



A QTL atlas for grain yield and its component traits in maize (*Zea mays*)

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Abstract

Grain yield and its component traits are essential targets in maize breeding. These traits are genetically complex and controlled by a large number of quantitative trait loci (QTL). The aim of this study was to compile reported QTL and major genes for grain yield and its component traits in a QTL atlas, as a valuable resource for the maize community. To this end, 1,177 QTL related to maize yield were collected from 56 studies published between 1992 and 2018. These QTL were projected to genetic map “IBM2 2008 Neighbors”, which led to the identification of 135 meta-QTL. Some genomic regions appear to be hotspots for yield-related meta-QTL, often affecting more than one of the investigated traits. Moreover, we catalogued 20 major maize loci associated with yield and identified 65 maize homologs of 21 rice yield-related genes. Interestingly, we found that a significant proportion of them are located in meta-QTL regions. Collectively, this study provides a reference for QTL fine-mapping and gene cloning, as well as for molecular marker-assisted breeding of yield-related traits in maize.

KEYWORDS

candidate genes, grain yield, maize, meta-analysis, meta-QTL, yield components

1 | INTRODUCTION

Maize is one of the most important cereal crops for food, feed and energy worldwide, and consequently, grain yield is an agronomic trait of utmost importance. Grain yield is a highly complex, quantitative trait controlled by numerous genes with small effects (Hallauer & Miranda, 2010). In the last 2–3 decades, a large number of QTL for grain yield and yield-related traits have been identified through QTL mapping studies. However, despite this large body of information that has been generated

on the genetic control underlying grain yield and yield component traits, such QTL information has not been widely adopted and utilized in maize breeding programmes or by maize researchers. This is partly due to the quantitative nature of these traits and many QTL being population-specific and thus not transferable to other populations. Moreover, different marker systems and population-specific genetic linkage maps used for QTL mapping complicate the comparison of results across studies.

Meta-analysis is a statistical approach that combines the results from previous studies by analysing the information through statistical

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TABLE 1 List of grain yield and its component traits considered in this meta-QTL study

	Abbreviation	Traits included	No. of studies
Grain yield	GY	Grain yield per plant Grain yield per plot	27
Ear weight per plant	EWPP	Ear weight per plant	3
Ear length	EL	Ear length	29
Ear diameter	ED	Ear diameter	21
Cob diameter	CD	Cob diameter	5
Kernel row number	KRN	Kernel row number Ear row number	30
Kernel number per row	KNPR	Kernel number per row Grain number per row	20
Grain weight	GW	Grain weight One hundred kernel weight 300-Kernel weight	33
Kernel length	KL	Kernel length 10-Kernel length 20-Kernel length	10
Kernel thickness	KT	Kernel thickness 10-Kernel thickness 20-Kernel thickness	6

merging and comprehensive evaluation (Glass, 1976), which can also be applied to QTL mapping results (Mace et al., 2018; Martinez et al., 2016; Salvi & Tuberosa, 2015). In maize, the “IBM2 2008 Neighbors” map (Lee et al., 2002), a genetic map with high-density molecular markers, has laid the foundation for the integration of QTL from different experiments. Based on such an integrated map, a mathematical model can be built to identify “consistent” QTL, defined as meta-QTL, and narrow down their confidence intervals through meta-analysis

TABLE 2 Chromosomal distribution of QTL reported for maize grain yield and its component traits

Trait	Chr.1	Chr.2	Chr.3	Chr.4	Chr.5	Chr.6	Chr.7	Chr.8	Chr.9	Chr.10	Total
GY	30	8	9	11	13	12	9	7	6	9	114
EWPP	1	6	7	2	1	4	3	2	8	4	38
EL	32	19	20	7	14	12	27	15	7	18	171
ED	19	21	18	9	11	7	15	17	7	11	135
CD	7	6	1	3	4	0	3	1	1	0	26
KRN	24	17	28	34	28	8	19	13	17	19	207
KNPR	13	8	3	8	14	5	20	8	8	10	97
GW	67	21	36	34	25	24	42	14	24	19	306
KL	13	7	9	5	3	6	2	5	2	2	54
KT	5	7	2	2	2	3	1	1	1	5	29
Total	211	120	133	115	115	81	141	83	81	97	1,177

Abbreviations: CD, cob diameter; ED, ear diameter; EL, ear length; EWPP, ear weight per plant; GW, grain weight; GY, grain yield; KL, kernel length; KNPR, kernel number per row; KRN, kernel row number; KT, kernel thickness.

(Goffinet & Gerber, 2000). For example, Wang, Wu, Ding, and Xi (2009) collected 400 yield-related QTL from different experiments and found 96 meta-QTL (Wang et al., 2009). In another study, Wang, Weng, Lu, Wang, and Li (2011) collected 411 yield and yield-related QTL and constructed an integrated QTL map containing 221 QTL for yield and its component traits (Wang et al., 2011). More recently, Chen et al. (2017) collected 999 QTL for maize yield traits from 33 published studies and obtained 76 meta-QTL through meta-analysis (Chen et al., 2017).

The aim of this study was to provide the most comprehensive and up-to-date inventory of the yield-related QTL landscape, the maize QTLome and major loci reported to affect yield. To this end, we first collected 1,177 QTL of maize yield traits from 56 studies published between 1992 and 2018 and then integrated them on the “IBM2 2008 Neighbors” reference map. In addition, major yield loci from maize and homologs of rice genes were analysed with regard to their genomic co-localization with the identified meta-QTL. Taken together, this QTL atlas can serve as a resource for maize breeding and research towards further improvement and genetic understanding of yield and its component traits.

2 | MATERIALS AND METHODS

2.1 | Data collection

QTL data were collected from 56 studies published between 1992 and 2018. A total of ten maize (*Zea mays* L.) yield and yield-related traits were considered in this study, including grain yield (GY), ear weight per plant (EWPP), ear length (EL), ear diameter (ED), cob diameter (CD), kernel row number (KRN), kernel number per row (KNPR), grain weight (GW), kernel length (KL) and kernel thickness (KT). For QTL without physical map position, we identified the physical map position in the B73 genome (B73_RefGen_v4) based on the left and right markers' physical location. Subsequently, we converted the physical map position to APGv4 version by assembly converter (http://ensembl.gramene.org/Oryza_sativa/Tools/AssemblyConverter?db=core).

