Euphytica (2013) 193:303–316
DOI 10.1007/s10681-013-0901-7

Quantitative trait loci mapping for yield components and kernel-related traits in multiple connected RIL populations in maize

Chunhui Li · Yongxiang Li · Baocheng Sun · Bo Peng · Cheng Liu · Zhizhai Liu · Zhaozhao Yang · Qingchao Li · Weiwei Tan · Yan Zhang · Di Wang · Yunsu Shi · Yanchun Song · Tianyu Wang · Yu Li

Received: 18 October 2012 / Accepted: 26 February 2013 / Published online: 29 March 2013

Abstract Grain yield is one of the most important and complex quantitative traits in maize breeding. In the present study, a total of 11 connected RIL populations, derived from crosses between elite inbreed "Huangzaosi" as the common parent and 11 elite inbreeds, were evaluated for five yield components and kernel-related traits under six environments. Quantitative trait loci (QTL) were detected for the traits under each environment and in joint analysis across all environments for each population. A total of 146 major QTL with $R^2 > 10$ % in at least one environment and also detected based on joint analysis across all environments were identified in the 11 populations. *Lqkwei4* conferring kernel weight and *Lqklen4-1* conferring kernel length both located in the adjacent marker intervals in bin 4.05 were stably expressed in four environments and in joint analysis across six environments, with the largest R^2 over 27 and 24 % in a single environment, respectively. Moreover, all major QTL detected in the 11 populations were aligned on the IBM2 2008 neighbors reference map. Totally 16 common QTL (CQTL) were detected. Seven important CQTL (CQTL1-2, CQTL1-3, CQTL4-1, CQTL4-2, CQTL4-3, CQTL4-4, and CQTL6-1) were located in bin 1.07, 1.10, 4.03, 4.05, 4.08, 4.09 and 6.01–6.02, respectively. These chromosomal regions could be targets for fine mapping and marker-assisted selection.

Keywords Maize · QTL · Yield · Kernel-related traits

Y. Li—Co-author, equally contribute to the work

Electronic supplementary material The online version of this article (doi:10.1007/s10681-013-0901-7) contains supplementary material, which is available to authorized users.

C. Li · Y. Li · B. Peng · Z. Liu · Z. Yang · Q. Li · W. Tan · Y. Zhang · D. Wang · Y. Shi · Y. Song · T. Wang (✉) · Y. Li (✉)
Institute of Crop Science, Chinese Academy of Agricultural Sciences, Beijing 100081, China
e-mail: wangtianyu@263.net

Y. Li
e-mail: yuli@mail.caas.net.cn

B. Sun · C. Liu
Institute of Food Crops, Xinjiang Academy of Agricultural Sciences, Urumqi 830000, China

Introduction

Maize (*Zea mays* L.) is one of major crops in the world, with the production quantity of more than 844 million tonnes in 2010 (http://faostat.fao.org). Grain yield is the most important trait of interest in maize breeding programs; nevertheless it is a very complex quantitative trait and usually has a low heritability, which often results in a slow genetic gain in breeding (Lee and Austin 1998). Consequently, it has become important to understand the genetic basis of yield component traits, since these traits can be employed in indirect selection in maize breeding.

Kernel weight is one of the yield component traits and is seriously affected by kernel size, measured by thickness, length and width. The kernel size is an important target of breeding, not only as a component of grain yield (Messmer et al. 2009) but also as a judgment of early vigor of maize (Revilla et al. 1999). In addition, the kernel size is an important attribute for determining the market value of maize grain since it influences flour yield and protein content (Gupta et al. 2006). Therefore, it is necessary to dissect the genetic basis of kernel thickness, kernel length and kernel width.

During the past decade, with the advent of molecular marker techniques and quantitative trait loci (QTL) analysis approaches, many QTL for kernel weight and seed size have been identified in rice, wheat and barley (Li et al. 1998; Lin et al. 1996; Qiao et al. 2008; Rahman et al. 2007; Xing et al. 2002). Especially, a few genes for kernel-related traits have been detected in rice, e.g. *GS3* (Fan et al. 2006), *GW2* (Song et al. 2007) and *qSW5* (Shomura et al. 2008; Wan et al. 2008). However, mapping QTL for kernel size in maize is rare so far (Austin and Lee 1996; Veldboom and Lee 1994; Lee and Veldboom 1996; Smith et al. 1994; Li et al. 2009a, b; Peng et al. 2011).

Although there has been substantial QTL researches for grain yield and kernel weight in maize, such studies often use individual biparental mapping populations (Ajnone-Marsan et al. 1995; Austin and Lee 1996; Lee and Veldboom 1996; Ribaut et al. 1997; Yan et al. 2006; Tang et al. 2010), which could not reveal the genetic variation of broader genetic reference populations and restrains the identification of different genetic background alleles (Holland 2007). It has been reported that different populations originated from different parents have a great influence on the results of QTL detection (Beavis et al. 1991; Stuber et al. 1992; Austin et al. 2000). Some authors have proposed analyzing jointly the different populations. Using this method, previous studies have been performed by using independent populations (no known pedigree relationship between the parents of different populations) (Muranty 1996; Xu 1998). Under this condition, the QTL effect are nested (in the statistical sense) within populations and the estimated number of parameters increases with the increasing number of populations. In addition, due to a lack of connection between populations, it is not possible to globally compare the effects of all QTL alleles segregating in the different populations. Therefore, the development of connected populations with a common parent among populations which capture a broad spectrum of phenotypic variation is an alternative approach. Using connected populations, the effects of alleles segregating are estimated simultaneously, which facilitates a global comparison. This is of particular interest to identify the common parental origin(s) of favorable allele(s) at each QTL and to identify the common QTL in different populations for a given trait. In USA, the maize nested association mapping (NAM) population was created by crossing 25 diverse lines of maize to one common line, then producing about 5,000 RILs (McMullen et al. 2009). Using the NAM population, it has been effectively used to dissect the genetic architecture of the maize flowering time (Buckler et al. 2009), leaf architecture (Tian et al. 2011), male and female inflorescence traits (Brown et al. 2011) and maize kernel composition traits (Cook et al. 2012).

