

The meta analysis provides further insights into the genetic basis of maize low temperature tolerance



ARTICLE INFO

Article history:

Received 7 February 2022

Accepted 18 May 2022

Available online 23 May 2022

Keywords:

Cold injury

Crops

Low temperature

Maize

Meta-analysis

QTL

Quantitative trait

Tolerance

Zea mays

ABSTRACT

Background: Cold injury is one of the most important limiting factors for maize production in mid-high latitude regions in the world. A total of 314 QTLs for maize low temperature tolerance have been identified in different populations using different statistical methods. However, few identical QTLs have been identified in different research studies.

Results: A consensus map of QTLs related to maize low temperature tolerance was constructed, based on the public genetic map, IBM2 2008 Neighbors as a reference map, along with a set of 314 QTLs reported in the literature over the past 20 years. A total of 187 QTLs were projected onto the IBM2 2008 Neighbors by software BioMercator. Forty-seven consensus QTLs were detected. The confidence interval at all sites ranged from 0.04 cM to 102.73 cM, and the proportion of the phenotypic variance associated with each of them ranged from 3.32% to 20.11%. Major chromosomal sites were identified on Chr.6 (MQTL29, MQTL30, and MQTL31).

Conclusions: This study provides further insights into the genetic basis of maize low temperature tolerance. Moreover, the MQTLs reported here could be harnessed for functional marker development and candidate gene mining of maize low temperature tolerance.

How to cite: Yu T, Zhang J, Cao J, et al. A meta-analysis of low temperature tolerance QTL in maize. Electron J Biotechnol 2022;58. <https://doi.org/10.1016/j.ejbt.2022.05.002>

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Abbreviations: AIC, akaike information criteria; CI, confidence interval; CIM, composite interval mapping; DH, double haploid; MAS, marker-assisted selection; MQTLs, MetaQTLs; QTL, quantitative trait locus; R2, proportion of phenotypic variance; RIL, recombinant inbred line.

Peer review under responsibility of Pontificia Universidad Católica de Valparaíso

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<https://doi.org/10.1016/j.ejbt.2022.05.002>

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1. Introduction

Maize (*Zea mays* L.) is one of the most important cereal crops worldwide, accounting for 40% (>800 mt) of the global food production [1]. Maize is highly sensitive to low temperatures, and it can grow at the lowest temperature of 5–18°C [2]. Low temperature and cold injury occur in mid-high latitude regions of the

world, which cause serious yield loss of maize [3,4]. Maize resistance to low temperature is a complex quantitative trait controlled by polygenes, and it is easily influenced by environment. To date, more than 300 QTLs for maize low temperature tolerance have been identified in different populations under different temperatures using different statistical methods. Jin et al. [5] identified 12 maize low temperature-related QTLs with an F_2 population of the W72 \times W10 cross. Using recombinant inbred line (RIL) populations derived from the cross of B73 and Mo17, Hu et al. [3] detected 15 maize low temperature-related QTLs. Using a double haploid (DH) population, Presterl et al. [6] mapped 25 low temperature-related QTLs of maize through the Composite Interval Mapping (CIM) method. Hund et al. [7] identified 60 maize low temperature-related QTLs with an $F_{2:3}$ population of the Lo964 \times Lo1016 cross. Fracheboud et al. [8] used RIL populations derived from the cross of Ac7643 and Ac7729/TZ and detected 25 maize low temperature-related QTLs. However, few identical QTLs have been identified in different research studies.

Meta-analysis, as developed by Goffinet and Gerber [9], is a statistical approach to combine the results of several individual related research studies. Software BioMercator [10] and MetaQTL [11] have been developed for meta-analysis to determine the number of consensus QTLs and narrow the QTL confidence intervals. In maize, Kaur et al. [12] applied meta-analysis to integrate 99 QTLs related to popping traits; 10 MetaQTLs (MQTLs) were detected with physical distance varying from 0.43 and 12.75 Mb. Zhong et al. [13] used this approach to integrate 128 QTLs for four leaf shape traits and identified 13 MQTLs with phenotypic variance ranging from 5.60% to 39.20% and physical distance ranging between 0.57 and 28.91 Mb. Zhou et al. [14] collected 1177 QTLs for maize yield traits and retrieved 135 MQTLs through BioMercator. A similar result was obtained with 49 consensus QTL controlling maize yield-related traits [15].

In this study, 314 published maize low temperature tolerance QTLs were collected. A consensus map of QTLs relevant to low temperature tolerance in maize was then created with the IBM2 2008 Neighbors genetic linkage map as a reference map. Next, consensus positions and QTLs were acquired through the meta-analysis method. The MQTLs reported here provide valuable information for candidate gene mining and functional marker development of maize low temperature tolerance.

2. Materials and methods

2.1. Collection and integration of mapping information for maize low temperature tolerance QTLs

Mapping information for 314 low temperature tolerance QTLs in maize, including the names of the parents, the QTL number, the type of plant populations, the population size, and the analysis methods for phenotypic values (Table 1) was collected from the public database PubMed (<http://www.ncbi.nlm.nih.gov/pubmed>) and the MaizeGDB (<http://www.maizegdb.org>). For each QTL, map position (most likely position and CI around this position) and the proportion of phenotypic variance (R^2) are the two most important parameters. In cases where the CI for the QTL position was not available in the published paper, a 95% CI was estimated using the equation proposed by Darvasi and Soller [16] as follows:

$$CI = 530/(N \times R^2) \quad (1)$$

$$CI = 163/(N \times R^2) \quad (2)$$

where CI is the confidence interval of a QTL, N is the size of the mapping population, and R^2 is the explained phenotypic variance. **Equa-**

tion 1 is suitable for both backcross and F_2 populations. **Equation 2** is suitable for recombinant inbred line (RIL) population.

