Euphytica (2009) 169:273–284
DOI 10.1007/s10681-009-9966-8

Dent corn genetic background influences QTL detection for grain yield and yield components in high-oil maize

Y. L. Li · X. H. Li · J. Z. Li · J. F. Fu · Y. Z. Wang · M. G. Wei

Received: 20 May 2008 / Accepted: 13 May 2009 / Published online: 30 May 2009

Abstract Despite the well-recognized importance of grain yield in high-oil maize (*Zea mays* L.) breeding and production, few studies have reported the application of QTL mapping of such traits. An inbred line of high-oil maize designated 'GY220' was crossed with two dent maize inbred lines to generate two connected $F_{2:3}$ populations with 284 and 265 $F_{2:3}$ families. Our main objective was to evaluate the influence of genetic background on QTL detection of grain yield traits through comparisons between the $F_{2:3}$ populations. The field experiments were conducted during the spring in Luoyang and summer in Xuchang, Henan, China. Two genetic linkage maps were constructed with a genetic distance of 2111.7 and 2298.5 cM using 185 and 173 polymorphic SSR markers, respectively. In total, 18 and 15 QTL were detected for six grain yield traits in the two populations. Only one common QTL marker was shared between the two populations. A QTL cluster associated with five traits was identified at bin 1.05–1.06, including the shared QTL for 100GW, which demonstrated the largest effect (16.7%). Among the detected QTL, 12 digenic interactions were identified. Our results reflect the substantial influence of dent maize genetic background on QTL detection of grain yield traits.

Y. L. Li (✉) · X. H. Li · J. Z. Li · J. F. Fu · Y. Z. Wang · M. G. Wei
College of Agriculture, Henan Agricultural University, 95 Wenhua Rd, Zhengzhou, China
e-mail: yuling_li@126.com

Keywords High-oil maize · Dent corn inbred · Grain yield traits · Genetic background · $F_{2:3}$ family lines · QTL inconsistency

Abbreviations

A	Additive
CIM	Composite interval mapping
D	Dominance
ED	Ear diameter
EL	Ear length
GPR	Grains per row
100GW	100-Grain weight
GWP	Grain weight per plant
IHP	Illinois high protein
IHO	Illinois high oil
ILP	Illinois low protein
ILO	Illinois low oil
MAS	Marker-assisted selection
MIM	Multiple interval mapping
NILs	Near isogenic lines
OD	Over-dominance
PD	Partial dominance
QTL	Quantitative trait locus/loci
RPE	Rows per ear
SSR	Simple sequence repeat

Introduction

Grain yield is one of the most important attributes of maize. Consequently, the literature is rich in reports

of QTL mapping for grain yield and yield component traits in normal maize (Stuber et al. 1987, 1992; Veldboom and Lee 1994; Austin and Lee 1996, 1998; Austin et al. 2000; Song 2003). A survey of the literature reveals that several hundred related QTL have been detected on all ten maize chromosomes. QTL can only be detected when the two parents possess polymorphisms both at the respective marker locus and at the trait locus for bi-parental populations. Therefore only a subset of QTL could generally be detected in a given population. In some cases, QTL mapping results are strongly dependent on the mapping population(s). The influence of genetic background on QTL detection has generally been reported in different populations derived from various parents (Beavis et al. 1991; Stuber et al. 1992; Austin et al. 2000), different generations derived from the same crosses (Austin and Lee 1996, 1998; Li et al. 2007), or with several test crosses and connected populations (Blanc et al. 2006; Mihaljevic et al. 2004). Therefore, to reveal the genetic characteristics of any quantitative trait, it is vital that QTL mapping be conducted using a large number of populations derived from different parents with various genetic backgrounds. Several connected multi-parental crosses will increase the probability of QTL detection and consequently reveal the effects of genetic background on QTL and phenotypic traits (Blanc et al. 2006; Meyer et al. 2007; Mihaljevic et al. 2004).

The most outstanding characteristic of high-oil maize is an increase in grain oil content compared with normal maize. However, grain yield is also an important factor in high-oil maize breeding and production. To date, only Song (2003) has reported QTL mapping for grain yield traits using the $F_{2:3}$ population derived from the cross between B73 and a high-oil maize inbred line BY804 (developed from the Beinongda high-oil maize population). IHO (Illinois High Oil) /ILO (Illinois Low Oil) are the current high-oil germplasms used to detect QTL for grain chemical composition (Dudley et al. 2007; Goldman et al. 1994); however, no reports for grain yield or yield component traits have reported using IHO/ILO or other high-oil germplasm samples. In this study, a high-oil maize inbred line GY220 (developed from an Alexander high-oil maize background) was crossed with two elite dent maize inbred lines to generate two connected $F_{2:3}$ populations. Our main objective was to evaluate the influence of genetic background on QTL detection in six grain yield and yield component traits through comparisons between the $F_{2:3}$ populations grown under the same environmental conditions. Since few QTL studies have been conducted for grain yield and yield component traits in high-oil maize, comparison of the results of this study with previous work in normal maize or popcorn may provide insights into the effects of high-oil and dent maize genetic background. In addition, Alexander high-oil maize QTL mapping has not been reported for any trait prior to this report.

Materials and methods

Population development

Dent corn inbred lines 8984 and 8622 were chosen as maternal parents to generate two connected crosses with the common high-oil maize inbred line GY220 as the paternal parent, 8984 × GY220 (Pop.1) and 8622 × GY220 (Pop.2). GY220 was derived from the cycle 27 Alexander high-oil maize population and was selected and provided by China Agricultural University. The Alexander high-oil population was initiated in the 1950s and developed by Alexander through single kernel selection at the University of Illinois. It belongs to the Lancaster heterotic group (Jiang et al. 2005). The two dent corn inbred lines 8984 and 8622 were developed in our laboratory and belong to the Chinese Reid heterotic group. The two crosses were self-pollinated to produce 284 and 265 $F_{2:3}$ lines for the F_1 derived from lines 8984 and from 8622, respectively.

