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ORIGINAL ARTICLE

Identification and stability of QTLs for grain traits in the elite wheat variety 'Chuanmai104'

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Abstract

Chuanmai104 (CM104), an elite wheat (*Triticum aestivum* L.) variety that currently produces the highest yield per unit area in southwestern China, plays a critical role in wheat production. The high quality and stability of grain traits are important factors that ensure the high, stable yields of CM104 in different production areas. In this study, six grain traits of CM104 sampled from 19 environments in five provinces of China during 2018–2022 were evaluated. The traits comprised thousand-kernel weight, grain length, grain width, grain length–width ratio, grain circumference, and grain surface area. Fifteen quantitative trait loci (QTLs) associated with the grain traits were identified based on a recombinant inbred lines (F_{9-10}) population derived from the cross between CM104 and the landrace Baimaomai (BMM), nine and six QTLs derived from CM104 and BMM, respectively. Three mainly pleiotropic QTLs derived from CM104, namely QTL10 (grain circumference, grain surface area), QTL11 (grain length, grain circumference), and QTL12 (grain length, grain circumference), were expressed significantly and stably in multiple environments, and explained 3.34–5.06%, 5.32–6.50%, and 6.00–12.13% of the phenotypic variation, respectively. The pyramiding of multiple genes is hypothesized to have contributed to the stability of the CM104 grain traits in different environments. The results provide a basis for future improvement of yield and its stability in wheat.

Keywords Quantitative trait loci · Grain traits · Linkage map · Stability

Introduction

Wheat is an economically important crop that is a major energy and nutrient source for humans. Against the background of a growing global population and climate change, human food demands are increasing rapidly. Wheat breeders are currently focused on developing varieties with high and stable yields to meet the increase in food demand (Eltaher et al. 2021). However, it is difficult to increase wheat yields quickly, which jeopardizes future food security (Li et al. 2016).

Previous studies have indicated that wheat yield is mainly determined by three traits: spike number per area, kernels per spike, and thousand-kernel weight (TKW) (Yang et al. 2016). Thousand-kernel weight is mainly controlled by grain morphology and grain-filling degree (Okamoto et al. 2013). Generally, grain morphology mainly affects TKW through grain length (GL), grain width (GW), grain length–width ratio (GR), grain circumference (GC), and grain surface area (GSA), and ultimately impacts on wheat yield (Wang et al. 2012; Gao et al. 2021; Cristina et al. 2016; Liu et al. 2017).

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Therefore, research on grain morphology has important applications for improvement of the grain weight in wheat. Identification of the key genes associated with grain morphology is crucial for further improvement of wheat yield. Many quantitative trait loci (QTLs) that contribute to grain morphology or grain weight traits have been identified in durum wheat (Varshney et al. 2000) and in hexaploid wheat distributed on all 21 chromosomes Huang et al. 2003 and 2006; Li et al. 2022; Williams et al., 2014; Okamoto et al. 2013; Patil et al. 2013; Simmonds et al. 2014; Zhang et al. 2015; Kumar et al. 2019; Cabral et al. 2018; Liu et al. 2017). Some of the genes that influence grain morphology have been cloned. For instance, *TaGW2* negatively regulates wheat GW and TKW (Su et al. 2011; Wang et al. 2018). The gene *DA1-RELATED 1* (*TaDA1*) is a negative regulator of grain size and can interact with *TaGW2* to affect grain weight in wheat (Liu et al. 2020). *TaPGS1* is a transcription factor that regulates wheat grain size and grain weight. Overexpression of *TaPGS1* significantly increases grain weight, GL, and GW. Further investigation showed that *TaPGS1* binding to the *FI3* promoter to knockdown *FI3* expression significantly reduces grain weight, GL, and GW (Guo et al. 2022). In addition, many genes, such as *TaCKX*, *TaGS5*, *TaAGP-L*, *TaSDIR1*, *TaCYP78A3*, *TaGS3*, *TaGW7*, and *TaGW8*, have been confirmed to be involved in the regulation of wheat grain morphology or grain weight (Jabłoński et al. 2020; Wang et al. 2015, 2020; Zhang et al. 2019; Ma et al. 2015, 2017; Zhang et al. 2019; Yan et al. 2019).

Chuanmai104 (CM104), an elite synthetic hexaploid wheat-derived variety bred by the Crop Research Institute, Sichuan Academy of Agricultural Sciences, exhibits numerous desirable traits, including high yield, good grain quality, broad adaptability, and resistance to stripe rust, powdery mildew, and pre-harvest sprouting under the unique ecological conditions of Sichuan Province in China (Li et al. 2014). From 2010 to 2020, CM104 consistently maintained the highest yield increase recorded in the southwestern China wheat production region, and set a record yield of 10,947 kg per hectare for southwestern China in 2020. Recently, CM104 has been widely used as an elite breeding material in the wheat breeding program in southwestern China, and a total of 21 varieties are derived from CM104 in this growing region (Liu et al. 2021). However, the genetic mechanism for the high and stable yield of CM104 remains uncertain.

In this study, CM104 grains were sampled in different years and from different regions to analyze the genetic basis for the high yield and its stability. The grain morphology and grain weight phenotypes were recorded for a population of 251 recombination inbred lines (RILs; F_{9-10}) derived from the cross of CM104 and the wheat landrace Baimaomai (BMM) grown in three environments. The results provide a foundation for analysis of the genetic mechanism for the high yield and stability of CM104, and provide valuable information for pyramiding of multiple genes associated with grain traits for future improvement of wheat varieties.

