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QTL Detection for Grain Water Relations and Genetic Correlations with Grain Matter Accumulation at Four Stages after Pollination in Maize

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Abstract

Grain water relations were closely correlated with matter accumulation during grain development. In this study, QTL mapping for Grain Water Content (GWC) at four stages after pollination and Grain Dehydration Rate (GDR) during six intervals were done using 258 Recombinant Inbred Lines (RIL). Meta-QTL (mQTL) was revealed by meta-analysis using Bio Mercator for both traits herein and together with seven traits related with grain matter accumulation in our previous research. Among 40 QTL detected for GWC and 35 QTL for GDR, 45 QTL were stage/period specific. QTL on chromosome 5 could be considered as full-stage QTL. Eight of 11 mQTL included QTL for both traits. Grain matter traits were positively correlated with GWC, but negatively correlated with GDR in most cases. Low coincidences in QTL position and opposite allelic effects for two kinds of traits suggested that their simultaneous improvement might be realized. Selection for low grain moisture could be focused on QTL at bins 1.07-1.08, 2.08, 4.03-4.04 and 5.03-5.04, while it should be followed to QTL at bins 7.02-7.03, 1.03-1.04 and 10.05-10.06 for high grain weight. However, this should be proved through practical selection, and the related marker intervals needed to be narrowed down in further research.

Keywords: Grain water relations; Grain matter accumulation traits; Genetic correlation; QTL detection; meta-QTL analysis

Introduction

Both dry-matter and water content of grain changes simultaneously during grain development after pollination in maize *Zea mays L.* Although several environmental factors had great influence on them [1,2], they were all genetically controlled quantitative traits with middle to high heritability [3-14]. According to the theory of developmental genetics, genes are expressed selectively at different growth stages [15] and the development of morphological traits occurs through the actions and interactions of many genes differentially expressed during growth periods [16]. Therefore, the genetic basis for dynamic traits should be revealed through major developmental stages.

For dry-matter, Quantitative Trait Loci (QTL) mapping for grain weight at harvest had been extensively conducted in previous research [17-27]. Recently, QTL for Grain Fresh Weight (GFW) and Grain Dry Weight (GDW) at several stages after pollination have been reported by Capelle et al. and Liu et al. [28,29]. Most QTL showed stage specificity in both research.

Grain Water Content (GWC) was closely correlated with dry-matter content [8]. In early developmental stages, grain accumulated more water than dry-matter. Therefore, grain water relations were good indicators of grain developmental progress during grain filling [30-32]. Besides, low GWC and high Grain Dehydration Rate (GDR) at harvest were very important for maize production in temperate regions (mid- to short-season areas, such as *Huanghuihai maize* belt in China), which could facilitate machinery harvest, shelling efficiency, grain quality and reduce additional drying cost and shrinkage penalties [28,33-36]. Previous research has shown that selection of inbred lines based on low ear-moisture content at a given date after pollination was an effective way to result in low grain moisture content at harvest for inbred lines and associated hybrids [37-39]. However, QTL mapping for grain water relations had been reported mostly for Grain Water Content at harvest [21,36,40-42]. Detected QTL for field grain drying rate from physiological maturity to grain harvest. Recently, QTL detection for three traits related with grain water relations at 30, 40, 60 and 80 Days After Pollination (DAP) was conducted by Capelle et al. [28] using intermitted recombinant $F_{3:4}$ population derived from cross between inbreeds F2 and F252. Obvious stage-specific QTL were revealed for all traits. Besides, there were no other records in the literature regarding QTL for GWC and GDR at different stages after pollination.

In this study, 258 Recombinant Inbred Lines (RIL) developed from a cross between two contrasting genotypes, a popcorn inbred N04 with small grain size and high GDR, and a dent inbred Dan 232 with large grain size and low GDR, was used to measure and detect QTL for GWC at four stages and for GDR during all periods. The same population had been used to map QTL for seven traits related with grain matter accumulation in our previous study [43]. Our main objectives in this study were to (1) reveal the phenotypic and QTL characteristics of GWC and GDR at different stages after pollination; (2) to compare the result of QTL detection for traits related with grain matter accumulation in our previous research to identify main genetic regions for grain development worthy of elucidation in further research and marker assisted selection (MAS) in maize.

Materials and Methods

Plant materials and field experiment

The population development used in this study and the field

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Table 1: Combined analysis of variances and heritabilities (h_B^2) for all traits, and their performance for two parents and in the RIL population.

Trait	Stages	Parents		RIL population									
		Dan232	N04	Range	Average	CV%	Skewness	Kurtosis	σ_g^2	σ_e^2	$\sigma_{g\times e}^2$	h_B^2	h_B^2CI on 95%
GWC [a]	10 DAP	88.09	81.91	80.16-88.94	84.39	1.78	-0.21	-0.06	4.32**	11.00**	1.63**	0.77	0.70-0.82
	20 DAP	70.36	51.30	44.33-70.23	59.83	6.37	0.13	0.58	7.78**	12.14**	1.97**	0.87	0.84-0.90
	30 DAP	50.81	30.93	31.29-54.24	42.75	9.74	0.23	-0.14	3.31**	57.68**	2.81**	0.70	0.61-0.76
	40 DAP	44.09	24.66	17.53-45.09	30.72	14.87	0.19	0.61	3.34**	18.04**	1.69**	0.70	0.62-0.77
GDR	12 DAP	1.77	3.06	1.65-2.97	2.45	11.34	-0.43	-0.20	4.26**	9.88**	1.54**	0.77	0.70-0.82
	13 DAP	1.86	2.55	1.57-2.70	2.08	8.53	-0.14	0.25	2.67**	41.78**	2.26**	0.63	0.52-0.71
	14 DAP	1.47	1.91	1.41-2.12	1.79	7.65	0.11	0.50	2.52**	23.94**	1.59**	0.60	0.49-0.69
	23 DAP	1.96	2.04	1.14-2.40	1.71	13.95	0.06	-0.08	1.34*	8.63**	1.99**	0.25	0.05-0.42
	24 DAP	1.31	1.33	0.99-1.97	1.45	12.12	0.24	0.37	1.96**	14.88**	1.52**	0.49	0.35-0.60
	34 DAP	0.67	0.63	0.34-2.23	1.18	27.64	0.58	1.01	1.26*	0.73	1.78**	0.21	0.02-0.38

Notes: * and ** indicate significances at 0.05 and 0.01 levels, respectively.
CI: Confidence Interval.
a GWC: Grain Water Content; GDR: Grain Dehydration Rate.

experiment has been described in our previous research [27,43]. Briefly, 258 F_9 RILs were derived from a cross between two contrasting inbred lines, Dan232 and N04 by single-seed descent method. The α-design with three-row plots and two replications was used to evaluate the RIL population and both parents at Zhengzhou, Henan, China in 2008 and 2009. All plants were self-pollinated within each plot by hand when more than 80% silks appeared.