In this study, the 11 connected RIL populations with the common parent "Huangzaosi" were used to detect QTL for five yield-related traits based on 6 individual environments and joint analysis across all environments. The main objectives of this work were: (1) to produce a powerful permanent resource to promote the identification of QTL for a great diversity of traits; (2) to detect QTL for yield components and kernel-related traits in each of the 11 RIL populations; (3) to integrate detected QTL in the 11 RIL populations and identify some important common QTL among different populations; (4) to analyze the influence of different genetic backgrounds and environments on QTL detection for yield components and kernel-related traits; and (5) to find identical QTL and important genetic regions for further studies in fine mapping and marked-assisted breeding in the future.

Materials and methods

Generation of the RIL populations

Twelve inbred lines (Zheng58, Ye478, Qi319, Weifeng322, Lv28, Pa405, Duo229, K12, Mo17, Huobai, Huangyesi3 and Huangzaosi) are elite inbred lines in China maize breeding and are representative members of several popular heterotic groups used in China. For example, Ye478 belongs to the Reid group, Mo17 the Lancaster group, Lv28 the Luda Red Cob group, K12 and Huangyesi3 the Tangsipingtou group (Li and Wang 2010). Particularly, the common parent "Huangzaosi" from the Tangsipingtou group is an important elite foundation parent in China, which has many merits,

including wide adaptability and high combining ability (Zhao et al. 2008; Liu et al. 2009). Parents K12 and Huangyesi3 were the derived inbred lines of common parent "Huangzaosi". Parent Zheng58 was the derived inbred line of parent Ye478. Other parents did not have direct relationship. 11 RIL populations were derived from the crosses between Huangzaosi as the male parent and the 11 diverse inbreds as the females by single seed descent to the F_7 generation. These RIL populations hereafter referred to as Zheng58H, Ye478H, Qi319H, Weifeng322H, Lv28H, Pa405H, Duo229H, K12H, Mo17H, HuobaiH and Huangyesi3H), consisted on 183, 184, 167, 184, 184, 184, 183, 184, 151, 183 and 184 families (RILs), respectively.

Field experimental design and phenotyping

The parents and the RIL families of the 11 populations were field evaluated across a total of six environments. In 2008, the evaluation of the populations was carried out in Beijing. In 2009, the experiment was grown in three locations: Beijing, Xinxiang of Henan province and Urumqi of Xinjiang province. In 2010, the experiment was again evaluated in Xinxiang of Henan province and Urumqi of Xinjiang province. Each location × year combination was considered as an environment in the following statistical analysis. For each environment, the experiment was divided into 11 separate sets and each set contained one population and its two parents. For each set, all the RIL were randomly assigned within each replication with one-row plot. Two replications of each set were planted adjacently. The rows included 11 plants were 3 m length and 0.6 m apart. The final plant density was 52,400 plants per hectare in all environments.

The traits evaluated included: (1) grain yield per plant (GYPP), evaluated from the average of 5 plants in the center of each row, in grams; (2) 100-kernel weight (KWEI), measured in grams estimated from the average of three samples of the weight of 100 randomly selected seeds; (3) 10-kernel thickness (KTHI), measured from the average of five samples of the thickness of 10 seeds in the center of an ear, in cm; (4) 10-kernel length (KLEN), measured from the average of five samples of the length of 10 seeds in the center of an ear, in cm; (5) 10-kernel width (KWID), measured from the average of five samples of the width of 10 seeds in the center of an ear, in cm.

Phenotypic data analysis

Analysis of variance for five traits was performed for each of the 11 RIL populations by PROC GLM (SAS Institute Inc. 1999) with genotype, environments, interaction between genotype and environments, and replications as random effects. The broad-sense heritability (h^2) on a plot basis was estimated as $h^2 = \sigma_g^2/\left(\sigma_g^2 + \sigma_{ge}^2/n + \sigma_\varepsilon^2/nk\right)$, where σ_g^2 is genotypic variance, σ_{ge}^2 is the interaction of genotype with environment (genotype × environment variance), σ_ε^2 is experimental error variance, n is the number of environments and k is the number of replications per environment (Hallauer and Miranda 1988).

Mean values of the six environments for each population were used to calculate the Pearson's phenotypic correlation coefficients between all traits by the SAS PROC CORR procedure (SAS Institute Inc. 1999). Estimates for the genetic correlation coefficients among all traits were obtained with PLABSTAT software (Utz 1997).

Genotyping and genetic map construction

For the 11 RIL populations, young leaves from 10 plants for each RIL family and each parent line were harvested in bulk to conduct genomic DNA extraction using CTAB method (Chen and Ronald 1999). The genotypes of the 11 RIL populations (1971 RIL lines) were determined using a set of 757 SNPs that uniformly covered the whole genome at Pioneer Hi-bred international. Marker positions were projected on the IBM2 2008 neighbors reference map obtained from MaizeGDB.

A total of 201, 165, 206, 194, 205, 211, 191, 163, 179, 191 and 103 polymorphic SNP markers were employed to construct individual RIL genetic map for Zheng58H, Ye478H, Qi319H, Weifeng322H, Lv28H, Pa405H, Duo229H, K12H, Mo17H, HuobaiH and Huangyesi3H, respectively, using Mapmaker v3.0 software (Lander et al. 1987). Haldane mapping function was applied for calculating genetic distance.

QTL analysis

A mixed-model based on composite interval mapping method was used to conduct QTL mapping in

QTLNetwork software version 2.0 (Yang et al. 2007), with a walking speed of 1 cM. The threshold for indicating the existence of a significant QTL for all traits in each environment was obtained by 1,000 permutations at a significance level of $p = 0.05$. The confidence interval calculated by the odd ratio reduced by a factor 10 was averaged for each of the QTL (Yang et al. 2007). For all traits in each of the 11 populations, joint analysis across all environments and analysis for each of the six environments were both carried out. If the confidence intervals of QTL detected for the same trait in different environments overlapped, they were accepted as the same QTL. The sign of the additive effects was employed to determine the parent from which the favorable alleles came. If the additive effects had positive sign, the alleles which increased a given trait originate from the common parent "Huangzaosi", otherwise from the other parents. Major QTL with $R^2 > 10$ % in at least one environment and also detected based on joint analysis across all environments were identified in all populations. The major QTL in the original maps were projected on the IBM2 2008 neighbors reference map using markers shared between both maps. More than three QTL with overlapping marker intervals or same marker intervals were considered as common QTL (CQTL) among all populations.

