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ORIGINAL PAPER

QTL consistency and meta-analysis for grain yield components in three generations in maize

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Abstract Grain yield is the most important and complex trait in maize. In this study, a total of 258 F_9 recombinant inbred lines (RIL), derived from a cross between dent corn inbred Dan232 and popcorn inbred N04, were evaluated for eight grain yield components under four environments. Quantitative trait loci (QTL) and their epistatic interactions were detected for all traits under each environment and in combined analysis. Meta-analysis was used to integrate genetic maps and detected QTL across three generations (RIL, $F_{2:3}$ and BC_2F_2) derived from the same cross. In total, 103 QTL, 42 pairs of epistatic interactions and 16 meta-QTL (mQTL) were detected. Twelve out of 13 QTL with contributions (R^2) over 15% were consistently detected in 3–4 environments (or in combined analysis) and integrated in mQTL. Only q100GW-7-1 was detected in all four environments and in combined analysis. 100qGW-1-1 had the largest R^2 (19.3–24.6%) in three environments and in combined analysis. In contrast, 35 QTL for 6 grain yield components were detected in the BC_2F_2 and $F_{2:3}$ generations, no common QTL across three generations were located in the same marker intervals. Only 100 grain weight (100GW) QTL on chromosome 5 were located in adjacent marker intervals. Four common QTL were detected across the RIL and $F_{2:3}$ generations, and two between the RIL and BC_2F_2 generations. Each of five important mQTL (mQTL7-1, mQTL10-2, mQTL4-1, mQTL5-1 and mQTL1-3) included 7–12 QTL associated with 2–6 traits. In conclusion, we found evidence of strong influence of genetic structure and environment on QTL detection, high consistency of major QTL across environments and generations, and remarkable QTL co-location for grain yield components. Fine mapping for five major QTL (q100GW-1-1, q100GW-7-1, qGWP-4-1, qERN-4-1 and qKR-4-1) and construction of single chromosome segment lines for genetic regions of five mQTL merit further studies and could be put into use in marker-assisted breeding.

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Introduction

Maize (*Zea mays* L.) is widely used for food, forage, industrial and energy throughout the world. As the increase in population, decrease in cultivated land and occurrence of food crisis in recent years, improvement in grain yield becomes more and more important in maize breeding. However, grain yield is the most complex quantitative trait, which is not only controlled by many genes with relatively small effects and easily influenced by environments, but is also determined by several component traits correlated at different degrees. With the application of molecular markers, several studies on quantitative trait loci (QTL) mapping for grain yield and its component traits have been done, and detected QTL were distributed on all ten maize chromosomes (Stuber et al. 1987, 1992; Veldboom and Lee 1994; Austin and Lee 1996, 1998; Austin et al. 2000; Mihaljevic et al. 2004; Blanc et al. 2006; Yan et al. 2006; Li et al. 2007, 2009; Ma et al. 2007). Therefore, the genetic characteristics of grain yield and its components should be revealed through extensive studies using many distinct populations tested in diverse environments. Only major QTL with consistency across populations and environments could be put into broad

use in marker-assisted breeding and are worthy to be cloned in further studies.

Since different populations (Stuber et al. 1992; Austin et al. 2000), generations (Austin and Lee 1996, 1998; Li et al. 2007), and environments (Li et al. 2003; Lan et al. 2005) were commonly found to have great influence on the results of QTL detection experiments, direct comparisons of QTL data across different studies were difficult. Through meta-analysis QTL detected across several independent studies could be integrated and true QTL with more accurate confidence intervals and small target regions for candidate genes could be provided (Goffinet and Gerber 2000; Arcade et al. 2004; Khowaja et al. 2009). Using this method, Wang et al. (2009) obtained 96 meta-QTL from 400 QTL for grain yield and seven component traits detected using 17 mapping populations in 21 reports and from public data in maizeGDB (http://www.maizeGDB.org/). Chardon et al. (2004) identified 62 consensus-QTL from 313 QTL detected in 22 reports for flowering time in maize. Also, 401 consensus-QTL were revealed from 785 QTL by Shi et al. (2009) for eight yield traits in rapeseed, in which 82.5% QTL were clustered and were integrated into 111 unique pleiotropic QTL.

Popcorn germplasm is generally inferior to normal maize in grain yield. Normal maize germplasm could be introduced to improve grain yield and yield components in popcorn (Ziegler and Ashman 1994). In our previous study, QTL mapping for grain yield components were conducted using both $F_{2:3}$ and BC_2F_2 generations derived from the same cross between Dan232 and N04 (Li et al. 2007). To date, no other such studies using popcorn germplasm have been reported. In this paper, 258 recombinant inbred lines (RIL) derived from the same cross between Dan232 and N04 were used to detect QTL for eight grain yield components in four environments. Our first objective was to identify consistent QTL across three generations and different environments. The second objective was to integrate detected QTL in three generations. Consistent and consensus-QTL may be considered as the main objective QTL for further studies in QTL cloning, candidate gene identification and marker-assisted breeding for grain yield in maize.

Materials and methods

Plant materials and field experiments

The population used in this study consisted of 258 F_9 RIL derived by single-seed descent from a cross between dent corn inbred Dan232 and popcorn inbred N04. Dan232 was derived from Lu 9 kuan × Dan340. N04 was derived from a Chinese popcorn variety BL03 (Li et al. 2007).

The 258 F_9 RIL and both parents were evaluated using completely random design with one-row plots in four environments in Henan, China, three at Zhengzhou (07Zhengzhou), Wenxian and Xinxiang in 2007 with two replications, and one at Zhengzhou in 2008 (08Zhengzhou) with no replication. The rows were 4 m long with 0.67 m spacing between rows. Plots were planted by hand at a density of 60,000 plants per ha. Standard cultivation management practices were used in each environment. Ten plants from the middle of each plot were chosen for the evaluation of eight grain yield components. Harvested ears were dried naturally to 13.5% grain moisture. The traits measured were ear weight per plant (EWP, g), grain weight per plant (GWP, g), 100 grain weight (100GW, g), ear length (EL, cm), kernel number per row (RKN), ear diameter (ED, cm), row number per ear (ERN), and kernel ratio (KR, %). KR was calculated as the ratio of GWP to EWP. Trait measurements averaged over the two replications were used as the preliminary data in QTL analysis.

Phenotypic data analysis

Using the statistical software package SPSS 12.0, combined analyses of variance for each trait in 2007 and correlation coefficients among traits were calculated following a mixed model, with RIL effect random and effects for environments and replications fixed. Broad-sense heritabilities (H_B^2) on an entry mean basis were calculated as $H_B^2 = 1 - 1/F$, where $F = MS_g/MS_{ge}$. $MS_g = nr\sigma_g^2 + r\sigma_{ge}^2 + \sigma_e^2$, $MS_{ge} = r\sigma_{ge}^2 + \sigma_e^2$, where σ_g^2 was the variance of families, σ_{ge}^2 was the variance of interaction between families and environments, σ_e^2 was the error variance, r was the number of replications, and n was the number of locations. Confidence intervals on heritability estimates were calculated according to Knapp et al. (1985).