2.2. QTL projection of BioMercator

IBM map (Intermated B73 \times Mo17) is a high-density genetic linkage map with more than 1000 RFLP and 700 SSR markers, of which 90 markers are the core markers, and the map is divided into 100 bin intervals [17]. Sharopova et al. [18] added 385 new SSR markers to the IBM map, which was called the IBM neighbors map. The IBM2 2008 Neighbors map is the latest version of the map with 20,925 loci, including RFLP, SSR, RAPD, and gene and sequence probe (<http://www.MiazeGdb.org>, updated in March 2021). In this study, the original maps of QTLs were compared with the reference map IBM2 2008 Neighbors. The information of all these QTLs, especially the beginning and ending positions of the CI, was imported into the program and mapped on their own linkage maps; this was then further projected to the reference map based on their relative distances to flanking framework markers, while maintaining constant distances between the framework markers. Each QTL was then transferred to the reference map using a homothetic function provided with the software BioMercator (V4.2), which contains algorithms from the MetaQTL, to create a consensus map of QTLs relevant to low temperature tolerance in maize. If the order of flanking markers of a given QTL were inverted with that in the reference map, there was no influence for the QTL projection. If more than one QTL was linked to the same marker, the formula proposed by Darvasi and Soller [16] was used to calculate the CI. Otherwise, the QTL was not projected.

2.3. Meta-analysis of low temperature tolerance in maize

Meta-analysis was applied to validate the existence of the proposed consensus QTL and to refine their CI [19,20]. QTLs from different independent experiments and associated on the same chromosome and at the neighboring interval are used to calculate a consensus QTL. Five models (1-, 2-, 3-, 4-, or N-QTL models) were given, and the minimum Akaike Information Criteria (AIC) value was the best model, designated the consensus QTL. The formula given by Goffinet and Gerber [9] was applied to estimate the number of QTL present on a linkage group or chromosome. The consensus QTL positions were determined using the mean of the QTL distribution maximizing the likelihood. We estimated the variance of QTL consensus position as follows:

$$\text{var}(QTL) = \frac{1}{\sum \frac{1}{\delta_i^2}} \quad (3)$$

where δ_i^2 represented the phenotypic variance for each of the QTL on the linkage group. The 95% CI of the consensus QTL position was calculated from the var (QTL) as follows:

$$CI = 3.92 \times \sqrt{\text{var}(QTL)} \quad (4)$$

The mean R^2 values of the original QTLs in that region were the explained variance of this consensus QTL.

3. Results

3.1. Collection of maize low temperature tolerance QTLs

A total of 314 QTLs related to maize low temperature tolerance published in the last 20 years were downloaded and collected from PubMed and MaizeGDB, 15 mapping populations, and the results above in this research (Table 1). The population types involved in RIL, DH, $F_{2:3}$ and $F_{2:4}$. The QTL mapping method is mainly CIM (composite interval mapping).

Table 1
QTL mapping information of maize low temperature tolerance.

Reference	Parent	QTL number	Cross type	Population size	Analysis method
Presterl et al. (2007) [6]	SL, TH	25	DH	720	CIM
Leipner et al. (2008) [26]	ETH-DH7, ETH-DL3	25	F _{2:3}	226	CIM
Rodríguez et al. (2013) [27]	A661, EP42	1	F _{2:3}	393	CIM
Rodríguez et al. (2008) [28]	B73, Mo17	2	RIL	302	CIM
Rodríguez et al. (2014) [29]	EP42, A661	4	F _{2:3}	210	CIM
Jompuk et al. (2005) [30]	ETH-DH7, ETH-DL3	29	F _{2:3}	226	CIM
Hund et al. (2005) [31]	Lo964, Lo1016	3	F _{2:4}	168	CIM
	ETH-DL3, ETH-DH7	4	F _{2:3}	226	CIM
Hund et al. (2004) [7]	Lo964, Lo1016	60	F _{2:3}	168	CIM
Fracheboud et al. (2004) [32]	ETH-DH7, ETH-DL3	19	F _{2:3}	226	CIM
Fracheboud et al. (2002) [8]	Ac7643, Ac7729/TZ	25	RIL	233	CIM
Guerra-Peraza et al. (2011) [33]	B73, Mo17	19	RIL	295	CIM
Hu et al. (2016) [3]	B73, Mo17	15	RIL	243	CIM
Jin et al. (2021) [5]	W72, W10	12	F ₂	210	CIM
Li et al. (2014) [34]	Huangzao4, CML343	44	RIL	119	SMA, ICIM
Leipner and Evan (2008)[35]	ETH-DH7, ETH-DL3	27	F _{2:3}	226	CIM

Table 2
QTL for maize low temperature tolerance.