Results

Segregation and linkage maps

The average frequencies of parental alleles in each population were approximately close to expected ratio (Mendelian 1:1) for the RILs. The linkage maps obtained for the 11 RIL populations were composed of a mean of 183 SNPs with the range of 103 (Huangyesi3H) to 211 (Pa405H) (Table 1). The total length of the linkage maps was in the range of 858.1 cM (Huangyesi3H) to 1,946.7 cM (Weifeng322H). The average interval lengths between two adjacent markers ranged from 6.8 cM (K12H) to 10.0 cM (Weifeng322H).

Phenotyping data analyses

The ANOVA suggested that genotypic and environmental effects were highly significant ($p < 0.001$) for all traits in all populations. Genotype × environment interactions

Table 1 Overall genotyping data for the eleven RIL populations

	Zheng58H	Ye478H	Qi319H	Weifeng322H	Lv28H	Pa405H	Duo229H	K12H	Mo17H	HuobaiH	Huangyesi3H
No. of genotyped lines	183	184	167	184	184	184	183	184	151	183	184
No. of markers scored	201	165	206	194	205	211	191	163	179	191	103
% of Huangzaosi-allele	49.7	51.9	51.1	50.2	50.1	51.4	53.1	50.8	51.8	49.7	49.8
Estimated genome size (cM)	1495.2	1495.3	1532.2	1946.7	1568.1	1580.3	1697.7	1101.5	1525.3	1774.5	858.1
Average interval between markers (cM)	7.4	9.1	7.4	10.0	7.6	7.3	8.9	6.8	8.5	9.3	7.6

Table 2 Analysis of variance for yield components and kernel-related traits for the eleven populations in six environments

Source	Mean square										
	Zheng58H	Ye478H	Qi319H	Weifeng322H	Lv28H	Pa405H	Duo229H	K12H	Mo17H	HuobaiH	Huangyesi3H
Grain yield per plant (g)											
Genotype(G)	2946.6***	5836.3***	3188.8***	3173.9***	1270.5***	2204.5***	1872.9***	2192.2***	2220.5***	1424.3***	1689.3***
Environment(E)	290004.5***	384172.3***	229714.5***	131524.2***	222821.7***	198218.2***	240050.0***	440358.2***	161544.0***	169580.0***	292368.6***
G × E	561***	1167.4***	929.0***	515.4***	423.5***	440.1***	387.0**	638.2***	520.1***	396.0***	429.6***
Block	463.6	1892.9	5118.4**	127.8	1434.2*	17955.7**	18285.7**	2387.2*	2467.9**	78.9	13792.0**
Error	345.5	542.1	426.4	228.5	256.3	328.6	331.0	385.2	336.4	272.2	303.5
H^2	0.81	0.80	0.71	0.84	0.67	0.80	0.79	0.71	0.77	0.72	0.75
100-Kernel weight (g)											
Genotype(G)	103.6***	127.2***	98.1***	100.5***	105.4***	59.1***	109.3***	89.3***	63.6***	73.5***	36.8***
Environment(E)	7189.5***	5907.4***	4208.6***	3327.3***	2148.3***	3930.1***	2640.1***	5998.2***	4139.4***	4089.9***	2224.8***
G × E	16.9***	12.7***	18.2***	11.1***	12.2***	8.8***	9.6***	13.2***	16.5***	11.9***	6.6***
Block	3.7	37.3	64.1*	1.2	0.02	167.3**	362.1**	16.0	320.6**	6.1	38.4*
Error	8.8	9.4	10.1	6.5	6.3	5.4	6.4	8.5	9.0	6.5	4.1
H^2	0.84	0.90	0.81	0.89	0.88	0.85	0.91	0.85	0.74	0.84	0.82
10-Kernel thick (cm)											
Genotype(G)	1.16***	1.22***	1.29***	1.23***	1.31***	1.01***	1.02***	1.50***	0.74***	0.93***	0.61***
Environment(E)	3.89***	6.12***	17.69***	15.82***	13.34***	17.22***	8.13***	6.28***	11.78***	10.99***	20.48***
G × E	0.15***	0.16***	0.21***	0.20***	0.16***	0.15***	0.13***	0.16***	0.19**	0.16***	0.12***
Block	1.22**	1.71**	5.79**	3.05***	1.99***	4.61**	2.00***	0.28	2.81**	8.26***	0.14
Error	0.11	0.12	0.16	0.13	0.12	0.11	0.08	0.12	0.16	0.11	0.10
H^2	0.87	0.86	0.84	0.84	0.88	0.86	0.87	0.89	0.74	0.83	0.80
10-Kernel length (cm)											
Genotype(G)	3.21***	5.07***	3.26***	5.42***	3.07***	3.18***	3.54***	2.36***	3.16***	2.12***	1.95***
Environment(E)	133.62***	142.7***	119.79***	97.12***	82.67***	105.5***	79.35***	111.8***	80.76***	86.37***	69.37***
G × E	0.34***	0.52***	0.47***	0.45***	0.29***	0.44***	0.31***	0.3***	0.49***	0.33***	0.28***
Block	2.28**	1.18	4.52**	2.98***	0.01	4.53***	0.63	4.09***	2.18*	14.56**	0.05
Error	0.22	0.33	0.24	0.26	0.21	0.22	0.21	0.21	0.33	0.22	0.21
H^2	0.90	0.90	0.86	0.92	0.90	0.86	0.91	0.87	0.85	0.84	0.86
10-Kernel width (cm)											
Genotype(G)	2.31***	3.15***	2.41***	3.11***	2.41***	2.00***	2.67***	2.01***	2.08***	2.25***	1.02***
Environment(E)	48.35***	40.9***	50.0***	48.05***	37.65***	48.47***	24.97***	51.4***	35.48***	37.25***	19.74***

Table 2 continued

Source	Mean square											
	Zheng58H	Ye478H	Qi319H	Weifeng322H	Lv28H	Pa405H	Duo229H	K12H	Mo17H	HuobaiH	Huangyesi3H	
G × E	0.23***	0.23***	0.27***	0.23***	0.21***	0.18***	0.22***	0.20**	0.24**	0.22***	0.18***	
Block	0.25	0.72*	0.94*	0.84*	4.06***	4.36***	0.05	0.09	1.09*	3.26***	0.61*	
Error	0.15	0.17	0.20	0.16	0.15	0.13	0.14	0.17	0.19	0.16	0.14	
H^2	0.90	0.93	0.89	0.93	0.91	0.91	0.92	0.90	0.89	0.90	0.83	

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, respectively

were also found significant (Table 2). The broad sense heritability (h^2) was medium for grain yield (0.67–0.84) across six environments in the 11 populations. Compared with the heritability of GYPP, the heritability of the other traits was relatively high ($0.80 < h^2 < 0.93$), with the exception of KWEI and KTHI in Mo17H (both 0.74). 100-kernel weight and kernel-related traits were the most heritable traits on average.