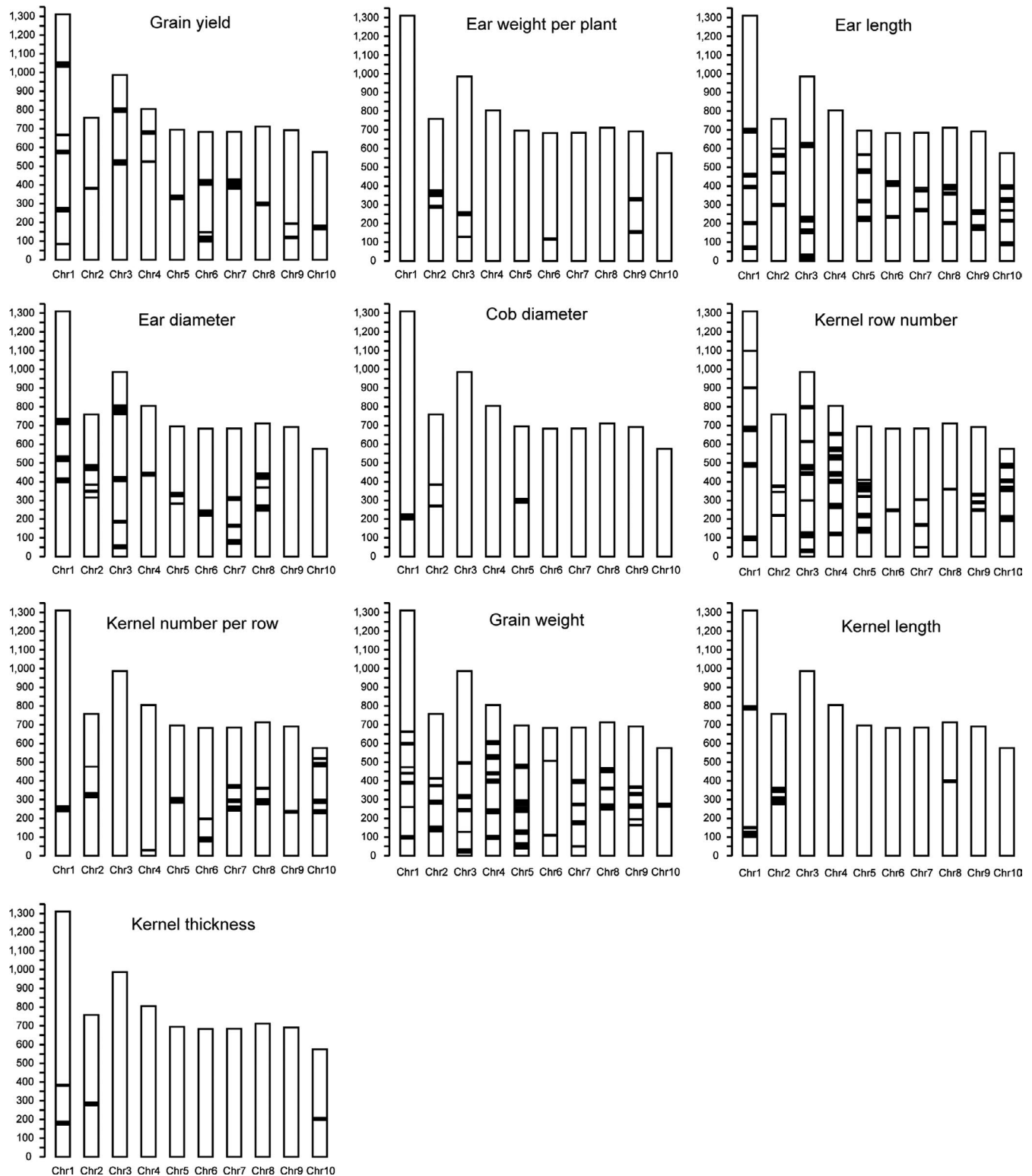


FIGURE 1 Distributions of the 202 meta-QTL identified for grain yield and its component traits. The axis shows the genetic map distance in cM; the black bars represent the meta-QTL regions

2.2 | Map projection

All collected QTL were projected to the target map “IBM2 2008 Neighbors” based on their left and right markers or the nearest marker. For markers, which were not on the IBM2 map, we used

the physical position of the QTL to project them on the IBM2 map. This means that we searched the marker on the IBM2 map, which is physically closest to the QTL marker, to project the QTL to the IBM2 map. It should be noted that we only used markers on the IBM2 map for which the distance to the original marker is <10Kb.