SSR and QTL analysis

A total of 207 SSR markers were used to genotype the 258 RIL using the same method described by Li et al. (2007). The linkage maps covered 10 maize chromosomes with a total length of 2,408.8 cM, and an average interval of 11.6 cM (Zhang 2009).

Composite interval mapping (CIM) was used to map QTL and estimate their effects for each trait (Zeng 1993, 1994). Model 6 of the Zmapqtl procedure in QTL Cartographer Version 2.5 (Wang et al. 2006) was employed, specifying the five markers identified by stepwise regression that explained most of the variation for a given trait as genetic background parameters and a window size of 10 cM on either side of the markers flanking the test site. To identify an accurate significance threshold for each trait, an empirical threshold was determined using 1,000

permutations (Churchill and Doerge 1994). QTL positions were assigned to relevant regions at the point of the maximum likelihood odds ratio (LOD). QTL confidence intervals were calculated by subtracting one LOD unit on each side from the maximum LOD position. Based on the results of QTL mapping, interactions among detected QTL were analyzed using MIM in WinQTLCart (Kao et al. 1999; Wang et al. 2006).

Meta-QTL analysis with BioMercator

Quantitative trait loci for the same or related traits detected in different experiments and mapped to the same or similar chromosome regions might be several estimates for a single QTL. Algorithms for meta-analysis were used to estimate the numbers and positions of meta-QTL (mQTL) using BioMercator 2.1 software (Goffinet and Gerber 2000; Arcade et al. 2004). The meta-analysis involved two stages: first the integration of the different genetic maps and then the meta-QTL analysis itself. For each chromosome with 10 and more QTL, meta-analysis was carried out separately. If one chromosome was longer than 200 cM or included more than 40 QTL it was broken up, and meta-analysis conducted separately on each genomic region.

In our previous studies, two genetic linkage maps were constructed using the $F_{2:3}$ and RIL populations derived from the same two inbreds, dent corn inbred D232 and popcorn inbred N04 (Li et al. 2007; Zhang 2009). A total of 35 QTL for six grain yield components (GWP, 100GW, EL, RKN, ED, and ERN) were detected in both BC_2F_2 and $F_{2:3}$ populations (Li et al. 2007), 16 QTL in $F_{2:3}$ and 19 QTL in BC_2F_2. The integrated genetic map was obtained by projecting the genetic linkage map of $F_{2:3}$ population onto that of RIL population (Goffinet and Gerber 2000; Arcade et al. 2004). Meta-QTL analysis was conducted according to data for multiple individual QTL. A modified Akaike's criterion was calculated to select among models with varying numbers of mQTL. For each mQTL, a confidence interval was calculated (Shi et al. 2009).

Results

Trait analysis of variance, performance, heritability and correlation in RIL population

According to the result of combined analyses of variance, genetic variances among RIL (σ_g^2) were significant or highly significant for all traits. Variances of environments (σ_e^2) were significant or highly significant for five traits, EW, GWP, 100GW, EL, and ED. Variances of genotype × environment interactions (σ_{ge}^2) were all significant or highly significant except for ED (Table 1). All traits differed greatly between the two parents. The popcorn inbred N04 had lower EWP, GWP, 100GW, EL, ED, and ERN, but higher RKN and KR than the dent corn inbred Dan232 (Table 2). According to the values of skewness and kurtosis, all traits were normally distributed in the RIL population except KR at Zhengzhou, Wenxian and Xinxiang in 2007. Transgressive segregations were observed for all traits. The coefficients of variation (CV%) for EWP and GWP were consistently larger than those for other six traits.

Broad-sense heritabilities (H_B^2) for all traits were high, ranging from 0.83 to 0.94 (Table 3). Phenotypic and genetic correlations among eight traits differed little across four environments (data not shown for each environment). Based on combined data across four environments, both EWP and GWP were positively correlated with all other six traits. Except for significant negative correlations between 100GW and both RKN and ERN, and insignificant correlations between EL and both ERN and KR, all other correlations were positively significant.

QTL identification for each trait in RIL population and comparison across three generations

Since σ_{ge}^2 were significant for all traits except ED, QTL detections were conducted for data in each individual environment, and also using mean values across all four environments. A total of 103 QTL were detected for eight traits (Table 4; Fig. 1), 19 QTL at 07Zhengzhou, 15 QTL at Wenxian, 28 QTL at Xinxiang, 15 QTL at 08Zhengzhou and 26 QTL in combined analysis. These QTL were located on all ten chromosomes. Many QTL were located on chromosomes 4, 1, 7, 10 and 5, with 23, 18, 16, 13 and 9 QTL, respectively. Individual QTL explained between 4.2 and 24.6% of the phenotypic variation, with 40 QTL over 10% and 13 over 15%.

EWP and GWP

Seven QTL detected for EWP were located on chromosomes 4, 6, 7 and 10. Each QTL explained phenotypic variation ranging from 6.1 to 12.5%, with three QTL explaining over 10%. qEWP-10-1 was consistently detected in the same marker interval umc1677–umc2122 (bin 10.05–10.06) at 07Zhengzhou, Xinxiang, and in combined analysis. All the positive alleles came from the dent corn parent Dan232. EWP was not studied in the $F_{2:3}$ and BC_2F_2 generations.

Ten QTL were detected for GWP, located on chromosomes 4, 7, and 10. Individual QTL explained from 6.0 to 15.6% of the phenotypic variation, with eight QTL accounting for over 10% and two QTL for over 15%. Three QTL were consistently found in the same marker intervals,

Table 1 Combined analysis of variances for eight grain yield components in the RIL population under three environments in 2007 (*F* values)

Sources	EWP	GWP	100GW	EL	RKN	ED	ERN	KR
Family	8.13**	9.28**	17.77**	8.00**	5.95**	6.62**	11.56**	7.63**
Environment	46.63**	31.81**	75.84**	75.46**	4.81	12.74*	6.80	0.52
Family × environment	1.22**	1.25**	1.70**	1.20*	1.62**	1.06	1.60**	1.21**

*, ** Significance at 0.05 and 0.01 levels, respectively

qGWP-4-1 in phi072–umc1757 (bin 4.01) at 07Zhengzhou, Wenxian and in combined analysis, qGWP-4-2 in bnlg1126–umc1117 (bin 4.03–4.04) and qGWP-10-1 in umc1677–umc2122 (bin 10.05–10.06) at 07Zhengzhou, Xinxiang and in combined analysis. In both $F_{2:3}$ and BC_2F_2 generations, five QTL on chromosomes 1, 4, 5, 8 and 10 were detected. However, QTL on chromosomes 4 and 10 were located in different marker intervals.