Field trials and trait evaluation

The 285 and 265 $F_{2:3}$ lines, including the F_1 and parental lines, were evaluated in two adjacent trials with one-row plots and two replications. The study employed an α-design under the same environmental conditions for each population and was conducted in 2006 during the spring in Luoyang and summer in Xuchang, Henan, China. Each row was 4 m long with 0.67 m between rows. Plots were planted by hand at a density of 60,000 plants ha^{-1}. Standard cultivation management practices were used at each study site.

Ten consecutive plants from the middle of each row were chosen to evaluate each of six grain yield

and yield component traits. The traits measured included the following: grain weight per plant (GWP, g), 100-grain weight (100GW, g), ear length (EL, cm), grains per row (GPR), ear diameter (ED, cm) and rows per ear (RPE). Trait measurements averaged over the two replications across two environments were used as the preliminary data in the analyses.

Phenotypic data analysis

The correlation coefficients among six grain yield and yield component traits were calculated using the statistical software package SPSS 12.0. Broad sense heritabilities and their confidence intervals were calculated for all traits in the $F_{2:3}$ families according to Knapp et al. (1985).

SSR analysis and map construction

Leaf samples were collected at seedling stage from each F_2 plant, two F_1 and the three parental lines, 8984, 8622 and GY220, and stored at −80°C. The CTAB method of Saghai Maroof et al. (1984) was used for DNA extraction. SSR analysis was conducted as reported in Senior and Heun (1993).

A total of 665 SSR primer pairs were chosen from the Maize GDB (http://www.maizegdb.org) according to their uniform distribution throughout all ten maize chromosomes. The primer pairs were initially screened for polymorphisms between the two pairs of parents, 8984/GY220 and 8622/GY220. Ultimately, 212 and 205 polymorphic markers were selected that clearly showed co-dominant segregation in the two respective populations. Excluding 27 and 32 SSR markers showing serious segregation distortion and failing to be assigned to any linkage group in the two populations, the two genetic linkage maps were constructed with 185 and 173 SSR markers using Mapmaker 3.0 at an LOD threshold >3.0 (Lincolin 1992). The recombination frequency between linked loci was transformed into centimorgan (cM) distances by applying Kosambi's mapping function (Kosambi 1944).

QTL analysis

Composite interval mapping (CIM) was applied to map QTL and estimate QTL effects for each trait (Zeng 1994). Five markers were identified by stepwise regression that explained most of the variation for a given trait. The five markers were specified in Model 6 of the Zmapqtl procedure in QTL Cartographer Version 2.5 (Wang 2006) using 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 for CIM using 1,000 permutations (Churchill and Doerge 1994). QTL positions were assigned to relevant regions at the point of a maximum LOD score. If two peaks for the same trait on the same chromosome were observed, and at least two markers and a minimum distance of 20 cM separated the two peaks, they were accepted as two different QTL (Groh et al. 1998). QTL confidence/support intervals were calculated as the point along the significance peak where the LOD score was 1.0 unit less than the peak LOD score.

The dominance effects calculated for the $F_{2:3}$ family lines were expected to be reduced by half compared with F_2 plants, so the effects were doubled. Average levels of dominance were calculated as the ratio $DR = |D|/|A|$ with the additive (A) and the dominance (D) effects estimated for the $F_{2:3}$ populations. Gene action was based on the dominance average employing the criteria of Stuber et al. (1987): additive (A) = 0–0.2; partial dominance (PD) = 0.21–0.80; dominance (D) = 0.81–1.20; and overdominance (OD) >1.20. Based on the CIM results, interactions between QTL were analyzed using the multiple interval mapping (MIM) method in WinQTLCart (Kao et al. 1999; Wang 2006).

Results

Marker segregation and genetic linkage maps for the two populations

One hundred four markers were identical between the two populations, accounting for 49.1 and 50.7% of the total polymorphic markers, respectively. In Pop.1, Chi-square tests revealed that 82 markers associating with all ten chromosomes deviated from the expected 1:2:1 Mendelian ratio, with 11 marker loci toward GY220, 7 toward 8984 and 64 toward the F_1. Twelve SSR markers that showed serious segregation distortion were excluded from the analysis. Fifteen markers failed to be assigned to any linkage group. Finally,

185 SSR markers that clearly demonstrated co-dominant segregation were used to construct the linkage map for Pop.1. The markers were assigned to all ten maize chromosomes with a total length of 2111.7 cM and an average interval of 11.4 cM (Fig. 1).

In Pop.2, Chi-square tests of 64 markers on all 10 chromosomes showed deviation from the expected Mendelian ratio of 1:2:1. Nine, 20, 33 and 2 marker loci were toward GY220, 8622, their F_1 and both parents, respectively. Fourteen SSR markers that showed serious segregation distortion were excluded from the analysis. Eighteen markers failed to be assigned to any linkage group; therefore, the final linkage map for Pop.2 was constructed with 173 SSR markers, clearly depicting co-dominant segregation. The pairs of markers were assigned to all ten chromosomes with a total length of 2298.5 cM and an average interval of 13.29 cM (Fig. 2).