The phenotypic (r_p) and genetic (r_g) correlation coefficients between five traits in each of the 11 populations were listed in Table 3. GYPP had significant negative correlations with KTHI across all populations. KWEI had significant positive correlations with traits KTHI, KLEN and KWID in all populations. The correlation coefficients between GYPP and kernel size traits (KLEN, KWEI and KWID) indicate that a lot of the QTL mapped for these traits may be linked or have pleiotropic effect in the present study. It was worthwhile to note that the correlation coefficients between GYPP and KLEN were significant in the 11 populations. Peng et al. (2011) also obtained significant positive correlations and linear fit between GYPP and KLEN in two $F_{2:3}$ populations. Hence, we could conclude that the correlation between GYPP and KLEN was very robust in different genetic backgrounds and populations.

QTL analysis

A total of 146 major QTL were detected, including 19 in Zheng58H, 17 in Ye478H, 11 in Qi319H, 18 in Weifeng322H, 21 in Lv28H, 9 in Pa405H, 14 in Duo229H, 12 in K12H, 6 in Mo17H, 8 in HuobaiH and 11 in Huangyesi3H (supplemental table). These QTL were projected on the IBM2 2008 neighbor's reference map which allowed us to compare the QTL detected in the 11 RIL populations (Fig. 1). These QTL were distributed across the genome. Many QTL were distributed on chromosomes 1, 3, 4 and 5 (27, 16, 29 and 17 QTL, respectively). Individual QTL explained between 1.4 and 20.5 % of the total intrapopulation phenotypic variation of the target trait. The detailed information of individual QTL detected was presented in Supplemental table.

GYPP

Eleven QTL detected for GYPP were found in eight of the 11 populations, except for Ye478H, Lv28H and

Table 3 Phenotypic and genetic correlation coefficients among five traits in the eleven populations

	GYPP/KWEI	GYPP/KTHI	GYPP/KLEN	GYPP/KWID	KWEI/KTHI	KWEI/KLEN	KWEI/KWID	KTHI/KLEN	KTHI/KWID	KLEN/KWID
Zheng58H	0.16*/0.16*	-0.32**/-0.24**	0.60**/0.58**	0.08ns /0.02ns	0.49**/0.60**	0.46**/0.52*	0.69**/0.78**	-0.19** /-0.14*	0.39**/0.45**	0.34**/0.31**
Ye478H	0.38**/0.50**	−0.39**/−0.36**	0.66**/0.73**	0.16*/0.29**	0.40**/0.46**	0.54**/0.68**	0.70**/0.84**	-0.11^{ns}/−0.10*	0.47**/0.51**	0.37**/0.46**
Qi319H	0.29**/0.34**	−0.37**/−0.27**	0.56**/0.58**	0.20**/0.22**	0.39**/0.52**	0.46**/0.54**	0.67**/0.80**	−0.22**/−0.14*	0.39**/0.48**	0.45**/0.47**
Weifeng322H	0.41**/0.39**	−0.33**/−0.31**	0.73**/0.70**	0.13^{ns}/0.13*	0.46**/0.64**	0.59**/0.66**	0.69**/0.78**	-0.14^{ns}/-0.01^{ns}	0.52**/0.59**	0.28**/0.30**
Lv28H	0.11^{ns}/0.02^{ns}	−0.22**/−0.18**	0.54**/0.47**	0.05^{ns}/-0.01^{ns}	0.70**/0.82**	0.38**/0.44**	0.76**/0.84**	-0.05^{ns}/-0.07^{ns}	0.58**/0.64**	0.20**/0.24**
Pa405H	0.26**/0.29**	−0.35**/−0.38**	0.62**/0.64**	0.09^{ns}/0.12*	0.51**/0.59**	0.40**/0.41**	0.73**/0.82**	−0.22**/−0.28**	0.45**/0.45**	0.22**/0.21**
K12H	0.23**/0.27**	−0.28**/−0.27**	0.63**/0.72**	0.06^{ns}/0.14*	0.57**/0.71**	0.26**/0.40**	0.74**/0.86**	−0.31**/−0.19**	0.58**/0.64**	0.27**/0.25**
Mo17H	0.26**/0.29**	−0.44**/-0.59**	0.62**/0.61**	0.32**/0.26**/0.31**/0.34**	0.31**/0.34**	0.45**/0.55**	0.69**/0.81**	-0.25**/-0.32**	0.26**/0.25**	0.50**/0.45**
HuobaiH	0.16* /0.03ns	-0.29**/-0.34**	0.53**/0.54**	0.17* /0.05ns	0.54**/0.75**	0.47**/0.46**	0.66**/0.76**	-0.12ns/-0.07ns	0.35**/0.46**	0.46**/0.44**
Huangyesi3H	0.30**/0.25**	-0.35**/-0.36**	0.73**/0.78**	0.08ns/0.07ns	0.42**/0.57**	0.39**/0.43**	0.68**/0.86**	-0.36**/-0.35**	0.41**/0.54**	0.16*/0.14*

The values in front of "/" indicate phenotypic correlation coefficients, and the values behind of "/" indicate genetic correlation coefficients

NS not significant

** $p < 0.01$; * $p < 0.05$

Mo17H. These QTL were located on chrom. 2, 3, 4, 6, 8 and 9. Each QTL explained phenotypic variation ranging from 2.2 to 6.7 %. Most of these QTL were population specific, except one in bin 9.03 which was detected in Weifeng322H and HuobaiH (other parents' alleles increases GYPP).