Reference	QTL	chromosome	LOD score	R ² (%)	position	marker
Presterl et al. (2007) [6]	pres1	ch2	3.2	2.5	28	bnlg1017
	pres2	ch2	13.1	13	84	umc1635
	pres3	ch2	3	2.2	120	umc2005
	pres4	ch3	17.1	11.9	76	bnlg1456
	pres5	ch3	28.6	17.8	112	bnlg1047a
	pres6	ch3	14.9	8.4	132	umc1489
	pres7	ch3	12.7	7.5	142	bnlg1257
	pres8	ch4	61.2	33.7	36	umc1117
	pres9	ch4	4.8	3.3	108	bnlg292b
	pres10	ch5	13.5	7.2	10	bnlg1046
	pres11	ch5	26.7	15.4	24	bnlg1700
	pres12	ch5	8.2	5.5	70	umc1941
	pres13	ch5	21.8	13.9	74	bnlg609
	pres14	ch6	7.8	5.3	18	phi075(fdx1)
	pres15	ch6	7.9	4.9	70	umc1413
	pres16	ch7	13.7	8.1	36	bnlg2203
	pres17	ch7	5	3.4	38	bnlg1792
	pres18	ch9	112.3	52.4	18	bnlg1583
	pres19	ch9	8.2	4.9	62	bnlg1401
	pres20	ch9	4.2	3.2	84	bnlg1191
	pres21	ch10	3.7	2.6	64	umc1507
	pres22	ch10	14.3	4.4	74	phi035(umc57a)
Leipner and Evan (2008) [35]	leip1	ch1	4.57	8.6	68	umc1397
	leip2	ch1	3.04	6.6	193	mmc0041
	leip3	ch1	3.91	8.2	246	bnlg1502a
	leip4	ch2	3.44	7.1	112	bnlg1909
	leip5	ch2	3.05	5.3	123	dupssr21
	leip6	ch3	3.27	9	104	mmc0022
	leip7	ch3	3.37	10.6	202	bnlg1108
	leip8	ch3	2.6	5.2	223	bnlg1257
	leip9	ch3	3.42	7.3	225	bnlg1754
	leip10	ch6	3.09	8.1	99	umc1887
	leip11	ch6	6.01	17.5	217	bnlg1740
	leip12	ch8	2.73	4.8	23	umc1034
	leip13	ch8	4.44	9	101	dupssr14
	leip14	ch8	3.83	8.1	109	umc1663
	leip15	ch10	2.94	12.3	18	phi041
	leip16	ch10	3.33	5.9	66	umc1995
Jompuk et al. (2005) [30]	Jom1	ch1	3.74	4.1	0	bnlg1112
	Jom2	ch1	4.44	7.9	167	umc1128
	Jom3	ch1	5.31	4.2	181	mmc0041
	Jom4	ch2	0.49	0.5	108	phi109642
	Jom5	ch2	3.13	5	125	bnlg121
	Jom6	ch2	6.79	12.5	138	dupssr21
	Jom7	ch3	4.23	10.6	11	umc1394
	Jom8	ch3	4.48	10.8	86	mmc0022
	Jom9	ch4	4.52	8.2	6	phi072(mt11)
	Jom10	ch4	6.29	8.3	12	umc1276(bx5)

Table 2 (continued)

Reference	QTL	chromosome	LOD score	R ² (%)	position	marker
Hund et al. (2004, 2005) [7,31]	Jom11	ch4	4.54	7	138	bnlg2291
	Jom12	ch6	19.15	30.3	227	bnlg1740
	Jom13	ch6	8.86	15.9	235	umc1653
	Jom14	ch8	6.63	15.2	39	bnlg1863
	Jom15	ch8	4.99	7.5	66	bnlg1782
	Jom16	ch8	4.52	7.6	74	mmc0181
	Hund1	ch1	5	0.08	0	pgamcta310
	Hund2	ch1	4.3	2.5	8	pgamccc210
	Hund3	ch1	4.9	4	38	umc11a
	Hund4	ch1	6.1	14.2	44	csu145c(pck1)
	Hund5	ch1	5.6	9.2	49	asg45
	Hund6	ch1	5.4	6.4	70	pgamccc280
	Hund7	ch1	3.9	7.1	93	pgamcta205
	Hund8	ch1	5	12.4	81	umc67(a)
	Hund9	ch1	5.4	7.9	164	cdo122a
	Hund10	ch2	4.1	8.4	17	pgamcta210
	Hund11	ch2	4.2	1.7	57	pgamcca590
	Hund12	ch3	5.7	6.5	20	umc32a
	Hund13	ch3	5.3	2.8	41	pgamcca250
	Hund14	ch3	5.5	0.6	56	umc16a
	Hund15	ch3	3.9	2	96	umc48c
	Hund16	ch3	4.2	6.7	100	csu58a
	Hund17	ch4	11.1	1.7	10	umc156a
	Hund18	ch4	4.9	1.7	54	pgamcta345
	Hund19	ch4	4.3	2.2	69	pgamctt300
	Hund20	ch4	4.6	10.8	110	cdo127a
	Hund21	ch4	3.6	2.5	119	pgamctt430
	Hund22	ch5	3.7	8.3	104	pgcmcta260
	Hund23	ch5	6.1	11.7	109	pgamcca500
	Hund24	ch5	6.3	6.2	113	pgamcgt165
	Hund25	ch5	4.8	3.2	123	umc108
	Hund26	ch5	4.9	0.6	141	pgamcgg330
	Hund27	ch5	3.9	7.8	171	php10017
	Hund28	ch6	2.9	2.9	2	umc59a
	Hund29	ch6	7.9	2.1	20	pgcmcga450
	Hund30	ch6	4.3	5.7	55	csu116a
	Hund31	ch6	4.1	7.9	57	pgamcta175
	Hund32	ch7	4.9	3.6	20	umc5b
	Hund33	ch7	3.9	0.4	74	pgamcgg150
	Hund34	ch9	4.1	1.4	11	pgamcca100
Hund35	ch9	3.9	0.4	13	csu134c	
Hund36	ch10	4.3	0.1	10	php20075a	
Hund37	ch10	5	12.5	56	umc130	
Hund38	ch10	6.1	11.7	61	pgamctt250	
Hund39	ch10	4	0.7	69	pgamctg300	
Hund40	ch10	5.5	7	81	umc49b	
Fracheboud et al. (2002, 2004) [8,32]	Fra2002-1	ch1	2.94	6	146	bnl5.59a
	Fra2002-2	ch1	2.87	6.2	158	umc119(umc119a)
	Fra2002-3	ch3	3.37	4.91	68	npi114b
	Fra2002-4	ch3	4.47	6.51	72	umc10(umc10a)
	Fra2002-5	ch3	3.75	5.97	289	umc317(cyp1)
	Fra2002-6	ch4	2.29	2.2	202	umc133(umc133a)
	Fra2002-7	ch4	0.73	0.4	239	umc326(rps8)
	Fra2002-8	ch1	4.3	6.9	176	bnlg1564
	Fra2002-9	ch1	3.5	6.7	201	bnlg1502
	Fra2002-10	ch2	3.5	6.69	4	bnlg1017
	Fra2002-11	ch2	3.6	54.5	47	umc1823
	Fra2002-12	ch2	6.4	10	121	bnlg1909
	Fra2002-13	ch6	3.7	5.8	120	bnlg1617
	Fra2002-14	ch6	4.1	10.7	201	umc1859
	Fra2002-15	ch6	21.6	37.4	221	bnlg1740
Guerra-Peraza et al. (2011) [33]	Gue-1	ch5	6.26	6.4	218	umc1447
	Gue-2	ch5	25.86	23	254	php15024
	Gue-3	ch5	8.9	9.2	257	ufg60
	Gue-4	ch5	15.8	16.1	263	bnlg1902
	Gue-5	ch5	6.56	5.1	289	bnlg1208
	Gue-6	ch5	7.15	6.3	360	umc2026(gst17)
	Gue-7	ch6	9.15	8.5	424	umc1490
	Gue-8	ch6	6.83	7.1	453	umc1350
	Gue-9	ch6	7.76	7.4	483	agp2
	Gue-10	ch6	9.08	7.9	487	umc2059
	Gue-11	ch7	6.23	5.6	139	gta101a
	Gue-12	ch7	9.08	7.2	159	uaz187
	Gue-13	ch7	8.75	6.3	161	bnlg1094
	Gue-14	ch7	7.06	7.2	242	umc116a