Trait evaluation

Grain sample collections had been described by Li et al. [43]. At 10 DAP, 20 DAP, 30 DAP, and 40 DAP, three to five years with uniform grain sets were harvested and the kernels on the middle two third of each ear were shelled manually and bulked within plot. According to 100-Grain Fresh Weight (GFW) and 100-Grain Dry Weight (GDW), Grain Water Content (GWC, %) at four stages (10 DAP, 20 DAP, 30 DAP, and 40 DAP) were calculated as ((GFW-GDW)/GFW) ×100. Grain Dehydration Rate (GDR, %/d) were calculated for six DAP periods, including 10-20 DAP (WDR12), 10-30 DAP (WDR13), 10-40 DAP (WDR14), 20-30 DAP (WDR23), 20-40 DAP (WDR24) and 30-40 DAP (WDR34).

The measurements of seven traits related with grain matter accumulation had been described by Li et al. [43], including GFW, GDW, Grain-Filling Rate (GFR, g/d) during six periods, increasing rate in fresh weight (FWIR, g/d) for five periods, and the activities of three enzymes AGPP, GBSS and SSS at 30 DAP. Trait measurements averaged over the two replications were used as the preliminary data in further analysis.

Simple sequence repeat (SSR) analysis and map construction

The leaf tissues (< 2 weeks old) of five plants were collected and bulked for each entry. DNA was extracted using a CTAB procedure [44]. SSR analysis was conducted as reported in Senior and Heun [45].

A total of 723 SSR primer pairs, chosen from Maize GDB (http://www.maizegdb.org) for their uniform distribution throughout all ten maize chromosomes, were initially screened for their polymorphism between the two parents. Ultimately, 212 markers that clearly showed co-dominant segregation were used to genotype the 258 RIL families for which phenotypic data were available. Five SSR markers that showed serious segregation distortion were excluded from the analysis. Finally, 207 SSR markers were used to construct the linkage map with Join map 3.0b [46]. This linkage map covered 10 maize chromosomes with a total length of 2408.8 cM and an average interval of 11.6 cM [27,43].

Phenotypic data and QTL analysis

Phenotypic data and QTL analysis were conducted using the same methods as in Li et al. [43]. Briefly, the statistical software package SPSS12.0 was used to do variance analysis for each trait and correlation coefficients among traits. Heritability and the confidence intervals of the measured traits were computed according to Knapp et al. [47].

QTL mapping for each trait was conducted using Composite Interval Mapping (CIM) [48,49] according to model 6 of the *Zmapqtl* procedure in QTL Cartographer Version 2.5 [50]. An accurate significance threshold for each trait was identified through 1,000 permutations and chromosome -wise type I error/p value was set as 0.05 [51]. 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 Win QTL Cart [50].

Meta-QTL analysis with Bio Mercator

To integrate QTL information for GWC at four stages and GDR during six periods detected in this study, mQTL were identified by meta-analysis [52-54]. As reported by Li et al. and Li et al. [27,43], algorithms for meta-analysis were used to estimate the numbers and positions of meta-QTL (mQTL) using Bio Mercator 2.1 software [52,53]. According to data for multiple individual QTL, a modified *Akaike's Criterion* (AIC) was calculated for testing models in which how many meta-QTL existed. The model with the lowest statistic test was the most probable model. In each model, a confidence interval was calculated for each mQTL [55].

Results

Variance analysis, performance, heritability and correlation for GWC and GDR in RIL population

Except environment (σ_e^2) for WDR34, variances for genotype (σ_g^2), σ_e^2 and genotype × environment interactions (σ_{ge}^2) were significant for all traits (Table 1). Heritability estimates for GDR at 23 DAP and 34 DAP were low, but those for other traits were middle to high, with ranges from 0.49 to 0.87.

Both GWC and GDR showed similar patterns of decline after pollination for two parents and the RIL population, except WDR23 for both parents. All traits differed greatly between the two parents. The popcorn inbred N04 had lower values than the dent corn inbred Dan232 for GWC at all stages. But the reverse was for GDR during

Table 2: Phenotypic correlations among all traits according to the data in combined analysis.

Trait	Stage	GWC				GDR					
		10 DAP	20 DAP	30 DAP	40 DAP	12 DAP	13 DAP	14 DAP	23 DAP	24 DAP	34 DAP
GWC [a]	20 DAP	0.668**	1								
	30 DAP	0.563**	0.751**	1							
	40 DAP	0.459**	0.596**	0.686**	1						
GDR	12 DAP	-0.372**	-0.923**	-0.722**	-0.575**	1					
	13 DAP	-0.246**	-0.600**	-0.940**	-0.609**	0.683**	1				
	14 DAP	-0.150*	-0.422**	-0.563**	-0.947**	0.502**	0.591**	1			
	23 DAP	0.110	0.155*	-0.443**	-0.213**	-0.11	0.575**	0.270**	1		
	24 DAP	0.129*	0.185**	-0.096	-0.623**	-0.166*	0.159*	0.742**	0.408**	1	
	34 DAP	0.049	0.096	0.255**	-0.486**	-0.100	-0.280**	0.564**	-0.271**	0.720**	1

Notes: * and ** indicate significances at 0.05 and 0.01 levels, respectively.
[a] GWC: Grain Water Content; GDR: Grain Dehydration Rate.

Table 3: QTL detected for GWC at four stages and GDR during six periods under two environments and in combined analysis.