Eighty-three of the 185 and 173 markers constructed on the 10 maize chromosomes were shared

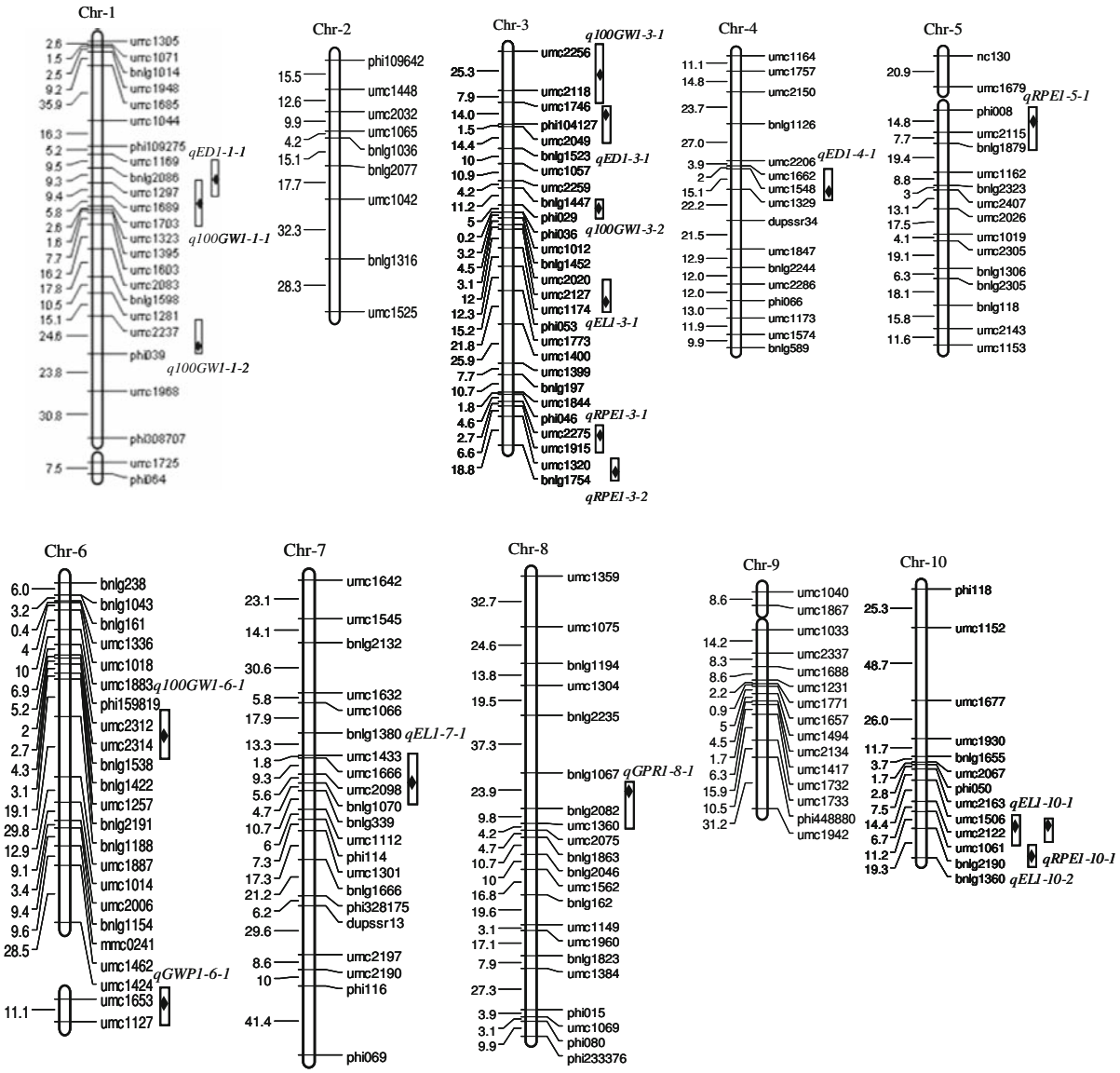

Fig. 1 SSR linkage map for 8984 × GY220 $F_{2:3}$ families. QTL one-LOD support intervals are indicated by *vertical bars*, and the maximum LOD peak positions are indicated by *solid diamonds*

(accounting for 44.9 and 48.0% of the total markers constructed), and between the 130 and 141 markers showing an expected 1:2:1 ratio, 40 markers were shared (accounting for 30.8 and 28.4% of the total markers constructed) between Pop.1 and Pop.2. For the 11 and 9 markers skewing to the same high-oil parent GY220 in Pop.1 and Pop.2, the populations did not share any common markers. Seven and 20 markers skewed toward the dent maize parent 8622 in Pop.2 and 8984 in Pop.1, accounting for 8.5 and 31.3% of the total skewed markers. Although high numbers of markers skewed to their relative F_1 in both populations, this was higher in Pop.1 than in Pop.2, with 64 and 33 markers exhibiting a skewed