TABLE 3 Meta-QTL identified for maize grain yield and its component traits

Meta-QTL	Chr.	Position	Left marker	Right marker	Interval (cM)	Physical interval (bp)	Traits
MQTL1	1	212.07	crr8	gpm559	196.765–226.76	28,614,414–39,461,267	CD, EL
MQTL2	1	407.78	psei7	expb6	396.225–419.335	80,601,549–93,847,218	ED
MQTL3	1	522.54	umc1812	rnr6	508.82–536.26	182,705,449–190,964,811	ED
MQTL4	1	721.12	bcd207a	IDP126	706.23–736.01	227,583,574–234,435,868	ED
MQTL5	1	71.04	hyd6	IDP4725	62.7–79.38	5,466,250–7,386,352	EL
MQTL6	1	458.29	IDP8606	az19D1	449.63–466.95	155,927,725–163,308,047	EL
MQTL7	1	696.31	gpm802	umc1128	685.52–707.1	220,037,238–227,870,996	EL
MQTL8	1	390.87	nrx1	IDP1986	384.6–402.32	71,675,538–85,098,449	GW, EL
MQTL9	1	441.28	AY109678	IDP831	437.57–444.99	105,529,216–117,006,192	GW
MQTL10	1	473.57	umc1395	umc2233	472.64–474.5	166,197,012–167,087,181	GW
MQTL11	1	599.32	umc1335	umc2236	593.845–604.795	199,526,569–200,686,322	GW
MQTL12	1	663.13	umc1486	TIDP5582	660.55–665.71	212,544,411–214,041,602	GW
MQTL13	1	84.17	bnlg1014	bhlh35	82.98–85.36	7,034,080–8,017,653	GY
MQTL14	1	268.56	TIDP2962	p2	257.575–279.545	41,838,164–48,424,617	GY, GW
MQTL15	1	576.43	TIDP3582	TIDP5292	568.495–584.365	195,402,576–197,842,950	GY
MQTL16	1	666.88	IDP8950	cncr1	663.745–670.015	212,827,329–214,573,739	GY
MQTL17	1	1,043.42	apr18	AY106825	1,031.195–1055.645	295,636,319–299,188,693	GY
MQTL18	1	114.3	lls1	umc115	99.53–129.07	10,265,855–15,175,214	KL
MQTL19	1	150.77	IDP209	IDP4230	147.17–154.37	16,019,272–18,325,785	KL
MQTL20	1	790.88	mab7	umc1991	781.32–800.44	244,210,054–249,131,104	KL
MQTL21	1	251.53	tgdl	pdcl	236.895–266.165	41,838,204–45,724,685	KNPR
MQTL22	1	97.88	gst31	TIDP8778	87.15–108.61	8,130,156–11,584,664	KRN, GW
MQTL23	1	489.96	umc1603	TIDP4573	479.905–500.015	167,093,959–179,013,478	KRN
MQTL24	1	682.02	IDP4480	IDP8154	669.135–694.905	214,316,529–218,581,439	KRN
MQTL25	1	900.86	emp4	rps10	898.255–903.465	276,804,885–279,386,535	KRN
MQTL26	1	1,099.64	fdx3	gpm671a	1,098.955–1100.325	301,512,118–301,727,825	KRN
MQTL27	1	180.94	sfp1	ifa1	172.195–189.685	24,778,825–26,771,165	KT
MQTL28	1	383.55	myb156	IDP511	380.36–386.74	65,079,230–72,422,461	KT
MQTL29	2	270.42	IDP4687	prpo2	266.815–274.025	33,458,523–36,238,478	CD
MQTL30	2	474.86	IDP8607	TIDP5694	460.395–489.325	208,366,773–212,551,977	ED, EL, KNPR
MQTL31	2	299	fl1	umc8b	292.83–314.5	43,020,779–53,960,657	EL, KL
MQTL32	2	564.84	TIDP5645	IDP7660	557.275–572.405	221,963,944–224,116,168	EL
MQTL33	2	600.37	IDP7614	umc1256	600.17–600.57	231,387,026–231,641,052	EL
MQTL34	2	373.59	IDP8402	umc1755	368.025–380.33	153,602,981–179,457,271	EWPP, GW, KRN
MQTL35	2	142.61	TIDP5615	gpm7	128.995–156.225	10,502,839–14,135,350	GW
MQTL36	2	412.97	TIDP2671	mbd117	410.86–415.08	190,977,198–193,814,484	GW
MQTL37	2	382.28	TIDP3735	IDP866	378.665–385.895	170,387,400–175,801,116	GY, CD, ED
MQTL38	2	352.62	IDP8654	bnlg1831	340.825–368.2	66,446,831–156,922,169	KL, ED, EWPP, KRN
MQTL39	2	324.14	IDP267	IDP4221	311.675–336.605	50,707,050–63,284,690	KNPR, ED
MQTL40	2	220.48	ole1	IDP296	216.895–224.065	22,072,283–29,993,501	KRN
MQTL41	2	283.16	IDP7686	IDP7152	273.675–295.34	35,909,767–43,541,448	KT, EWPP, GW, KL
MQTL42	3	52.17	mmp38	TIDP5337	42.9–61.44	2,791,471–3,620,134	ED
MQTL43	3	186.1	umc1495	umc1655	181.1–191.1	19,238,843–25,820,717	ED

(Continues)

TABLE 3 (Continued)

Meta-QTL	Chr.	Position	Left marker	Right marker	Interval (cM)	Physical interval (bp)	Traits
MQTL44	3	414.4	IDP4091	IDP9062	402.54–426.26	173,523,604–180,791,331	ED
MQTL45	3	769.92	TIDP5764	IDP7486	759.825–780.015	224,987,243–227,491,948	ED
MQTL46	3	798.01	IDP4108	phot1	788.48–807.875	227,921,572–233,046,742	ED, GY, KRN
MQTL47	3	10.94	amyb4	umc1394	3.505–18.375	826,368–1,687,515	EL
MQTL48	3	158.63	gpm423a	umc2158	147.755–169.505	11,887,709–19,237,887	EL
MQTL49	3	223.84	mmc0132	gpm279	210.07–237.61	33,380,642–58,919,893	EL
MQTL50	3	619.77	IDP4731	umi8	608.43–631.11	213,455,933–217,057,372	EL, KRN
MQTL51	3	26.74	IDP703	tcptf33	17.415–38.25	1,408,232–2,709,285	GW, EL, KRN
MQTL52	3	243.81	gpm279	mmp9	238.175–261.65	58,920,338–112,398,360	GW, EWPP
MQTL53	3	316.12	IDP8406	IDP8616	306.945–325.295	133,872,675–149,518,417	GW
MQTL54	3	496.29	obf3	mrpi2	491.625–500.955	190,259,712–192,962,985	GW
MQTL55	3	519.62	mrpi2	gst8	506.94–532.3	192,965,166–197,152,506	GY
MQTL56	3	117.5	cg1	umc2259	103.3–131.7	6,928,913–9,366,966	KRN, EWPP, GW
MQTL57	3	300.21	hsp70–4	TIDP3027	298.755–301.665	126,865,908–128,772,746	KRN
MQTL58	3	444.51	na1	umc60	436.315–452.705	181,822,989–183,976,488	KRN
MQTL59	3	477.59	gpm298	IDP149	465.96–489.22	185,592,577–189,987,406	KRN
MQTL60	4	97.82	IDP3934	IDP4153	88.715–106.925	5,769,308–7,348,868	GW
MQTL61	4	237.53	umc1963	umc1969	226.78–248.28	29,284,165–33,819,646	GW
MQTL62	4	400.13	gln5	umc2038	391.34–410.825	170,035,992–175,877,003	GW, KRN
MQTL63	4	605	IDP666	IDP3866	595.845–614.155	233,621,521–236,808,104	GW
MQTL64	4	679.85	IDP4019	umc1109	671.9–687.8	242,144,623–243,421,992	GY
MQTL65	4	31.33	IDP578	TIDP5763	29.095–33.565	3,000,281–3,464,978	KNPR
MQTL66	4	121.31	IDP85	IDP5997	114.42–128.2	7,407,162–11,329,629	KRN
MQTL67	4	271.36	umc2282	his2b2	259.315–283.405	37,786,012–65,618,139	KRN
MQTL68	4	441.81	IDP1421	ppr5	431.21–452.41	177,028,170–184,369,041	KRN, ED, GW
MQTL69	4	530.76	IDP7593	umc2200	516.635–542.715	193,549,219–207,028,261	KRN, GW, GY
MQTL70	4	574.05	mlo4	gpm871	562.56–585.54	211,843,655–230,200,724	KRN
MQTL71	4	655.44	IDP7548	IDP414	649.215–661.665	240,522,788–241,795,463	KRN
MQTL72	5	331.93	nip1a	IDP7914	322.71–344.645	151,838,198–168,108,235	ED, GY
MQTL73	5	315.22	sbp1	TIDP8860	312.11–318.33	91,109,100–140,714,979	EL
MQTL74	5	323.6	TIDP8860	rps24	318.795–328.405	140,717,468–155,336,754	EL, GY, KRN
MQTL75	5	568.14	atpc1	gpm874b	564.615–571.665	213,494,647–213,761,423	EL
MQTL76	5	53.1	umc1445	umc1260	38.105–68.095	2,184,882–3,149,222	GW
MQTL77	5	126.9	IDP150	bhlh154	116.08–137.72	6,407,653–9,460,784	GW
MQTL78	5	247.14	IDP7560	gpm157	233.48–260.8	22,866,124–47,752,003	GW
MQTL79	5	283.51	IDP6078	TIDP5078	269.55–310.34	58,018,845–149,303,626	GW, CD, ED, KNPR
MQTL80	5	478.68	gpm41	pac1	469.4–489.735	193,954,983–201,801,849	GW, EL
MQTL81	5	141.48	phyC2	umc1587	128.295–154.665	7,382,139–10,404,954	KRN
MQTL82	5	219.01	mbd109	cpn1	209.31–237.05	16,891,070–31,979,596	KRN, EL
MQTL83	5	362.19	ppi1	IDP1648	348.555–375.825	171,711,252–173,177,267	KRN
MQTL84	5	387.08	aasr6	TIDP5775	385.11–389.05	175,170,821–176,050,924	KRN
MQTL85	5	392.06	pza02040	magi62442	389.83–394.29	176,186,882–177,531,199	KRN
MQTL86	5	408.87	TIDP9188	umc1155	407.75–409.99	179,681,601–184,662,295	KRN
MQTL87	6	233.07	ebe2	umc1250	218.31–253.01	113,548,492–131,419,705	ED, EL, KRN
MQTL88	6	414.55	gpm908b	pebp7	400.5–427.995	160,518,805–163,368,049	EL, GY