KWEI

Twenty-six QTL detected for KWEI were found in ten of the 11 populations, except for Pa405H. These QTL were distributed across the genome, with the exception of chromosomes 2. Most of these QTL were population specific, but four QTL were found at the same location in two populations: on bin 4.03 in Ye478H and K12H (Huangzaosi allele increased KWEI); on bin 4.05–4.06 in Huangyesi3H and Duo229H (Huangzaosi allele increased KWEI); on bin 4.09 in K12H and Mo17H (Huangzaosi allele increased KWEI); on bin 5.06–5.07 in HuobaiH and Lv28H (other parents' alleles increases KWEI). In addition, one QTL on bin 4.05 was mapped in Duo229H, HuobaiH and Lv28H, with the Huangzaosi allele increasing KWEI in the three populations.

KTHI

Thirty-one QTL detected for KTHI were found in the 11 RIL populations. One to six QTL were detected depending on the RIL set. Chrom. 1 and 5 presented the largest number of QTL. On chrom. 1, all QTL alleles that increased KTHI came from Huangzaosi, except Dqkthi1 and HYqkthi1. However, on chrom. 5, all QTL alleles that increased KTHI came from other parents, except Pqkthi5 and HYqkthi5. Most of these QTL were population specific except one on bin 1.10 which was detected in Weifeng322H, Ye478H and Zheng58H (Huangzaosi allele increased KTHI) and one on bin 3.07 in HuobaiH and Lv28H (Huangzaosi allele increased KTHI).

KLEN

Thirty-five QTL detected for KLEN were found in the 11 RIL populations. One to six QTL were detected depending on the RIL set. These QTL were distributed genome wide. Chromosomes 1 and 4 presented the largest number of QTL. On chrom. 1, all QTL alleles that increased KLEN came from other parents, except

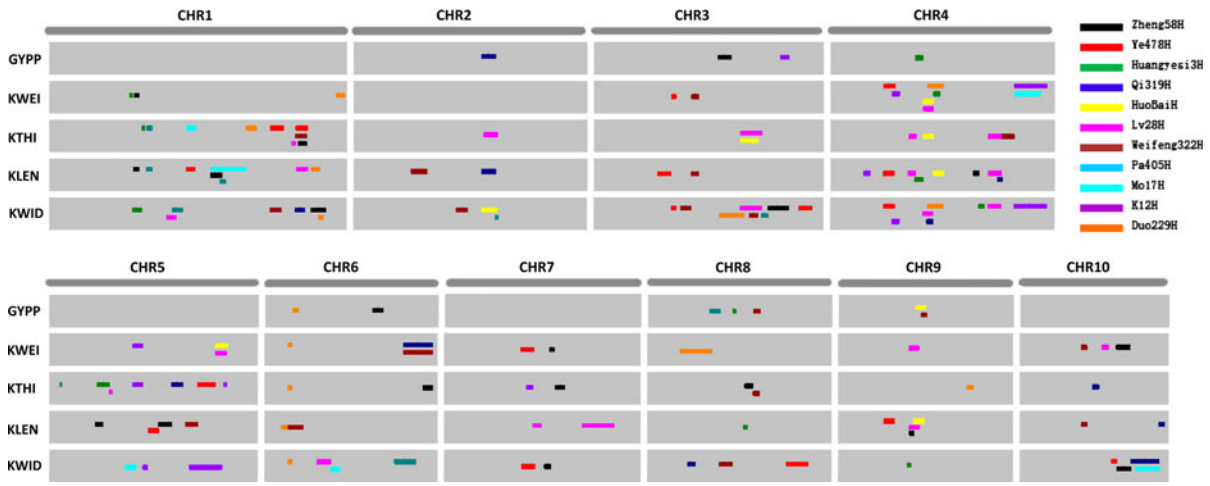

Fig. 1 Schematic representation of the QTL detected in the 11 populations for the five traits analyzed: grain yield per plant (GYPP),100-kernel weight (KWEI),10-kernel thickness (KTHI), 10-kernel length (KLEN) and 10-kernel width (KWID). QTL with $R^2 > 10$ % in at least one environment and also detected based on joint analysis across all environments were projected on the IBM2 2008 neighbors reference map. QTL for each RIL population are color coded

Dqklen1. On chrom. 4, all QTL alleles that increased KTHI came from Huangzaosi, except Zqklen4, Qqklen4 and Lqklen4. Most of these QTL were population specific, but three QTL were found at the same location in two populations: on bin 4.08 in Qi319H and Lv28H (other parents' alleles increased KLEN); on bin 9.03 in Zheng58H and Lv28H (other parents' alleles increased KLEN); and on bin 9.03 in HuobaiH and Lv28H (other parents' alleles increased KLEN). In addition, one QTL on bin 1.07 was mapped in Zheng58H, Mo17H and Pa405H, with the other parents' alleles increasing KLEN in three populations.

KWID

Forty-three QTL detected for KWID were found in the 11 RIL populations. One to six QTL were detected depending on the RIL set. These QTL were distributed across the genome. Chrom. 1, 3 and 4 presented the largest number of QTL. Most of these QTL were population specific, but seven QTL were found at the same location in two populations: on bin 1.04 in Pa405H and Lv28H (Huangzaosi allele increased KWID); on bin 1.11 in Zheng58H and Duo229H (Huangzaosi allele increased KWID); on bin 2.07 in Pa405H and HuobaiH (Huangzaosi allele increased KWID); on bin 3.07 in Lv28H and Duo229H (Huangzaosi allele increases KWID); on bin 3.07 in Lv28H and Weifeng322H (Huangzaosi allele increased KWID); on bin 4.03 in K12H and Ye478H (Huangzaosi allele increased KWID); and on bin 10.07 in Mo17H and Qi319H (other parents' alleles increased KWID). In addition, one QTL on bin 4.05 was mapped in Lv28H, Duo229H and Qi319H, with Huangzaosi allele increasing KWID in the three populations.

Effects of QTL alleles and prediction of parental kernel-related traits

We used individual effects associated with parental alleles at each QTL, and arranged the 11 RIL populations based on the sum of effects (Fig. 2a, b). Most populations showed positive and negative effects. A few of populations were dominated by effects in a single direction. For example, the effects for KWEI and KLEN in Zheng58H were both negative, while those for KWEI in Mo17H and KLEN in Duo229H were positive (Fig. 2a, b). Our results showed that the difference for kernel-related traits among inbred lines was not caused by only a gene of large effect, but by the cumulative effects of several QTL (Fig. 2a). We used the summed QTL effects to predict the parental difference for KWEI and KLEN and were able to accurately predict the parental difference with the R^2 of 0.80 and 0.75 for KWEI and KLEN, respectively (Fig. 2c, d).