100 Grain weight

Twenty-two QTL were detected for 100GW located on chromosomes 1, 2, 5, 6, 7 and 10. Each QTL explained from 4.2 to 24.6% of the phenotypic variation, with 10 QTL explaining over 10% and seven QTL over 15%. q100GW-1-1 and q100GW-5-1 were consistently detected at 07Zhengzhou, Wenxian, Xinxiang and in combined analysis in the same marker intervals phi001–umc2227 (bin 1.03–1.04) and umc1478–bnlg565 (bin 5.01–5.02), respectively. q100GW-1-1 always explained above 19.3% of the phenotypic variation. q100GW-7-1 was consistently detected in the same marker interval umc2057–umc1567 (bin 7.02–7.03) in all four environments and in combined analysis. Positive alleles of all QTL came from the dent corn parent Dan232. In both $F_{2:3}$ and BC_2F_2 generations, six QTL on chromosomes 1, 5, 7 and 8 were detected. Although QTL on chromosomes 1 and 5 were all detected across three generations, they were not located in the same marker intervals. Two QTL on chromosomes 5 and 7 detected in the $F_{2:3}$ generation were located in the same marker intervals.

EL and RKN

Fourteen QTL were detected for EL, and located on chromosomes 1, 2, 3, 4 and 7. Each QTL explained from 4.5 to 8.7% of the phenotypic variation. qEL-1-1, qEL-1-2, and qEL-3-1 were consistently detected in two environments and in combined analysis in the same marker intervals bnlg1007–umc1403 (bin 1.02–1.03), bnlg1556–phi039 (bin 1.07–1.08), and bnlg1452–umc1773 (bin 3.04), respectively. qEL-7-1 was consistently detected in marker interval umc2057–umc1567 (bin 7.02–7.03) at Xinxiang and 08Zhengzhou. Positive alleles of all QTL came from the dent corn parent Dan232, except qEL-1-1 and qEL-3-1. In both $F_{2:3}$ and BC_2F_2 generations, six QTL on chromosomes 1, 3, 4, and 7 were detected. The QTL on chromosome 3 were all detected across three generations and located in adjacent marker intervals. The QTL detected on chromosome 4 in the $F_{2:3}$ generation was also located in adjacent marker interval bnlg2291–dupssr228 (bin 4.06–4.08).

Eight QTL were detected for RKN, located on chromosomes 1, 4, 5 and 7. Each QTL explained from 7.2 to 12.1% of the phenotypic variation, with three QTL explaining over 10%. Two QTL were consistently detected in the same marker intervals, qRKN-1-1 in umc1269–phi427913 (bin 1.01) at 07Zhengzhou and in combined analysis, and qRKN-5-1 in umc1478–bnlg565 (bin 5.01–5.02) at Wenxian and in combined analysis. Except for qRKN-1-2, qRKN-4-1 and qRKN-4-2, the positive alleles came from the popcorn parent N04. Two QTL on chromosomes 7 and 8 were detected in the $F_{2:3}$ and BC_2F_2 generations. But the QTL on chromosome 7 detected in $F_{2:3}$ generation was located in different marker intervals.

ED and ERN

Nineteen QTL were detected for ED. These QTL were located on chromosomes 1, 2, 3, 4, 7, 8 and 10. Each QTL explained from 5.0 to 18.2% of the phenotypic variation, with six QTL explaining over 10% and one QTL over 15%. Two QTL were consistently detected in the same marker intervals, qED-1-1 in umc1269–phi427913 (bin 1.01) at 07Zhengzhou, Wenxian, Xinxiang and in combined analysis, and qED-3-1 in umc2277–umc1052 (bin 3.08–3.09) at Xinxiang, 08Zhengzhou, and in combined analysis. Positive alleles of all QTL came from the dent corn parent Dan232 except qED-1-1 and qED-1-2. In both $F_{2:3}$ and BC_2F_2 generations, 10 QTL on chromosomes 2, 4, 5, 8 and 10 were detected. QTL on chromosome 10 were located in the same or adjacent marker interval. But QTL on chromosomes 4 and 8 detected across three generations, and QTL on chromosome 2 detected across two generations, were all located in different marker intervals.

Thirteen QTL were detected for ERN. These QTL were located on chromosomes 3, 4, 6, 9 and 10. Each QTL explained from 4.7 to 17.8% of the phenotypic variation,

Table 2 Performance of eight grain yield components for two parents and in the RIL population

Trait	Environment	Parent		RIL population				
		N04	Dan232	Range	Average	CV (%)	Skewness	Kurtosis
EWP	07Zhengzhou	35.00	45.80	9.05–102.38	38.37	33.83	0.76	1.99
	Wenxian	27.60	48.10	12.50–92.50	50.14	30.03	−0.01	−0.25
	Xinxiang	23.50	60.75	11.35–92.75	43.03	36.04	0.50	−0.06
	08Zhengzhou	16.50	59.60	13.70–107.80	38.04	39.47	0.89	1.26
	Average	25.65	53.56	18.50–78.01	42.26	28.78	0.27	−0.22
GWP	07Zhengzhou	27.70	32.50	5.10–74.63	28.74	38.47	0.61	0.96
	Wenxian	22.25	32.20	6.04–73.91	38.05	34.95	0.07	−0.18
	Xinxiang	18.85	40.50	6.30–76.20	32.39	41.61	0.55	0.01
	08Zhengzhou	13.00	45.00	7.90–74.60	29.11	42.11	0.07	0.26
	Average	20.45	37.55	10.81–61.63	31.98	32.90	0.27	−0.23
100GW	07Zhengzhou	9.20	23.20	7.24–24.67	15.82	19.96	−0.04	0.15
	Wenxian	10.11	23.06	9.10–25.33	16.20	19.35	0.11	−0.28
	Xinxiang	9.43	26.56	8.62–28.64	18.06	19.10	0.27	0.45
	08Zhengzhou	7.92	22.17	6.99–24.91	15.53	20.90	0.07	−0.03
	Average	9.16	23.75	9.08–25.85	16.41	17.80	0.09	0.33
EL	07Zhengzhou	11.08	12.77	7.60–17.75	12.20	13.69	0.10	0.35
	Wenxian	11.85	13.65	7.20–17.63	13.42	12.18	−0.51	0.93
	Xinxiang	11.49	15.25	8.93–18.76	13.71	12.67	−0.11	−0.09
	08Zhengzhou	11.10	11.22	5.83–16.90	11.54	17.57	0.14	0.44
	Average	11.38	13.22	8.87–17.14	12.73	11.59	0.05	0.04
RKN	07Zhengzhou	22.10	16.40	12.00–30.15	21.70	16.56	−0.15	−0.11
	Wenxian	22.40	18.60	10.47–32.50	22.60	18.16	−0.27	0.08
	Xinxiang	23.50	20.70	16.20–32.50	23.75	13.56	0.22	−0.15
	08Zhengzhou	28.00	19.80	12.67–36.60	22.45	17.27	1.09	2.23
	Average	24.00	18.88	15.28–30.90	22.62	13.28	0.15	−0.22
ED	07Zhengzhou	2.39	4.10	1.69–4.74	3.24	10.99	0.37	2.64
	Wenxian	2.53	4.18	1.44–4.53	3.46	11.15	−0.85	4.31
	Xinxiang	2.58	4.32	2.57–4.62	3.45	10.37	0.04	0.12
	08Zhengzhou	2.10	4.12	2.25–4.36	3.12	10.91	0.23	0.88
	Average	2.40	4.18	2.35–4.27	3.33	9.42	−0.02	0.06
ERN	07Zhengzhou	13.20	15.20	10.95–21.4	14.92	11.33	0.64	0.61
	Wenxian	13.60	15.80	9.20–20.80	15.51	12.13	0.33	0.13
	Xinxiang	14.40	16.00	11.80–20.20	15.02	9.98	0.54	0.28
	08Zhengzhou	14.00	17.20	8.50–19.60	15.03	10.89	0.20	0.35
	Average	13.80	16.05	10.89–20.50	15.12	9.73	0.48	0.20
KR	07Zhengzhou	0.79	0.71	0.37–0.87	0.74	10.48	−1.70	4.12
	Wenxian	0.81	0.67	0.38–0.87	0.75	9.92	−1.85	5.40
	Xinxiang	0.80	0.67	0.44–0.89	0.74	10.49	−1.04	1.30
	08Zhengzhou	0.79	0.76	0.50–0.98	0.75	9.40	−0.87	1.45
	Average	0.80	0.70	0.52–0.95	0.75	8.47	−0.65	1.11