(Continues)

TABLE 3 (Continued)

Meta-QTL	Chr.	Position	Left marker	Right marker	Interval (cM)	Physical interval (bp)	Traits
MQTL89	6	507.66	psah1	gpm378	507.395–507.925	168,208,191–168,918,648	GW
MQTL90	6	111.71	bnlg1641	oec33	98.41–125.01	50,574,770–91,338,946	GY, EWPP, GW
MQTL91	6	147.34	TIDP6248	mab26	145.845–148.835	94,189,094–96,204,324	GY
MQTL92	6	87.57	umc2312	umc2314	75.84–99.3	29,796,545–39,661,638	KNPR
MQTL93	6	197.26	gpm824	umc1979	194.25–200.27	109,439,900–109,836,884	KNPR
MQTL94	7	78.36	IDP2360	gpm47	68.27–88.45	5,054,424–6,928,657	ED
MQTL95	7	165.13	umc2327	si605085g01	158.885–185.325	22,055,193–48,965,520	ED, GW, KRN
MQTL96	7	309.78	umc1713	IDP96	301.655–317.905	133,907,560–136,123,538	ED, KRN
MQTL97	7	272.13	zim28	pza02365	264.865–280.605	125,135,827–131,101,945	EL, GW
MQTL98	7	398.16	cdpk8	psb29	388.545–410.565	158,305,234–162,636,525	GW, EL, GY
MQTL99	7	384.03	IDP9042	IDP2483	379.27–388.79	148,351,442–149,326,156	GY
MQTL100	7	420.41	kik1	IDP4109	410.445–430.375	161,582,076–164,518,386	GY
MQTL101	7	252.77	IDP8670	IDP4336	240.58–264.96	107,532,516–125,155,948	KNPR
MQTL102	7	293.28	IDP5896	TIDP3761	286.255–300.305	133,385,851–135,156,136	KNPR
MQTL103	7	371.48	lon1	umc1865	363.635–380.535	148,273,453–152,313,978	KNPR, EL
MQTL104	7	50.55	umc1426	prp4	48.605–52.55	3,206,895–3,653,618	KRN, GW
MQTL105	8	368.68	IDP689	IDP2365	367.165–370.195	137,868,133–139,922,670	ED
MQTL106	8	430.8	AY109883	IDP2426	415.815–445.785	165,746,628–169,441,892	ED
MQTL107	8	202.82	csu849	pza01209	197.095–208.545	56,949,909–67,046,926	EL
MQTL108	8	360.78	mrp1	IDP8682	354.11–367.45	132,314,587–139,029,418	EL, GW, KNPR, KRN
MQTL109	8	394.64	IDP8541	crr4	381.27–408.01	144,288,735–162,775,996	EL, KL
MQTL110	8	260.3	umc2075	IDP179	245.64–275.06	96,826,817–102,988,442	GW, ED
MQTL111	8	458.35	IDP2426	TIDP3577	446.795–469.905	169,445,215–171,222,519	GW
MQTL112	8	289.86	act1	AY110056	275.19–307.585	102,417,640–115,386,449	KNPR, GY
MQTL113	9	178.31	pza01272	TIDP3100	164.925–191.695	18,809,336–21,877,254	EL
MQTL114	9	155	znod1	TIDP5595	148.835–161.165	16,775,891–18,531,201	EWPP
MQTL115	9	330.73	TIDP4605	TIDP5562	323.765–337.695	132,744,545–133,463,093	EWPP, GW, KRN
MQTL116	9	164.77	pza01272	TIDP3390	162.45–167.09	18,809,336–19,064,567	GW
MQTL117	9	264.86	IDP5001	pza00152	250.615–273.9	101,928,077–113,591,821	GW, EL
MQTL118	9	367.48	apx1	IDP102	363.125–371.835	136,739,519–141,024,529	GW
MQTL119	9	120.03	TIDP2976	umc2336	115.1–124.96	13,846,424–15,127,325	GY
MQTL120	9	193.69	baf1	umc1258	191.695–195.685	21,787,375–23,398,386	GY, GW
MQTL121	9	234.95	vpp2	knox2	229.38–240.52	81,455,307–96,269,799	KNPR
MQTL122	9	249.05	acp1	AY103770	243.73–254.37	97,680,959–102,858,558	KRN
MQTL123	9	290.87	gpm246b	IDP6873	284.995–296.745	113,592,370–117,527,271	KRN
MQTL124	10	92.43	bnlg1451	gpm657	83.575–101.285	4,474,953–5,236,890	EL
MQTL125	10	215.14	tps23	AY112073	188.63–220.08	58,557,438–83,290,724	EL, KRN, KT
MQTL126	10	325.55	gpm411b	gpm503	314.705–336.395	129,115,164–133,899,066	EL
MQTL127	10	395.94	IDP134	IDP8314	386.18–412.555	140,145,611–142,612,745	EL, KRN
MQTL128	10	266.85	clx2	IDP8244	262.845–272.21	113,484,076–114,249,089	GW, EL
MQTL129	10	276.61	IDP2458	cl32758_1	272.195–281.025	115,195,221–119,056,861	GW
MQTL130	10	173.48	IDP3820	glu1	162.765–184.195	13,315,394–35,174,831	GY
MQTL131	10	235.85	TIDP2980	umc1995	226.975–244.725	85,135,233–93,373,491	KNPR
MQTL132	10	290.83	cl32758_1	hag103b	281.43–300.23	119,059,431–127,154,778	KNPR

