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Genetic characteristics of a wheat founder parent and a widely planted cultivar derived from the same cross

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Abstract

Founder parents have contributed significantly to the improvement of wheat breeding and production. In order to investigate the genetic characteristics of founder parents and widely planted cultivars, Mazhamai (M), Biyumai (B) and six sibling lines (BM1–6) derived from the cross M×B were phenotyped for eight yield-related traits over multiple years and locations and genotyped using the the wheat 90K single nucleotide polymorphism (SNP) assay. BM4 has been used as a founder parent, and BM1 has been widely planted, whereas BM2, 3, 5, and 6 have not been used extensively for breeding or planting in China. Phenotypic comparisons revealed that BM4 and BM1 displayed a better overall performance than the other sibling lines. BM1 showed higher thousand-grain weight than BM4, whereas BM4 exhibited a lower coefficient of variation for most of the yield-related traits across different years and locations, indicating that BM4 was widely adaptable and more stable in different environments. SNP analysis revealed that BM4 and BM1 inherited similar proportions of the M genome but are dissimilar to BM2, 3, 5, and 6. Both BM1 and BM4 have specific alleles that differ from the other BM lines, and most of these alleles are concentrated in specific chromosomal regions that are found to associate with favorable QTLs, these SNPs and their surrounding regions may carry the genetic determinants important for the superior performance of the two lines. But BM4 has more genetic diversity than BM1 with more specific alleles and pleiotropic regions, indicating that the genome of BM4 may be more complex than the other sibling lines and has more favorable gene resources. Our results provide valuable information that can be used to select elite parents for wheat and self-pollinating crop breeding.

Keywords: wheat, founder parents, widely planted cultivars, SNP

1. Introduction

Wheat (*Triticum aestivum* L.) is one of the most important crops affecting the global economy and food security, and most of the world's wheat is produced by China, which produces >120 million tons per year (National Bureau of Statistics of the Republic of China, http://www.stats.gov.cn/; and Food and Agriculture Organization of the United Nations, FAO, http://www.fao.org/statistics/en/). Since

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the 1950s, thousands of wheat cultivars have been bred in pedigree selection programs, which have significantly increased the yield and total production of wheat in China. Pedigree analysis indicates that most released cultivars are derived from 16 founder parents (Zhuang 2003). Among these founder parents, Bima 4, Beijing 8 (Li *et al*. 2012), Nanda 2419 (Jia *et al*. 2013), Abbondanza, Funo, Xiaoyan 6, and Youzimai are also widely planted (>667 000 ha) in China (Zhuang 2003). Founder parents have played a crucial role in modern crop breeding for have bred many wheat cultivars, especially widely planted cultivars, and have introduced favorable gene resources, such as the "reduced height genes" (*Rht* genes) from Akakomughi and Norin 10 (Gale and Youssefian 1985; Borojevic and Borojcvic 2005a). Pedigree analysis has also been used to identify the founder parents of other crops, including rice (*Oryza sativa* L.; Tian *et al*. 2006; Zhou *et al*. 2012; Zhang *et al*. 2013), maize (*Zea mays* L.; Lu *et al*. 2009), soybean (*Glycine max* L. Merr.; Lorenzen *et al*. 1996; Lee *et al*. 2004), and barley (*Hordeum vulgare* L.; Russell *et al*. 2000; Sjakste *et al*. 2003). Many studies have reported the genetic contribution of founder parents to derivative lines, and important founder parents quantitative trait loci (QTLs) have been identified by molecular markers and pedigree analysis (Pestsova and Röder 2002; Borojevic and Borojcvic 2005b; Ma *et al*. 2007; Han *et al*. 2009; Li *et al*. 2009, 2012; Zhou *et al*. 2012; Jia *et al*. 2013; Xiao *et al*. 2014; Wu *et al*. 2015). However, the basic genetic characteristics of founder parents are still poorly understood.

Mazhamai (M), a local landrace of the Guanzhong District in Shaanxi Province of China, was a major founder parent for wheat breeding in the 1950s. M has ecological adaptability, high tolerance to abiotic stress, and a high number of grain numbers per spike (GNS), but it is susceptible to stripe rust. Biyumai (B), which is highly resistant to stripe rust, was introduced from the United States (Zhuang 2003). In China, six wheat cultivars named BM1–6 are derived from the cross M×B. BM1 has been planted over 6 000 000 ha, but few cultivars have been bred from it. BM4 has been planted over 867000 ha, and 80 released cultivars have been bred from it, including six widely planted cultivars (> 667000 ha) and the founder parents Beijing 8 (Zhuang 2003; Li *et al*. 2012) and Jing 411 (Xiao *et al*. 2014). However, the other four sibling lines (BM2, 3, 5, and 6) have not been used extensively for breeding or planting. Because the six BM sibling lines are derived from the same cross but exhibit different performances, they provide an ideal system to analyze the genetic characteristics of founder parents and widely planted cultivars.