Materials and methods

Plant materials and mapping population

Nineteen samples of CM104 grains were collected from five provinces in China during 2018–2022, and three BMM samples were collected from Sichuan in 2021–2022 (Fig. 1**,** Table 1). Recombination inbred lines were derived from the cross between CM104 and BMM (Fig. 2), comprising 251 RILs-F_9 (2021) and RILs-F_{10} (2022) lines. The RILs were grown at Guanghan in 2021 (2021GH) and 2022 (2022GH), and at Shifang in 2022 (2022SF). Approximately 30 seeds of each line were uniformly sown in a single 1-m-long row with 25 cm spacing between rows. Standard field management practices were applied.

Evaluation of grain traits and statistical analysis

Thousand-kernel weight, GL, GW, grain length–width ratio (GR), GC, and GSA of each accession from different environments were recorded using an automatic seed test analyzer (Mini1600, Jie Lai Mei Technology Co., Ltd., Chengdu, China). Regression analysis of the CM104 grain traits was performed with Excel software (Microsoft, Redmond, WA, USA). The correlations among the grain traits were analyzed using the two-tailed Pearson method implemented in IBM SPSS Statistics 25 (IBM Corporation, Armonk, NY, USA). Analysis of variance (ANOVA) was conducted, and then, the accessions were ranked with Duncan's test and plotted using GraphPad Prism V8.0.2.263. R software (i386 4.1.0) and the lme4

Fig. 1 CM104 grain samples collection location in 2018–2022

Table 1 CM104 and BMM planting environment and year

Accessions	Years	City	Province	Group	Environments
CM104	2018	Chongzhou	Sichuan	SC	2018_CZ
	2021	Guanghan	Sichuan	SC	2021_GH
	2022	Guanghan	Sichuan	SC	2022_GH
	2022	Jiangyou	Sichuan	SC	2022_JY
	2022	Langzhong	Sichuan	SC	2022_LZ
	2022	Mianyang	Sichuan	SC	2022_MY
	2022	Neijiang	Sichuan	SC	2022_NJ
	2022	Pixian	Sichuan	SC	2022_PX
	2022	Shifang	Sichuan	SC	2022_SF
	2022	Shehong	Sichuan	SC	2022_SH
	2022	Shunqing	Sichuan	SC	2022_SQ
	2022	Xindu	Sichuan	SC	2022_XD
	2022	Yilong	Sichuan	SC	2022_YL
	2022	Zhongjiang	Sichuan	SC	2022_ZJ
	2022	Guiyang	Guizhou	SC	2022_GY
	2022	Jingmen	Hubei	SW	2022_JM
	2022	Lijiang	Yunnan	SW	2022_LJ
	2022	Zhengzhou	Henan	SW	2022_ZZ
	2022	Xinxiang	Henan	SW	2022_XX
BMM	2021	Guanghan	Sichuan		2021_GH
	2022	Guanghan	Sichuan		2022_GH
	2022	Shifang	Sichuan		2022_SF

package were used to calculate the broad-sense heritability (H^2; Smith et al. 1998) of the wheat grain traits. High-quality images of wheat grains were captured with a Leica M205 FA stereomicroscope (Leica, Germany).

QTL mapping

Genotyping of the CM104 × BMM RILs was performed using the wheat 50 K SNP (single nucleotide polymorphism) genotyping array developed by CapitalBio Corporation (Beijing, China) and synthesized by Affymetrix (California, America). In a previous study, we constructed genetic linkage maps with 3779 polymorphic SNP markers (Liu et al. 2017). The QTL analysis was conducted with inclusive composite interval mapping using GAHP software (Zhang et al. 2022). The QTLs were mapped at a logarithm of odds threshold of 4 based on 1000 permutations and a walking speed of 1.0 cM, with $P = 0.001$ in a stepwise regression. The QTL effects were estimated as the proportion of phenotypic variance explained by the QTL. The QTLs for a trait with identical, overlapping, or adjacent marker intervals in a linkage group were treated as identical and given a common name. Only QTLs identified in two or three environments were considered. The physical distance between the marker interval of a QTL was analyzed using the International Wheat Genome Sequencing Consortium (http://www.wheatgenome.org/) and EnsemblPlants (http://plants.ensembl.org/info/website/ftp/index.html) databases based on the flanking sequences.

Results

Phenotypic variation and diversity analysis

Nineteen samples of CM104 grains from different environments in China were collected to evaluate phenotypic variation in grain morphology and grain weight (Table 2). Of

Fig. 2 Comparison of grain phenotype of Baimaomai and Chuanmai104

Table 2 Phenotypic performance of CM104 in diverse environments for thousand-kernel weight (TKW), grain length (GL), grain width (GW), grain length–width ratio (GR), grain circumference (GC), and grain surface area (GSA). The environment is designated by the trait, year, and location