(Continues)

TABLE 3 (Continued)

Meta-QTL	Chr.	Position	Left marker	Right marker	Interval (cM)	Physical interval (bp)	Traits
MQTL133	10	520.28	umc1113	dba3	517.005–523.555	149,200,759–149,278,822	KNPR
MQTL134	10	362.04	krp15	umc1045	348.965–375.115	134,575,911–139,063,429	KRN
MQTL135	10	485.1	TIDP3378	lhcb6	473.845–498.335	148,715,856–149,775,316	KRN, KNPR

2.3 | Meta-analysis

Meta-analysis was performed for each trait with the BioMercator4 (Arcade et al., 2004) software. This integrates the QTL which are closely located to the meta-QTL and refines the meta-QTL confidence intervals. Generally, five different models, including 1-, 2-, 3-, 4- or N-QTL models, with different Akaike information criterion (AIC) values were tested for the meta-QTL analysis (Goffinet & Gerber, 2000). The model with the lowest AIC value was then considered as the optimal model. If several meta-QTL for different traits were located at the same position with an overlapping confidence interval greater than 70%, they were integrated to one meta-QTL.

2.4 | Mining of homologous rice candidate genes in the meta-QTL regions

Thirty-three rice genes related to grain yield and yield component traits were collected from the CHINA RICE DATA CENTER (<http://www.ricedata.cn/>). The protein sequences of maize were downloaded from EnsemblPlants (<https://plants.ensembl.org/>). We then used the protein sequences of the 33 rice genes for alignment with all maize proteins and the BLAST+ (Camacho et al., 2009) software to identify homologous genes in maize. The criteria for these searches used an *E*-value of $<1e-10$, identity $>60\%$, alignment length $>60\%$ of the rice proteins length and an alignment score >200 to select homologous genes.

3 | RESULTS

A total of 1,177 QTL for maize yield as well as yield-related QTL were collected from 56 published studies (Table 1; Table S1). The size of the mapping populations ranged from 74 to 498, while recombinant inbred lines (RIL) and F2:3 families were the most often used population types for QTL mapping. Across all evaluated experiments, "Mo17", "Huangzaosi", "Qi319" and "Ye478" were the most widely used parents. The reported QTL were distributed on all ten chromosomes, with the highest number of QTL on chromosome 1 (211) and the lowest number of QTL on chromosomes 6 and 9 (Table 2). The number of QTL for per trait ranged from 26 for cob diameter to 306 for grain weight, while for the trait grain yield 114 QTL have been reported.

Of the 1,177 QTL, 608 were directly projected to the IBM2 map based on their flanking markers, whereas the remaining 569 QTL were

projected onto this map using their physical map positions and closely located markers. The meta-analysis identified a total of 202 meta-QTL, including 22 for grain yield, 8 for ear weight per plant, 34 for ear length, 22 for ear diameter, 4 for cob diameter, 41 for kernel row number, 17 for kernel number per row, 43 for grain weight, 7 for kernel length and 4 for kernel thickness (Figure 1; Table S2). Especially for grain yield, kernel row number and grain weight, meta-QTL for each trait were found on all ten chromosomes. Finally, we derived 135 meta-QTL, named MQTL1 to MQTL135, by merging overlapping meta-QTL for the different traits (Table 3; Figure 2). These meta-QTL are unevenly distributed on the maize genome (Figure 2). Remarkably, 41 out of the 135 meta-QTL affected two or more traits. Four of them, MQTL38 on chromosome 2 (340.825 cM –368.2 cM), MQTL41 on chromosome 2 (273.675–295.34 cM), MQTL79 on chromosome 5 (269.55–310.34 cM) and MQTL108 on chromosome 8 (354.11–367.45 cM), were identified to affect even four of the yield traits. Regarding grain yield, the highest number of joint meta-QTL was found for grain weight, which, however, is also the trait with the highest number of identified meta-QTL (Figure 3). Across all traits, the highest number of joint meta-QTL was found for kernel row number and grain weight, with 12 shared meta-QTL.