with six QTL over 10% and two QTL over 15%. Three QTL were consistently detected in the same marker intervals, qERN-4-1 in bnlg1621–bnlg1189 (bin 4.06–4.07) at Wenxian, Xinxiang and in combined analysis, qERN-9-1 in umc1636–umc1267 (bin 9.02–9.03) at Wenxian and Xinxiang, and qERN-10-1 in umc1677–umc2122 (bin 10.05–10.06) at Wenxian and in combined analysis. Except for qERN-9-1 positive alleles of all QTL came from the dent corn parent Dan232. In both $F_{2:3}$ and BC_2F_2 generations, six QTL on chromosomes 4, 5, 7 and 10 were detected. Two QTL on chromosomes 4 and 10 detected in the $F_{2:3}$ generation were located in the related or same

Table 3 Correlations among eight grain yield components in the RIL population and trait heritabilities based on combined data across three environments in 2007

Trait	EWP	GWP	100GW	EL	RKN	ED	ERN	KR
EWP	1	0.98**	0.34**	0.54**	0.63**	0.73**	0.41**	0.54**
GWP	0.98**	1	0.34**	0.47**	0.60**	0.70**	0.40**	0.68**
100GW	0.35**	0.35**	1	0.15**	−0.24**	0.43**	−0.22**	0.16**
EL	0.55**	0.48**	0.15**	1	0.74**	0.24**	0.01	0.03
RKN	0.67**	0.63**	−0.26**	0.76**	1	0.25**	0.30**	0.29**
ED	0.77**	0.74**	0.45**	0.24**	0.26**	1	0.57**	0.37**
ERN	0.42**	0.41**	−0.23**	−0.01	0.30**	0.60**	1	0.26**
KR	0.57**	0.70**	0.17**	0.03	0.31**	0.37**	0.27**	1
Heritability (h_B^2)	0.88	0.89	0.94	0.88	0.8	0.85	0.91	0.87
Confidence intervals on 95% h_B^2	0.85–0.90	0.87–0.91	0.93–0.95	0.85–0.90	0.79–0.86	0.81–0.88	0.89–0.93	0.84–0.89

Phenotypic correlations above diagonal and genotypic correlations below

EWP ear weight per plant, *GWP* grain weight per plant, *100GW* 100 grain weight, *EL* ear length, *RKN* kernel number per row, *ED* ear diameter, *ERN* row number per ear, *KR* kernel ratio

marker intervals. But no common QTL across three generations were detected.

Kernel ratio

Ten QTL for KR were detected, located on chromosomes 2, 4, 7 and 8. Each QTL explained from 4.3 to 19.2% of the phenotypic variation, with four QTL explaining over 10% and one over 15%. qKR-4-1 was consistently detected in the same marker interval phi072–umc1757 (bin 4.01) at 07Zhengzhou, Xinxiang and in combined analysis. Positive alleles of all QTL came from the dent corn parent Dan232, except for qKR-2-1, qKR-4-2 and qKR-4-3. KR was not included in the $F_{2:3}$ and BC_2F_2 generations.

Digenic epistasis among detected QTL

Forty-two pairs of epistatic interactions were detected among 103 QTL for eight traits (data not shown). These involved 68 loci distributed on all ten chromosomes. However, the interaction effects were all very low, explaining from 0.1 to 6.0% of the phenotypic variation. These results indicated that the contributions of digenic interactions to grain yield components were small in most instances.

Meta-QTL analysis

The integrated genetic map consisted of 237 SSR markers, and was 2,452.2 cM long with an average marker interval of 10.35 cM (Fig. 1). For 138 QTL (103 QTL in this study and 35 in the $F_{2:3}$ and BC_2F_2 generations) detected for eight grain yield components in three generations, 16 distinct QTL clusters were found (Table 5). Ninety-one QTL (65.9%) were integrated in those regions, 69 QTL in RIL, 12 QTL in $F_{2:3}$ and 10 QTL in BC_2F_2 generations. These mQTL were located on eight chromosomes, four on chromosome 1, three on chromosome 4, two on chromosomes 3, 5 and 10, and one on chromosomes 2, 7 and 9. On average, one mQTL included 5.7 QTL with a range from 3 to 12 for one to six traits. QTL included in mQTL1-1, mQTL1-2, mQTL1-4, mQTL3-1, mQTL3-2 and mQTL9-1 were all only detected in the RIL generation, while those in mQTL1-3, mQTL5-1, mQTL7-1 and mQTL10-2 were detected across three generations. mQTL7-1 included 12 QTL for six traits (EWP, GWP, 100GW, EL, ED and ERN), with the Dan232 allele favoring EWP, GWP, 100GW, ED and EL and the N04 allele favoring ERN. The twelve QTL involved in mQTL10-2 associated with four traits (EWP, GWP, ERN and ED), with all favorable alleles coming from Dan232. mQTL4-1 included eight QTL for four traits (EWP, GWP, ED and KR), with all favorable alleles coming from Dan232. mQTL5-1 included eight QTL for two traits (100GW and RKN), with all favorable alleles coming from Dan232. However, mQTL1-2, mQTL3-1 and mQTL9-1 included QTL only for one trait, EL, 100GW, EL and ERN, respectively.

Discussion

Consistent QTL detected across three generations for grain yield components

Three generations (RIL, $F_{2:3}$ and BC_2F_2) derived from the same two parents were used to detect QTL for grain yield components. In this study, a total of 103 QTL for 8 traits were detected in the RIL generation in 4 environments and in combined analysis. In our previous research, 16 and 19 QTL for 6 grain yield components were found in $F_{2:3}$ and

Table 4 QTL detected for eight grain yield components in each environment and in combined analysis in the RIL population