Accessions	TKW	GL	GW	GR	GC	GSA
CM104-2018CZ	46.02	7.00 ± 0.80	3.64 ± 0.48	1.96 ± 0.32	17.92 ± 1.71	18.80 ± 3.65
CM104-2021GH	46.47	7.02 ± 0.43	3.66 ± 0.37	1.93 ± 0.20	17.89 ± 1.18	18.89 ± 2.77
CM104-2022GH	42.88	7.07 ± 0.58	3.64 ± 0.40	1.96 ± 0.18	17.86 ± 1.48	18.63 ± 3.21
CM104-2022JY	59.62	7.55 ± 0.30	4.02 ± 0.22	1.88 ± 0.12	19.30 ± 0.71	22.40 ± 1.73
CM104-2022LZ	47.33	7.19 ± 0.57	3.73 ± 0.37	1.94 ± 0.17	18.24 ± 1.52	19.64 ± 3.21
CM104-2022MY	55.23	7.32 ± 0.40	3.96 ± 0.26	1.86 ± 0.14	18.85 ± 0.90	21.54 ± 2.12
CM104-2022NJ	55.52	7.71 ± 0.63	3.69 ± 0.45	2.11 ± 0.20	19.29 ± 1.69	20.89 ± 3.72
CM104-2022PX	45.16	7.05 ± 0.51	3.59 ± 0.45	1.98 ± 0.21	17.79 ± 1.51	18.55 ± 3.45
CM104-2022SF	52.57	7.27 ± 0.54	3.83 ± 0.42	1.91 ± 0.18	18.57 ± 1.53	20.64 ± 3.57
CM104-2022SH	40.12	7.04 ± 0.54	3.48 ± 0.46	2.05 ± 0.24	17.65 ± 1.63	18.02 ± 3.46
CM104-2022SQQ	40.26	7.12 ± 0.40	3.43 ± 0.35	2.09 ± 0.20	17.74 ± 1.06	17.88 ± 2.50
CM104-2022XD	48.34	7.19 ± 0.50	3.75 ± 0.38	1.93 ± 0.16	18.22 ± 1.40	19.81 ± 3.26
CM104-2022YL	44.79	7.19 ± 0.66	3.66 ± 0.48	1.99 ± 0.25	18.23 ± 1.72	19.29 ± 3.81
CM104-2022ZJ	50.60	7.46 ± 0.34	3.93 ± 0.21	1.90 ± 0.10	19.02 ± 0.87	21.71 ± 1.85
CM104-2022GZ	30.93	6.97 ± 0.54	3.12 ± 0.42	2.26 ± 0.25	17.01 ± 1.38	15.56 ± 2.75
CM104-2022JM	44.56	7.01 ± 0.47	3.60 ± 0.36	1.96 ± 0.17	17.71 ± 1.22	18.56 ± 2.85
CM104-2022LJ	31.16	6.78 ± 0.23	3.33 ± 0.33	2.05 ± 0.20	16.92 ± 0.69	16.34 ± 1.92
CM104-2022ZZ	37.86	7.28 ± 0.44	3.27 ± 0.41	2.25 ± 0.22	17.88 ± 1.36	17.37 ± 2.49
CM104-2022XX	51.14	7.22 ± 0.53	3.81 ± 0.41	1.91 ± 0.12	18.47 ± 1.64	20.49 ± 3.42

these samples, 14 samples were harvested in Sichuan Province during 2018–2022 (SC group) and five samples were harvested outside Sichuan Province in 2022 (SW group) (Fig. 3). Differences in the means for the grain morphology and grain weight traits between the SC and SW groups were analyzed by performing an ANOVA. The TKW, GW, GC, and GSA traits in the SC group were significantly higher than those in the SW group ($P < 0.05$; Fig. 3a), suggesting that Sichuan is the most suitable production zone for CM104. Furthermore, ANOVA and a regression analysis were used to evaluate the stability of the grain morphology and grain weight traits. Two CM104 samples (2018CZ and 2021GH) were compared with 12 CM104 samples collected in 2022 from different environments in Sichuan Province, but no significant differences were observed between the two groups (Fig. 3b).

Regression analysis showed that the grain morphology and grain weight traits of CM104 grown in Sichuan Province