Trait	Environment	Stage	QTL	Marker interval	Bin loci [a]	Position	LOD [b]	R^2 (%)[c]	A[d]
GWC [e]	2008	10 DAP	q8GWC10-1-1	bnlg1007-umc1403	1.02-1.03	49.11	3.85	7.81	-0.45
			q8GWC10-1-2	bnlg1556-phi039	1.07-1.08	263.21	3.26	7.86	0.45
			q8GWC10-3-1	umc1489-umc1844	3.07-3.08	30.01	3.20	4.96	0.36
			q8GWC10-5-1	umc1389-umc1162	5.03-5.04	110.71	6.67	11.08	0.54
			q8GWC10-8-1	umc1360-umc1741	8.02- 8.03	79.91	4.92	7.28	0.43
		20 DAP	q8GWC20-1-1	umc1976-bnlg1803	1.02	32.51	5.14	8.26	-1.13
			q8GWC20-1-2	bnlg1556-phi039	1.07-1.08	267.21	5.07	12.98	1.41
			q8GWC20-3-1	umc2277-umc1052	3.08- 3.09	95.41	3.15	4.47	-0.83
			q8GWC20-4-1	nc005-bnlg1265	4.05	98.71	3.27	4.33	0.83
			q8GWC20-5-1	bnlg1287-umc2111	5.04	124.61	9.64	18.69	1.70
		30 DAP	q8GWC30-4-1	umc1964-bnlg1621	4.05	109.01	3.66	7.42	1.23
			q8GWC30-5-1	umc1389-umc1162	5.03-5.04	112.71	8.08	13.39	1.68
			q8GWC30-5-2	bnlg1346-bnlg2305	5.07	212.91	3.82	7.27	1.24
		40 DAP	q8GWC40-5-1	umc1389-umc1162	5.03-5.04	110.71	4.88	9.12	1.61
			q8GWC40-5-2	bnlg2305-umc1225	5.07-5.08	228.21	3.23	9.20	1.61
	2009	10 DAP	q9GWC10-1-1	umc1976-bnlg1803	1.02	30.51	3.05	5.25	-0.40
			q9GWC10-5-1	bnlg565-phi109188	5.02-5.03	69.41	3.03	11.24	0.60
			q9GWC10-5-2	bnlg1287-umc2111	5.04	122.61	3.25	6.49	0.45
		20 DAP	q9GWC20-1-1	bnlg1007-umc1403	1.02-1.03	51.11	3.27	7.77	-1.12
			q9GWC20-1-1	umc2083-umc1281	1.05- 1.06	205.71	5.30	8.59	1.17
			q9GWC20-4-1	bnlg1126-umc1117	4.03-4.04	77.71	4.28	10.37	1.29
			q9GWC20-5-1	umc1389-umc1162	5.03-5.04	112.71	4.04	6.80	1.06
		30 DAP	q9GWC30-4-1	nc005-bnlg1265	4.05	98.71	3.91	6.09	1.30
			q9GWC30-5-1	umc1389-umc1162	5.03-5.04	110.71	4.32	8.06	1.49
			q9GWC30-5-2	bnlg1346-bnlg2305	5.07	212.91	3.45	6.69	1.34
			q9GWC30-9-1	phi065-umc2337	9.03	98.51	4.15	6.67	-1.34
		40 DAP	q9GWC40-2-1	mmc0381-umc1992	2.08	233.51	3.31	6.00	1.29
			q9GWC40-5-1	umc1389-umc1162	5.03-5.04	106.71	3.66	7.32	1.40
	Combined	10 DAP	qcGWC10-1-1	umc1976-bnlg1803	1.02	30.51	5.31	8.63	-0.45
			qcGWC10-3-1	umc1489-umc1844	3.07- 3.08	30.01	4.13	6.39	0.38
			qcGWC10-5-1	bnlg1287-umc2111	5.04	122.61	5.19	10.21	0.49
		20 DAP	qcGWC20-1-1	umc1976-bnlg1803	1.02	30.51	5.96	9.57	-1.19
			qcGWC20-1-2	umc2083-umc1281	1.05- 1.06	205.71	5.34	8.21	1.10
			qcGWC20-4-1	bnlg1621-bnlg1189	4.06-4.07	137.71	3.77	11.37	1.29
			qcGWC20-5-1	bnlg1287-umc2111	5.04	122.61	6.15	10.98	1.28
			qcGWC20-5-1	bnlg1346-bnlg2305	5.07	214.91	3.43	5.66	0.92
		30 DAP	qcGWC30-4-1	bnlg1126-umc1117	4.03-4.04	77.71	4.74	10.99	1.40
			qcGWC30-5-1	umc1389-umc1162	5.03-5.04	110.71	6.80	11.78	1.46
			qcGWC30-5-2	bnlg1346-bnlg2305	5.07	212.91	4.26	7.73	1.18
		40 DAP	qcGWC40-5-1	umc1389-umc1162	5.03-5.04	110.71	4.36	8.31	1.33
GDR	2008	12 DAP	q8GDR12-1-1	umc1245-dupssr12	1.07-1.08	290.71	3.11	5.03	-0.07
			q8GDR12-4-1	bnlg1126-umc1117	4.03-4.04	77.71	3.36	8.80	-0.10
			q8GDR12-5-1	bnlg1287-umc2111	5.04	124.61	4.80	10.58	-0.11
			q8GDR12-5-2	bnlg1346-bnlg2305	5.07	212.91	4.28	8.76	-0.10