(continued on next page)

Table 2 (continued)

Reference	QTL	chromosome	LOD score	R ² (%)	position	marker
Hu et al. (2016) [3]	Hu-1	ch5	9.66	11.29	246.41	umc1
	Hu-2	ch5	6.08	8.11	419.21	mmc0481
	Hu-3	ch6	5.17	7.03	75.51	uck1
	Hu-4	ch6	3.88	5.75	342.61	mmp150
	Hu-5	ch6	4.1	5.17	459.11	umc62
	Hu-6	ch7	3.72	7.78	190.01	umc1983
	Hu-7	ch7	4.77	5.72	244.71	mmp127
Leipner et al. (2008) [26]	Leip2-1	ch1	15.32	9.6	4	bnlg1112
	Leip2-2	ch1	6.72	3.6	13	phi096
	Leip2-3	ch1	9.35	7.15	105	bnlg1884
	Leip2-4	ch2	7.89	1.25	0	bnlg1338
	Leip2-5	ch2	6.03	7.4	140	dupssr21
	Leip2-6	ch2	7.55	7.05	240	bnlg1520
	Leip2-7	ch3	7.41	0.85	0	umc1746
	Leip2-8	ch3	8.25	3.45	86	bnlg1019(a)
	Leip2-9	ch3	11.42	11.55	108	mmc0022
	Leip2-10	ch5	7.78	4.8	0	umc1060
	Leip2-11	ch5	6.27	8.7	82	bnlg1346
	Leip2-12	ch7	10.32	4.9	31	umc1001
	Leip2-13	ch7	6.42	4.65	110	umc1760
	Leip2-14	ch8	9.33	7.1	43	umc1562
	Leip2-15	ch8	6.82	0.8	88	bnlg1823
	Leip2-16	ch9	9.17	5.25	50	phi027(wx1)
	Leip2-17	ch9	7.43	6.95	75	nc134(gl15)
Li et al. (2015) [34]	Li1-1	ch3	4.14	22	77	bnlg1144
	Li1-2	ch3	2.8	11.09	159	umc1012(umc59e)
	Li1-3	ch5	2.53	10.35	260.2	umc1315
	Li1-4	ch5	2.94	11.43	346.5	umc1349
	Li1-5	ch5	2.84	11.56	518	umc2216
	Li1-6	ch7	3.41	12.21	13.8	umc1241(cka4)
	Li1-7	ch7	2.61	11.13	190.4	bnlg1792
	Li1-8	ch7	5.07	18.93	252.4	umc1787
	Li1-9	ch7	3.12	12.48	284	bnlg657
	Li1-10	ch7	3.71	14.51	292.7	mmc0411
	Li1-11	ch7	2.5	10.23	322.7	bnlg1070
	Li1-12	ch9	3.22	12.33	12	bnlg1272a
	Li1-13	ch9	2.63	11.89	30	bnlg1583
	Li1-14	ch9	2.62	11.03	101.1	umc1170
	Li1-15	ch9	3.04	12.35	162.93	umc1893
	Li1-16	ch9	3.08	11.31	226.76	phi065(pep1)
	Li1-17	ch9	2.62	9.49	322.59	umc1519
	Li1-18	ch9	4.39	15.94	381.1	umc2341
	Li1-19	ch9	3.33	13.4	461.6	bnlg1191
	Li2-1	ch2	3.48	35.89	34.67	umc1622(crr1),bnlg1017
	Li2-2	ch2	3.3	21.83	265.67	bnlg2248,umc1448
Li2-3	ch2	3.13	9.08	302.67	bnlg1175,bnlg1909	
Li2-4	ch2	3	10.15	306.67	bnlg1909,umc1003(zpu1)	
Li2-5	ch2	2.71	11.81	368.7	umc1065(pbf1),umc1875	
Li2-6	ch3	2.74	22.54	4	umc2118,umc2257	
Li2-7	ch3	3.98	22.62	74	umc2376,bnlg1144	
Li2-8	ch3	3.21	24.54	753	bnlg1182,phi047(npi425a)	
Li2-9	ch4	3.17	9.23	307.6	bnlg1265,umc1891	
Li2-10	ch4	3.27	25.92	482.6	bnlg2162,phi093(ssu1)	
Li2-11	ch5	3.86	13.57	346	phi047(npi425a)	
Li2-12	ch7	8.34	25.4	252.8	umc2161(mmp58),umc1349	
Li2-13	ch7	3.06	14.75	294.8	mmc0411,bnlg1070	
Li2-14	ch7	3.51	25.16	272.8	umc1787,bnlg657	
Li2-15	ch8	2.71	27.37	229.58	umc1904,umc2503(rgp2)	
Li2-16	ch9	2.78	15.28	14	bnlg1272a,bnlg1583	
Li2-17	ch9	3.01	13.3	101	bnlg1810,umc1170	
Li2-18	ch9	2.93	6.81	248	nc134,umc1519	
Li2-19	ch9	2.77	21.81	350	umc1519,umc2341	
Li2-20	ch9	5.6	16.16	380	umc2341,umc2343	
Li2-21	ch9	2.64	11.15	462	bnlg1191,umc2131	