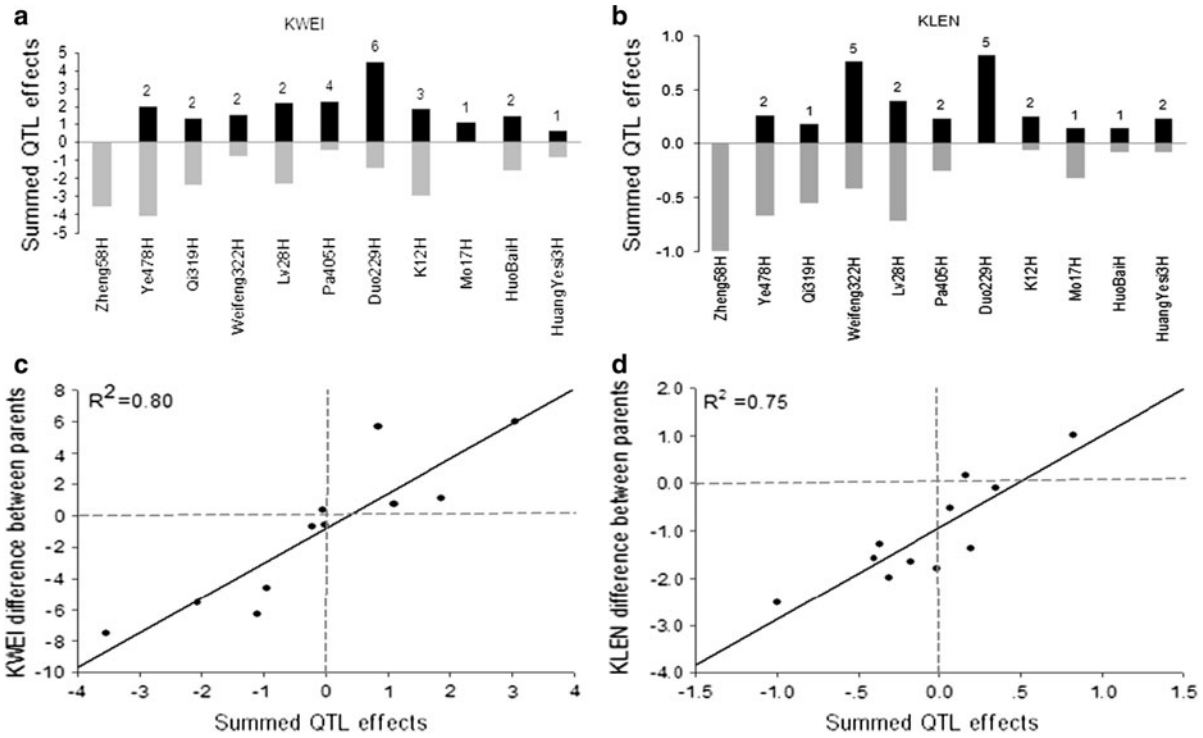

Fig. 2 Sums of the estimated additive positive (*black*) and negative (*grey*) QTL allele effects for 11 populations and predicted of parental kernel-related traits using summed QTL effects. **a** Sums of the estimated additive positive and negative QTL allele effects for 100-kernel weight (KWEI) in 11 populations, numbers indicate count of QTL. **b** Sums of the estimated additive positive and negative QTL allele effects for 10-kernel length (KLEN) in 11 populations, numbers indicate count of positive QTL. **c, d** Parental difference can be predicted from the summed QTL effects for KWEI and KLEN, respectively

Common QTL among all populations

For 146 major QTL detected for the five traits in 11 populations, 16 CQTL were obtained (Table 4). These CQTL were located on eight chromosomes, four on chrom. 4, three on each of chrom. 1 and 6, two on chrom. 5, and one on each of chrom. 2, 3, 7 and 9. On average, one CQTL covered 3.8 QTL with a range of from 3 to 7 for one to four traits.

Discussion

Comparison of QTL in the 11 connected populations

Quantitative trait loci (QTL) could be generally detected in a segregating population derived from two parental inbred lines. However, there have been many repetitive reports about the inconsistencies in QTL detection for the same trait among populations derived from different parents (Stuber et al. 1992; Austin et al. 2000) and different populations with the same cross (Li et al. 2007, 2009a, b). The effect of different genetic backgrounds may mainly cause inconsistent results on the QTL detection. In this study, the same parent Huangzaosi was used, the field management was identical and the same method was used to detect QTL. Although a total of 146 major QTL for five traits were detected in the 11 populations, no common QTL for a given trait were found in the same marker intervals across all populations. The great inconsistency across all populations in QTL detection could be mainly attributable to different genetic backgrounds. Previous studies also reported only poor to moderate QTL congruency for agronomic traits in different maize biparental mapping populations (Beavis et al. 1991; Melchinger et al.