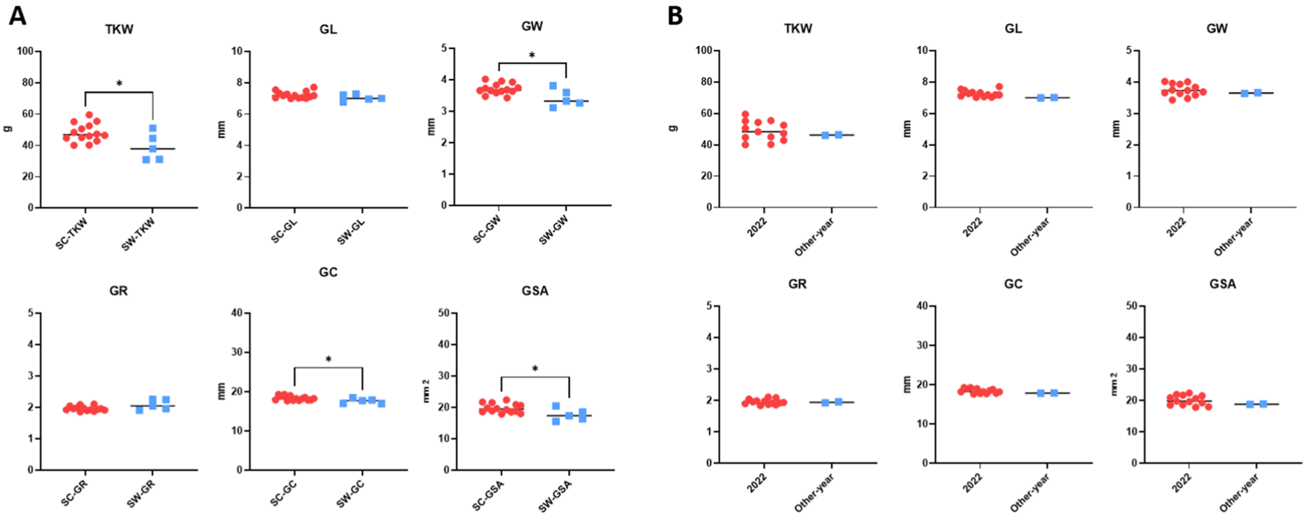


Fig. 3 Variance analysis of grain morphology and grain weight traits in CM104 in multiple environments. **a** the grain phenotypes were compared between groups Sichuan (SC) and outside Sichuan (SW); **b** the grain phenotypes were compared between groups 2022 and other years (2018 and 2021). *means $P < 0.05$

were highly stable. A highly significant correlation was observed between grain morphology and grain weight traits for all 14 environments ($R^2 = 0.88$–0.95; Fig. 4).

QTL mapping of grain traits

Among the three environments for the RILs, significant differences in TKW, GL, GC, and GSA between CM104 and BMM were observed ($P < 0.05$; Fig. 5a). The frequency distributions of the investigated traits revealed continuous variation in the RILs population, suggesting that the phenotypic data for the four grain traits were normally distributed and these traits were controlled by multiple QTLs (Fig. 5b).

The estimated H^2 values for TKW, GL, GC, and GSA were greater than 0.5 (range 0.52–0.84) (Table 3). Thus, it was assumed that the traits were influenced by genetic factors. Pearson correlation coefficients for the four grain morphologies and grain weight traits in the three environments ranged from 0.58 to 0.96 (Fig. 6).

In the three environments, 15 QTLs were identified for GC, GL, GSA, and TKW. Three detected QTLs for TKW explained 6.08–6.84% of the phenotypic variation, 11 QTLs for grain morphology explained 3.35–12.13%, and one QTL for GSA

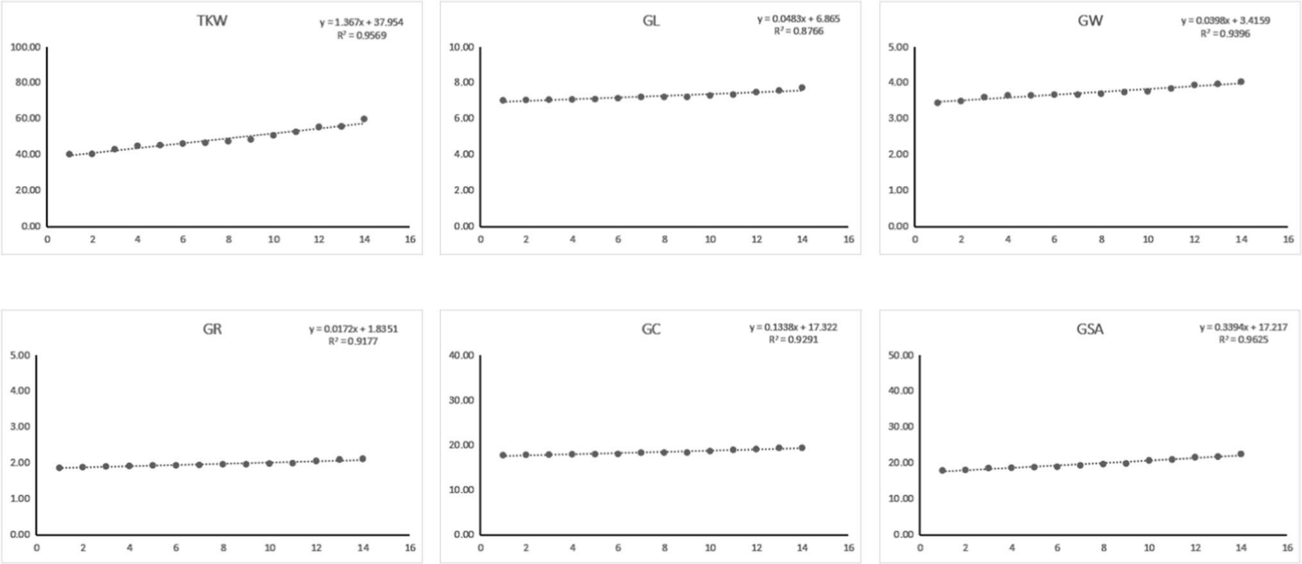


Fig. 4 Regression analysis of grain morphology and grain weight traits in CM104 in Sichuan during 2018–2022