3.2. Maize low temperature tolerance QTLs' projection

QTLs related to low temperature tolerance in maize were loaded into their original maps according to MapName, QTLName, Chromosome, LODScore, R², and SM position. A total of 314 QTLs were projected onto the reference map IBM 2 2008neighbors, and 187 QTLs with common markers were projected successfully

(Table 2). The projected QTLs covered the whole genome of IBM 2 2008neighbors (Fig. 1).

3.3. Meta analysis of low temperature tolerance QTLs in maize

Meta-analysis was carried out and a total of 47 MQTLs were identified. These MQTLs were unevenly distributed in all 10 chro-

mosomes and named MQTL1 to MQTL47 after the order from Chr.1 to Chr.10: 7 MQTLs on Chr.1; 3 MQTLs on Chr.2, Chr.4 and Chr.8 each; 4 MQTLs on Chr.3, Chr.7 and Chr.10 each; 8 MQTLs on chr.5; 6 MQTLs on chr.6 and 5 MQTLs on chr.9 (Table 3). Meta-analysis significantly narrowed the CIs of the original QTLs; CIs of the 47 MQTLs ranged from 0.04 cM to 102.73 cM, and 23 out of them were less than 1 cM (Table 3). Every MQTL contained at least three original QTLs; the original QTL number of 47 MQTLs ranged from 3 to 14, and the original QTL number of MQTL10, MQTL29, MQTL30 and MQTL31 were more than 10 (Table 3). The proportion of the phenotypic variance associated with each of the 47 MQTLs ranged from 3.32% to 20.11%. The mean R^2 values of MQTL29, MQTL30, MQTL31 and MQTL33 were more than 15% (Table 3). Remarkably, MQTL29, MQTL30 and MQTL31 on Chr.6 integrated more than 10 original QTLs, and the mean R^2 values were more than 15%. MQTL29 and MQTL31 integrated 14 QTLs from 4 populations. Flanking markers of MQTL29 lay at 510.64 cM and 538.17 cM, and the R^2 value of MQTL29 was 18.32%. Flanking markers of MQTL31 lay at 593.35 cM and 603.46 cM, and the R^2 value of MQTL31 was 18.04%. MQTL30 integrated 13 QTLs from 3 populations. The flanking markers for this site lay at 568.30 cM and 575.38 cM, and the R^2 value of MQTL30 was 19.08%.

4. Discussion

IBM2 2008 neighbors is a public map based on the isolated population of B73 × Mo17. The parent inbred line B73 has been sequenced and used to construct the physical map. The IBM population has high recombination rate and resolution, and it is an excellent population for the detection of microeffect QTLs. The

IBM2 2008 neighbors map is 8054.28 cM in length and contains 20,925 markers of various types. There are many common markers with completed or in-process QTL mapping maps, which can improve the accuracy of MQTLs.

In recent years, some progress has been made in accelerating the genetic improvement process of crop stress tolerance traits by using MAS [21,22,23,24,25]. However, as most genes controlling crop stress tolerance traits are inherited from quantitative traits and limited by the effectiveness, operability and economy of QTL mapping, MAS has not been widely applied in maize breeding practice.

In this study, 314 published QTLs related to maize low temperature tolerance were integrated using IBM2 2008 Neighbors as a reference map, and the “consensus QTLs” with large effect values that could be detected in different genetic populations and under different environmental conditions were obtained by meta-analysis. The relationship between the effect and location of QTLs related to maize low temperature tolerance was evaluated. The study finding will provide powerful support for the development of molecular markers that can be applied to MAS technology in the corresponding sections in the future and greatly improve the assisted breeding efficiency of MAS. The advantages of applying meta technology to maize low-temperature tolerance traits (MAS) are as follows: limited by various factors, it is difficult to locate all target QTLs in a single QTL mapping, and the estimated QTL phenotypic contribution rate is often unreliable. In this study, meta-analysis was used to integrate previous maize low temperature tolerance-related QTLs to provide more reliable molecular markers for MAS development. Generally, the genetic map constructed by QTL mapping has the problem of low molecular marker