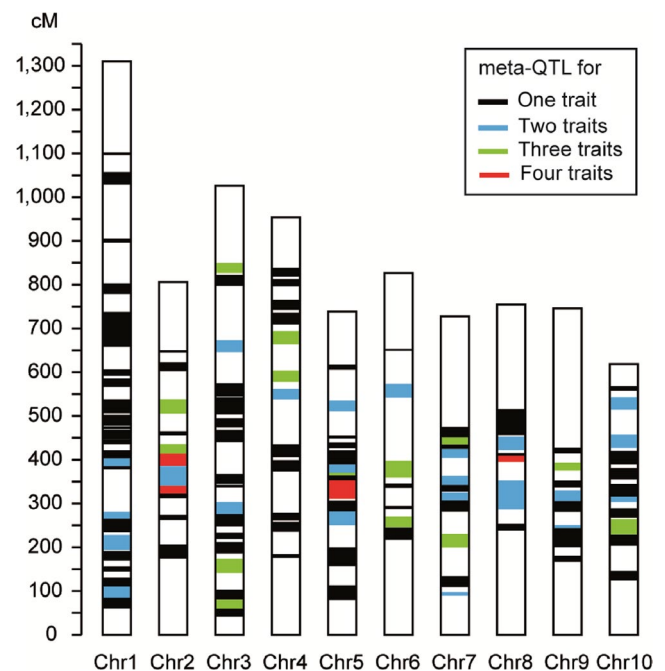
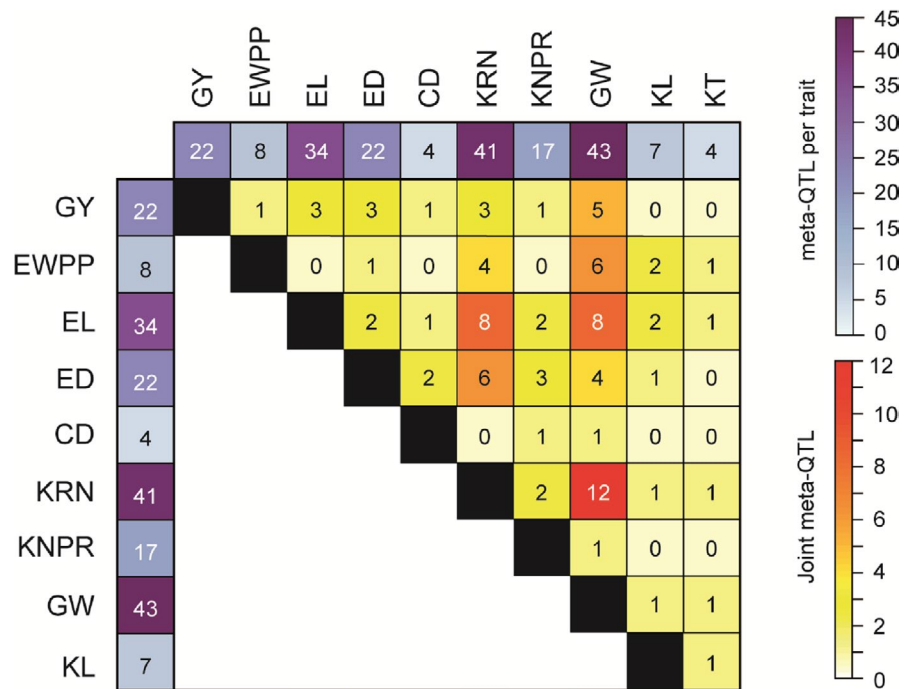


FIGURE 2 Distribution of the 135 meta-QTL on the ten chromosomes. The axis shows the genetic map distance in cM; the coloured bars represent meta-QTL regions affecting a single trait, two, three or four traits

FIGURE 3 Identified meta-QTL per trait and meta-QTL shared between traits



We next catalogued major maize loci reported to affect yield or a yield component trait (Table 4). The analysis of their genomic localization revealed that 13 out of the 20 genes are located in meta-QTL regions. In addition, we used the protein sequences of 33 rice yield genes and aligned them to the maize protein database to identify their corresponding maize genes. This revealed 65 homologs of 21 of the rice genes in the maize genome (Table S4), while for the other 11 rice genes no homologs were found. We then aligned these homologs to the meta-QTL regions in order to identify additional candidate genes underlying the meta-QTL. Thirty-one of the 65 homologs (47.7%), derived from 19 rice genes, were found to be located in the meta-QTL regions (Table 5), which are a significant ($p = .0003$) proportion considering that the meta-QTL regions account for only 27.2% of the genetic map. Four candidate genes *Zm00001d014793*, *Zm00001d003776*, *Zm00001d052890* and *Zm00001d031451*, which are located in the meta-QTL regions MQTL79, MQTL39, MQTL69 and MQTL3, respectively, are known as *td1* (Bommert et al., 2005), *mn1* (Cheng, Taliario, & Chourey, 1996), *ub3* and *ub2* (Chuck, Brown, Meeley, & Hake, 2014), and have previously been reported to affect maize yield. Others affect various processes and as in rice, may well play important roles in the formation of maize yield.

4 | DISCUSSION

4.1 | Identification of yield meta-QTL in maize

Since Goffinet and Gerber first proposed to apply meta-analysis for the integration of QTL (Goffinet & Gerber, 2000), several such studies have been performed for a range of crops, including maize (Chen et al., 2017; Jiang et al., 2013; Wang et al., 2009; Wang et al., 2013; Wang et al., 2016). The aim of this study was to provide the

most comprehensive meta-QTL analysis for yield and yield component traits in maize to date, as a resource for maize research and breeding.

Yield and its component traits are genetically complex, highly quantitative traits, that are controlled by many small-effect QTL. Consistently, we identified 1,177 QTL for the ten yield-related traits investigated in this study. However, QTL reported in the literature are often population- and/or environment-specific, and thus, a meta-analysis holds the potential to identify the most robust and therefore most promising regions for use in maize breeding as well as for further research towards fine-mapping and cloning of the underlying genes. Our meta-analysis identified 202 meta-QTL, which, after the merging of co-located meta-QTL for different traits, resulted in 135 meta-QTL. Some of the identified meta-QTL overlapped with previously reported ones, even though the applied methods differed to a certain degree (Table S5) (Chen et al., 2017; Wang et al., 2013; Wang et al., 2016). Among these overlapping meta-QTL, seven were consistently identified in this and three surveyed studies, making them promising targets for further research (Table S5).