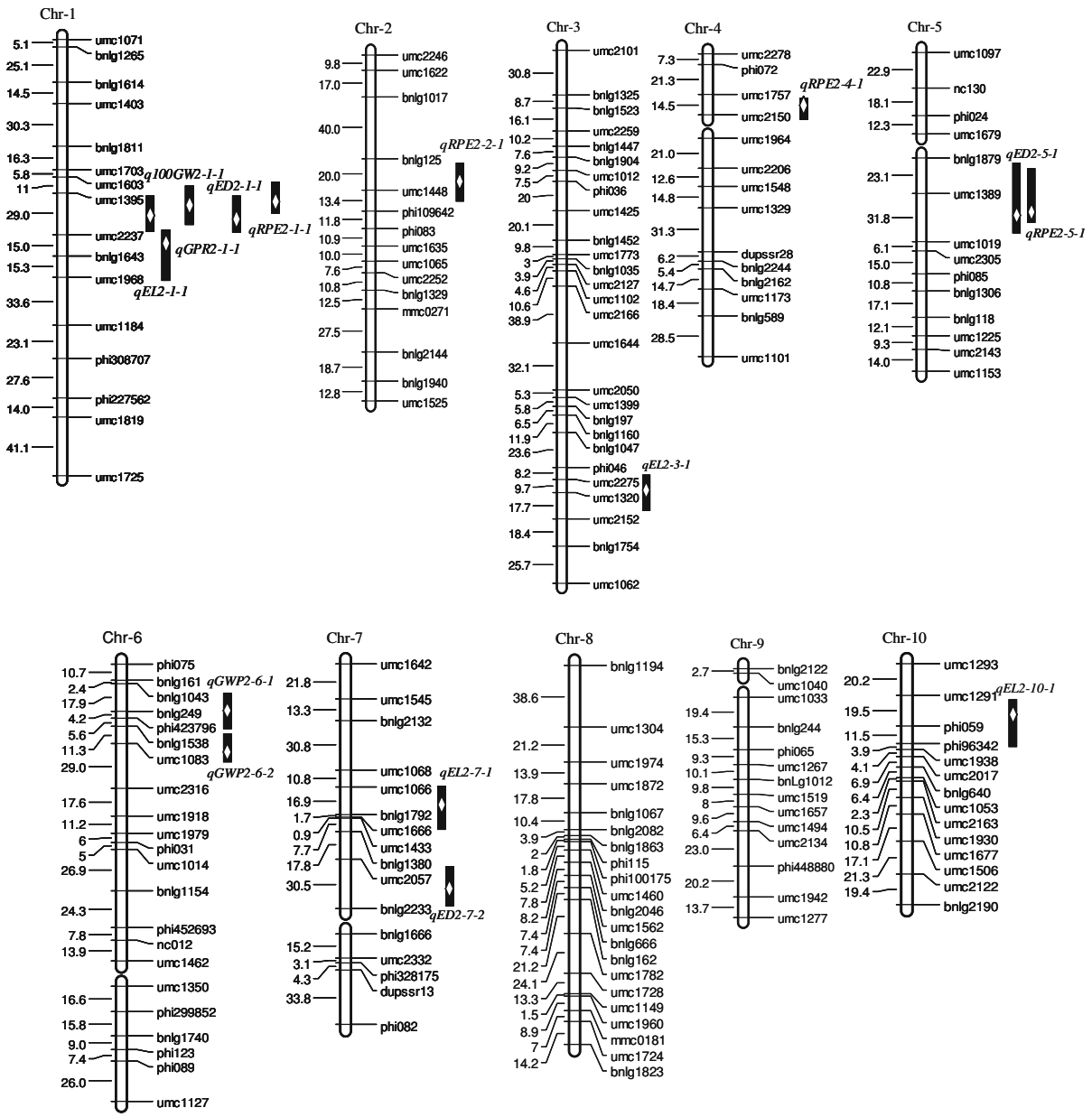

Fig. 2 SSR linkage map for 8622 × GY220 $F_{2:3}$ families. QTL one-LOD support intervals are indicated by *vertical bars*, and the maximum LOD peak positions are indicated by *open diamonds*

distribution, accounting for 78.0 and 51.6% of the skewed markers, respectively. All markers were located in regions similar to those in the MaizeGDB map, with the exception of umc1336 in Pop.1 and umc1782 in Pop.2. These two markers were, respectively, located in bin 6.0 and 8.05 in our study and in bin 10.03 and 7.04 in the MaizeGDB map.

Performance of six grain yield and yield component traits in the two connected populations

The six traits differed between the two population parents, especially for GWP and 100GW. For the two normal corn parent lines, 8984 had a higher value for GWP, but all other traits did not differ. In the two $F_{2:3}$ populations, all traits showed a continuous distribution pattern around the mean with a wide variance and transgressive segregation exceeding the high and low parent values (Table 1). Heritability estimates for all traits ranged from 0.22 and 0.63 in Pop.1 and from 0.33 and 0.58 in Pop.2 (Table 2).

Phenotypic and genotypic correlations among the six traits and between the two populations were not equal, reflecting the influence of genetic differences (Table 2). Lower genotypic correlation values were observed than phenotypic correlation values. Correlations between GWP and other component traits were largely significant, which indicated that all traits were integral in determining GWP.

QTL detection for each trait in Pop.1

In Pop.1, a total of 18 QTL were detected for all six traits. The QTL were determined to reside on chromosomes 1 (three), 3 (six), 4, 5, 6 (two), 7, 8, 10 (three) (Fig. 1; Table 3). Only one QTL was detected for both GWP and GPR. The two QTL were located on chromosomes 6 and 8, contributing 9.8 and 11.9% to the phenotypic variation, respectively. Parent GY220 (high-oil content) or 8984 (dent) contributed the positive allele.

Five QTL were detected for 100GW, located on chromosomes 1 (two), 3 (two), and 6. The contributions to phenotypic variation for a single QTL varied from 7.5 to 13.1%, with q100GW1-3-2 providing the highest contribution. The total contribution of the five QTL was 45.8%. The positive allele in q100GW1-1-1 was contributed by GY220, while those of the other four QTL were contributed by 8984.

