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Characterization of four favorable alleles conferring high thousand-kernel weight of common wheat (*Triticum aestivum L.*) in the Huang-huai wheat-growing region of China

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Abbreviations: MTKW: Mean Thousand-Kernel Weight; SSR: Simple Sequence Repeat; QTL: Quantitative Trait Locus; PCR: Polymerase Chain Reaction; PIC: Polymorphism Information Content

Abstract

Improving grain yield is a priority for wheat breeding. Here, we report favorable alleles at four different thousand-kernel weight (TKW)-related Simple Sequence Repeat (SSR) loci (*Xgwm259, Xcfe172, Xbarc186,* and *Xbarc322*) in a panel of 82 wheat genotypes from the Huang-huai wheat-growing area in China. Two allelic variations were detected at each locus, one having positive effect on TKW. Apart from the favourable allele, $cfe172_{-122\ bp}$, with a frequency of 84.81%, the frequency of the other three favoured alleles was 29.51-56.79%, suggesting that the favourable alleles at these loci have not been strongly selected for and fixed. Moreover, the results showed that the favourable alleles have additive genetic effects. The highest mean TKW of 52.0 g corresponded to the presence of four favoured alleles at 69 critical marker loci, whereas varieties with 0-2 favoured alleles exhibited a relatively lower mean TKW, ranging from 45.6 to 49.1 g. More importantly, less modern wheat cultivar in our experiment contained favoured alleles at all those four loci and indicated the genetic potential for TKW improvement by identifying and pyramiding favourable alleles into new cultivars. Our results showed the identification of favoured alleles will be useful in breeding high-yielding wheat varieties in the future.

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Introduction

Common wheat (*Triticum aestivum* L.) is an important staple crop worldwide. Wheat breeders have placed particular emphasis on improving yields in varied environments, as well as on the end-products quality. Although improving grain yield has been a priority for wheat breeding programs for decades, the rate of improvement still lags behind the increasing world population and the decrease in cultivatable land [1]. The number of spikes per plant, number of kernels per spike, and Thousand-kernel Weight (TKW) are three major factors affecting wheat yields. Previous studies have shown that among these factors, TKW has the highest heritability [2]. Moreover, TKW can be measured easily and used to approximate the agronomic yield of a wheat genotype [3]. Selection for a high TKW in the early generations of wheat breeding is highly effective for improving the overall yield [4].

In common wheat, grain weight is an important trait contributing to grain quality and yield. Therefore, it has drawn major attention from the wheat breeding community all over the world. Based on previous efforts, numerous molecular markers related to TKW have been identified and validated in different genetic back grounds and environments. Röder et al. [5] fine mapped a Quantitative Trait Locus (QTL) in the telomeric region of chromosomal arm 7DS that correlates with grain weight. QTLs associated with TKW in wheat were also identified by studies assessing agronomic yield components [6]. Wang et al. [7] found a haplotype block associated with TKW on chromosome 5DS by validating 27 Simple Sequence Repeat (SSR) TKW-related loci in an $F_{2:5}$ breeding population of common wheat in four different environments. However, whether favourable alleles at these high yield-related loci are also dominant in different breeding populations is unknown. The genetic effect of these favourable alleles during wheat breeding in the Huang-huai wheat region is still unclear. The answers to these questions will provide a more detailed understanding of high yield-related favourable loci or alleles distributed among modern wheat varieties. This information will also be useful for future molecular breeding and for the release of new cultivars in this area.

Molecular breeding aims to select the most valuable genotypes or alleles and to combine them in order to develop a desirable cultivar [8]. The identification of favourable alleles helps in the selection of parents for crosses to ensure pyramiding of the maximum number of favourable alleles in the most desirable genetic background. A linear correlation between TKW and favourable alleles was previously reported [4,8]. Guo et al. [6] evaluated the effects of favourable alleles among various loci associated with yield in both wheat cultivars and a doubled haploid breeding population. However, low number of polymorphic markers is a limitation in most wheat programs since the germplasm is often based on a narrow gene pool [9]. This is particularly significant for the D genome of wheat [10], which has important loci associated with bread-making quality.