The development of the wheat 9K and 90K single nucleotide polymorphism (SNP) wheat assays has allowed the determination of detailed haplotype structure and the genetic basis of trait variation (Cavanagh *et al*. 2013; Wang *et al*. 2014). These assays have been widely used to identify genomic regions targeted by breeding and improvement selection, to characterize genetic variation in allohexaploid and allotetraploid populations, and to dissect complex traits by QTL (Wu *et al*. 2015) and association mapping (Sela *et al*. 2014; Zanke *et al*. 2014a, b; Maccaferri *et al*. 2015). In the present study, the wheat 90K SNP assay was used to genotypes BM 1–6 and their parents to identify the genomic characteristics of founder parents and widely planted cultivars.

The objectives of the present study were to (1) analyze the phenotypic characteristics of the founder parent BM4 and the widely planted cultivar BM1; (2) analyze the genetic characteristics of BM4 and BM1 by evaluating the genomic similarities and differences of BM1–6. The present study provides theoretical guidance for the selection of parents for wheat and self-pollinating crop breeding.

2. Materials and methods

2.1. Plant materials and field trials

B, M, and BM1–6 were evaluated over three consecutive years from 2007 to 2009 in five major wheat ecological regions in China, including Shijiazhuang in Hebei Province (114.36′E, 37.38′N), Tai'an in Shandong Province (116.02′E, 35.38′N), Yangling in Shaanxi Province (108.82′E, 34.36′N), Chengdu in Sichuan Province (104.06′E, 34.66′N), and Yangzhou in Jiangsu Province (119.4′E, 32.15′N). A randomized complete block design was used at all locations with three replications per site. Each plot consisted of five rows (2 m long and 30 cm wide), and 40 seeds were planted in each row. Ten plants from the center of each plot were harvested for each line to measure eight yield-related traits including plant height (PH), grain number per spike (GNS), thousand-grain weight (TGW), effective tiller number (ETN), spike length (SL), spikelet number per spike (SNS), sterile spikelet number per spike (SS), and heading date (HD). Details about the measurements and timing of measurements are described in Li *et al*. (2006).

2.2. Statistical analysis

Basic statistics for each trait were calculated for B, M, and BM1–6. Analysis of variance (ANOVA) was used to test the statistical significance of various sources of variation using SAS software (Release 9.1.3; SAS Institute, Cary, NC, USA). Duncan's new multiple range test (MRT) was used to conduct multiple comparison analysis tests for B, M, and BM1–6 (Duncan 1955).

2.3. SNP genotyping

DNA was extracted from fresh leaf tissue of each individual using a modified cetyltrimethyl ammonium bromide (CTAB) method (Allen *et al*. 2006). SNP genotyping was performed on purified DNA by Capital Bio Technology of Beijing, using the Illumina iSelect 90K SNP assay (Wang *et al*. 2014) according to the manufacturer's protocols (Illumina, USA). SNP allele clustering and genotype calling was performed using GenomeStudio polyploid clustering v1.0 software (Wang *et al*. 2014).

2.4. SNP data analysis

The Illumina iSelect 90K SNP assay contains 81 587 SNPs in total, and 40 267 of these SNPs were genetically mapped onto the consensus map of 21 wheat chromosomes (Wang *et al*. 2014). SNPs were filtered by removing monomorphic SNPs and those with a large number of missing values (>10%). Based on the 40 267 mapped SNPs, 8 331 SNPs polymorphic between B and M were used to evaluate the genomic differences of BM1–6.