Four QTL for EL were detected on chromosomes 3, 7 and 10 (two). The contributions to phenotypic variation for a single QTL ranged from 5.8 to 7.5%, with a total contribution of 26.2%. The positive allele in qEL1-3-1 was contributed by 8984, and the

Table 1 Phenotypic performance for three parents and their two $F_{2:3}$ families based on combined data across two environments

Population	Trait	Parents		$F_{2:3}$ families				
		GY220	8984/8622[a]	Range	Mean	CV (%)	Skewness	Kurtosis
Pop.1	GWP (g)	44.15	77.50	20.00–123.75	65.53	31.97	0.19	−0.36
	100GW (g)	13.17	22.63	7.92–26.75	18.47	17.99	−0.06	0.29
	EL (cm)	14.17	14.94	11.00–22.58	16.56	11.16	0.16	0.43
	GPR	30.06	28.63	17.00–42.67	32.13	13.44	−0.43	0.56
	ED (cm)	3.52	3.75	3.30–5.05	4.07	7.11	0.27	0.61
	RPE	13.21	16.00	11.00–18.50	15.18	8.08	−0.13	0.49
Pop.2	GWP (g)	44.15	57.5	20.00–120.48	63.63	30.72	0.27	−0.36
	100GW (g)	13.17	22.21	12.05–37.10	23.81	16.23	−0.23	0.77
	EL (cm)	14.17	15.43	10.88–19.38	14.89	9.99	0.34	0.47
	GPR	30.06	27.58	12.00–46.00	28.79	16.08	0.03	1.51
	ED (cm)	3.52	3.68	3.23–5.05	3.96	6.68	0.45	1.29
	RPE	13.21	12.50	10.00–16.25	12.98	8.75	0.44	0.44

GWP grain weight per plant, *100GW* 100 grain weight, *EL* ear length, *GPR* kernel number per row, *ED* ear diameter, *RPE* row number per ear

[a] 8984 was the parent in Pop.1, and 8622 was the parent in Pop.2

Table 2 Phenotypic and genotypic correlations among six traits and their heritabilities (h_B^2) for the two populations based on combined data across two environments

Trait	GWP	100GW	EL	GPR	ED	RPE
GWP		0.11 (0.054)	0.05 (0.29**)	0.08 (0.24**)	0.20** (0.22**)	0.06** (0.17*)
100GW	0.22** (0.13)		−0.0284 (−0.1)	−0.09 (0.06)	−0.17* (0.04)	−0.23** (−0.12)
EL	0.33** (0.20**)	0.16* (−0.14)		0.24** (0.45**)	0.06 (0.30**)	−0.06 (−0.01)
GPR	0.38** (0.248**)	−0.12 (−0.29**)	0.505** (0.61**)		0.09 (0.26**)	−0.04 (0.12)
ED	0.32** (0.36**)	0.39** (0.32**)	0.16* (−0.07)	0.07 (−0.12)		0.15*(0.35**)
RPE	0.20** (0.14*)	−0.11 (−0.15*)	−0.01 (−0.06)	0.22** (0.05)	0.40** (0.41**)	
h_B^2/C.I. on h_B^2	0.27/0.07–0.42 (0.33/ 0.15–0.47)	0.22/0.02–0.39 (0.42/ 0.27–0.55)	0.45/0.30–0.56 (0.50/ 0.37–0.61)	0.26/0.06–0.41 (0.46/ 0.32–0.58)	0.52/0.40–0.62 (0.57/ 0.45–0.66)	0.63/0.54–0.71 (0.58/ 0.46–0.67)

Genotypic correlations above diagonal, phenotypic correlations below

The first line numbers outside the brackets were for Pop.1, those in the brackets were for Pop.2

GWP grain weight per plant, *100GW* 100 grain weight, *EL* ear length, *GPR* kernel number per row, *ED* ear diameter, *RPE* row number per ear, *C.I.* 95% confidence interval on h_B^2

* $P < 0.05$, ** $P < 0.01$

high-oil parent GY220 contributed the remaining three. This was consistent with their performance, since the EL of GY220 was longer than that of 8984.

Three QTL for ED were detected and were located on chromosomes 1, 3 and 4. The contribution to phenotypic variation for a single QTL varied from 4.8 to 11.0% with a total contribution of 22.6%. The positive allele on chromosome 4 was contributed by GY220, and 8984 was responsible for two positive alleles on chromosomes 1 and 3.

Chromosomes 3 (two), 5 and 10 harboured four QTL for RPE. The contributions to phenotypic variation for a single QTL ranged from 5.1 to 10.7%, with a total contribution of 30.3%. All positive alleles were contributed by 8984.

QTL detection for each trait in Pop.2

Fifteen total QTL were detected in Pop.2 located on chromosomes 1 (five), 2, 3, 4, and 5 (two), 6 (two), 7 (two) and 10 (Table 3, Fig. 2). For GWP two QTL were detected on chromosome 6, making a 7.7 and a 6.3% contribution to the phenotypic variation with a total contribution of 14.0%. The dent corn parent 8622 was responsible for all positive alleles.

One QTL was detected for both 100GW and GPR located on chromosome 1, with a contribution to phenotypic variation of 16.7% in 100GW and 11.8% in GPR. Parent 8622 provided the positive alleles.

Four QTL for EL were detected, which resided on chromosomes 1, 3, 7 and 10. The contribution to phenotypic variation for a single QTL varied from 5.3 to 9.0%, and the total contribution was 28.5%. The positive alleles in qEL2-1-1 and qEL2-10-1 were contributed by GY220, while the other two alleles were derived from 8622.

Three QTL located on chromosomes 1, 5 and 7 were detected for ED. The contribution to phenotypic variation for a single QTL varied from 6.2 to 10.7%, with a total of 23.8%. GY220 contributed the positive allele to qED2-5-2, and the remaining positive alleles were derived from 8622.