		13 DAP	q8GDR13-4-1	nc005-bnlg1265	4.05	96.71	3.58	5.93	-0.05
			q8GDR13-5-1	umc1389-umc1162	5.03-5.04	112.71	4.95	8.33	-0.06
			q8GDR13-5-2	bnlg1346-bnlg2305	5.07	210.91	5.25	10.72	-0.07
		14 DAP	q8GDR14-2-1	bnlg1940-umc2214	2.08-2.1	262.11	3.24	14.11	-0.06
			q8GDR14-5-1	umc1389-umc1162	5.03-5.04	110.71	3.52	7.08	-0.04
			q8GDR14-5-2	bnlg2305-umc1225	5.07-5.08	230.21	3.80	11.57	-0.06
		24 DAP	q8GDR24-7-1	umc1409-phi057	7.01	52.01	3.13	6.52	-0.06
	2009	12 DAP	q9GDR12-1-1	umc1976-bnlg1803	1.02	199.81	7.19	13.32	-0.11
			q9GDR12-4-1	umc1964-bnlg1621	4.05	111.01	3.53	7.69	-0.09
		13 DAP	q9GDR13-2-1	umc1042-dupssr25	2.07- 2.08	214.71	3.21	5.80	-0.05
			q9GDR13-4-1	nc005-bnlg1265	4.05	98.71	4.64	7.64	-0.06
			q9GDR13-5-1	bnlg1346-bnlg2305	5.07	212.91	3.83	7.83	-0.06
			q9GDR13-9-1	phi065-umc2337	9.03	96.51	3.88	6.11	0.06
		14 DAP	q9GDR14-2-1	mmc0381-umc1992	2.08	233.51	3.46	6.57	-0.04
		23 DAP	q9GDR23-2-1	bnlg1940-umc2214	2.08	260.11	0.97	4.66	0.08
			q9GDR23-5-1	dupssr28-umc1313	4.08-4.09	196.01	2.88	7.69	-0.10
		34 DAP	q9GDR34-9-1	phi065-umc2337	9.03	98.51	2.89	5.96	-0.13
	Combined	12 DAP	qcGDR12-1-1	umc2083-umc1281	1.05- 1.06	205.71	3.82	6.44	-0.08
			qcGDR12-4-1	umc1964-bnlg1621	4.05	111.01	3.70	8.88	-0.09
			qcGDR12-5-1	bnlg1287-umc2111	5.04	122.61	3.18	6.34	-0.08
			qcGDR12-5-2	bnlg1346-bnlg2305	5.07	212.91	3.17	5.93	-0.08
		13 DAP	qcGDR13-4-1	nc005-bnlg1265	4.05	96.71	7.01	11.01	-0.06
			qcGDR13-5-1	umc1389-umc1162	5.03-5.04	110.71	4.22	7.48	-0.05
			qcGDR13-5-2	bnlg2305-umc1225	5.07-5.08	228.21	4.25	11.42	-0.06
			qcGDR13-9-1	phi065-umc2337	9.03	98.51	3.54	5.56	0.04
		14 DAP	qcGDR14-2-1	mmc0381-umc1992	2.08	235.51	3.88	7.06	-0.04
			qcGDR14-2-2	bnlg1940-umc2214	2.08-2.1	262.11	3.60	14.97	-0.05
		23 DAP	qcGDR23-2-1	umc1042-dupssr25	2.07- 2.08	214.71	3.21	6.15	-0.07
		24 DAP	qcGDR23-2-1	mmc0381-umc1992	2.08	235.51	3.88	7.07	-0.05
		34 DAP	qcGDR24-2-1	mmc0381-umc1992	2.08	233.51	3.77	7.39	-0.12
			qcGDR34-4-1	umc1313-bnlg589	4.09-4.1	225.61	2.83	7.86	0.10

[a] Bin locations for the flanking markers.
[b] LOD, The Likelihood Odds Ratio.
[c] R2, percent of phenotypic variance explained by each QTL.
[d] The additive effects of QTL, positive values indicated that alleles from Dan 232 increased the trait scores.
[e] GWC: Grain Water Content; GDR: Grain Dehydration Rate.

most periods except 34 DAP. According to the values of skewness and kurtosis, all traits showed normal distributions and transgressive segregations exceeding both parent values in the RIL population. The variance coefficients (CV%) were high in most cases, from 1.78% for GWC at 10 DAP to 27.64% for WDR34.

For correlations among traits, almost the same tendency was observed for data in 2008, 2009 and in combined analysis. According to the result in combined analysis (Table 2), all significant positive correlations were shown among GWC at four stages and among GDR except early (12 DAP) and late periods (34 DAP). But most negative correlations were observed between GWC and GDR, especially GWC at 40 DAP with GDR during all periods, and GWC at other three stages with GDR during 12 DAP, 13 DAP and 14 DAP periods. Positive correlations were observed in four cases, GWC at 10 DAP with WDR24, GWC at 20 DAP with WDR23 and WDR24, and GWC at 30 DAP with WDR34.

QTL identification for GWC at four stages after pollination and GDR during six periods

According to the significant σ_{ge}^2 for both traits in all cases, QTL mapping was conducted for data under each environment. Combined analyses using means across the two environments were also conducted for comparison (Table 3). A total of 40 QTL were detected for GWC at four stages, which were located on chromosomes 1, 3, 4, 5, 8 and 9. Individual QTL explained phenotypic variance from 4.96% to 18.69%, with 11 QTL over 10% and only one QTL over 15%. N04 contributed the positive alleles of eight QTL located at bins 1.02 and 1.02-1.03, and of all QTL on chromosomes 3 and 9. The QTL on chromosome 5 was consistently detected at all stages both under each environment and in combined analysis. They were located on three marker intervals at bins 5.03-5.04, 5.04 and 5.07. QTL on chromosome 1 were detected at 10 DAP and 20 DAP under all cases, which were related with six bins, 1.02, 1.02-1.03, 1.05-1.06 and 1.07-1.08. QTL on chromosome 4 were detected at 20 DAP and 30 DAP under five cases, which were related with five bins, 4.03-4.04, 4.05 and 4.06-4.07. On chromosome 3 QTL were detected at 10 DAP and 20 DAP in 2009 and at 10 DAP in combined analysis. Both QTL on chromosomes 8 and 9 were only detected in one case, at 10 DAP and 30 DAP, respectively.