4.2 | Genome distribution and co-localization of meta-QTL

The meta-QTL identified in this study were found on all chromosomes, indicating that loci throughout the entire genome contribute to the expression of the yield traits (Table 2; Figure 1). Nevertheless, the meta-QTL were not evenly distributed along the ten chromosomes, but certain meta-QTL hotspots were apparent, affecting two or even up to four traits (Figure 2). This may be due to clusters of linked genes affecting different traits or to

TABLE 4 Major maize genes related to yield

Gene symbol	Trait	Gene product	Maize gene	Chr.	Position (bp)	Meta-QTL	Reference
CT2	Shoot meristem size	GTP-binding protein	Zm00001d027886	1	16,722,740 – 16,730,676	MQTL19	Bommert et al. (2013)
<i>tb1</i>	Ear size	TCP transcription factor	Zm00001d033673	1	63,456,839 – 63,460,120	-	Lauren et al. (2002)
<i>ub2</i>	Grain yield	SBP-box transcription factor	Zm00001d031451	1	190,382,979–190,387,086	MQTL3	Chuck et al. (2014)
<i>ZmZHOUPI</i>	Kernel size and weight	Transcription factor	Zm00001d003677	2	53,849,188 – 53,854,880	MQTL39, MQTL31	Grimault et al. (2015)
<i>zfl2</i>	Ear morphology	-	Zm00001d002449	2	12,914,134 – 12,917,141	MQTL35	Bombliés and Doebley (2006)
<i>mn1</i>	Kernel development	Cell wall invertase	Zm00001d003776	2	58,876,057 – 58,879,338	MQTL39	Cheng et al. (1996)
<i>emp2</i>	Kernel development	Heat shock-binding factor protein	Zm00001d005675	2	183,064,072–183,068,902	-	Fu et al. (2002)
<i>Cg1</i>	Ear morphology	MicroRNA 156	GRMZM5G838324	3	6,928,278–6,928,401	-	Chuck et al. (2007)
<i>ra2</i>	Ear morphology	RA2 LOB domain protein	Zm00001d039694	3	12,158,280–12,159,065	MQTL48	Bortiri et al. (2006)
<i>KRN4</i>	Kernel row number	-	-	4	203,675,518–203,678,518	MQTL69	Liu et al. (2015)
<i>fea2</i>	Fasciated ear	Leucine-rich repeat receptor protein kinase	Zm00001d051012	4	136,765,307–136,767,795	-	Peter et al. (2013)
<i>Gln1–4</i>	Kernel size	Glutamine synthetase isoenzymes	Zm00001d051804	4	170,036,839–170,039,970	MQTL62	Martin et al. (2006)
<i>ub3</i>	Grain yield	SBP-box transcription factor	Zm00001d052890	4	203,611,347–203,615,518	MQTL69	Chuck et al. (2014)
<i>td1</i>	Fasciated ear	Leucine-rich repeat receptor protein kinase	Zm00001d014793	5	63,456,839–63,460,120	MQTL79	Bommert et al. (2005)
<i>ZmINCW1</i>	Kernel size and weight	Cell wall invertase	Zm00001d016708	5	173,403,817–173,408,283	-	Liu, Huang, et al. (2017)
<i>ubl1</i>	Kernel size	Phosphodiesterase	Zm00001d017432	5	195,844,968 – 195,847,238	MQTL80	Li et al. (2016)
<i>Gln1–3</i>	Kernel number	Glutamine synthetase isoenzymes	Zm00001d017958	5	210,867,756–210,871,269	-	Martin et al. (2006)
<i>ra1</i>	Ear morphology	Transcription factor	Zm00001d020430	7	113,572,410–113,572,937	MQTL101	Vollbrecht et al. (2005)
<i>tsh4</i>	Ear morphology	SBP-box transcription factor	Zm00001d020941	7	137,273,600–137,277,139	-	Chuck et al. (2010)
<i>zfl1</i>	Ear morphology	-	Zm00001d026231	10	141,561,796–141,564,817	MQTL127	Bombliés and Doebley (2006)

pleiotropic gene action of a single or several genes. Moreover, different marker densities on each chromosome may have had an impact on the number of detected QTL (Yu et al., 2011). Shared meta-QTL between grain yield and its component traits were found for all traits, except for kernel length and kernel thickness (Figure 3). Eleven of the 22 grain yield meta-QTL co-located with a meta-QTL for a yield component trait, indicating that the respective grain yield meta-QTL may actually trace back to the component trait and its effect on yield. The other half of the grain yield meta-QTL are likely to depend on other traits that, despite not being direct yield components, can affect yield.

4.3 | Assessing maize and rice candidate genes

In recent years, several genes related to grain yield traits, particularly to kernel characteristics, have been identified in maize. The CLAVATA–WUSCHEL feedback loop is an important signalling pathway in plants that primarily affects stem cell maintenance in the inflorescence meristem, but in maize also grain shape and grain yield (Liu et al., 2015; Schoof et al., 2000). We found that the CT2 (Bommert, Je, Goldshmidt, & Jackson, 2013) and *td1* (Bommert et al., 2005) genes from this signalling pathway are located in the MQTL19 and MQTL79 regions,

TABLE 5 Candidate homologs of rice genes located within the meta-QTL regions in maize