Crop domestication usually results in a decrease in genetic diversity across the entire genome. Modern breeding of wheat involves further directional selection for a high TKW or other favoured traits. Modern Chinese wheat varieties produced over the last 60 years are mainly based on 16 founder parents [11], which has lowered the genetic diversity of the breeding population. Identifying new favourable or dominant alleles at high yield-related loci and further pyramiding them together to release new wheat cultivars would not only broaden the gene pools of modern Chinese wheat cultivars, but also improve their yield potential and bread-making quality.

In this study, we set out to dissect the genetic effects of high yield-related allelic variation during wheat breeding in the Huang-huai wheat region and to evaluate the association of allelic variations and TKW for the marker-assisted selection of high TKW and grain yields in wheat.

Materials and methods

Eighty-two wheat varieties from the Huang-huai wheat-growing region were collected and used for a marker-trait association analysis (Table 1). These varieties were representative historical and modern wheat cultivars mainly cultivated in this area. In 2013 and 2014, wheat varieties were planted in plots at Zhaoxian, Hebei Province, China. The plots were 2 m long. Each plot had three rows with 25 cm between the rows, and 60 seeds were sowed in one row. All plots were well irrigated and fertilized during the growing season in Zhaoxian, Hebei Province, China. Field management followed local practices at Zhaoxian. Because counting 1000 grains is time consuming and labor cost, three independent samples of 200 grains each were weighed in practical applications and the TKW was estimated by converting the average values for each variety.

Genomic DNA was extracted from leaves according to the standard cetyl trimethylammonium bromide method [12]. Genotypes were fingerprinted at 69 marker loci following Polymerase Chain Reaction (PCR) amplification. These markers were reported to be associated with TKW in previous studies [4,8, 13-20]. The primer sequences, annealing temperature, and genetic locations of the marker loci were obtained from Grain Genes (http://wheat.pw.usda.gov) and references [21]. The details of markers used in this study are listed in supplementary table S1. PCR primers used to fingerprint genotypes were synthesized by Life Technologies (Beijing). PCR amplification was performed in a total volume of 20 µl containing DNA 1.5 µl (50-100 ng/µl), 10 ul 2X Taq Mastermix (CWBIO, Beijing, China), 1.5 µl of the forward and reverse primers (5 µM) and add 5.5 µl ddH_2O. The PCRs were performed with a Veriti Thermal Cycler (Applied Biosystems, Foster City, CA, USA) and the reaction was carried out with the following procedure: Pre-denaturation at 94°C for 5 min, followed by 30 cycles of 94°C for 30 s, 55°C for 1 min, 72°C for 30s, and a final extension step at 72°C for 2 min (or adjusted to give the best results).

The amplified products were separated on an ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, CA, USA) after purification of the PCR products. Fragment sizes were determined using an internal size standard (GeneScan-500LIZ; Applied Biosystems), and the outputs were analyzed using GeneMapper software (http://www.appliedbiosystems.com.cn/).

Based on the phenotypic and genotypic data, parameters of the genetic effects of each marker locus, including allele frequency, allele number, genetic diversity, and Polymorphism Information Content (PIC), were evaluated by single marker analysis. Statistical analysis were performed by Excel 2013.