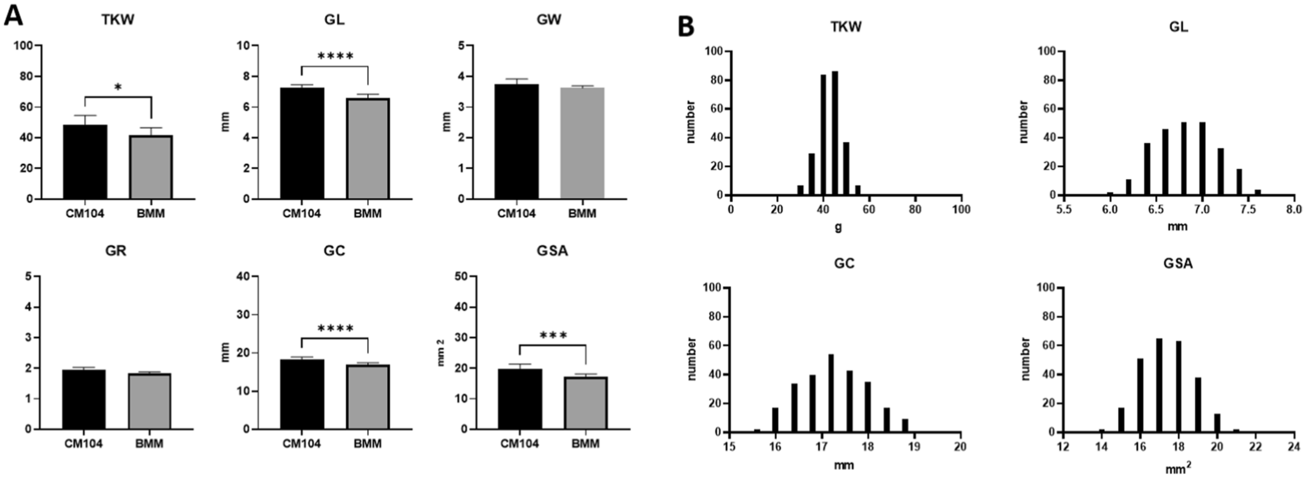


Fig. 5 Grain phenotypes were analyzed in RILs populations and parents. A) variance analysis of grain morphology and grain weight traits in CM104 and BMM; B) phenotypic distribution for TKW, GL, GC, and GSA in CM104XBMM RILs populations. *means $P < 0.05$, ***means $P < 0.001$, ****means $P < 0.0001$

Table 3 Grain phenotype of the parents and RILs in this study. H^2 broad-sense heritability

Environments	Types	Accessions	TKW (g) Min	TKW (g) Max	TKW (g) Mean	TKW (g) H^2	GL (mm) Min	GL (mm) Max	GL (mm) Mean	GL (mm) H^2	GW (mm) Min	GW (mm) Max	GW (mm) Mean	GW (mm) H^2	GR Min	GR Max	GR Mean	GR H^2	GC (mm) Min	GC (mm) Max	GC (mm) Mean	GC (mm) H^2	GSA (mm^2) Min	GSA (mm^2) Max	GSA (mm^2) Mean	GSA (mm^2) H^2
2021GH	parents	CM104	43.53	49.40	46.67	0.52	6.89	7.15	7.02	0.84	3.57	3.75	3.66		1.92	1.94	1.93		17.50	18.27	17.89	0.80	18.14	19.63	18.88	0.69
		BMM	40.32	43.14	41.73		6.54	6.54	6.54		3.57	3.71	3.64		1.78	1.84	1.81		16.75	17.02	16.88		16.86	17.31	17.05	
	population	RILs	29.04	87.75	42.76		6.04	7.70	6.83		3.03	4.02	3.52		1.66	2.35	1.96		15.54	19.25	17.27		13.89	22.57	17.36	
2022GH	parents	CM104	40.17	56.80	46.87		7.00	7.46	7.19		3.46	4.09	3.77		1.83	2.06	1.92		17.56	19.34	18.28		17.62	22.90	19.96	
		BMM	36.14	43.80	39.38		6.27	6.79	6.52		3.55	3.63	3.58	0.27	1.77	1.88	1.83	0.86	16.21	17.25	16.74		15.83	17.71	17.00	
	population	RILs	17.00	53.74	38.03		5.77	7.93	6.87		2.73	3.92	3.44		1.66	2.43	2.02		14.60	19.56	17.23		11.45	21.60	17.06	
2022SF	parents	CM104	52.57	53.22	52.89		7.21	7.23	7.22		3.80	3.84	3.82		1.82	1.90	1.90		18.48	18.49	18.84		20.28	20.72	20.50	
		BMM	37.67	50.81	44.24		6.42	6.99	6.70		3.55	3.72	3.63		1.89	1.91	1.86		16.48	17.82	17.15		16.13	18.87	17.50	
	population	RILs	22.52	62.90	47.88		6.13	7.96	7.10		2.82	4.04	3.64		1.68	2.34	1.96		15.06	19.93	17.97		12.51	23.28	19.01	

and TKW explained 4.33–5.35%. Three stable putative QTLs (QTL10, QTL11, and QTL12) for grain morphology associated with GC, GL, and GSA were detected in this study. These QTLs were located on chromosomes 5B and 5D, and explained 3.35–12.13% of the phenotypic variation (Table 4, Fig. 7). The additive effect of the individual QTLs indicated that CM104-positive alleles contributed to the three traits.