Trait	Environment	QTL	Marker interval	Bin locus	Position	LOD	R^2 (%)[a]	A[b]
EWP	07Zhengzhou	*q7zEWP-10-1*	*umc1677–umc2122*	10.05–10.06	81.7	3.3	8.4	3.77
	Wenxian	*qwEWP-4-1*	*phi072–umc1757*	4.01	16.0	3.5	12.5	5.34
	Xinxiang	*qxEWP-4-2*	*bnlg1126–umc1117*	4.03–4.04	77.7	3.9	10.4	5.08
		qxEWP-10-1	*umc1677–umc2122*	10.05–10.06	81.7	4.4	11.1	5.21
	08Zhengzhou	*q8zEWP-6-1*	*umc1296–umc2165*	6.07	212.4	3.0	6.1	3.78
		q8zEWP-7-1	*umc1666–umc2057*	7.02	64.6	3.5	6.4	3.80
	Average	*qcEWP-10-1*	*umc1677–umc2122*	10.05–10.06	81.7	3.2	8.6	3.58
GWP	07Zhengzhou	*q7zGWP-4-1*	*phi072–umc1757*	4.01	16.0	2.8	10.5	3.64
		q7zGWP-4-2	*bnlg1126–umc1117*	4.03–4.04	75.7	4.0	12.1	3.90
		q7zGWP-10-1	*umc1677–umc2122*	10.05–10.06	81.7	3.4	8.8	3.31
	Wenxian	*qwGWP-4-1*	*phi072–umc1757*	4.01	16.0	4.0	15.3	5.22
	Xinxiang	*qxGWP-4-2*	*bnlg1126–umc1117*	4.03–4.04	75.7	4.4	12.4	4.81
		qxGWP-10-1	*umc1677–umc2122*	10.05–10.06	81.7	4.2	10.9	4.47
	Average	*qcGWP-4-1*	*phi072–umc1757*	4.01	18.0	4.8	15.6	4.21
		qcGWP-4-2	*bnlg1126–umc1117*	4.03–4.04	77.7	3.8	10.7	3.49
		qcGWP-7-1	*umc2057–umc1567*	7.02–7.03	71.2	3.2	6.0	2.60
		qcGWP-10-1	*umc1677–umc2122*	10.05–10.06	81.7	4.3	11.4	3.56
100GW	07Zhengzhou	*q7z100GW-1-1*	*phi001–umc2227*	1.03–1.04	129.3	6.2	22.9	1.52
		q7z100GW-5-1	*umc1478–bnlg565*	5.01–5.02	45.5	4.0	8.5	0.93
		q7z100GW-5-2	*bnlg565–phi109188*	5.02–5.03	73.4	3.1	12.0	1.1
		q7z100GW-6-1	*umc1883–umc1018*	6.00–6.01	0.01	3.8	5.1	0.73
		q7z100GW-7-1	*umc2057–umc1567*	7.02–7.03	73.2	3.1	5.7	0.76
	Wenxian	*qw100GW-1-1*	*phi001–umc2227*	1.03–1.04	129.3	5.1	20.5	1.43
		qw100GW-5-1	*umc1478–bnlg565*	5.01–5.02	45.5	3.7	8.2	0.92
		qw100GW-7-1	*umc2057–umc1567*	7.02–7.03	75.2	6.9	11.6	1.16
	Xinxiang	*qx100GW-1-1*	*phi001–umc2227*	1.03–1.04	129.3	7.9	24.6	1.72
		qx100GW-2-1	*phi402893–umc1227*	2.00–2.01	10.0	3.2	5.6	0.81
		qx100GW-2-2	*umc1776–umc1448*	2.03–2.04	82.4	3.4	7.5	0.95
		qx100GW-5-1	*umc1478–bnlg565*	5.01–5.02	45.5	3.1	6.1	0.86
		qx100GW-5-2	*bnlg565–phi109188*	5.02–5.03	75.4	3.3	11.7	1.19
		qx100GW-7-1	*umc2057–umc1567*	7.02–7.03	75.2	9.0	15.8	1.38
		qx100GW-10-1	*umc1938–umc2163*	10.03–10.04	56.1	4.8	7.3	0.95
	08Zhengzhou	*q8z100GW-5-3*	*umc1502–umc1941*	5.05–5.06	156.7	3.0	5.7	0.78
		q8z100GW-7-1	*umc2057–umc1567*	7.02–7.03	75.2	8.1	16.7	1.34
	Average	*qc100GW-1-1*	*phi001–umc2227*	1.03–1.04	127.3	6.3	19.3	1.29
		qc100GW-2-3	*phi083–umc1459*	2.04–2.05	121.8	3.04	6.9	0.77
		qc100GW-5-1	*umc1478–bnlg565*	5.01–5.02	45.5	3.49	7.3	0.80
		qc100GW-7-1	*umc2057–umc1567*	7.02–7.03	75.2	9.11	17.0	1.21
		qc100GW-10-2	*umc1677–umc2122*	10.03–10.04	63.5	3.1	4.2	0.60
EL	07Zhengzhou	*q7zEL-1-2*	*bnlg1556–phi039*	1.07–1.08	261.2	3.1	6.5	0.43
		q7zEL-3-1	*bnlg1452–umc1773*	3.04	108.2	3.1	5.5	−0.4
	Wenxian	*qwEL-1-1*	*bnlg1007–umc1403*	1.02–1.03	43.1	3.0	5.2	−0.41
	Xinxiang	*qxEL-1-1*	*bnlg1007–umc1403*	1.02–1.03	47.1	4.0	8.1	−0.5
		qxEL-1-2	*bnlg1556–phi039*	1.07–1.08	265.2	3.2	7.7	0.48
		qxEL-2-1	*umc1992–mmc0381*	2.08	235.5	3.0	4.5	0.37
		qxEL-4-1	*dupssr28–umc1313*	4.08–4.09	200.0	3.1	7.2	0.47
		qxEL-7-1	*umc2057–umc1567*	7.02–7.03	73.2	3.1	5.7	0.42
		qxEL-7-2	*umc2190–phi116*	7.06	220.9	4.5	6.9	0.46
	08Zhengzhou	*q8zEL-3-1*	*bnlg1452–umc1773*	3.04	108.2	3.4	7.1	−0.54
		q8zEL-7-1	*umc2057–umc1567*	7.02–7.03	77.2	2.9	7.0	0.55
	Average	*qcEL-1-1*	*bnlg1007–umc1403*	1.02–1.03	47.1	4.3	8.7	−0.44
		qcEL-1-2	*bnlg1556–phi039*	1.07–1.08	265.2	3.6	8.3	0.43
		qcEL-3-1	*bnlg1452–umc1773*	3.04	108.2	3.1	5.1	−0.34