For GDR, a total of 35 QTL were detected during six periods, which were located on chromosomes 1, 2, 4, 5, 7 and 9. Individual QTL explained phenotypic variance from 4.66% to 14.97%, with eight QTL over 10% and none QTL over 15%. N04 contributed the positive alleles of 31 QTL, while Dan232 contributed those of other four QTL. No QTL were detected consistently under all cases. Three QTL on chromosome 1 and three QTL on chromosome 9 were all detected during only one period, 12 DAP or 13 DAP. Nine QTL on chromosome 2 and 12 QTL on chromosome 5 were all related with four periods, 13 DAP, 14 DAP, 23 DAP and 24 DAP, and 12 DAP, 13 DAP, 14 DAP and 23 DAP. Seven

Table 4: Meta-QTL identified by meta-analysis for GWC at four stages and GDR during six periods under two environments and in combined analysis.

mQTL	AIC [a]	Position (cM)	Confidence interval (cM)	Adjacent marker	Bin	QTL number	Related trait	QTL integrated [b]
mQTL1-1	118.02	30.75	24.85-36.65	umc1568-bnlg1007	1.02	4	GWC	q8GWC2-1-1, q9GWC1-1-1, qcGWC1-1-1, qcGWC2-1-1
mQTL1-2	118.02	50.64	39.14-62.14	bnlg1803-phi001	1.02-1.03	2	GWC	q8GWC1-1-1, q9GWC2-1-1
mQTL1-3	118.02	203.1	197.98-208.23	umc1906-umc1281	1.05-1.06	4	GWC, GDR	q9GWC2-1-2, qcGWC2-1-2, q9GDR12-1-1, qcGDR12-1-1
mQTL1-4	118.02	273.46	262.14-284.78	bnlg1556-umc1245	1.07	2	GWC	q8GWC1-1-2, q8GWC2-1-2
mQTL2-1	78.64	230.26	224.79-235.74	dupssr24-mmc0381	2.08	5	GWC, GDR	q9GWC4-2-1,q9GDR14-2-1, qcGDR14-2-1, qcGDR24-2-1, qcGDR34-2-1
mQTL2-2	78.64	262.01	257.14-266.88	bnlg1940-umc2214	2.08-2.10	3	GDR	q8GDR14-2-1, q9GDR23-2-1, qcGDR14-2-2
mQTL3-1	21.91	30.01	20.96-39.06	umc2118-bnlg1647	3.0-3.02	2	GWC	qcGWC1-3-1,q8GWC1-3-1
mQTL4-1	134.55	77.71	71.58-83.84	bnlg1126-umc1117	4.02-4.04	3	GWC, GDR	q9GWC2-4-1, qcGWC3-4-1, q8GDR12-4-1
mQTL4-2	134.55	102.34	97.79-106.9	nc005-bnlg1621	4.05-4.06	3	GWC, GDR	q8GWC2-4-1, q9GWC3-4-1, q9GDR13-4-1
mQTL5-1	260.93	114.74	112.12-117.37	umc1389-umc2111	5.03-5.05	3	GWC, GDR	q8GDR13-5-1,q9GWC2-5-1,q8GWC3-5-1
mQTL5-2	260.93	212.95	209.13-216.77	bnlg1346-bnlg2305	5.07	8	GWC, GDR	q8GWC3-5-2, q9GWC3-5-2, qcGWC2-5-2, qcGWC3-5-2, q8GDR12-5-2, q8GDR13-5-2, q9GDR13-5-1, qcGDR12-5-2
mQTL5-3	260.93	229.05	223.29-234.81	bnlg2305-umc1225	5.07-5.08	3	GWC, GDR	q8GWC4-5-2, q8GDR14-5-2, qcGDR13-5-2
mQTL9-1	26.13	98.09	90.4-105.78	umc1267-umc2121	9.03-9.04	4	GWC, GDR	q9GWC3-9-1, q9GDR13-9-1, q9GDR34-9-1, qcGDR13-9-1

[a] AIC: Akaike's Criterion.
[b] GWC: Grain Water Content; GDR: Grain Dehydration Rate.

QTL on chromosome 4 were related with three periods, 12 DAP, 13 DAP and 34 DAP. One QTL on chromosome 7 were detected during 24 DAP.

Digenic epistasis among QTL for GWC and GDR

For both traits in all cases, 29 pairs of digenic interactions were identified, 15 and 14 pairs for GWC, GDR, respectively (data not shown). Phenotypic variance explained by the interaction between marker intervals umc2275-umc1844 and umc2275-umc1273 at the same bin 3.07-3.08 for WDR23 was 12.6%. But the contribution values of other digenic interactions were all low, ranging from 0.1% to 5.7%. These results suggested that the contributions of digenic interactions to GWC and GDR were minimal.

Meta-QTL analysis for GWC and GDR under all cases

Considering 75 QTL for GWC at four stages and GDR during six periods detected in this study, 13 distinct QTL clusters (mQTL) were found (Table 4). Forty-six QTL were located in those cluster regions, accounting for 61.33%. Fifteen QTL for GWC and 14 QTL for GDR failed to be integrated. These mQTL were located on six chromosomes, four, three, two, two, one and one on chromosomes 1, 5, 2, 4, 3 and 9, respectively. One meta-QTL included 3.54 QTL on average, with a variation between 1 and 8 QTL. mQTL1-1, mQTL1-2, mQTL1-4, mQTL3-1 included QTL only for GWC, while only QTL for GDR were included in mQTL2-2. Other eight mQTL included QTL for both traits.

Four mQTL on chromosome 1 and mQTL3-1 included QTL for both traits at early stages/periods (GWC at 10 DAP and 20 DAP, and GDR during 12 DAP). mQTL4-1, mQTL4-2, mQTL5-1 and mQTL5-2 included QTL for both traits at middle stages/periods (GWC at 20 DAP and 30 DAP, and GDR during 12 DAP and 13 DAP). mQTL2-2 and mQTL9-1 included QTL for both traits at middle to late stages/periods (GWC at 30 DAP, and GDR during 13 DAP, 23 DAP, 14 DAP and 34 DAP). mQTL2-1 and mQTL5-3 included QTL for both traits at late stages/periods (GWC at 40 DAP, and GDR during 13 DAP, 14 DAP, 24 DAP and 34 DAP).

Correlation and meta-QTL analysis for two traits herein and seven traits related with grain matter accumulation in our previous research

Using the same RIL population, the performance and QTL detection for seven traits related with grain matter accumulation had been revealed in our previous research, including GFW and GDW at four stages, GFR during six periods, FWIR during five periods, and the activities of three enzymes AGPP, GBSS and SSS at 30 DAP [43]. Their phenotypic correlations with GWC and GDR showed positive correlations with GWC in most cases (69/88), but negative correlations with GDR in most cases (82/132) (Table 5). Particularly, GWC at four stages were positively correlated with GDW at 40 DAP, GFR during 14 DAP, 23 DAP, 24 DAP and 34 DAP, GFW at four stages, FWIR during all five periods, and the activities of AGPP and SSS. But GDR34 was negatively correlated with GDW at four stages, GFR during 12 DAP, 13 DAP, 14 DAP and 23 DAP, GFW at 10 DAP, 30 DAP and 40 DAP, FWIR during 10 DAP, 13 DAP, 14 DAP and 23 DAP.