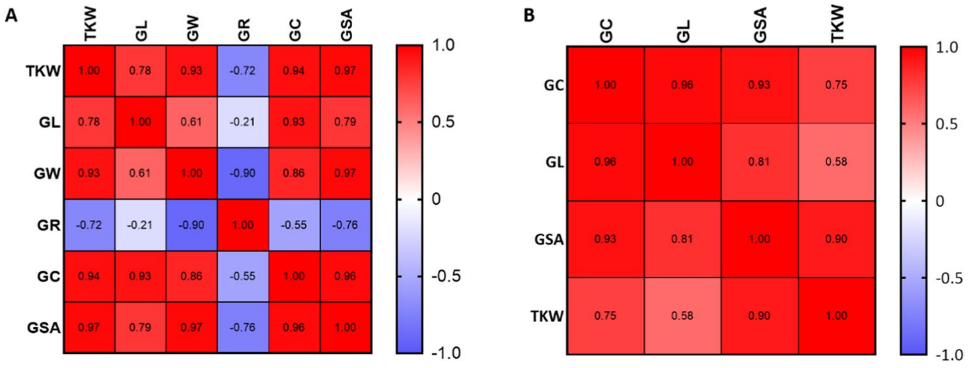
Discussion

Grain traits of CM104 showed high stability in different environments

Thousand-kernel weight is positively correlated with grain morphology and is an important trait owing to its phenotypic stability and high heritability (Kuchel et al. 2007). Selection for a higher TKW has been conducted during domestication, and therefore, it has been argued that the grain morphology of cereals is a component of the domestication syndrome (Brown et al. 2009). Larger grains generally favor TKW, seedling vigor, and flour yield characteristics (Chastain et al. 1995). Stable wheat production is crucial to global food security (Macholdt and Honermeier 2017). Many factors, such as the phenotypic stability of wheat varieties and genotype × environment interactions, affect wheat yield to different extents (Nielsen and Vigil 2018). Regression analysis and ANOVA are widely used to evaluate the relationship between wheat yield and environment (Chen et al. 2018; Pepó and Győri 2005; Ayalneh et al. 2014; van Frank et al. 2020; Ji et al. 2023). In the present study, CM104 samples were collected from different environments; grain traits in the SC group were significantly higher than those in the SW group. The highest TKW was recorded in the 2022_JY sample (59.62 g/1000 grains), which indicated that JY was the most suitable production location for CM104. As the highest yielding wheat variety grown in Sichuan, CM104 exhibits its broad adaptability and stable high yield. However, its adaptability is generally poor outside of Sichuan Province, with the exception of the 2022_XX sample (51.14 g/1000 grains) in Henan Province, which suggested that CM104 can maintain favorable grain traits in specific environments. Correlation analysis showed that the TKW of CM104 was positively correlated with GL, GW, GC, and GSA, but was negatively correlated with GR (Fig. 6). This result indicated that modern breeders prefer rounded seeds, consistent with previous findings (Cheng et al. 2020; Zhang et al. 2022).

Stable QTLs associated with grain morphology and grain weight traits

Grain morphology and grain weight are complex quantitative traits, and are influenced by many main and micro-effect QTLs (Slafer et al. 2014). In previous studies, more



A

	TKW	GL	GW	GR	GC	GSA
TKW	1.00	0.78	0.93	-0.72	0.94	0.97
GL	0.78	1.00	0.61	-0.21	0.93	0.79
GW	0.93	0.61	1.00	-0.90	0.86	0.97
GR	-0.72	-0.21	-0.90	1.00	-0.55	-0.76
GC	0.94	0.93	0.86	-0.55	1.00	0.96
GSA	0.97	0.79	0.97	-0.76	0.96	1.00

B

	GC	GL	GSA	TKW
GC	1.00	0.96	0.93	0.75
GL	0.96	1.00	0.81	0.58
GSA	0.93	0.81	1.00	0.90
TKW	0.75	0.58	0.90	1.00

Fig. 6 Pearson's correlation coefficients (r) between thousand-kernel weight (TKW), grain length (GL), grain width (GW), grain length–width ratio (GR), grain circumference (GC), and grain surface area (GSA). **a** Grain phenotypic correlation analysis of CM104 was performed in nineteen environments; **b** grain phenotypic correlation analysis of CM104 × BMM RILs population in three environments