The proportion of the genome inherited from each parent and the alleles specific to each line were identified by comparing the BM1–6, B and M alleles in Excel. The genetic similarity between B, M, and BM1–6 was evaluated by principal coordinates analysis (PCoA) based on a similarity matrix calculated on the Flapjack platform (downloaded from https://ics.hutton.ac.uk/flapjack/) (Milne *et al*. 2010). Based on the 90K consensus map (Wang *et al*. 2014), we constructed a heatmap of BM1–6 where 8 331 SNPs with alleles derived from B and M are shown as different colored blocks (red and blue). We were able to visualize the important genomic variation by comparing the colored blocks. For example, in the heatmap, a switch from B to M (i.e., a change in color) indicates a recombination breakpoint in the chromosomal region. We compared the genotypic data of BM1–6, and alleles that differentiated one line from the other five lines were viewed as being specific to that line. Similarly, a chromosomal region (<20 cM in length) harboring alleles specific to one line was viewed as a region specific to that line. We compared the SNP markers in these genomic regions to the locations of previously identified QTLs. When any SNP in the specific region was within the confidence interval of a QTL, this region was viewed as being specifically associated with the trait of interest.

3. Results

3.1. Comparison of phenotypic characteristics

Combined ANOVA indicated that there was a significant (P<0.01) difference among B, M, and BM1–6 for five traits (PH, GNS, TGW, SL, and SNS), but not for ETN, SS and HD (Table 1). The variation explained by year was significant for most traits, except for SL and SS, whereas the variation explained by location was significant for all traits except ETN. All interactions between the eight cultivars and three years, and between the eight cultivars and five locations were not significant, indicating that genotypic variation was the primary contributor to the observed phenotypic variation in the eight traits.

Phenotypic variation was observed among the six sibling lines (BM1–6) and their two parents (B and M) (Tables 1 and 2). GNS, TGW, SL, SNS, and HD of the B and M were significantly different (Table 2). M had higher GNS and SNS, and B had higher TGW and SL. Compared with phenotypes observed in the parental lines, transgressive phenotypes were observed in BM1–6, in both directions for PH and in one direction for GNS, TGW, ETN, SNS, SS, and HD. Furthermore, the means of GNS and SNS of BM1–6 were closer to those of M, whereas the means of TGW and SL were closer to those of B, which indicated that all the six cultivars inherited good phenotypic characters from their parents and were superior to the parents.

Among the six sibling lines, BM1 had the highest TGW and SL, whereas BM4 had the most ETN, shortest SL, and minimum SS (Table 2). Compared with the other four cultivars (BM2, 3, 5, and 6), BM4 and BM1 had higher TGW and shorter HD. Although there were no significant differences in the yield components (TGW, GNS, and ETN) between BM1 and BM4, BM4 had fewer SS, shorter PH,

Table 1 ANOVA for eight yield-related traits in the six sibling lines (BM1–6) and their parents (Mazhamai (M) and Biyumai (B)) across five locations and three years[1)]

Source	PH	GNS	TGW	ETN	SL	SNS	SS	HD
Line	4.99***	21.12***	41.25***	0.23	20.37***	23.60***	2.22	1.57
Year	14.14***	12.14***	6.13**	20.12***	0.63	3.35*	0.26	11.97***
Location	9.00***	28.86***	3.25*	2.47	22.37***	33.17***	3.78*	302.80***
Year×Line	0.49	0.78	0.73	0.29	0.95	1.03	0.61	0.21
Location×Line	0.82	1.35	1.13	0.23	0.70	0.49	0.36	0.32

[1)] PH, plant height; GNS, grain number per spike; TGW, thousand grain weight; ETN, effective tiller number; SL, spike length; SNS, spikelet number per spike; SS, sterile spikelet number per spike; HD, heading date.
*, **, and ***, significant at P<0.05, 0.01, and 0.001, respectively.

Table 2 Descriptive statistics for eight traits measured for BM1–6 and their parents (Mazhamai (M) and Biyumai (B)) across five locations and three years