In our previous research, 161 QTL had been detected for six traits related with grain matter accumulation, including GDW, GFW, GFR, FWIR, AGPP and SSS. Simultaneously considering 75 QTL for GWC and GDR herein, and 161 QTL for six traits before, 11 distinct QTL clusters (mQTL) were found (Table 6). Ninety-four QTL (accounting for 39.83%) were located in those cluster regions, which included 14 QTL for two traits herein (5 QTL for GWC, 9 QTL for GDR) and 80 QTL for six traits before (22 QTL both for GDW and GFW, 20 QTL for GFR, 14 QTL for FWIR, and one QTL both for AGPP and SSS). Correspondingly, 61 QTL and 81 QTL failed to be integrated.

These mQTL were located on six chromosomes, three on chromosomes 1, two on chromosomes 2, 3 and 7, and one on chromosome 9 and 10. One meta-QTL included 8.55 QTL on average, with a variation between 2 and 32 QTL. mQTL1-3, mQTL2-1 and mQTL2-1 included QTL only for two traits herein, while only QTL for six traits before were included in mQTL1-1, mQTL3-1, mQTL7-1, mQTL7-2 and mQTL10-1. Three mQTL (mQTL1-2, mQTL3-2 and mQTL9-1) included QTL both for two traits herein and for six traits before. The positive alleles of three QTL included in mQTL3-2 were

Table 5: Phenotypic correlations between GWC and GDR with seven traits related with grain matter accumulation according to the data in 2008.

Trait [a]	GDW10	GDW20	GDW30	GDW40	GFR12	GFR13	GFR14	GFR23	GFR24	GFR34	SSS
GWC10	-0.273**	0.01	0.197**	0.258**	0.067	0.235**	0.283**	0.309**	0.307**	0.141*	0.177**
GWC20	-0.086	-0.130*	0.097	0.249**	-0.130*	0.109	0.258**	0.261**	0.360**	0.222**	0.213**
GWC30	-0.182**	-0.07	0.087	0.321**	-0.042	0.109	0.340**	0.197**	0.432**	0.410**	0.261**
GWC40	-0.013	0.094	0.300**	0.498**	0.107	0.315**	0.511**	0.410**	0.595**	0.415**	0.199**
GDR12	-0.013	0.157*	-0.043	-0.245**	0.179**	-0.044	-0.247**	-0.198**	-0.372**	-0.277**	-0.171**
GDR13	0.091	0.082	-0.02	-0.270**	0.075	-0.03	-0.282**	-0.104	-0.379**	-0.422**	-0.223**
GDR14	-0.08	-0.088	-0.254**	-0.461**	-0.081	-0.258**	-0.467**	-0.342**	-0.551**	-0.410**	-0.157*
GDR23	0.116	-0.056	0.039	-0.074	-0.086	0.029	-0.086	0.108	-0.082	-0.224**	-0.115
GDR 24	-0.052	-0.172**	-0.213**	-0.349**	-0.183**	-0.217**	-0.354**	-0.192**	-0.364**	-0.281**	-0.06
GDR34	-0.184**	-0.186**	-0.280**	-0.316**	-0.171**	-0.275**	-0.311**	-0.298**	-0.316**	-0.115	0.012
GWC10	0.313**	0.395**	0.391**	0.331**	0.313**	0.370**	0.350**	0.280**	0.183**	0.164**	0.079
GWC20	0.304**	0.450**	0.383**	0.356**	0.304**	0.409**	0.341**	0.311**	0.101	0.152*	0.085
GWC30	0.149*	0.370**	0.454**	0.441**	0.149*	0.424**	0.479**	0.447**	0.293**	0.258**	0.147*
GWC40	0.259**	0.426**	0.538**	0.697**	0.259**	0.445**	0.541**	0.702**	0.413**	0.154*	0.151*
GDR12	-0.228**	-0.362**	-0.328**	-0.345**	-0.228**	-0.367**	-0.301**	-0.318**	-0.068	-0.104	-0.065
GDR13	-0.056	-0.274**	-0.372**	-0.381**	-0.056	-0.344**	-0.414**	-0.407**	-0.266**	-0.225**	-0.132*
GDR14	-0.172**	-0.326**	-0.450**	-0.649**	-0.172**	-0.355**	-0.468**	-0.673**	-0.389**	-0.114	-0.133*
GDR23	0.170**	0.033	-0.126*	-0.115	0.170**	-0.052	-0.205**	-0.176**	-0.267**	-0.198**	-0.101
GDR 24	0.013	-0.061	-0.223**	-0.456**	0.013	-0.091	-0.268**	-0.512**	-0.342**	-0.052	-0.074
GDR34	-0.157*	-0.118	-0.166*	-0.394**	-0.157*	-0.081	-0.144*	-0.394**	-0.167*	0.088	-0.005

[a] AGPP, ADP-Glc pyrophosphorylase; GBSS: Granule-Bound Starch Synthase; GDW: 100-grain dry weight; GFR: Grain-Filling Rate; GFW: 100-Grain Fresh Weight; GWC: Grain Water Content; FWIR: Increasing Rate In Fresh Weight; SSS: Soluble Starch Synthase; GDR: Grain Dehydration Rate.