Chromosomes 1, 2, 4 and 5 harboured four QTL for RPE. The contributions to phenotypic variation for a single QTL varied from 6.0 to 15.3%, with a total of 36.5%. The positive alleles of qRPE2-1-1 and qRPE2-5-1 were contributed by GY220, while the other two positive alleles were from parent 8622.

Table 3 QTL detected for six grain yield and yield component traits in the two $F_{2:3}$ families

Trait	Population	QTL	Marker interval	Bin locus	Position	LOD	A	D	Action	R^2
GWP	Pop.1	qGWP1-6-1	umc1653–umc1127	6.07–6.08	6.0	4.8	−10.55	−0.40	A	9.8
	Pop.2	qGWP2-6-1	bnlg1043–bnlg249	6.0–6.01	23.1	2.6	8.98	−14.34	OD	7.7
		qGWP2-6-2	bnlg1538–umc1083	6.01–6.02	44.8	3.0	9.10	−10.38	D	6.3
100GW	Pop.1	q100GW1-1-1	umc1297–umc1689	1.05	98.0	5.6	−0.49	4.30	OD	10.1
		q100GW1-1-2	umc2237–phi039	1.06–1.08	188.7	3.2	0.45	2.52	OD	7.5
		q100GW1-3-1	umc2256–umc2118	3.01–3.0	18.0	3.5	1.44	−1.00	PD	6.5
		q100GW1-3-2	bnlg1447–phi029	3.03–3.04	92.2	7.5	1.62	0.16	A	13.1
		q100GW1-6-1	umc2312–umc2314	6.01	32.5	5.4	1.44	0.50	PD	8.6
	Pop.2	q100GW2-1-1	umc1395–umc2237	1.05–1.06	122.1	4.6	1.88	1.36	PD	16.7
EL	Pop.1	qEL1-3-1	umc2127–umc1174	3.05	119.4	3.0	0.26	0.80	OD	5.8
		qEL1-7-1	umc1666–umc2098	7.02–7.03	110.6	4.3	−0.75	0.30	PD	7.5
		qEL1-10-1	umc1506–umc2122	10.05–10.06	135.4	3.7	−0.70	−0.14	PD	7.1
		qEL1-10-2	umc1061–bnlg2190	10.06	154.5	3.2	−0.45	−0.72	OD	5.8
	Pop.2	qEL2-1-1	umc2237–bnlg1643	1.06–1.08	145.1	3.3	−0.50	−0.02	A	6.4
		qEL2-3-1	umc2275–umc1320	3.08	300.4	4.3	0.47	0.24	PD	7.8
		qEL2-7-1	umc1066–bnlg1792	7.01–7.02	88.7	2.6	0.48	−1.30	OD	5.3
		qEL2-10-1	umc1291–phi059	10.01–10.02	32.2	4.2	−0.63	0.06	A	9.0
GPR	Pop.1	qGPR1-8-1	bnlg1067–bnlg2082	8.03	141.9	4.6	1.03	3.10	OD	11.9
	Pop.2	qGPR2-1-1	umc1395–umc2237	1.05–1.06	118.1	4.9	−2.27	0.40	A	11.8
ED	Pop.1	qED1-1-1	bnlg2086–umc1297	1.04–1.05	86.7	7.4	0.09	0.26	OD	11.0
		qED1-3-1	umc1746–phi104127	3.01	43.2	4.6	0.09	0.12	OD	6.8
		qED1-4-1	umc1548–umc1329	4.05–4.06	82.5	3.7	−0.08	−0.02	PD	4.8
	Pop.2	qED2-1-1	umc1395–umc2237	1.05–1.06	128.1	3.1	0.10	−0.04	PD	6.2
		qED2-5-1	umc1389–umc1019	5.03–5.06	35.1	4.5	−0.10	−0.04	PD	10.7
		qED2-7-2	umc2057–bnlg2233	7.02	133.7	2.7	0.11	0.06	PD	6.9
RPE	Pop.1	qRPE1-3-1	umc2275–umc1915	3.08	227.4	6.0	0.30	0.52	OD	7.8
		qRPE1-3-2	umc1320–bnlg1754	3.08–3.09	246.7	6.0	0.38	0.64	OD	10.7
		qRPE1-5-1	phi008–umc2115	5.03–5.02	14.0	3.8	0.44	0.14	PD	5.1
		qRPE1-10-1	umc1506–umc2122	10.05–10.06	137.4	4.0	0.56	−0.42	PD	6.7
	Pop.2	qRPE2-1-1	umc1395–umc2237	1.05–1.06	112.1	3.7	−0.34	−0.20	PD	6.9
		qRPE2-2-1	bnlg125–umc1448	2.03–2.04	82.8	3.7	0.33	0.22	PD	6.0
		qRPE2-4-1	umc1757–umc2150	4.01–4.02	36.6	4.7	0.58	−0.70	D	8.3
		qRPE2-5-1	umc1389–umc1019	5.03–5.06	35.1	6.3	−0.54	−0.14	PD	15.3

In most cases, additive effects were greater than dominance effects. Higher dominance effects were only detected in five QTL for 100GW, EL, EKN and ED in Pop.1 and one QTL for EL in Pop.2. Five, 15, 2, and 11 QTL expressed additive, partial dominance, dominance and over-dominance effects for all six traits, respectively. The results indicated that partial dominance and over-dominance might play the greatest role in grain yield and yield component traits in maize, followed by additive and dominance effects.