Table 4 continued

Trait	Environment	QTL	Marker interval	Bin locus	Position	LOD	R^2 (%)[a]	A[b]
RKN	07Zhengzhou	*q7zRKN-1-1*	*umc1269–phi427913*	1.01	10.4	4.3	7.9	−1.02
		q7zRKN-7-1	*umc1936–phi328175*	7.03–7.04	155.9	3.0	10.6	−1.18
	Wenxian	*qwRKN-4-1*	*bnlg1126–umc1117*	4.03–4.04	77.7	4.0	11.2	1.38
		qwRKN-5-1	*umc1478–bnlg565*	5.01–5.02	45.5	4.6	12.1	−1.43
	Xinxiang	*qwRKN-4-2*	*dupssr28–umc1313*	4.08–4.09	204.0	3.0	7.2	0.87
	08Zhengzhou	*q8zRKN-1-2*	*bnlg1556–phi039*	1.07–1.08	265.2	3.2	9.6	1.21
	Average	*qcRKN-1-1*	*umc1269–phi427913*	1.01	12.4	3.8	7.3	−0.82
		qcRKN-5-1	*umc1478–bnlg565*	5.01–5.02	41.5	3.2	7.6	−0.83
ED	07Zhengzhou	*q7zED-1-1*	*umc1269–phi427913*	1.01	8.4	3.9	6.7	−0.11
		q7zED-1-2	*bnlg1643–umc2047*	1.08–1.09	314.1	2.8	6.3	−0.1
		q7zED-10-1	*umc1938–umc2163*	10.03–10.04	56.1	3.4	5.7	0.10
	Wenxian	*qwED-1-1*	*umc1269–phi427913*	1.01	8.4	3.4	5.8	−0.09
		qwED-8-1	*bnlg1812–umc1960*	8.05	139.0	3.3	6.9	0.10
	Xinxiang	*qxED-1-1*	*umc1269–phi427913*	1.01	8.4	3.2	6.0	−0.08
		qxED-3-1	*umc2277–umc1052*	3.08–3.09	89.2	4.1	10.9	0.12
		qxED-4-1	*phi072–umc1757*	4.01	22.0	4.9	18.2	0.15
		qxED-7-1	*umc2057–umc1567*	7.02–7.03	71.2	4.0	7.3	0.10
		qxED-10-2	*umc1677–umc2122*	10.05–10.06	79.7	3.9	9.5	0.11
	08Zhengzhou	*q8zED-2-1*	*bnlg1940–umc2214*	2.08–2.10	260.1	3.1	12.9	0.12
		q8zED-3-1	*umc2277–umc1052*	3.08–3.09	93.2	4.4	11.6	0.12
		q8zED-4-2	*dupssr28–umc1313*	4.08–4.09	194.0	3.3	8.8	0.10
		q8zED-7-2	*phi057–umc1409*	7.01	50.0	4.8	10.1	0.11
	Average	*qcED-1-1*	*umc1269–phi427913*	1.01	8.4	3.4	5.4	−0.07
		qcED-2-2	*phi402893–umc1227*	2.00–2.01	4.0	3.0	5.8	0.08
		qcED-3-1	*umc2277–umc1052*	3.08–3.09	91.2	4.2	12.1	0.11
		qcED-4-3	*bnlg1189–umc1808*	4.07–4.08	167.4	3.09	5.85	0.08
		qcED-7-3	*bnlg2233–umc1068*	7.02	12.0	3.1	8.98	0.1
ERN	07Zhengzhou	*q7zERN-3-1*	*bnlg1647–umc2259*	3.02–3.03	67.6	3.3	6.5	0.43
	Wenxian	*qwERN-4-1*	*bnlg1621–bnlg1189*	4.06–4.07	141.7	3.5	15.8	0.75
		qwERN-9-1	*umc1636–umc1267*	9.02–9.03	72.3	3.0	11.6	−0.64
		qwERN-10-1	*umc1677–umc2122*	10.05–10.06	79.7	3.1	9.1	0.57
	Xinxiang	*qxERN-4-1*	*bnlg1621–bnlg1189*	4.06–4.07	141.7	4.0	17.8	0.64
		qxERN-4-2	*bnlg1189–umc1808*	4.07–4.08	165.4	3.3	6.7	0.39
		qxERN-9-1	*umc1636–umc1267*	9.02–9.03	72.3	3.6	13.0	−0.54
	08Zhengzhou	*q8zERN-3-2*	*umc1052–umc1594*	3.09	111.1	4.0	8.7	0.49
		q8zERN-6-1	*umc1296–umc2165*	6.07	206.4	3.1	7.2	0.44
		q8zERN-10-1	*phi323152–umc2021*	10.05–10.07	133.9	4.7	10.2	0.53
	Average	*qcERN-4-1*	*bnlg1621–bnlg1189*	4.06–4.07	143.7	3.9	14.8	0.57
		qcERN-9-1	*umc1267–umc1271*	9.03	86.8	3.0	4.7	−0.32
		qcERN-10-1	*umc1677–umc2122*	10.05–10.06	81.7	3.5	9.5	0.45
KR	07Zhengzhou	*q7zKR-4-1*	*phi072–umc1757*	4.01	12.0	3.3	9.0	0.03
		q7zKR-4-2	*umc1313–bnlg589*	4.09–4.10	213.6	2.7	5.2	−0.02
	Wenxian	*qwKR-7-1*	*bnlg2233–umc1068*	7.02	24.0	2.8	7.3	0.02
		qwKR-8-1	*bnlg2046–bnlg666*	8.04–8.05	124.1	2.8	4.3	0.02
	Xinxiang	*qxKR-2-1*	*umc1065–bnlg1329*	2.06–2.08	150.5	3.5	11.2	−0.03
		qxKR-4-1	*phi072–umc1757*	4.01	16.0	5.3	19.2	0.03
	08Zhengzhou	*q8zKR-4-3*	*umc1294–bnlg1126*	4.02–4.03	53.8	2.9	4.9	−0.02
	Average	*qcKR-2-1*	*umc1065–bnlg1329*	2.06–2.08	150.5	3.1	10.5	−0.02
		qcKR-4-1	*phi072–umc1757*	4.01	16.0	3.7	13.4	0.02
		qcKR-7-2	*phi057–umc1409*	7.01	52.0	2.9	5.6	0.02

[a] R^2 percent of phenotypic variations explained by each QTL

[b] A additive effect of QTL, positive values indicated that alleles from Dan232 increased the trait score