Table 6: Meta-QTL identified by meta-analysis for two traits in this study and GDW, GFW, GFR, FWIR, GWC, GDR, AGPP and SSS using the same populations in our previous research.

mQTL	AIC [a]	Position	C.I.(cM)	Adjacent marker	Bin locus	Trait	QTL integrated	QTL integrated [b]
mQTL1-1	486.47	131.07	129.91-132.24	phi001-umc2227	1.03-1.04	GFR,GFW, GDW,FWIR	11	qcGFR14-1-1,qcGFW40-1-1,qcGFW30-1-1,qcGDW40-1-1,qcGDW30-1-1,q9FWIR14-1-1,q9FWIR13-1-1,q9GFR34-1-1,q9GFR13-1-1,q9GFW30-1-1,q9GDW30-1-1
mQTL1-2	486.47	201.5	198.74-204.26	umc1906-umc1281	1.05-1.06	FWIR,GFW,GDR	8	q8FWIR10-1-2,qcFWIR12-1-1,qcGFW20-1-1,q9GDR12-1-1,q9FWIR12-1-1,q8FWIR12-1-1,q9GFW20-1-1,q8GFW20-1-1
mQTL1-3	486.47	268.57	262.14-274.99	bnlg1556-phi039	1.07-1.08	GWC	2	q8GWC20-1-2,q8GWC10-1-2
mQTL2-1	87.56	230.55	224.98-236.13	dupssr24-mmc0381	2.08	GDR,GWC	5	qcGDR23-2-1,qcGDR14-2-1,qcGDR24-2-1,q9GDR14-2-1,q9GWC40-2-1
mQTL2-2	87.56	262.01	257.14-266.88	bnlg1940-umc2214	2.08-2.10	GDR	3	q9GDR23-2-1,qcGDR14-2-2,q8GDR14-2-1
mQTL3-1	57.14	38.61	32.25-44.96	umc2049-bnlg1647	3.01-3.02	GFR,GDW	2	q9GFR12-3-1,q9GDW20-3-1
mQTL3-2	57.14	89.7	76.75-102.66	umc2258-umc1773	3.02-3.04	GFR,GWC,GFW	3	q8GFR24-3-1,q8GWC20-3-1,q9GFW20-3-1
mQTL7-1	412.47	18.24	13.11-23.37	bnlg2233-umc1068	7.02	FWIR,GFR,GFW	3	q8FWIR10-7-1,qcGFR24-7-1,q8GFW10-7-1
mQTL7-2	412.47	75.59	74.5-76.69	umc2057-umc1567	7.02-7.03	GDW,AGPP, SSS,GFW, GFR,FWIR	32	q8GDW30-7-1,q8GDW40-7-1,qAGPP30-7-1,qSSS30-7-1,q9GDW20-7-1,q9GDW30-7-1,q8GFW20-7-1,q8GFW40-7-1,q9GFW10-7-1,q9GFW20-7-1,q9GFW30-7-1,q9GFW40-7-1,q8GFR14-7-1,q8GFR24-7-1,q9GFR12-7-1,q9GFR13-7-1,q8FWIR13-7-1,q8FWIR14-7-1,q9FWIR12-7-1,qcGDW10-7-1,qcGDW20-7-1,qcGDW30-7-1,qcGDW40-7-1,qcGFW10-7-1,qcGFW20-7-1,qcGFW30-7-1,qcGFW40-7-1,qcGFR12-7-1,qcGFR13-7-1,qcGFR14-7-1,qcGFR23-7-1,qcFWIR10-7-1
mQTL9-1	55.39	102.47	96.63-108.31	umc2337-umc2121	9.03-9.04	GDR,GWC,FWIR, GFW,GDW	5	qcGDR13-9-1,q9GWC30-9-1,q9FWIR10-9-1,q9GFW10-9-1,q9GDW10-9-1
mQTL10-1	235.19	75.62	73.51-77.73	umc1677-umc2122	10.05-10.06	FWIR,GFR, GDW,GFW	20	q9FWIR10-10-1,q9GFR13-10-1,q9GFR12-10-1,q8GFR12-10-1,q9GDW30-10-1,q9GDW20-10-1,q9GDW10-10-1,qcFWIR10-10-1,qcGFR12-10-1,qcGFW10-10-1,qcGDW30-10-1,qcGDW-20-10-1,qcGDW10-10-1,q9GFW20-10-1,q9GFW10-10-1,q8GDW20-10-1,qcGFR13-10-1,qcGDW40-10-1,qcGFR14-10-2,q9GDW40-10-1

[a] AIC: Akaike's criterion.
[b] AGPP: ADP-Glc Pyrophosphorylase; GDW: 100-Grain Dry Weight; GFR: Grain-Filling Rate; GFW: 100-Grain Fresh Weight; GWC: Grain Water Content; FWIR: Increasing Rate In Fresh Weight; SSS: Soluble Starch Synthase; GDR: Grain Dehydration Rate.

all contributed by inbred N04. But for mQTL1-2 and mQTL9-1, N04 contributed the positive alleles of QTL for GWC or GDR, those for traits before were all contributed by inbred Dan232.

Discussion

Correlations among GWC and GDR at different stages

In previous research, several stages/periods for GWC, GDR and grain weight were rarely measured simultaneously. Few reports for correlations among different traits and among different stages/periods for a single trait could be found [35]. Considered that drying rate influenced hybrid grain moisture at harvest. A negative correlation between late-season drying rate and grain moisture at harvest was reported by Kang and Zuber [56]. Selection of inbred lines based on low GWC at early stages has been proved effective in reducing GWC at harvest [37-39].

In this study, all significant positive correlations were observed for GWC among four stages and for GDR among periods with overlapping stages. For correlations between GWC and GDR, negative correlations were observed between GWC at four stages and GDR during 12 DAP, 13 DAP and 14 DAP and between GWC40 and GDR during all six periods. For GDR during the latest period (34 DAP), insignificant correlations with GWC at 10 DAP and 20 DAP, and positive correlation with GWC at 30 DAP were obtained. Therefore, GWC at late stage could be predicted according to data at any early stages, which had been proved through selection of inbred lines and their crosses [37-39]. But GDR at late period could only be predicted according to periods with overlapping stages. High GDR during all periods was beneficial for low GWC at late stage.

In breeding, direct evaluation for GWC and GDR is labor-intensive and unpractical in large-scale selection [35]. Although kernel physiology, such as endosperm type, osmotic diffusion pressure of the kernels, and pericarp thickness was shown to be associated with drying rate [10,57-59], evaluation of these physiological traits was also labor intensive. In addition, selection for these traits could reduce kernel quality [35]. According to the evaluation of S_2 lines selected via four morphological traits (date of husk senescence, husk length, kernel number, and silking date) and their crosses, Sweeney et al. [35] considered that selection for early husk senescence in the inbreeds decreased grain moisture by 27 g/kg, hastened physiological maturity, and increased lodging in the associated hybrids with no effect on yield. Selection for the other three traits had no significant effect on grain moisture at harvest. Accordingly, they suggested that selection for early husk senescence in inbreeds would result in hybrids with low grain moisture and that evaluation of husk senescence might be useful in monitoring maturity. But effective morphological traits for indirect selection of low grain moisture had not been reported under the same maturity condition. MAS could be tried in case major QTL for GWC and GDR and their effective linking markers were obtained.