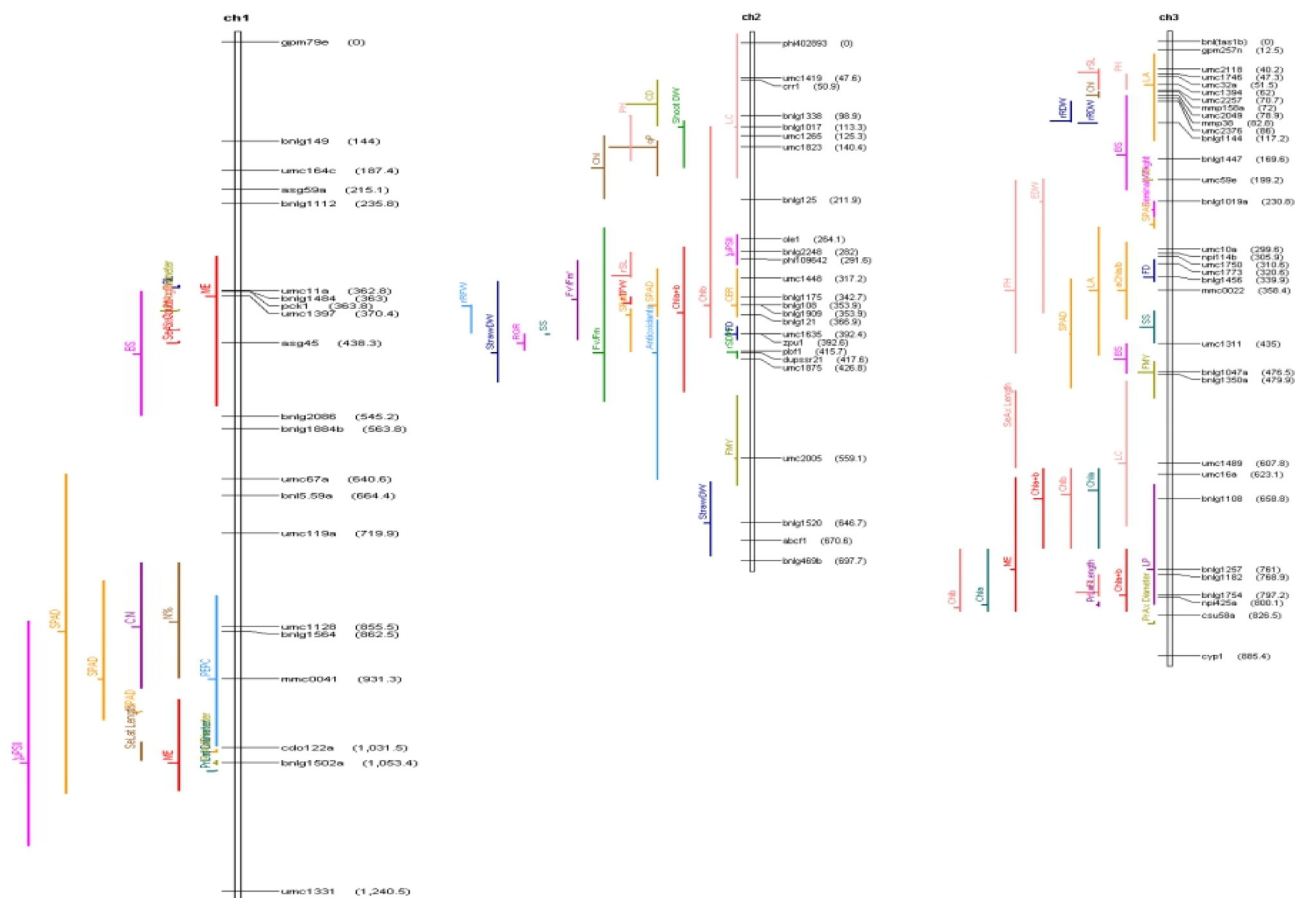


Fig. 1. Consensus map of QTLs relevant to low temperature tolerance in maize.