Trait[1)]	Line	Mean	SD[2)]	Range	CV (%)[3)]	MRT[4)]
PH	M	121.94	11.00	96.75–141.00	9.02	d
	B	122.61	8.20	107.52–132.00	6.69	dc
	BM1	129.71	6.47	116.83–141.90	4.99	ba
	BM2	120.88	7.83	106.90–136.00	6.48	d
	BM3	127.03	12.58	107.43–139.56	9.90	b
	BM4	126.18	9.13	111.60–145.00	7.23	bc
	BM5	131.09	10.32	113.75–150.00	7.87	a
	BM6	132.42	9.57	119.68–152.00	7.23	a
GNS	M	50.94	11.77	29.33–75.25	23.11	b
	B	34.02	6.47	22.38–45.70	19.02	d
	BM1	44.79	9.74	28.00–58.40	21.74	c
	BM2	54.42	12.95	32.70–75.05	23.81	b
	BM3	41.14	9.60	25.48–58.17	23.34	c
	BM4	43.53	7.75	28.03–53.83	17.79	c
	BM5	50.99	9.58	35.88–64.75	18.78	b
	BM6	58.95	12.88	38.50–74.55	21.86	a
TGW	M	27.03	3.03	22.43–31.93	11.23	d
	B	39.33	5.71	21.43–44.60	14.51	a
	BM1	35.88	3.98	28.93–43.95	11.09	b
	BM2	26.16	2.66	21.37–30.03	10.15	d
	BM3	34.47	3.57	26.50–37.63	10.35	b
	BM4	34.53	2.31	30.46–38.00	6.70	b
	BM5	29.89	4.18	20.80–35.30	13.98	c
	BM6	28.02	3.12	22.30–33.53	11.13	dc
ETN	M	11.81	4.78	6.53–19.67	40.47	a
	B	12.30	4.35	6.93–22.3	35.34	a
	BM1	11.15	3.78	5.77–17.23	33.88	a
	BM2	10.64	3.55	5.43–15.37	33.35	a
	BM3	10.14	2.31	7.37–13.55	22.74	a
	BM4	12.17	5.69	7.06–24.83	46.81	a
	BM5	11.28	3.85	5.30–16.13	34.11	a
	BM6	10.89	3.37	6.28–15.00	30.99	a
SL	M	7.21	1.07	5.50–9.72	14.81	f
	B	9.89	0.84	8.18–10.95	8.55	a
	BM1	9.79	0.99	7.88–10.99	10.11	ba
	BM2	9.26	1.06	6.99–10.50	11.50	dc
	BM3	9.37	1.05	7.98–11.20	11.22	bdc
	BM4	8.47	0.77	6.99–9.87	9.06	e
	BM5	9.62	1.14	7.31–12.41	11.81	bac
	BM6	8.97	0.98	6.90–10.63	10.96	d
SNS	M	20.53	2.29	16.23–24.58	11.17	d
	B	17.68	1.89	14.00–20.43	10.70	g
	BM1	18.63	1.75	15.70–21.15	9.41	f
	BM2	21.76	2.57	16.13–25.00	11.83	b
	BM3	21.02	1.99	17.27–23.62	9.45	cd
	BM4	19.51	1.75	15.33–21.60	8.98	e
	BM5	21.63	1.92	17.30–24.55	8.90	cb
	BM6	23.06	2.13	19.43–26.20	9.21	a
SS	M	1.34	0.41	0.78–2.00	30.68	d
	B	1.75	0.50	0.67–2.20	28.64	bcd
	BM1	1.85	0.74	0.89–2.80	40.12	bcd
	BM2	2.52	0.79	1.33–387	31.47	a
	BM3	2.14	0.92	0.67–2.97	43.05	ba
	BM4	1.41	0.57	0.22–2.07	40.02	cd
	BM5	1.90	0.49	0.78–2.40	26.06	bc

(Continued on next page)

Table 2 (Continued from preceding page)

Trait[1)]	Line	Mean	SD[2)]	Range	CV (%)[3)]	MRT[4)]
	BM6	1.60	0.75	0.67–2.80	46.80	cd
HD	M	184.68	22.09	149.00–214.00	11.96	bc
	B	181.92	23.56	141.00–215.00	12.95	d
	BM1	182.68	21.04	146.00–211.00	11.52	dc
	BM2	186.26	20.75	153.00–216.00	11.14	ba
	BM3	187.43	22.74	151.00–220.00	12.13	a
	BM4	184.33	20.45	152.00–212.00	11.09	bc
	BM5	182.14	23.27	142.00–215.00	12.78	d
	BM6	184.70	22.93	146.00–218.00	12.41	bc

[1)] PH, plant height; GNS, grain number per spike; TGW, thousand grain weight; ETN, effective tiller number; SL, spike length; SNS, spikelet number per spike; SS, sterile spikelet number per spike; HD, heading date.
[2)] SD, standard deviation.
[3)] CV, coefficient of variation.
[4)] MRT, Duncan's new multiple range test.

and a lower CV than BM1 for most traits across years and locations, which indicated that BM4 is more adaptable to various ecological zones (Table 2). BM2 had the lowest TGW (26.16 g) and the most SS (2.52); BM3 had the minimum GNS and the longest HD; and BM5 and 6 showed higher PH than the other four lines (Table 2). These negative characteristics partially explain why these lines have not been widely planted or used as founder parents in wheat breeding.