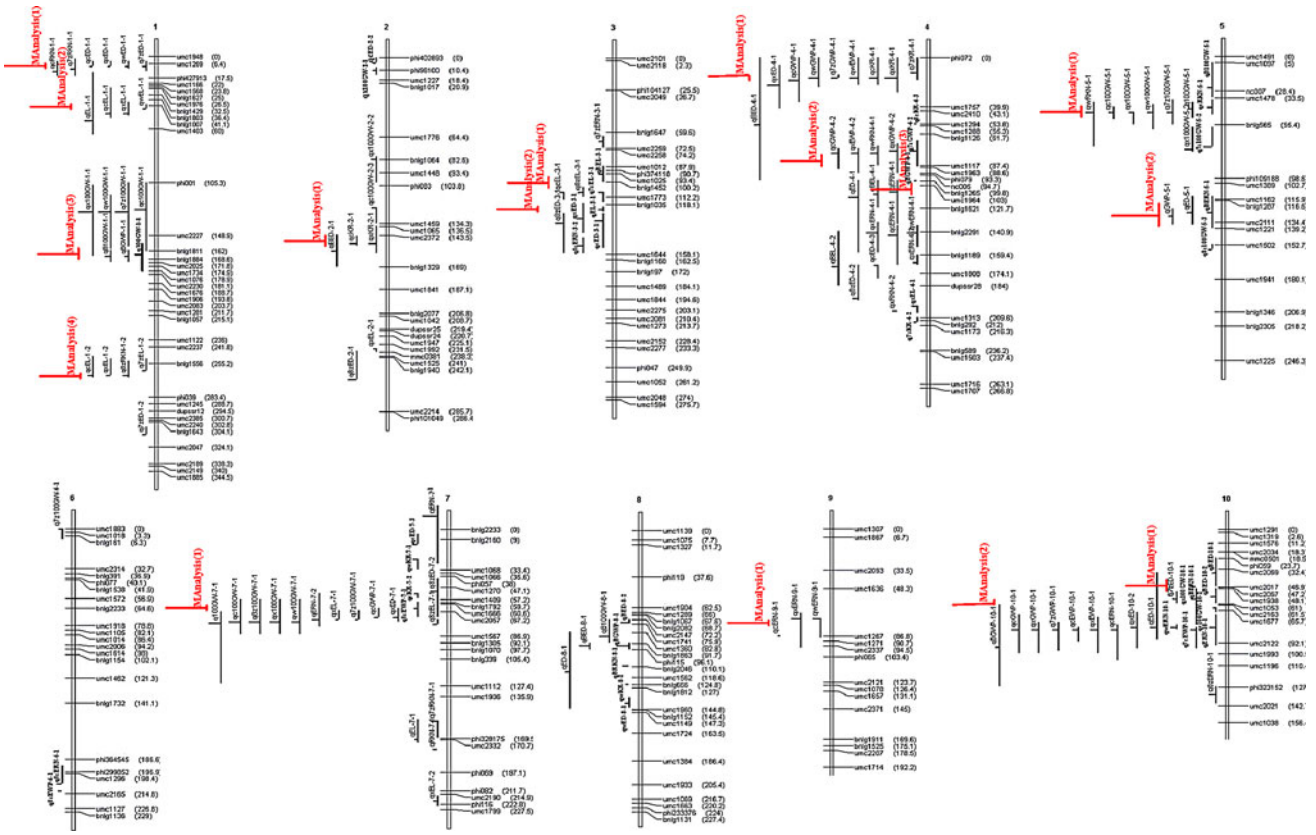

Fig. 1 The integrated map of the RIL and $F_{2:3}$ generations, and QTL and meta-QTL for eight grain yield components detected in three generations

BC_2F_2 populations, respectively (Li et al. 2007). Among the 138 QTL detected in total, no common QTL in the same marker intervals were found across three generations. The QTL for 100GW on chromosome 5 were located in adjacent marker intervals. Four common QTL across the RIL and $F_{2:3}$ generations were found in the same marker intervals, two for 100GW at bin 5.02–5.03 and 7.02–7.03, one for ED at bin 10.05–10.06, and one for ERN at bin 10.05–10.06. Two QTL were common between RIL and BC_2F_2 generations, which were located at the same bin 3.04 for EL and bin 10.03–10.04 for ED. Compared with previous studies, the QTL for EL at the same bin 3.04 was also detected by Austin and Lee (1998) in $F_{6:7}$ lines. In particular, QTL for 100GW located at bin 5.02–5.03 were frequently detected by Austin and Lee (1996) in an $F_{6:7}$ generation, Veldboom and Lee (1994) in an $F_{2:3}$ and Lan et al. (2005) in an $F_{2:3}$. These two QTL showed great consistency across both environments and populations, and might deserve further study in fine mapping and in MAS.

Three generations in our studies were derived from the same two parents and the same method was used to detect QTL. But the field experiments for the RIL generation were not conducted under the same environments as the $F_{2:3}$ and BC_2F_2 generations. Therefore, the great inconsistency across three generations in QTL detection could be mainly attributable to different genetic structures and environments. The allele frequency was 50% N04 to 50% Dan232 in the $F_{2:3}$, 83% N04 to 15% Dan232 in the BC_2F_2 (Li et al. 2007), and 46% N04 to 47% Dan232 in the RIL generation (Zhang 2009). Clearly, backcrosses and selections in the BC_2F_2 (Li et al. 2007) and successive meiosis in the RIL generation (Zhang 2009) led to large changes in genetic structure. Similar inconsistencies in QTL detection for nine plant traits and three kernel composition traits between the BC_2F_2 and $F_{2:3}$ generations were also observed in our previous studies (Li et al. 2008; Liu et al. 2008). Several other studies also showed that genetic structure has great impact on QTL detection (Moreno-Gonzalez 1993; Mihaljevic et al. 2004; Blanc et al. 2006). However, high QTL consistency was found in the $F_{2:3}$ and $F_{6:7}$ generations for eight grain yield and yield components by Austin and Lee (1996), in which 70% QTL detected in the $F_{6:7}$ were also identified in $F_{2:3}$. Therefore, QTL consistency across generations derived from the same parents might depend

Table 5 Meta-QTL for eight grain yield components identified by meta-analysis

Meta-QTL	Position (cM)	Confidence interval (cM)	Map distance (cM)	Adjacent marker	QTL number	Trait involved/(generation)[a]	QTL integrated
mQTL1-1	8.64	7.37–9.92	2.55	umc1269–phi427913	6	ED(R), RKN(R)	q7zED-1-1, qcED-1-1, qxED-1-1, qwED-1-1, q7zRKN-1-1, qcRKN-1-1
mQTL1-2	43.39	42.12–44.72	2.6	bnlg1007–umc1403	4	EL(R, F)	qwEL-1-1, qxEL-1-1, qcEL-1-1, qEL-1-1
mQTL1-3	165.49	162.26–168.73	6.47	bnlg1811–bnlg1884	7	100GW(R, F, B), GWP(B)	q7z100GW-1-1, qx100GW-1-1, qw100GW-1-1, qc100GW-1-1, q100GW-1-1, qB100GW-1-1, qBGWP-1-1
mQTL1-4	263.45	260.34–266.57	6.23	bnlg1556–phi039	4	EL(R), RKN(R)	q7zEL-1-2, qcEL-1-2, qxEL-1-2, q8zRKN-1-2
mQTL2-1	150.97	147.36–154.58	7.22	umc2372–bnlg1329	3	KR(R), ED(B)	qxKR-2-1, qcKR-2-1, qBED-2-1
mQTL3-1	106.77	104.81–108.72	3.91	bnlg1452–bnlg1773	4	EL(R, B)	q7zEL-3-1, qcEL-3-1, q8zEL-3-1, qBEL-3-1
mQTL3-2	122.85	121.05–124.65	3.6	bnlg1035–umc1644	4	ED(R), EL(F)	qxED-3-1, qcED-3-1, q8zED-3-1, qEL-3-1
mQTL4-1	15.99	15.01–16.96	1.95	phi072–umc1757	8	EWP(R), GWP(R), ED(R), KR(R)	qwEWP-4-1, qcGWP-4-1, qwGWP-4-1, q7zGWP-4-1, qxED-4-1, q7zKR-4-1, qxKR-4-1, qcKR-4-1
mQTL4-2	77.14	73.95–81.33	7.38	bnlg1126–umc1117	5	EWP(R), GWP(R), RKN(R)	qxEWP-4-2, q7zGWP-4-2, qxGWP-4-2, qcGWP-4-2, qwRKN-4-1
mQTL4-3	103.52	101.68–105.35	3.67	umc1964–bnlg1621	4	GWP(B), ED(F), EL(B), ERN(F)	qBGWP-4-1, qED-4-1, qERN-4-1, qBEL-4-1
mQTL5-1	43.71	41.21–46.2	4.99	umc1478–bnlg565	8	100GW(R, F, B), RKN(R)	qc100GW-5-1, qx100GW-5-1, qw100GW-5-1, q7z100GW-5-1, q100GW-5-1, qB100GW-5-1, qwRKN-5-1, qcRKN-5-1
mQTL5-2	123.77	119.78–127.76	7.98	bnlg1287–umc2111	3	GWP(F), ED(F), ERN(B)	qGWP-5-1, qED-5-1, qBERN-5-1
mQTL7-1	74.12	72.85–75.39	2.54	umc2057–umc1567	12	EWP(R), GWP(R), 100GW(R, F), ED(R), EL(R), ERN(F)	q8zEWP-7-1, qcGWP-7-1, q7z100GW-7-1, qc100GW-7-1, qx100GW-7-1, qw100GW-7-1, q8z100GW-7-1, qxED-7-1, qxEL-7-1, q8zEL-7-1, q100GW-7-1, qERN-7-2
mQTL9-1	72.31	72.31–88.81	16.5	umc1636–umc1271	3	ERN(R)	qcERN-9-1, qxERN-9-1, qwERN-9-1
mQTL10-1	61.66	59.82–63.5	3.68	umc1938–umc1677	4	100GW(R), ED(R, B)	qx100GW-10-1, qc100GW-10-2, q7zED-10-1, qBED-10-2
mQTL10-2	80.17	78.44–81.9	3.46	umc1677–umc2122	12	EWP(R), GWP(R, B), ED(R, F), ERN(R, F)	q7zEWP-10-1, qcEWP-10-1, qxEWP-10-1, q7zGWP-10-1, qcGWP-10-1, qxGWP-10-1, qBGWP-10-1, qxED-10-2, qED-10-1, qcERN-10-1, qwERN-10-1, qERN-10-1