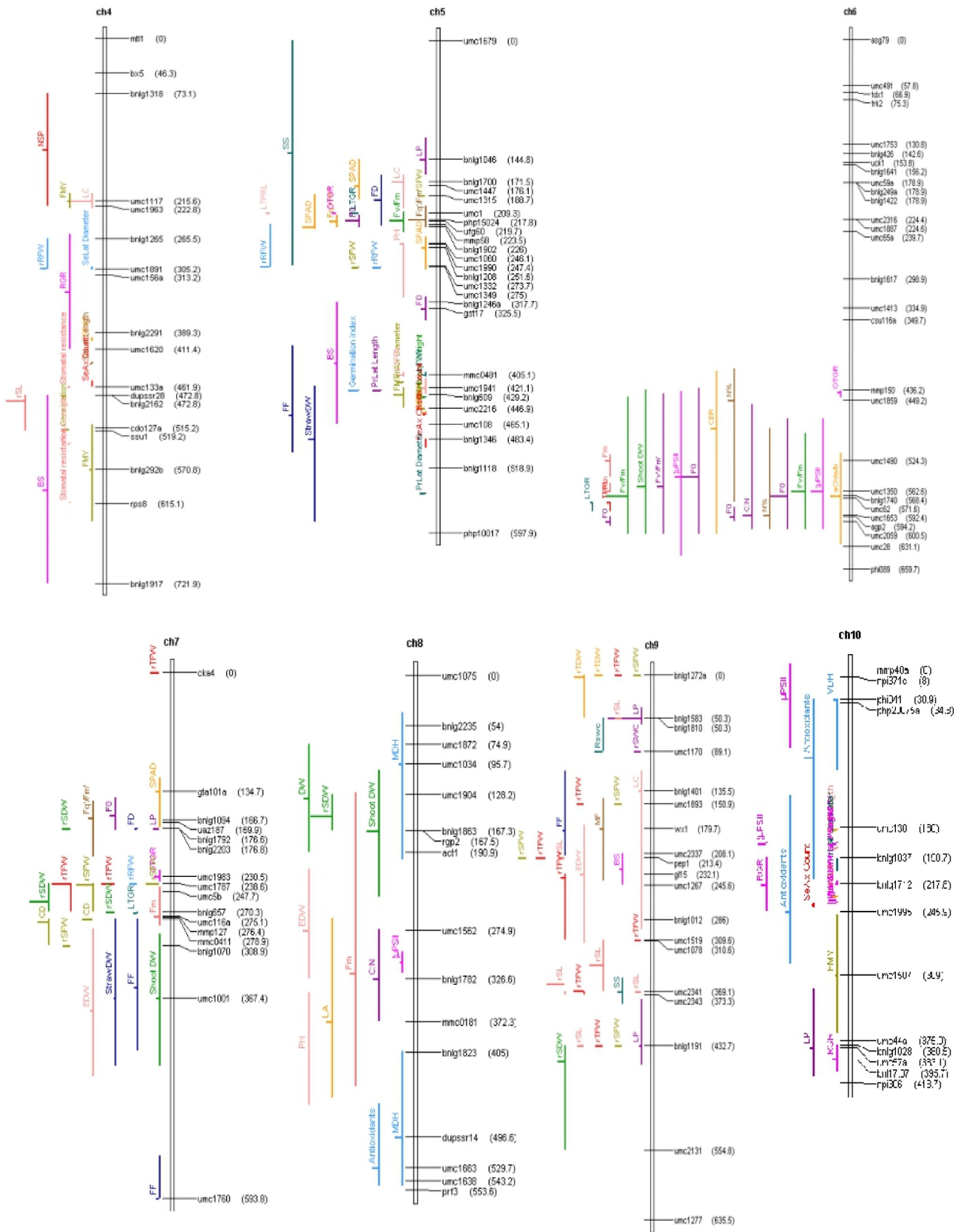


Fig. 1 (continued)

density and limited reference value for fine mapping, which ultimately leads to the low efficiency of MAS. In this study, an integrated map of maize low temperature tolerance-related QTLs

was constructed by integrating previous research results, which was rich in molecular markers. Using meta-analysis, MQTL that could be detected in different mapping populations could be

Table 3
Meta-analysis results of maize low temperature tolerance.