3.2. Comparison of genotypic characteristics

To determine the genetic variation of BM1–6, the proportion of the genome inherited from the parents B and M and similarity of the lines were evaluated by genotyping 8 331 polymorphic SNPs that effectively represent the genetic variation across the consensus map (Wang *et al*. 2014) (Appendix A). Except for BM3, five sibling lines inherited more than 55% of alleles from M (Fig. 1). BM3 inherited 45% of alleles from M and 55% from B, a proportion that is significantly different (P<0.05) from the other lines. PCoA analysis was performed to evaluate the genetic similarity of eight cultivars. B and M were clearly separated from BM1–6 and each other. BM1–6 could be separated into four groups: BM1 and 4, BM5 and 6, BM2 and 3 (Fig. 2). Overall, the genetic compositions of BM4 and 1 are similar to each other but dissimilar to those of BM2, 3, 5, and 6.

Using a heatmap constructed from the 8 331 SNPs, we detected the recombination events on each chromosome and found that the numbers and locations of recombination breakpoints in the six lines were diverse, with 32, 45, 40, 40, 39, and 37 recombination breakpoints identified for BM1–6, respectively (Table 3 and Fig. 3). Compared with BM1, there were more recombination breakpoints in BM4, especially on the A genome (Table 3). For BM1, no recombination events were identified on chromosomes 3A, 7A, 1B, and 6B, whereas for BM4, no recombination events were identified

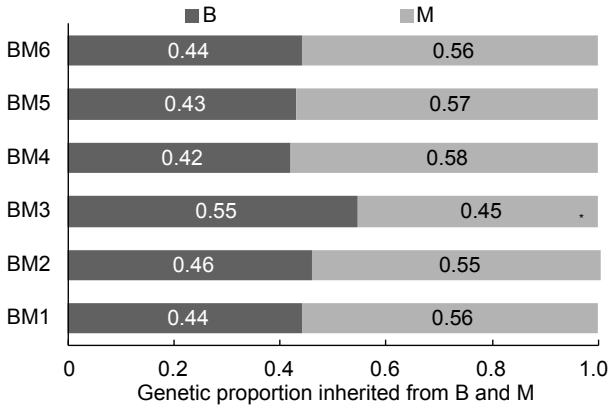

Fig. 1 Proportion of the BM1–6 genomes inherited from the Biyumai (B) and Mazhamai (M) parents based on 8 331 single nucleotide polymorphisms (SNPs). *, the proportion of BM3 inherited from B and M is significantly different from other lines at P<0.05.

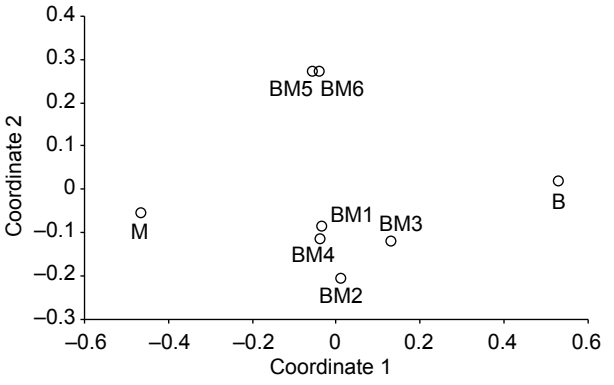

Fig. 2 Principal coordinate analysis (PCoA) based on a similarity matrix showing the genetic similarities between BM1–6 (six sibling lines).

on chromosomes 4A and 4B. The maximum number of crossovers in BM1 (n=3) was observed on chromosomes

Table 3 Distribution of breakpoints for the BM1–6 (six sibling lines) across 21 chromosomes and genomes

Chromosome	BM1	BM2	BM3	BM4	BM5	BM6	Total
1A	2	3	1	4	0	1	11
1B	0	3	3	2	4	3	15
1D	1	0	2	2	1	1	7
2A	3	4	3	2	0	0	12
2B	3	2	4	1	3	3	16
2D	2	1	3	2	2	1	11
3A	0	0	1	3	3	3	10
3B	3	6	2	5	2	2	20
3D	1	0	1	1	1	1	5
4A	1	3	0	0	0	0	4
4B	3	2	2	0	3	3	13
4D	1	0	1	1	1	1	5
5A	1	0	4	2	4	4	15
5B	2	5	5	3	3	3	21
5D	3	2	1	1	1	1	9
6A	1	3	2	2	2	2	12
6B	0	6	0	1	2	2	11
6D	2	1	1	3	2	0	9
7A	0	1	2	2	1	1	7
7B	2	1	2	2	3	3	13
7D	1	2	0	1	1	2	7
A genome	8	14	13	15	10	11	71
B genome	13	25	18	14	20	19	109
D genome	11	6	9	11	9	7	53
Total	32	45	40	40	39	37	233