Table 1: Thousand-kernel weight (TKW) and number of favorable alleles (FA) of 82 wheat varieties from the Huang-huai wheat-growing region of China

Varieties	Mean±SD	Range (g)	No. of FA	Varieties	Mean±SD	Range (g)	No. of FA
Baiyingdong2	40.67±0.76	40.0~41.5	3	NC2	42.33±0.58	42.0~43.0	0
Baofeng104	53.67±0.29	53.5~54	3	Nongda135	49.00±0.50	48.5~49.5	2
Baomai9	53.00±0.50	52.5~53.5	2	Nongda179	35.50±0.50	35.0~36.0	1
CA9722	45.50±1.00	44.5~46.5	1	Nongda211	49.67±0.76	49.0~50.5	1
Cangmai028	45.50±1.32	44.0~46.5	1	Nongda212	51.67±0.58	51.0~52.0	2
Cangmai6002	44.50±0.50	44.0~45.0	1	Nongda3488	50.00±0.50	49.5~50.5	3
Duofeng2000	49.17±1.04	48.0~50.0	3	Nongda3214	49.00±1.00	48.0~50.0	2
Gaoyou2018	49.67±2.75	46.5~51.0	1	Nongda3251	56.17±0.58	55.5~56.5	3
Hanyou3475	45.83±0.29	45.5~46	1	Nongda3432	45.83±1.04	45.0~47.0	3
Heima1	51.33±0.29	51.0~51.5	1	Nongdaduoxi1	46.83±0.76	46.0~47.5	1
Heng6599	47.17±0.76	46.5~48.0	2	Shannong12	49.50±0.87	49.0~50.5	1
Heng7228	46.17±0.29	46.0~46.5	2	Shannong14	51.50±0.50	51.0~52.0	2
Heng0628	52.17±0.58	51.5~52.5	2	Shannong15	52.83±0.29	52.5~53.0	2
Heng4399	51.50±1.00	50.5~52.5	2	Shannong18	52.17±0.76	51.5~53.0	2
Heng9526	53.33±0.76	52.5~54.0	3	Shannong8355	62.83±0.29	62.5~63.0	1
Henong4198	49.83±0.58	49.5~50.5	1	Shi4185	42.14±2.82	38.5~48.0	3
Henong58-3	42.00±0.50	41.5~42.5	2	Shijiazhuang10	49.17±0.29	49.0~49.5	1
Henong822	44.33±1.26	43.0~45.5	2	Shimai14	47.67±0.29	47.5~48.0	3
Henong827	44.67±0.29	44.5~45.0	3	Shimai16	46.67±0.76	46.0~47.5	3
Ji6358	48.67±0.76	48.0~49.5	1	Shimai18	40.83±0.29	40.5~41.0	2
Jidong3097	53.67±0.76	53.0~54.5	2	Shixin539	48.83±0.58	48.5~49.5	3
Jifeng703	51.17±0.76	50.5~52.0	2	Shixin733	54.67±0.76	54.0~55.5	3
Jing9428	54.67±0.76	54.0~55.5	2	Shixin828	46.17±0.58	45.5~46.5	2
Jingdong10	54.50±1.73	53.5~56.5	3	Shiyou17	50.83±0.29	50.5~51.0	2
Jingdong11	46.00±0.50	45.5~46.5	2	Taimai1	50.67±0.58	50.0~51.0	3
Jingdong20	53.67±0.76	53.0~54.5	4	Tainong18	48.83±0.76	48.0~49.5	1
Jingdong24	50.33±0.58	50.0~51.0	2	Taishan9818	57.00±0.50	56.5~57.5	2
Jingken49	45.83±0.29	45.5~46.0	2	Tangmai8	50.00±0.50	49.5~50.5	2
Jingmai9158	49.33±0.29	49.0~49.5	2	Weimai7	46.67±0.76	46.0~47.5	2
Jingshengmai1	59.50±0.00	59.5~59.5	2	Wennong5	48.50±1.00	47.5~49.5	2
Jining12	46.00±1.00	45.0~47.0	1	Xiaoyan81	57.50±1.73	55.5~58.5	3
Jining13	48.83±0.76	48.0~49.0	0	Yan2415	49.33±0.58	49.0~50.0	2
Jining16	55.83±1.53	54.5~57.5	2	Yannong19	49.33±0.29	49.0~49.5	2
Jinmai47	53.06±3.20	45.0~59.0	4	Yannong24	47.00±1.80	45.5~49.0	3
Jinmai54	47.67±0.29	47.5~48.0	4	Zhongmai12	50.67±0.29	50.5~51.0	2
Jinqiang5	52.33±0.29	52.0~52.5	4	Zhongmai24	46.83±0.29	46.5~47.0	3
Jinyin159	47.17±0.58	46.5~47.5	1	Zhongmai533	55.33±0.29	55.0~55.5	3
Laizhou95021	47.50±0.00	47.5~47.5	2	Zhongyou206	53.33±0.76	52.5~54.0	4
Liaomai16	54.00±1.00	53.0~55.0	3	Zhongyou335	47.83±2.84	47.0~51.0	2
Lunxuan061	51.50±1.50	50.0~53.0	3	Zhongyou9507	57.67±0.29	57.5~58.0	1
Luyuan301	52.33±0.76	51.5~53.0	2	Zhouyuan9369	50.50±0.87	49.5~51.0	2