Stage-specific QTL and comparison with QTL detected in previous research

In this study, 75 QTL were detected for GWC at four stages and GDR during six periods after pollination. According to QTL detected at different stages/periods and the result of mQTL analysis, those QTL could be clarified into four kinds: early stage, middle-to-late stage, late stage and full stage QTL. Seventeen QTL on chromosomes 1, 3 and 8 could be considered as early stage QTL, which were related with GWC at 10 DAP and 20 DAP, and GDR during 12 DAP. Seventeen QTL on chromosomes 4 and 9 included QTL for GWC at 20 DAP and 30 DAP, and GDR during 12 DAP, 13 DAP and 34 DAP, which could be considered as middle-to-late stage QTL. QTL on chromosome 2 were late stage QTL, which related with GWC at 40 DAP, and GDR during 13 DAP, 14 DAP, 23 DAP and 24 DAP. QTL for GWC at all stages, and for GDR during 12 DAP, 13 DAP, 14 DAP and 23 DAP were all detected on chromosome 5, which could be considered as full stage QTL. Overall, 45 QTL were stage or period specific, accounted for 60%.

In the report of QTL mapping for three traits related with grain water relations at 30, 40, 60 and 80 Days After Pollination (DAP) by Capelle et al. [28], 12, 4 and 3 QTL were detected for Water, Slope and Rate, respectively. No full-stage QTL were revealed for all traits. Even no common QTL across two stages were found. Much more stage-specific QTL were also shown for grain weight and grain filling rate in our previous study using the same population as in this study [43] and other research by Liu et al. [29]. This tendency was consistent with the theory of developmental genetics [15,16]. Therefore, genes selectively expressed during trait development could only be detected at specific stages.

Comparing with previous research in QTL detection for grain water relations, slope and rate at 30 and 40 DAP studied by Capelle et al. [28] could be considered as similar traits as in this study. But they used thermal time scales 300 and 400 degree × day for calculation. QTL for Slope 1, 2, 3 and 4 were detected at bins 2.04, 2.06, 3.04 and 4.03, respectively. QTL for Rate were only detected at bins 2.06 and 7.05 during 34 DAP, and at bin 3.03 during 46 DAP. In comparison with QTL detected for grain moisture at harvest in previous research by Austin et al., Sala et al., Beavis et al., Melchinger et al., Mihaljevic et al. and Ragot et al. [21,36,40-42,60], QTL on chromosome 5 were all detected except [41], and QTL on chromosomes 1 and 2 were all detected except [36]. QTL for field grain drying rate from physiological maturity to grain harvest were detected on chromosome 5. This was consistent with that QTL detected on chromosomes 2 and 5 in our present study were full stage or middle-to-late stage QTL. However, early-to-middle stage QTL on chromosome 4 herein were only detected by Austin et al. and Melchinger et al. [21,41]. Therefore, QTL detected on chromosomes 1, 2, and 5 in our present study could be considered as objective QTL in further research and MAS, especially QTL on chromosome 5. Actually, QTL with explained phenotypic variance over 10% were all related with chromosomes 1, 2, 4 and 5, accounting for 10.53%, 10.53%, 21.05%, and 57.89% of total 19 QTL, respectively.

Correlations between grain water relations and traits related with grain matter accumulation

Previous research had showed that GWC were not independent of grain weight or grain yield [28]. Positive correlations between grain yield and GWC at harvest have been reported in several research [8,32,61-63] found that maximum grain weight could be predicted from maximum GWC occurring at 40 to 60 DAP in maize hybrids grown at three densities.

In this present study, most positive correlations between GWC with seven traits related with grain matter accumulation, and most negative correlations between GDR with those traits were obtained, especially for GWC at the latest stage and for GDR during the latest period. Obviously, direct selection for low GWC and high GDR at late stage/period would result in decrease in grain weight at final stage, although this was favorable for maize production in temperate regions [28,33-38]. To obtain hybrids with low GWC and high GDR at harvest in such areas, increase in grain weight might be limited. Improvement in grain yield should be obtained through increase in grain numbers per ear

and per area. However, Capelle et al. [28] considered that the yield/moisture ratio at maturity was variable enough to allow selection for both high yield and low moisture at harvest [64-66] has successfully applied recurrent selection for reduction of kernel moisture by the introduction of tropical germplasm into temperate-a DAPted germplasm. So, correlation between grain yield and moisture at harvest might vary among different germplasms, high yield and low moisture might be realized through extensive selection.

According to the result of QTL detection for individual trait, QTL were detected on chromosomes 1, 2, 3, 4, 5, 7 and 9 for both kinds of traits. But the numbers of QTL located on chromosomes 1, 2, 4 and 7 were greatly different, 13, 10, 13 and 1 for two traits herein, and 43, 1, 2 and 54 for six traits before. In addition, 28 QTL were detected on chromosome 10 for six traits before, while no QTL were detected for two traits herein. The popcorn parent N04 contributed the positive alleles of QTL for the activities of AGPP and SSS, and most ones of QTL for GDR (33/37). The dent corn parent Dan232 contributed the positive alleles of most QTL for other traits (175/199). Among 11 mQTL obtained from meta-analysis for eight traits (GWC, GDR, GFW, GDW, GFR, FWIR, AGPP, and SSS), only three mQTL (mQTL1-2, mQTL3-2 and mQTL9-1) included QTL both for two traits herein and for six traits before. Obviously, both low coincidences in QTL position and opposite allelic effects for two traits related with grain water relations herein and for traits related with grain matter accumulation, suggested that simultaneous improvement in high grain weight and low grain moisture might be realized through MAS. In this RIL population, selection for grain weight should be focused on QTL at three bins 7.02-7.03, 1.03-1.04 and 10.05-10.06 [43], while selection for grain moisture could be followed to QTL located on chromosomes 1, 2, 4 and 5, especially at bins on 1.07-1.08, 2.08, 4.03-4.04 and 5.03-5.04. However, the result should be proved through practical selection, and the related marker intervals needed to be narrowed down in further research.

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