Table 4 Common QTL identified among all populations

Common QTL[a]	Marker interval (cM)[b]	Bin	QTL number	Trait invovled/(population)
CQTL1-1	198.4–226.4	1.03	3	KWEI(Zheng58H), KLEN(Zheng58H), KWID(Huangyesi3H)
CQTL1-2	638.3–649.5	1.07	3	KLEN(Zheng58H, Pa405H, Mo17H)
CQTL1-3	927.9–950.2	1.10	5	KTHI(Zheng58H,Ye478H,Weifeng322H), KLEN(Lv28H), KWID(Qi319H)
CQTL2-1	401.5–416.6	2.06	4	GYPP(Qi319H), KTHI(Lv28H), KLEN(Qi319H), KWID(HuobaiH)
CQTL3-1	544.6–579.5	3.07	4	KTHI(Lv28H,HuobaiH), KWID(Lv28H,Weifeng322H)
CQTL4-1	158.8–158.8	4.03	5	KWEI(Ye478H,K12H), KLEN(Ye478H), KWID(Ye478H,K12H)
CQTL4-2	277.8–304.3	4.05	7	KWEI(HuobaiH,Duo229H,Lv28H), KTHI(HuobaiH), KWID(Qi319H,Duo229H,Lv28H)
CQTL4-3	535.5–559.0	4.08	4	KTHI(Lv28H), KLEN(Lv28H,Qi319H), KWID(Lv28H)
CQTL4-4	603.3–687.8	4.09	3	KWEI(Mo17H,K12H), KWID(K12H)
CQTL5-1	257.8–281.2	5.03	3	KWEI(K12H), KTHI(K12H), KWID(Mo17H)
CQTL5-2	590.4–590.4	5.07	3	KWEI(HuobaiH,Lv28H), KTHI(K12H)
CQTL6-1	98.4–125.0	6.01–6.02	4	KWEI(Duo229H), KTHI(Duo229H), KLEN(Weifeng322H), KWID(Duo229H)
CQTL6-2	521.9–548.7	6.07	3	KWEI(Weifeng322H,Qi319H), KTHI(Zheng58H)
CQTL6-3	448.5–504.8	6.07	3	KWEI(Weifeng322H,Qi319H), KWID(Pa405H)
CQTL7-1	247.7–258.4	7.02	3	KWEI(Ye478H), KTHI(K12H), KWID(Ye478H)
CQTL9-1	230.6–251.8	9.03	4	GYPP(HuobaiH), KWEI(Lv28H), KLEN(Lv28H,HuobaiH)

[a] Only common QTL that correspond to more than three QTL for five traits among elenve populations are shown. CQTL is the abbreviation of common QTL.The number infront of "-" stands for chromosome, and the number behind of "-" stands for the serial number of CQTL

[b] Marker interval refers to the position of QTL flanking markers on the IBM2 2008 Neighbors map

2004). Eighteen identical QTL across two or more populations were found in the same marker intervals, one QTL for GYPP in bin 9.03, five for KWEI in bin 4.03, 4.05, 4.05–4.06, 4.09 and 5.06–5.07, two for KTHI in bin 1.01 and 3.07, three for KLEN in bin 1.07, 4.08 and 9.03, and seven for KWID in bin 1.04, 1.11, 2.07, 3.07, 4.03, 4.05 and 10.07. Two QTL in bin 4.03 and 4.05 were common for kernel weight and kernel width in two populations. This suggested that kernel weight and kernel width may have common genetic basis at these loci, which were supported by significant phenotypic and genetic correlations in both of the populations. Compared with previous studies, the QTL for grain yield in bin 9.03 was also detected by Ajmone Marsan et al. (2001) in an $F_{3:4}$ population. Peng et al. (2011) also reported one QTL for KWEI in bin 4.05 in one $F_{2:3}$ and its testcross progenies, one QTL for KTIH in bin 1.10 in one $F_{2:3}$ and its testcross progenies and one QTL for KWID in bin 10.07 in one $F_{2:3}$ population. In particular, QTL for KWEI located in bin 4.09 were frequently detected by Melchinger et al. (1998) in one $F_{2:3}$ generation, Yan et al. (2006) in one $F_{2:3}$ population and Tang et al. (2010) in an immortalized F_2 population. These QTL might be important genomic region for controlling GYPP, KWEI and kernel size traits.

Various genetic backgrounds may affect the QTL detection, but different environments simultaneously influence most quantitative traits. Among the 146 major QTL, 71, 38, 20, 9, 8 and 0 QTL were detected in one, two, three, four, five and six environments, respectively. No QTL was detected in six environments and in joint analysis across all environments. Only 17 QTL were consistently detected in more than four environments and in joint analysis across six environments. Hence, this result indicated that natural environments had large influence on QTL detection for yield components and kernel-related traits. However, about 29 % and 71 % in 17 QTL were stably expressed for 100-kernel weight and kernel size traits, respectively. No QTL were detected for grain yield per plant stably expressed in different environments. This

suggested that it was much easier to detect QTL for kernel-related traits stably expressed across different environments than grain yield. Several previous studies also reported that QTL for grain yield was less stable than flowering traits, plant structure traits and kernel-related traits (Vargas et al. 2006; Lima et al. 2006; Peng et al. 2011). Several QTL stably expressed should be paid great attention to in the future studies and MAS. *Yqkwid7*, with the largest R^2 over 17 % in single environment, was located in bin 7.02. A QTL for kernel width stably expressed in four of six environments and in joint analysis across six environments, with the largest R^2 over 23 % in single environment, have also been found in the same bin 7.02 as *Yqkwid7* in a previous study using one $F_{2:3}$ population with the same parents (Huangzaosi and Ye478) (Peng et al. 2011). This major QTL had high consistency across various environments and generations. *Lqkwei4* and *Lqklen4-1* were both detected in four environments and in joint analysis across six environments, with the largest R^2 over 27 and 24 % in single environment, respectively. These two QTL were consistently located at the same bin 4.05 and favorable alleles derived from the parent Huangzaosi. These major QTL might deserve further study in fine mapping and in MAS.

Common QTL analysis and comparison with known QTL

The phenomenon of QTL clusters for yield component and kernel-related traits have been reported in some independent studies (Austin and Lee 1996; Lee and Austin 1998; Li et al. 2007; Veldboom and Lee 1994; Wang et al. 2007). This phenomenon could be explained genetically by QTL with pleiotropy or tight linkage in control of multiple association traits. The collocations of QTL for yield component and kernel-related traits were consistent with significant correlations among yield component and kernel-related traits. In maize, 53 of 80 (66 %) QTL for grain yield were co-localized with other yield components traits (Austin and Lee 1996). In this study, although the common QTL for yield component and kernel-related traits among the 11 populations were distributed on ten chromosomes, the majority of the QTL were clustered in 16 chromosomal intervals (Fig. 1). The 16 intervals (16 CQTL), located on chromosomes 1, 2, 3, 4, 5, 6, 7 and 9, respectively, were found to be involved in control of one trait from more than three populations or two or more of the above traits from different populations (Table 4). These CQTL with high co-localization might be hot genetic regions for important QTL of related traits. Some significant CQTL and their value for further understanding the genetic basis of maize yield components and kernel-related traits were discussed below.