Results

Among the previously reported 69 marker loci related to grain yield, only 4 simple sequence repeat (SSR) marker loci showed polymorphisms in 82 wheat varieties released in the Huang-huai wheat-growing area. This suggests that genetic diversity was low in the population of wheat varieties tested. It may also indicate strong positive selection and fixation at TKW-related loci during wheat breeding because of agronomic importance. The four identified polymorphic SSR markers were *Xgwm259*, *Xcfe172*, *Xbarc186*, and *Xbarc322*, located on chromosomes 1B, 3D, 5A, and 5D, respectively (Table 2).

Two allelic variations were detected at each locus. The PIC value was 0.2577 at *Xcfe172*, whereas it ranged from 0.4160 to 0.4909 at the other three loci with no dominant alleles. The frequency distribution was extremely uneven at *Xcfe172*, which favoured the allele $cfe172_{-122bp}$ with a frequency of 84.81%. Compared with *Xbarc186* and *Xgwm259*, *Xbarc322* had an uneven allelic frequency distribution: Allele $barc322_{-235\ bp}$ had a frequency of 70.49%, while the frequency of the favoured allele $barc322_{-228bp}$ was only 29.51% (Table 2). At *Xgwm259*, the previously assigned favourable alleles [8] were not prominent in the current wheat population. *Xbarc322* and *Xcfe172* are located on chromosomes 5D and 3D, respectively, while *Xbarc186* and *Xgwm259* are located on chromosomes 5A and 1B, respectively. Both *Xbarc186* and *Xgwm259* had two allelic variations and PIC values above 49%. This suggests that the D genome was under strong selection during wheat evolution and cultivation while the A and B genomes exhibited characteristics of neutral selection.

During the domestication and cultivation of wheat, most favoured alleles at crucial loci have been selected for and fixed. The favoured allele at *Xcfe172* conferrred a high mean TKW (MTKW) of 50.0 g, while the other allele exhibited a MTKW of only 47.7 g. At *Xbarc186* and *Xgwm259*, the favoured alleles also confer a higher TKW compared with the other alleles, with one exception: At *Xbarc322*, the high-yield favoured allele was $barc322_{-228bp}$ with a MTKW of 51.5 g, while the dominant allele was $barc322_{-235\ bp}$ with a MTKW of 48.4 g. The frequency of these alleles was 25.91% and 70.49%, respectively (Table 2).

Modern wheat breeding has promoted the accumulation of favoured alleles in different varieties. The highest MTKW of 52.0 g corresponded to 4 favoured alleles at the 69 critical marker loci, whereas varieties with 0–3 favoured alleles exhibited lower MTKWs, ranging from 45.6 to 50.0 g (Table 3). These results indicate the reliability of identifying favoured alleles. More importantly, no modern wheat cultivar has favoured alleles at all marker loci, suggesting that the TKW can be improved further by marker-assisted selection.