Rice gene	Trait	Rice gene product	Homologous gene(s) in maize	Gene name in MaizeGDB	Meta-QTL region	Reference
BSG1	Grain size and grain weight	DUF640 domain-containing protein	Zm00001d051966		MQTL62	Ren et al. (2016)
			Zm00001d043011		MQTL59	
			Zm00001d015342		MQTL79	
D61	Grain yield	Systemin receptor SR160 precursor	Zm00001d011721	<i>bri1a</i> (<i>brassinosteroid insensitive1a</i>)	MQTL109	Yoichi et al. (2006)
FON1	Kernels per spike	Leucine-rich repetitive receptor protein kinase	Zm00001d014793	<i>td1</i> (<i>thick tassel dwarf1</i>)	MQTL79	Moon et al. (2006)
Ghd8	Grain yield	CCAAT box-binding protein HAP3 subunit	Zm00001d049485	<i>cadtfr5</i> (CCAAT-DR1-transcription factor 5)	MQTL61	Yan et al. (2011)
GIF1	Grain filling	Cell wall invertase	Zm00001d025354	<i>incw5</i> (<i>invertase cell wall5</i>)	MQTL129	Wang et al. (2008)
			Zm00001d003776	<i>mn1</i> (<i>miniature seed1</i>)	MQTL39	
			Zm00001d025355	<i>incw3</i> (<i>invertase cell wall3</i>)	MQTL129	
GS5	Grain size	OsSCP26—Putative serine carboxypeptidase homolog	Zm00001d040741		MQTL52	Li et al. (2011)
GSN1	Grain number and size	Dual specificity protein phosphatase	Zm00001d011037		MQTL108	Guo et al. (2018)
			Zm00001d035600		MQTL92	
GW2	Grain width and weight	Expressed protein	Zm00001d016164		MQTL79	Song, Huang, Shi, Zhu, and Lin (2007)
GW5	Grain width and weight	IQ calmodulin-binding motif family protein	Zm00001d010366		MQTL112	Liu, Chen, et al. (2017)
GW6a	Grain weight	HLS	Zm00001d015508	<i>hagtf24</i> (GNAT-transcription factor 24)	MQTL79	Song et al. (2015)
			Zm00001d046823	<i>hagtf35</i> (GNAT-transcription factor 35)	MQTL117	
HGW	Grain weight	Proline-rich cell wall protein-like	Zm00001d045263		MQTL114	Li et al. (2012)
IPA1	Grain yield	OsSPL14 - SBP-box gene family member	Zm00001d052890	<i>ub3</i> (<i>unbranched3</i>)	MQTL69	Jiao et al. (2010)
			Zm00001d031451	<i>ub2</i> (<i>unbranched2</i>)	MQTL3	
LP1	Panicle length	Remorin_C-containing protein	Zm00001d020708		MQTL97	Liu et al. (2016)
			Zm00001d005881		MQTL36	
OsAgs2	Grain size	Glucose-1-phosphate adenylyltransferase large subunit	Zm00001d032385	<i>agps1</i> (ADP glucose pyrophosphorylase small subunit leaf1)	MQTL7	Takashi, Kouichi, and Tatsuhito (2005)
			Zm00001d050032	<i>bt2</i> (<i>brittle endosperm2</i>)	MQTL67	
			Zm00001d005546	<i>agp1</i> (ADP glucose pyrophosphorylase small subunit embryo 1)	MQTL34	
OSSUT1	Grain weight	Sucrose transporter	Zm00001d033011	<i>sut3</i> (<i>sucrose transporter3</i>)	MQTL20	Kato, Taniguchi, and Horibata (2010)
GL3.1 (<i>qGL3</i>)	Grain length	Serine/threonine protein phosphatase	Zm00001d041307		MQTL52	Peng et al. (2012)
			Zm00001d013680		MQTL82	
			Zm00001d031088		MQTL23	

(Continues)

TABLE 5 (Continued)

Rice gene	Trait	Rice gene product	Homologous gene(s) in maize	Gene name in MaizeGDB	Meta-QTL region	Reference
SRS3	Grain shape	ATKINESIN-13A/ KINESIN-13A	Zm00001d037599	<i>krp9</i> (kinesin-related protein9)	MQTL87	Kanako et al. (2010)
SRS5	Grain size	Alpha-tubulin protein	Zm00001d013367	<i>tua4</i> (alpha tubulin4)	MQTL81	Segami (2011)
WTG1	Grain width and thickness	Ubiquitin thioesterase otubain-like	Zm00001d049873		MQTL67	Huang, (2017)

respectively. Furthermore, the *ra1* (Vollbrecht, Springer, Goh, Iv, & Martienssen, 2005), *ra2* (Bortiri et al., 2006), *zfl1*, *zfl2* (Bomblies & Doebley, 2006), *ub2* and *ub3* (GS Chuck et al., 2014) genes, which all affect ear morphology and thus yield by regulating the development of the spikelet-pair meristems and spikelet meristems (Liu et al., 2015), were found in MQTL101, MQTL48, MQTL127, MQTL35, MQTL3 and MQTL69, respectively. *KRN4*, which is located 60 Kb downstream of *ub3*, regulates the expression of *ub3* and affects the kernel row number of maize (Liu et al., 2015). In addition, *ubl1* (Li et al., 2016) and *ZmZHOUPI* (Grimault et al., 2015), which play an important role in the development of kernels, were found to be located in MQTL31 and MQTL80, respectively. The *mn1* (Cheng et al., 1996) gene, which is crucial for the development of the endosperm and pedicle of maize, is located in MQTL39. The *Gln1-4* (Martin et al., 2006) gene, which regulates the expression of glutamine synthetase mRNA and affects the kernel size, is located in MQTL62. However, some of the genes related to maize yield are not located in the identified meta-QTL regions, including *tb1* (Lauren, Paula, John, & Sarah, 2002), *emp2* (Fu, Robert, & Scanlon, 2002), *Cg1* (Chuck, Cigan, Saeteurn, & Hake, 2007), *fea2* (Peter, Namiko Satoh, & David, 2013), *ZmINCW1* (Liu, Huang, et al., 2017), *Gln1-3* (Martin et al., 2006) and *tsh4* (Chuck, Whipple, Jackson, & Hake, 2010). It should be noted that the *mn1* and *ZmINCW1* genes encode cell wall invertase proteins, while the candidate genes *Zm00001d025354* and *Zm00001d025355* identified in this study encode members of the same protein family. These four genes have recently been named *incw2*, *incw1*, *incw5* and *incw3*, respectively (Juárez-Colunga et al., 2018). The diverse nature of the genes related to yield illustrates the fact that the yield-related genes do not affect yield through a single pathway. Instead, yield-related genes participate in different molecular and physiological pathways and processes, and act at various developmental stages, which ultimately affect ear formation and therefore maize yield.

Next to linking known maize genes to the identified meta-QTL, we also took advantage of the progress made in rice in identifying yield-related genes. Intriguingly, for 19 rice genes related to grain yield, we identified homologous maize genes in 25 of our meta-QTL regions. Further research including functional analyses is required to verify these genes as underlying cause of the identified meta-QTL and to confirm their potential role in mediating grain yield in maize.

4.4 | Conclusions for the meta-analysis of maize yield

In this study, we performed a meta-analysis for QTL for grain yield and its component traits in maize, which resulted in a total of 135 identified meta-QTL. After validation in breeding programmes, these QTL appear to be promising candidates for utilization in marker-assisted or genomic selection. Moreover, QTL found consistently in several QTL mapping studies are more likely to be true QTL of broad relevance and thus warrant further research towards cloning of the underlying genes. The latter may be complemented by comparative genomic approaches based on candidate genes from maize or other crops. Collectively, this work presents a valuable resource for both, maize breeding and research.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

WL: designed the study. ZZ and ST: collected QTL mapping data. ZZ and GL: performed data analysis. ZZ, GL, DL, TMW, XW, SC, TW and WL: wrote the manuscript. All authors read and approved the final manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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