CQTL1-2 (bin 1.07) mainly controlled KLEN in three populations. This region included Mqklen1 with the larger effect (16.2 %) and stable expression in five environments, both *Zqklen1-2* and *Pqklen1-2* with stable expression in two environments. Clearly, QTL located at this genomic region shared high congruence across different genetic backgrounds and environments. Other parents rather than Huangzaosi conferred the favorable alleles at this locus across different genetic backgrounds and all environments. Several authors have reported QTL for kernel weight in this region (Veldboom and Lee 1994; Austin and Lee 1996; Lee and Veldboom 1996; Goldman et al. 1994). No other report about kernel shape was found.

CQTL1-3 (bin 1.10) controlled a range of different kernel-related traits in five populations. Previous studies have shown the existence of a large QTL cluster associated with kernel-related traits in bin 1.10, including kernel weight (Melchinger et al. 1994, 1998), kernel density and 10-kernel thickness (Peng et al. 2011), and starch concentration and yield (Azanza et al.1996; Lübberstedt et al. 1997). In our common QTL analysis, Five QTL (*Zqkthi1*, *Yqkthi1-2*, *Wqkthi1*, *Lqklen1* and *Qqkwid1*) associated with kernel thickness, kernel length and kernel width were co-localized at position 927.9–950.2 cM based on the IBM2 2008 Neighbors map. Except for Lqklen1, other QTL involved favorable alleles from the same parent, Huangzaosi. It could be concluded that this region may be the presence of kernel trait-related genes.

CQTL4-1 (bin 4.03) controlled KWEI, KLEN and KWID and harbored five QTL in two mapping populations. Five QTL (*Yqkwei4*, *Yqklen4*, *Yqkwid4*, *Kqkwei4-1*, *Kqkwid4-1*) were co-localized at position 158.8 based on the IBM2 2008 Neighbors map. The significant phenotypic and genetic correlations could explain the QTL cluster between different kernel traits. Huangzaosi contributed the favorable alleles at this locus across different genetic background and all environments. In the B73/Mo17 mapping population, a QTL for grain yield was also found in this genomic

region (Smith et al. 1994). The region may be specific in some genetic backgrounds.

CQTL4-2 (bin 4.05) seems to be very important for the genetic control of different kernel traits with pleiotropic effects. The seven QTL (*HBqkwei4*, *Dqkwei4* and *Lqkwei4* conferring KWEI, *Qqkwid4*, *Dqkwid4* and *Lqkwid4-1* conferring KWID, and *HBqkthi4* conferring KTHI), were consistently co-localized at position 277.8–304.3 cM based on the IBM 2008 Neighbors map. The significant phenotypic and genetic correlations could explain the genetic overlap between different kernel traits (Table 3). In addition, two QTL (*HYqkwei4* and *HBqklen4*) were located in the adjacent marker interval. Both *Lqkwei4* and *Lqkwid4-1* were stably expressed in four environments. Huangzaosi contributed the favorable alleles at this locus across different genetic backgrounds and all environments. Peng et al. (2011) also identified a QTL cluster for 100-kernel weight and kernel length in bin 4.05 with two $F_{2:3}$ mapping populations. This genomic region may be a core cluster for QTL controlling different kernel-related traits. It should be paid great attention in further investigation and breeding.

CQTL4-3 (bin 4.08) controlled kernel shape and harbored four QTL in two mapping populations. Especially, three QTL (*Lqkthi4-2*, *Lqklen4-2* and *Lqkwid4-2*) were stably expressed in at least two environments in Lv28H. Clearly, this genomic region may be very important for the control of kernel shape in Lv28H. QTL for kernel weight were also identified to be located in bin 4.08 by other authors (Veldboom and Lee 1994; Lee and Veldboom 1996; Rocheford and Berke 1995).

CQTL4-4 (bin 4.09) controlled KWEI in K12H and Mo17H and KWID in K12H. Three QTL (*Kqkwei4-2*, *Mqkwei4* and *Kqkwid4-2*) were co-localized at position 603.3-687.8 cM based on the IBM2 2008 Neighbors map. Huangzaosi contributed the favorable alleles at this locus across different genetic background and all environments. Previous studies have mapped many QTL for kernel weight to bin 4.09 (Melchinger et al. 1998; Yan et al. 2006; Tang et al. 2010). *ZmGW2* for 100-kernel weight was mapped between markers bnlg292 and umc1173 in bin 4.09 (Li et al. 2010; Tang et al. 2010). The genomic region for KWEI and KWID found in the present study was located within marker bnlg292 and umc1173 interval.

CQTL6-1 (bin 6.01–6.02) controlled KWEI, KTHI and KWID in Duo229H and KLEN in Weifeng322H. Four QTL (*Dqkwei6*, *Dqkthi6*, *Dqkwid6* and *Wqklen6*) were co-localized at position 98.4–125.0 cM based on the IBM2 2008 Neighbors map. Two QTL, *Dqgypp6* and *Dqklen6*, were located in the near marker interval. Huangzaosi contributed the favorable alleles at this locus across different genetic backgrounds and all environments. Four QTL (*Dqkwei6*, *Dqkwid6*, *Dqgypp6* and *Dqklen6*) were stably expressed in at least two environments. Clearly, the locus was very important for Duo229H. Several authors reported QTL for grain yield in bin 6.02 (Ajnone-Marsan et al. 1995; Ribaut et al. 1997).

Conclusion

Grain yield related traits possess a highly complex genetic mechanism. The influence of different genetic background on QTL detection for grain yield traits was reflected in this study. QTL for kernel shape traits stably expressed in different populations could be detected relatively easier. Hence, genetic improvement for kernel shape traits can be implemented to increase grain yield indirectly. Based on our study, two QTL for 100-kernel weight and 10-kernel length showing high congruence across different genetic backgrounds and stably expressing in various environments can be chosen as target QTL for conducting fine QTL mapping and marker-assisted selection. QTL cluster for the same trait in different populations and for several traits in different populations were detected. We identified some new genetic regions controlling kernel-related traits when compared with previous studies. The great development of high-throughput genotyping and next generation sequencing will provide more information for dissecting the candidate genetic regions.

Acknowledgments This work was partly supported by grants provided by the Ministry of Science and Technology of China (2011CB100100, 2009CB118401), International Science and Technology Cooperation Program of China (2011DFA30450) and Natural Science Foundation of China (U1138304). We thank the help of Prof. Jiankang Wang and Dr. Huihui Li in the data analysis and of Dr. Bailin Li for technique advice.

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