Table 2: Genetic effects of four simple sequence repeat (SSR) loci on thousand-kernel weight (TKW) in the Huang-huai wheat-growing area

	Locus							
	barc186		*barc322*		*cfe172*		*gwm259*	
Allele (bp) [a]	199	211	228	235	116	122	101	103
MTKW[b]±SD	49.30±4.84	49.94±4.17	51.51±3.89	48.44±4.18	47.74±4.42	49.96±4.41	49.54±4.65	49.71±4.09
No. of alleles[c]	35	46	18	43	12	67	32	42
Frequency (%)	43.21	56.79	29.51	70.49	15.19	84.81	43.24	56.76
PIC[d]	0.4908		0.4160		0.2577		0.4909	

[a]Allele (bp): fragment length of alleles at each locus, [b]MTKW: Mean thousand-kernel weight, [c]No. of alleles: Number of cultivars contains particular allele, [d]PIC: Polymorphism Index Content

Table 3: Effects of four favourable alleles accumulated on mean thousand-kernel weight (MTKW) in the Huang-huai wheat-growing area

No. of alleles	No.of genotypes	MTKW [a] ±SD
0	2	45.58±3.25
1	18	48.56±5.40
2	36	49.90±3.83
3	21	50.04±4.58
4	5	52.02±2.22

[a]MTKW: Mean thousand-kernel weight

Discussion

Crop domestication is an artificial evolutionary process. Strong selection in modern breeding has significantly reduced genetic diversity in domesticated populations [5], and only a small number of positively selected genes are conserved at crucial loci [22]. In this study, most of the previously reported polymorphic SSR loci did not generate allelic variations among wheat varieties. Moreover, among the four polymorphic SSR loci identified in this study, only two alleles were detected at each locus. These results suggest a relatively low level of genetic diversity in the Huang-huai wheat-growing area. This is likely because the founder parents of modern wheat varieties in this production area were from a narrow gene pool. Identification of new favourable alleles associated with grain yield will not only broaden the gene pool of current wheat breeding panels but will also improve the grain yield for breeding high-yield cultivars in this region of China.

Understanding the association between genotype and phenotype is a major biological question. Moreover, being able to predict phenotypes based on molecular genotypes is integral to marker-assisted selection. Many efforts have been made in wheat populations to identify marker-trait associations by mapping multiple traits and marker loci under different environmental conditions [23]. Peng et al. [24, 25] mapped several domestication syndrome factors and the involved QTLs in maps of wild emmer wheat, *Triticum dicoccoides*. *Xgwm259* was located more than 100 cM away from the QTL conferring grain weight on chromosome 1B. In this study, four SSR marker loci related to the grain yield trait TKW were identified. *Xgwm259* showed allelic variations related to TKW, with a PIC value of 0.4909. The relatively high TKW-favored allele was $gwm259_{-103\ bp}$, with a MTKW of 49.7 g. This suggests that *Xgwm259* underwent strong positive selection during modern

wheat breeding. Similarly, *Xbarc186* (with a PIC value of 0.4908) and *Xbarc322* (with a PIC value of 0.4160) have been strongly selected for and fixed during wheat breeding. The PIC value of *Xcfe172* was 0.2577, the lowest value among the four loci. However, the frequency distribution of $cfe172_{-122\ bp}$ was 84.81%, much higher than the other allelic variations, indicating that *Xcfe172* may have also undergone strong selection pressure during modern breeding. Moreover, the superior allele at *Xcfe172* has been strongly selected for and fixed during wheat breeding. We speculate that *Xcfe172* is located very close to target genes or loci that influence seed development.

During the domestication of common wheat, favored traits such as high TKW have been selected for and conserved. Strong allelic selection has occurred during wheat breeding because of an association with agronomically important traits [26]. In different wheat varieties, the allelic frequency distributions were uneven, and the alleles associated with favoured agronomic traits were present at a high frequency [26,27]. The identification of favoured alleles will aid in choosing parents for future crossing programs in order to ensure the maximum level of favoured alleles across sets of loci targeted for selection, and to promote fixation at these loci [4]. In this study, the frequency distribution of the alleles at *Xcfe172* was uneven: The favoured allele $cfe172_{-122\ bp}$ was present at a frequency of 84.81%, while the allele $cfe172_{-116bp}$ was only present at a frequency of 15.19%. Compared with the favoured allele at *Xcfe172*, favoured alleles at *Xbarc186*, *Xbarc322*, or *Xgwm259* have not been strongly selected for because of nearly even distribution frequencies. Strong selection pressure at these three loci to further select for the high-TKW favoured allele could improve overall grain yields.