than 100 QTLs for TKW, GL, GW, GC, and GSA in wheat have been identified and are distributed on all 21 chromosomes. In addition, wheat TKW is significantly positively correlated with grain morphology, and many QTLs associated with grain morphology have been co-localized with TKW QTLs (Börner et al., 2002; Huang et al. 2003; Huang et al. 2006; Li et al. 2022; Williams et al., 2014; Okamoto et al. 2013; Simmonds et al. 2014; Zhang et al. 2015; Kumar et al. 2019; Cabral et al. 2018; Liu et al. 2017). However, many QTLs for grain morphology are not detectable in different environments and explain only a small proportion of the phenotypic variation for grain weight. Taken together, these factors mean that such QTLs are unsuitable for use in marker-assisted selection for wheat breeding. However, such QTLs are strongly affected by the environment and not all major QTLs are repeatedly detected in all environments (Akram et al., 2020; Li et al. 2019; Suliman et al. 2021; Alemu et al. 2020; White et al. 2022; Gao et al. 2021). Therefore, molecular marker-assisted breeding for wheat grain traits is challenging. The present RIL populations were used for QTL analysis in multiple environments, which is a beneficial approach for breeding to select loci that can be detected in different environments. The present study detected 15 QTLs for grain morphology. With reference to previous studies, four QTLs for TKW identified in previous reports were detected on chromosomes 1A (1), 2A (2), and 2D (1). The co-localized GL and TKW locus QTL1 (537.54–544.74 Mb) is located at a similar position to that of the TKW QTL on chromosome 1A reported by Yang et al. (2020), and three QTLs located on chromosomes 2A and 2D have been reported in multiple studies. Interestingly, all of the favorable alleles associated with TKW were inherited from CM104 (Table 4). Among the 15 QTLs associated with grain morphology and grain weight identified in the present study, 14 QTLs have been located in previous studies except for QTL15. However, the physical location of QTL15 is near that of QTL14, and thus, they may represent a single QTL (Akram et al. 2021; Li et al. 2019; Suliman et al. 2021; Alemu et al. 2020; White et al. 2022; Gao et al. 2021; Okamoto et al. 2013; Tyagi et al. 2015; Gahlaut et al. 2021; Yang et al. 2020; Chidzanga et al. 2022; Sun et al. 2009; Azadi et al. 2015). In the current study, three QTLs associated with grain morphology were identified in multiple environments on chromosomes 5B and 5D, namely QTL10, QTL11, and QTL12, and their favorable alleles were all derived from CM104. Among these three stable QTLs, QTL10 and QTL11 explained 3.34–5.06% and 5.32–6.50% of the phenotypic variation, respectively, whereas QTL12 explained 6.00–12.13% of the phenotypic variation, which was significantly higher than that for QTL10 and QTL11. These results indicated that QTL12 was an important QTL for the grain morphology of CM104 (Table 4). These stable QTLs (QTL10, QTL11, and QTL12) detected in multiple environments provide a foundation for fine-mapping of TKW and grain morphology-related genes and improvement of the yield traits of CM104 by molecular marker-assisted selection. Additionally, the major and minor QTLs presented the excellent genetic basis to ensure the stable phenotype of grain traits of CM104 in multiple environments. It was also an effective strategy to cultivate high and stable yield wheat varieties with widely adaptation by pyramiding major and minor QTLs and utilizing the synergistic effect of major and minor QTLs.

Conclusion

The high-yielding and phenotypically stable wheat variety CM104 harbored favorable alleles for TKW and grain morphology. Eight previously reported QTLs were identified in CM104, but only three stable QTLs (QTL10, QTL11, and QTL12) were detected in multiple environments. Therefore, these three QTLs may be the genetic basis for the phenotypic stability of the TKW and grain morphology of CM104 in

Table 4 QTLs for grain morphology and grain weight traits by inclusive composite interval mapping in RIL population of Chuanmai104/Baimaomai in three environments, the physical position of markers was referenced to the Chinese Spring genome (IWGSCv1.0)

QTL	Trait	Env	Chr	Left Marker	Pos	Right Marker	Pos	Interval (Mb)	LOD	PVE(%)	Add	Origin	QTLs reported	Reported traits
QTL1	GSA	2021GH	chr1A	AX111548828	537,543,199	AX95630789	540,056,687	2.5135	5.4626	4.33	0.35	CM104	Yang et al. (2020)	TKW
	TKW	2021GH	chr1A	AX111174283	544,054,450	AX95652964	544,170,135	0.1157	4.1061	5.35	1.59	CM104		
QTL2	GC	2021GH	chr1B	AX94887858	423,205,018	AX109490291	437,183,983	13.9790	6.5704	7.24	0.22	BMM	Gao et al. (2021)	GSA
	GL	2021GH	chr1B	AX94887858	423,205,018	AX109490291	437,183,983	13.9790	4.3984	3.68	0.07	BMM		
QTL3	GC	2022SF	chr1D	AX95634375	243,462,018	AX94470806	249,023,870	5.5619	4.0799	5.53	0.20	BMM	Akram et al. (2021)	TKW
QTL4	GSA	2021GH	chr1D	AX94820546	318,497,325	AX95682418	362,320,692	43.8234	8.0513	6.68	0.44	BMM	Okamoto et al. (2013)	GW, GSA, GC
QTL5	TKW	2022GH	chr2A	AX109868961	619,770,018	AX109453394	639,752,951	19.9829	5.9849	6.84	2.00	CM104	Sun et al. (2009)	TKW, GW
QTL6	TKW	2022GH	chr2A	AX111007752	768,655,977	AX108730507	775,177,316	6.5213	5.5517	6.82	1.99	CM104	Gao et al. (2021); Li et al. (2019); Xin et al. (2019)	TKW, GL, GW, GC, GSA, GR
QTL7	TKW	2021GH	chr2D	AX86163393	35,683,268	AX109493327	43,780,514	8.0972	4.5485	6.08	1.70	CM104	Azadi et al. (2014); Chidzanga et al. (2022)	GY
QTL8	GL	2021GH	chr2D	AX110174570	585,137,768	AX109533227	600,406,415	15.2686	5.4962	5.53	0.08	CM104	Chidzanga et al. (2022); Li et al. (2019)	GY, TKW
QTL9	GC	2022GH	chr4B	AX95684402	12,892,078	AX111708768	13,944,454	1.0524	4.3267	4.81	0.18	BMM	Li et al. (2019)	TKW
QTL10	GC	2022SF	chr5B	AX109960007	37,480,209	AX109525345	37,797,184	0.3170	4.2262	5.72	0.20	CM104	Li et al. (2019); White et al. (2022)	GR, GW
	GSA	2022GH	chr5B	AX109852325	46,716,906	AX108954472	50,532,547	3.8156	4.0790	5.06	0.39	CM104		
QTL11	GC	2021GH	chr5B	AX112290807	273,139,244	AX86175380	279,305,011	6.1658	5.9584	6.51	0.20	CM104	Gao et al. (2021)	GY
	GC	2022GH	chr5B	AX112290807	273,139,244	AX86175380	279,305,011	6.1658	4.6771	5.32	0.18	CM104		
	GL	2022GH	chr5B	AX112290807	273,139,244	AX86175380	317,306,501	44.1673	4.3480	5.81	0.09	CM104		
QTL12	GC	2022GH	chr5D	AX108932356	27,261,491	AX109321838	47,532,080	20.2706	4.7094	6.00	0.20	CM104	Eltaher et al. (2021)	GY
	GL	2021GH	chr5D	AX108932356	27,261,491	AX109321838	47,532,080	20.2706	11.6912	11.25	0.12	CM104		
	GL	2022GH	chr5D	AX108932356	27,261,491	AX109321838	47,532,080	20.2706	7.7812	12.13	0.12	CM104		
QTL13	GC	2021GH	chr5D	AX94588037	346,877,508	AX111175437	370,951,342	24.0738	5.1252	5.81	0.19	CM104	Tyagi et al. (2015)	GC
QTL14	GL	2022GH	chr7B	AX109273671	111,306,072	AX109521272	113,537,778	2.2317	3.9401	5.24	0.08	BMM	Alemu et al. (2020); Suliman et al. (2021); Akram et al. (2021)	GW, GL, GY
	GC	2022GH	chr7B	AX111460060	126,059,975	AX94775218	128,772,842	2.7129	4.8473	5.40	0.19	BMM		
QTL15	GL	2021GH	chr7B	AX109280893	154,746,322	AX109632423	171,395,211	16.6489	4.5006	3.81	0.07	BMM		