[a] R, F and B in brackets indicate RIL, $F_{2:3}$ and BC_2F_2 generations, respectively

on other genetic reasons, such as germplasm, generations, selection and traits.

The great influences of different environments could be reflected in the significant variances of environments (σ_e^2) and genotype × environment interactions (σ_{ge}^2) for most traits in this study. Among the 103 QTL detected in four environments and in combined analysis, 40, 5, 12 and 3 QTL were detected in one, two, three and four instances, accounting for 38.8, 4.9, 11.7 and 2.9%, respectively. Only one QTL (q100GW-7-1) was consistently detected in four environments and in combined analysis. Such high proportions of environment specific QTL indicated that natural environments (such as soil and climates) had large effects on QTL detection for grain yield components. However, 12 out of 13 QTL (except qED-4-1) with R^2 over 15% were consistently detected in 2–3 environments and in combined analysis, which involved four traits, GWP, 100GW, ERN and KR. 100qGW-1-1 had the largest R^2 in three environments in 2007 and in combined analysis (from 19.3 to 24.6%), although it failed to be detected in 2008. This QTL was also detected in the near marker intervals (bnlg1811–bnlg1884 and umc2025–bnlg1811) in both $F_{2:3}$ and BC_2F_2 generations. q100GW-7-1 was also located in the same marker interval umc2057–umc15677 in the $F_{2:3}$ generation, with R^2 from 5.7 to 17.0%. qGWP-4-1, qERN-4-1 and qKR-4-1 were all detected in two environments in 2007 and in combined analysis, with R^2 from 10.5 to 15.6%, 14.8 to 17.8% and 9.0 to 19.2%, respectively. Moreover, QTL for 100GW at 10, 20, 30 and 40 days after pollination, and QTL for grain filling rate during most periods, have been found in the same marker interval as q100GW-7-1 in our recent study using the same RIL population (data not published). This indicated that major QTL had high consistency across different environments and generations, and combined analysis across several environments could reveal major QTL detected in each environment. These major QTL should be paid great attention in further studies and MAS. Now, NILs for five QTL (qGWP-4-1, q100GW-1-1, q100GW-7-1, qERN-4-1 and qKR-4-1) are being constructed using MAS.

Meta-QTL analysis and QTL coincidence for grain yield components

Because the results of QTL detection were greatly influenced by several interacting factors, such as genetic material (parents, populations, and generations), markers, mapping methods and environments, it is difficult to directly compare results across different studies (Moreno-Gonzalez 1993; Veldboom and Lee 1994; Austin and Lee 1996; Tanksley and Nelson 1996; Austin et al. 2000; Ho et al. 2002; Mihaljevic et al. 2004; Lan et al. 2005; Blanc et al. 2006; Li et al. 2007, 2009; Liu et al. 2008). Through meta-QTL analysis proposed by Goffinet and Gerber (2000), not only could QTL from independent studies be integrated, but also the genetic correlations among traits could be revealed. The chromosome regions for mQTL with high QTL co-localization might be hot spots for important QTL for associated traits. This should be paid great attention in further study and breeding.

In this study, 16 mQTL were obtained from 138 QTL for 8 grain yield components detected in three generations derived from the same two parents. Twelve QTL with R^2 higher than 15% were all integrated in these mQTL. Five mQTL, mQTL7-1, mQTL10-2, mQTL4-1, mQTL5-1 and mQTL1-3, were much more important. Each of these included 7–12 QTL associated with 2–6 traits, reflecting clusters of multiple QTL for grain yield components. For the compound trait GWP, 15 QTL were detected across 3 generations, 10 in RIL, 1 in $F_{2:3}$ and 4 in BC_2F_2. Except for the QTL detected in the BC_2F_2, the other 14 QTL were included in 7 mQTL. The component traits of these integrated QTL were 100GW in mQTL1-3, ED and KR in mQTL4-1, RKN in mQTL4-2, ED, EL and ERN in mQTL4-3, ED and ERN in mQTL5-2, 100GW, ED, EL and ERN in mQTL7-1, and ED and ERN in mQTL10-2. Co-integration of QTL for several grain yield components and of GWP QTL with QTL for its component traits were consistent with significant correlations among grain yield and its component traits. Austin and Lee (1996) found that 53 of 80 (66%) loci for grain yield and yield components were associated with 2 or more traits in maize. In *Brassica napus*, 47 of the 55 (85%) QTL for seed yield were co-localized with other yield traits (Shi et al. 2009).

The co-localization of QTL for yield correlated traits might mean pleiotropy and/or tight linkage. Previous studies in fine mapping and map-based cloning have found that several QTL/genes exhibited pleiotropic effects on multiple yield traits (Fan et al. 2006; Song et al. 2007; Xue et al. 2008). Through dissection of seven QTL for yield traits in a physical distance of 37.4 kb, Xie et al. (2008) considered that those co-localized QTL could be a single pleiotropic gene, which might act as a major regulator for plant development and control several traits simultaneously. In this study, the genetic regions for mQTL1-2, mQTL3-1 and mQTL9-1 might contain QTL for a single trait: EL, EL and ERN, respectively. The other 13 mQTL-related regions might contain tightly linked QTL for 2–6 traits or one single QTL with pleiotropic effects on several traits. The real situations can only be revealed by further study, through fine mapping for QTL and/or by development of single segment substitution lines for these mQTL-associated regions.

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