Digenic epistasis among QTL for all traits in the two populations

In the two study populations, 12 digenic interaction pairs were identified between QTL for all traits except GWP in Pop.2 (Table 4). The detected pairs were related to 18 marker loci distributed on eight chromosomes. The numbers of epistatic interactions identified as AA, AD and DD were 5, 2 and 5, respectively. The interaction effect values were low,

Table 4 Digenic epistatic interactions among QTL for six grain yield components in the two populations

Trait	Population	QTL1/Marker interval	QTL2/Marker interval	Interaction mode	LOD	Effect	R^2 (%)
GWP	Pop.1	phi036–umc1012 (3)	qGWP1-6-1(6)	AD	0.11	3.30	0.3
100GW	Pop.1	q100GW1-1-1 (1)	q100GW1-6-1 (6)	AA	1.01	−1.00	2.7
	Pop.2	bnlg1325–bnlg1523 (3)	umc1389–umc1019 (5)	DD	0.49	−1.55	0.2
EL	Pop.1	bnlg1380–umc1433 (7)	umc2163–umc1506 (10)	AA	1.41	0.65	1.5
	Pop.2	bnlg1329–mmc0271 (2)	phi059–phi96342 (10)	DD	1.72	1.03	3.5
GPR	Pop.1	umc2237–phi039 (1)	phi036–umc1012 (3)	AD	0.35	1.42	0.8
	Pop.2	qGPR2-1-1 (1)	bnlg1879–umc1389 (5)	DD	0.75	−3.97	4.4
ED	Pop.1	umc2049–bnlg1523 (3)	qED1-4-1 (4)	DD	1.46	−0.15	1.4
		qED1-4-1 (4)	phi118–umc1152 (10)	DD	1.39	−0.17	1.5
	Pop.2	qED2-2-1 (3)	umc1545–bnlg2132 (7)	AA	1.13	0.07	1.7
RPE	Pop.1	phi036–umc1012 (3)	qRPE1-10-1 (10)	AA	1.20	0.36	2.3
	Pop.2	qRPE2-1-1 (1)	bnlg1879–umc1389 (5)	AA	1.42	−0.40	2.3

Chromosome number in the brackets

ranging from 0.2 to 4.4%. These results suggest that interaction contributions to trait performance were minimal.

Discussion

Comparison of QTL detected in the two connected populations

Quantitative trait locus/loci are only detected when two parents possess polymorphisms at both a respective marker locus and at the trait locus for a bi-parental population. Mihaljevic et al. (2004) suggested that QTL exhibiting polymorphism in one cross but lacking polymorphism in another might be a biological cause. In general, only a subset of QTL could be detected in a given population (Blanc et al. 2006). Inconsistencies in QTL detection for the same trait have been repeatedly reported among populations with a range of different parents (Beavis et al. 1991; Stuber et al. 1992; Austin et al. 2000) and various populations derived from the same cross (Austin and Lee 1996, 1998; Li et al. 2007; Song 2003). Inconsistent results obtained from various testcrosses and connected populations might reflect the influence of genetic background on QTL detection (Mihaljevic et al. 2004; Blanc et al. 2006). Moreno-Gonzalez (1993) employed simulation studies and demonstrated that different generations provided varied success at estimating marker-associated QTL effects by multiple regressions.

Since various environments simultaneously influence most quantitative traits, the effect of genetic background on QTL mapping results can only be reflected through experiments conducted under the same environmental conditions. However, until now, few results have been reported using several connected populations under the same conditions. In most cases, few common QTL were detected (Beavis et al. 1991; Blanc et al. 2006; Charcosset and Gallais 1996; Meyer et al. 2007; Mihaljevic et al. 2004). However, most detected QTL having consistent and stable effects among genetic backgrounds were reported by Rebaï et al. (1997). These results demonstrated that common QTL detection results using connected populations were contingent on parents and traits. Traits with a complex genetic structure controlled by an increased number of small QTL, highly integrated epistatic complexes (Dudley 1993; Stuber et al. 1999) or varied control of traits via alternative metabolic pathways (Bost et al. 1999) must result in a high degree of incongruence in QTL detection.

In the present study, although the same high-oil corn parent GY220 was used and the field conditions were identical, minimal QTL congruence was found between the two populations. The most important factor might be different genetic interactions of the two dent corn parents with the same high-oil corn

parent GY220. According to specific combining ability (SCA) analysis between 30 dent/flint corn inbreds and 9 high-oil corn inbreds, SCA variances for all the six grain yield components were significantly different (Liu 2007). The value of SCA was also shown in high-oil maize breeding practices. In addition, a large decrease in grain yield and grain weight resulted from long-term selection for high-oil content. This fact might lead to a different or more complex genetic background in populations derived from high-oil and dent/flint maize inbreds. Comprehensive evaluation of our study revealed the clear influence of the dent maize genetic background on QTL detection for grain yield and yield component traits and a complicated genetic architecture. Of course, QTL-by-environment interactions should be analyzed in further studies under many environmental conditions using RILs with unlimited seed quantity.

For the digenic epistasis, five and seven pairs of digenic interaction were identified in the two populations, respectively. Although all traits showed digenic interactions except GWP in Pop.2, the interaction mode and the positions of related QTL or marker intervals were different in most cases. Otherwise, seven and four pairs of digenic interactions were detected between QTL and the marker interval, and between one marker interval and another, respectively. Similar results have been found in our previous study (Li et al. 2007). QTL for the respective traits might exist at these marker intervals. However, they were not detected in QTL analysis due to their small effects. Such marker intervals might have some role in digenic epistasis for grain yield and yield component traits.