MQTL	Chromosome	AIC value	MQTL position (cM)	MQTL CI (cM)	Map distance (cM)	Mean R ² (%)	No. of Population	No. of QTL	Left marker	Left marker position	Right marker	Right marker position
MQTL1	1	33.73	391.7	390.67–392.72	2.05	9.84	3	3	AY110028	390.3	IDP112	396.72
MQTL2	1	33.73	419.65	418.06–421.23	3.17	8.2	3	3	asn3	417.98	gpm498c	421.89
MQTL3	1	33.73	438.28	436.99–439.58	2.59	8.17	3	3	lim432	436.4	AY107489	439.64
MQTL4	1	135.27	979.33	978.29–980.37	2.08	6.75	4	6	kip1	977.76	umc252b	980.51
MQTL5	1	135.27	1,037.12	1,034.98–1,039.26	4.28	5.3	3	5	IDP9074	1034.91	gs1	149
MQTL6	1	135.27	1,053.97	1,050.13–1,057.82	7.69	4.94	3	5	BE639426	1051.1	aps1	1058
MQTL7	1	135.27	1,065.22	1,064.09–1,066.34	2.25	7.43	3	4	T1-3(5242)(1)	1062.28	mta1	1066.35
MQTL8	2	384.02	118.73	105.16–132.29	27.13	11.36	5	6	phi098	104.32	pza02081	132.35
MQTL9	2	384.02	345.36	340.56–350.15	9.59	8.27	5	8	fl1	340.4	mmp91	350.2
MQTL10	2	384.02	395.37	393.58–397.16	3.58	7.96	6	10	csu4a	393.48	csu1059	397.52
MQTL11	3	1301.1	117.2	117.17–117.23	0.06	14.32	3	3	IDP4911	117.15	bnlg1523	117.89
MQTL12	3	1301.1	199.21	199.15–199.27	0.12	9.12	3	4	gpm697	197.5	TIDP5269	199.37
MQTL13	3	1301.1	405.46	395.36–415.55	20.19	9.76	4	5	gpm375a	394.96	IDP8994	416.65
MQTL14	3	1301.1	807.57	803.76–811.39	7.63	5.85	3	6	csu1142	801.74	uaz114	811.72
MQTL15	4	702.91	517.32	517.01–517.63	0.62	11.57	4	4	mHbrMC217-B73	515.34	IDP7288	517.77
MQTL16	4	702.91	536.47	535.14–537.81	2.67	4.02	3	3	msh1	535.13	isu109b	538.11
MQTL17	4	702.91	615.08	614.75–615.41	0.66	3.32	3	3	vpp2	614.16	umc1740	615.7
MQTL18	5	146.48	188.7	188.63–188.76	0.13	10.69	4	6	gly1	188.54	agrr142	189.22
MQTL19	5	146.48	209.3	209.14–209.46	0.32	12.04	4	8	cl11868_1	208.98	td1	209.62
MQTL20	5	146.48	219.68	215.05–224.32	9.27	14.48	3	7	gpm419	215	dts1	225.28
MQTL21	5	146.48	275	274.95–275.05	0.1	8.97	4	5	TIDP8902	273.82	pza02981	275.28
MQTL22	5	688.14	414.4	414.02–414.77	0.75	5.28	4	4	pip1b	412.4	csu604b(trh)	416.67
MQTL23	5	688.14	424.86	424.68–425.03	0.35	8.76	4	7	gpm456e	423.69	mHbrBA93-Mo17	425.34
MQTL24	5	688.14	432.9	432.39–433.41	1.02	7.22	4	5	mHbrMC72-Mo17	431.76	sdg117b	433.63
MQTL25	5	688.14	446.92	446.86–446.98	0.12	8.29	4	5	pco112657	445.61	hsf1	448.48
MQTL26	6	327.78	178.56	176.82–180.29	3.47	8.09	3	6	gpm414b	176.17	rz444e	181.5
MQTL27	6	327.78	237.42	235.08–239.77	4.69	8.43	3	4	pgl1	233.79	elfg1	239.78
MQTL28	6	223.13	439.12	434.76–443.48	8.72	13.96	2	7	IDP330	434.11	umc38a	443.6
MQTL29	6	223.13	524.4	510.64–538.17	27.53	18.32	4	14	umc266c(ptk)	510.57	npi419a	538.8
MQTL30	6	223.13	571.84	568.30–575.38	7.08	19.08	3	13	gpm378	567.86	IDP9020	575.31
MQTL31	6	223.13	598.4	593.35–603.46	10.11	18.04	4	14	mmp105	592.4	cdo345c	603.6
MQTL32	7	25.86	176.6	176.55–176.66	0.11	7.23	3	5	IDP9119	176.08	bnlg2203	176.8
MQTL33	7	107.73	238.6	238.58–238.62	0.04	20.11	2	6	IDP8675	238.39	mHbrMG194-B73	239.21
MQTL34	7	107.73	270.33	270.28–270.39	0.11	11.95	3	3	ufg65	266.9	gpm793	270.71
MQTL35	7	107.73	278.9	278.86–278.94	0.08	8.45	4	5	gpm716m	278.47	gst23	280.89
MQTL36	8	141.28	147.88	130.38–165.38	35	12.3	4	5	umc1802	130.19	umc2075	166.5
MQTL37	8	141.28	312.61	301.63–323.59	21.96	6.34	2	5	IDP8541	301.15	csu125b(cah)	323.61
MQTL38	8	141.28	395.72	344.35–447.08	102.73	6.42	3	5	IDP4773	344.18	gpm716a	446.2
MQTL39	9	14.45	0	0–0.06	0.06	12.93	2	4	koln10b(hox2)	0	agrr41	1.49
MQTL40	9	162.08	150.88	150.84–150.92	0.08	7.53	3	5	pco067521	150.75	gpm78b	152.42
MQTL41	9	162.08	213.45	213.41–213.49	0.08	8.6	4	7	pep1	213.41	pza00925	213.9
MQTL42	9	162.08	309.59	309.52–309.66	0.14	13	3	3	gpm901	308.58	mHbrBT195-Mo17	309.88
MQTL43	9	2.25	432.71	432.68–432.74	0.06	9.72	3	5	gpm101g	432.63	gpm58b	434.75
MQTL44	10	866.47	162.7	162.36–163.04	0.68	10.23	2	3	IDP3820	161.3	npi105a	163.2
MQTL45	10	866.47	176.96	176.69–177.24	0.55	9.68	2	4	zn1	176.66	bcd1072b(hsp70)	177.5
MQTL46	10	866.47	234.2	233.96–234.44	0.48	7.91	3	3	mHbrMA330-B73	232.82	cdo551b	235.42
MQTL47	10	866.47	162.7	162.36–163.04	0.68	10.23	2	3	IDP3820	161.3	npi105a	163.2

obtained, and the efficiency of MAS could be improved by developing molecular markers closely linked to MQTL.

Maize low temperature tolerance is a typical quantitative trait, and its genetic mechanism is relatively complex, which is regulated by multiple genes and is easily affected by environment. Because of differences in mapping populations, statistical methods and experimental environments in previous studies, QTLs related to maize low temperature tolerance were located on 10 chromosomes. In the meta-analysis of this study, a phenomenon was noted wherein maize low temperature tolerance-related QTLs were widely distributed on 10 chromosomes. In addition, maize low temperature tolerance-related QTLs had the characteristics of chromosome cluster distribution (Fig. 1). The results further verified the phenomenon of QTL cluster distribution in maize [19], which was probably due to pleiotropic effect. The results provided a certain reference for obtaining the enrichment region of maize stress-resistant genes and had guiding significance for the future practice of MAS.

5. Conclusions

Maize resistance to low temperature is a complex quantitative trait controlled by polygenes, and this behavior is easily influenced by environment. The systems-level integration and reanalysis of maize low temperature-resistant QTLs are informative for the eventual QTL cloning and breeding application. In this study, 47 MQTLs were detected. The CIs at all sites ranged from 0.04 cM to 102.73 cM, and the proportion of the phenotypic variance associated with each of them from 3.32% to 20.11%. Major chromosomal sites were identified on Chr.6 (MQTL29, MQTL30, and MQTL31). The results presented here lay a foundation for the determination of genetic basis of maize low temperature tolerance. Moreover, information on MQTLs reported in this study is helpful for functional marker development and elite allele introgression in maize breeding programs.

Financial support

This research was funded by Heilongjiang Province “Ten Million” Special Project (2019ZX16B03-2) and Heilongjiang Academy of Agricultural Sciences “Agricultural Science and Technology Innovation Project” (HNK2019CX03).

Conflict of interest

The authors declare no conflict of interest.

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