TKW Thousand-kernel weight, *GL* grain length, *GW* grain width, *GR* grain length–width ratio, *GC* grain circumference, *GSA* grain surface area, *GY* grain yield

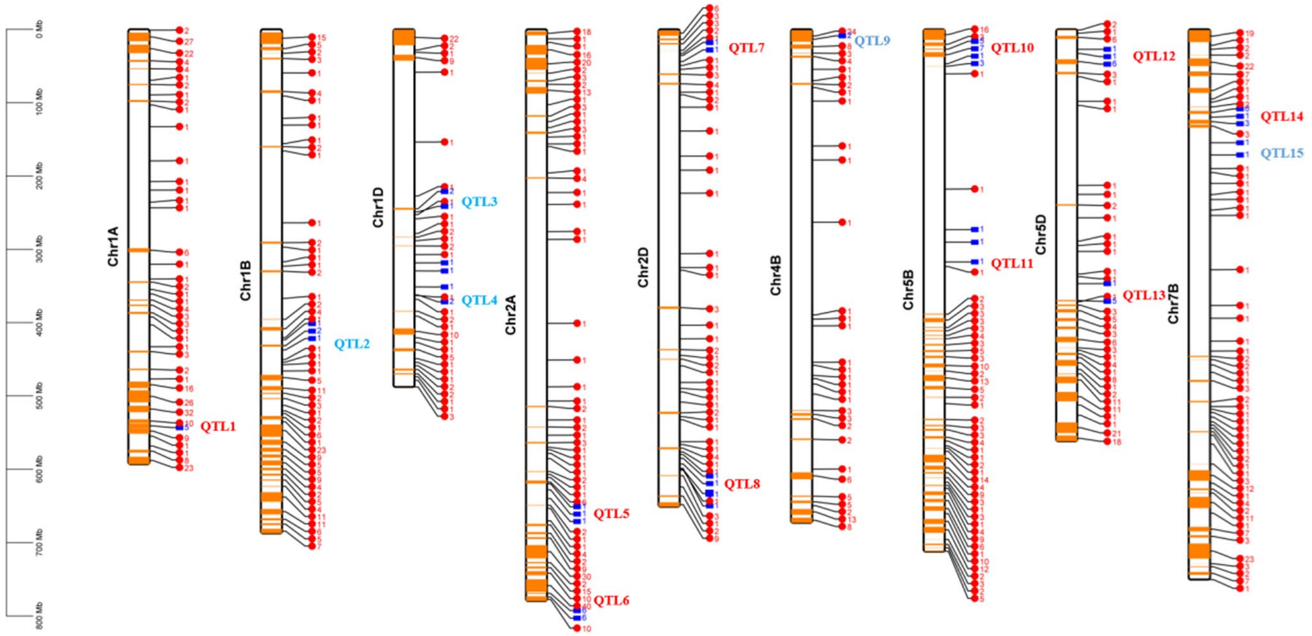


Fig. 7 Locations of the detected QTL that related the grain morphology in the CM104×BMM RILs population. A mega base (Mb) scale is shown on the left. *Red* QTLs mean donor of positive alleles come from CM104 and *blue* QTLs mean donor of positive alleles come from BMM

multiple environments. Pyramiding major and minor QTLs will be also useful to improve wheat varieties and contribute to the yield stability in multiple environments in future.

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Declarations

Conflict of interest The authors declared that they have no conflict of interest to this work. We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted.

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