Comparison of detected QTL for grain yield components with other studies

Grain yield plays the most important role both in normal maize and in specialty maize. Therefore, a body of literature exists on QTL mapping for grain yield and yield component traits using different kinds of populations derived from crosses of different normal corn inbred lines (Austin and Lee 1996, 1998; Austin et al. 2000; Stuber et al. 1987, 1992; Tang et al. 2007; Veldboom and Lee 1994; Wang et al. 2007; Yan et al. 2006), dent and popcorn inbreds (Li et al. 2007), and dent and high-oil maize inbreds (Song 2003). Several hundred related QTL have been detected across all chromosomes. Differences in mapping populations, mapping methods, few common loci, and environment are responsible for the challenges in making direct comparisons. However, comparisons of QTL data across different studies can provide preliminary/suggestive information. Because only a few QTL detections have been conducted in high-oil maize, comparison of the results in this study with previous results in normal maize or popcorn may provide insight into the effects of the high-oil maize genetic background. It is notable that the Alexander high-oil maize background has not been reported in QTL mapping for any trait prior to this report.

In the present study, most QTL (eight) were detected at both bin 1.05 and 1.06, including q100GW2-1-1 with the largest effect (16.7%), and qED2-1-1 and qGPR2-1-1 with contributions greater than 10% (11.0 and 11.8%). At these two bin loci and at nearby bins, a substantial number of QTL for GWP, 100/300GW, ear weight (EW), EL, ED, RPE, and GPR have been reported in previous research (Austin and Lee 1996, 1998; Li et al. 2007; Song 2003; Stuber et al. 1987, 1992; Tang et al. 2007; Veldboom and Lee 1994; Wang et al. 2007; Yan et al. 2006). Clearly, this region might play the most important role in determining maize grain yield and yield component traits. QTL located at this region share high congruence across different genetic backgrounds and environments. For our first attempts in conducting fine QTL mapping, we have chosen q100GW2-1-1 and hope to accomplish successful cloning. In fact, NILs for a 100GW QTL at bin 1.05–1.06, detected in our previous studies with dent and popcorn inbreds, have been completed, and fine mapping is in progress. Otherwise, at bin 3.04, 5.03 and 8.03 locating QTL with large effects for 100GW, GPR, ED in this study, QTL for most grain yield components have been detected in almost all previous related studies. QTL congruence in the present study with previous research reflects the potential for future progress. In addition, it is likely that newly detected major QTL share complementary roles in revealing the genetic nature of grain yield and yield component traits, especially in high-oil maize. Of course, knowledge regarding QTL function via cloning may lead to other viable approaches to improve grain yield. The success obtained in cloning grain/fruit weight QTL in rice (Fan et al. 2006; He et al. 2006; Li et al. 2004; Xie et al. 2007) and tomato (Alpert and Tanksley 1996;

Frary et al. 2000) can be vital to similar advances in maize.

QTL clusters associated with grain and yield component traits

Clustered QTL for grain yield and yield component traits have been reported in a number of independent studies (Austin and Lee 1996, 1998; Li et al. 2007; Song 2003; Veldboom and Lee 1994; Wang et al. 2007). Multiple trait associations can be explained genetically by QTL with pleiotropic effects or linked QTL in control of different traits. Among the 18 and 15 QTL detected in the two populations herein, 6 of 15 (40%) QTL were associated with two or four traits in Pop.2. In the region of marker interval umc1395–umc2237 at bin 1.05–1.06, four QTL for 100GW, GPR, ED and RPE were detected at position 122.1–128.1. In addition, one QTL for EL was located in the near marker interval umc2237–bnlg1643 at position 145.1. In this case, both parents contributed the favorable alleles. Two QTL for 100GW and one for ED were also detected in Pop.1 at bin 1.05, 1.06–1.08 and 1.04–1.05, respectively. This region might be a core cluster for QTL controlling different grain yield and yield components with pleiotropic effects. Two closely linked QTL with pleiotropic effects might be proposed, one for 100GW and ED, the other for GPR, RPE and EL. The exact position of the latter is uncertain, and it might be closer to marker umc2237. In fact, QTL with pleiotropic effects for GPR and EL are easily understood, since they were always correlated with each other in performance (Table 2). When the NILs for 100GW QTL with the largest effects are generated, this problem may show some resolution.

Another marker interval associated with multiple traits in Pop.2 was umc1389–umc1019 on chromosome 5. One QTL for ED and one for RPE were detected at interval bin 5.03–5.06. Since both favorable alleles were contributed by GY220 and the chromosome positions were the same (35.1), we can postulate that a single QTL with pleiotropic effects for ED and RPE might reside at this position. The significant phenotypic and genotypic correlations among these traits may provide some insight into this hypothesis, and due to the large effects of the two QTL (10.7 and 15.3%), further investigation is warranted. For the marker interval umc1506–umc2122 at bin 10.05–10.06 in Pop.1, where EL and RPE QTL were located, the two parents contributed favorable alleles for the traits. Therefore, two-clustered QTL might be individually controlling the two traits.

In conclusion, grain yield traits possess a highly complicated genetic structure. Substantial influence of dent maize genetic background on QTL detection for grain yield traits was reflected in this study. To elucidate the genetic nature of maize through QTL mapping, genetically different populations should be constructed and tested under various environmental conditions. Based on comparisons with previous results in normal maize or popcorn, two QTL for 100GW showing high congruence across different genetic backgrounds and environments were chosen as our objective QTL in conducting fine QTL mapping. QTL clusters associated with several traits were also identified in both populations.

Acknowledgments We greatly thank China Agricultural University for providing us the high-oil maize inbred line GY220. This work was funded by the Henan Innovation Project for University Prominent Research Talents (2005HANCET-12), the Henan Natural Science Foundation (0511032900).

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