The effect of favoured alleles at important loci was another consideration in the superior alleles' selection and fixation. In a natural population, allelic diversity at a locus under strong selection is significantly lower than diversity at other loci. Diversity in genomic regions flanking selected loci also declines in the process of selection [28,29]. In genetics, this is referred to as the hitchhiking effect or selection sweep, and it leads to increased linkage disequilibrium and changes in the distribution patterns of alleles within the selected region. These effects also provide the basis for the association of neutral markers with agronomic traits. Guo et al. [6] reported that the genetic effects of crucial loci were lower in modern cultivars than in the mini core collection of wheat. In this study, the genetic effects of *Xbarc186*, *Xbarc322*, and *Xgwm259*, compared with *Xcfe172*, may be more dramatic in different wheat varieties. Strong selection pressure at these loci in wheat breeding could be more effective at increasing grain yields.

Favourable alleles at crucial loci were not always the predominant ones in breeding panels [30]. High-yield favoured alleles were consistent with the dominant allele at most TKW-related loci in this study, with the exception of *Xbarc322*. One possible reason for this is that the yield QTL may overlap with QTLs for other important traits: The dominant allele $barc322_{-235\ bp}$ might also be favoured at other important loci conferring favored agronomic traits. Many quantitative and qualitative traits were co-selected during the domestication process of wheat yield traits, including plant height, spike number per plant, spike weight per plant, single spike weight, kernel number per plant, kernel number per spike, kernel number per spikelet, and spikelet number per spike [24]. Wang et al. [4] genotyped 531 SSR markers in the Chinese mini core collection of wheat. Twenty-two SSR marker loci were associated with TKW, each exhibiting phenotypic variation ranging from 1.56–21.99%. Using the same association panel, Zhang et al. [8] identified 23 SSR loci significantly associated with kernel number per spike and reported that favourable alleles combined with additive effects. They also identified favourable alleles at *Xgwm156-3B* with positive effects on both TKW and kernel number per spike. Song et al. [31] located *Xbarc186* on different arms of the same chromosome using physical and genetic mapping, indicating that *Xbarc186* could be a pleiotropic QTL. Therefore, favored alleles should be confirmed as dominant at the same locus before they are used in marker-assisted selection.

Most genes affecting grain yield have additive effects. Huang et al. [2] concluded that the accumulation of numerous rare superior alleles with positive dominance is an important contributor to heterotic phenomena in rice. Zhang et al. [32] performed association and favourable allele analyses of 209 genome-wide SSR markers and 4 types of water-soluble carbohydrates. The results showed that the dosage effects of pyramided favourable alleles for water-soluble carbohydrates played an important role in grain weight at the grain filling stage. Significant linear correlations were found between the number of favourable alleles for water-soluble carbohydrates and TKW: The more favourable alleles pyramided, the more grain weight improved. This is consistent with our finding that pyramiding more favourable alleles will be effective in improving grain yield in future wheat breeding programs.

Crucial loci have been selected for and fixed during wheat domestication and modern wheat breeding. Among the four SSR loci found to be polymorphic in this study, the frequencies of favoured alleles with positive effects on TKW exceeded 50%, suggesting that these loci have contributed to Chinese wheat breeding. On the other hand, strong selection in the breeding of released cultivars has already focused on some favourable alleles. The lower distribution frequency of favoured alleles means that these alleles could be selected to increase TKW for future wheat breeding. Furthermore, pyramiding more favourable alleles will likely be effective for improving overall wheat yields.

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