2A, 3B, 4B, and 5D, whereas in BM4, five crossovers were observed on chromosome 3B, and no fewer than three were observed on chromosomes 1A, 3A, 3B, 5B, and 6D (Table 3).

By compared the genotypes datasets of BM1-6, we identified alleles specific to each line that differentiate each line from the other five lines, and the number and distribution of these specific alleles differed between the six lines (Table 4 and Fig. 4). BM4 has 724 specific alleles that are mainly distributed on the homoeologous groups 5, 6, and 7, whereas BM1 has 409 specific alleles that are mainly distributed on the homoeologous groups 6 and 7 (Table 4 and Fig. 4). Of the 291 specific alleles shared by BM1 and BM4 but not found in the other four sibling lines, 244 and 47 were inherited from M and B, respectively (Table 4). Although the number of BM3-specific alleles was similar to the number of BM4-specific alleles, most of these alleles were inherited from B and are distributed on homoeologous groups 3 and 4 (Table 4 and Fig. 4).

Most of the specific alleles were concentrated on special chromosomal regions that were inherited as haplotypes from parents. For example, the region near 60 cM on chromosome 1A for BM4 was inherited from B (Fig. 3, blue block), whereas the same region was inherited from M in all the other lines (Fig. 3, red block). In total, the 676 BM4-specific alleles make up 13 specific regions on 11 chromosomes (1A, 1D, 3A, 3B, 4B, 5A, 5B, 6A, 6B, 6D, and 7B; Tables 4 and 5), and the 360 BM1-specific alleles make up 11 specific regions on 7 chromosomes (1B, 2A, 3D, 4B, 5B, 6A, and 7A; Tables 4 and 5). In addition, 236 of the 291 alleles specific to BM1 and BM4 form 10 genomic regions. Overall, the number and distribution of the specific alleles and regions in the six sibling lines were different from each other, and BM4 had more specific alleles and chromosomal regions than BM1, 2, 5, and 6.

4. Discussion

Increasing yield potential is a major goal of most crop breeding programs (Zhuang 2003; Reynolds *et al*. 2009). Thus, lines with favorable yield components have been preferentially selected as parents or elite cultivars. Furthermore, according to the rules for parents select in breeding, it is widely agreed that the parents of a cross should mostly have superior and complementary phenotypes and not have obvious flaws (Zhuang 2003). In present study, the founder parent BM4 and the widely planted cultivar BM1 were selected from tens of thousands of progeny derived from the cross M×B due to their enhanced phenotypic performance, especially higher TGW and shorter PH (Table 2). Compared with BM1, BM4 had shorter PH, fewer SS, and a lower CV for most yield-related traits across years and locations (Table 2). This indicates that better comprehensive performance could be an important characteristic of founder parents, as reported for the founder parent Beijing 8 (Li *et al*. 2012) and Nanda 2419 (Jia *et al*. 2013).

In the present study, the genomic characteristics of the six sibling lines were investigated using the wheat 90K SNP assay. BM1 and BM4 inherited similar proportions of genetic components from their parents but are dissimilar to BM2, 3, 5, and 6 (Figs. 1 and 2). Compared with BM1, BM4 has more specific alleles, chromosomal regions and recombination breakpoints (Table 3), which indicates that BM4 has more genetic diversity than BM1. Similarly, based on 481 SSR loci, Ge *et al*. (2009) found that the founder parents BM4 and St2422-464 contain more favorable alleles and more diversity than their sister lines, the widely planted cultivars BM1 and St1472-506, respectively.

All 1 424 BM1- and BM4-specific alleles (409 specific to BM1, 724 specific to BM4, and 291 specific to BM1 and BM4) are distributed across 18 chromosomes and comprise 34 genomic regions. These regions might be critical for breeding a founder parent or widely planted cultivar. To better understand the functions of these specific regions, we searched for QTLs from a recombinant inbred line (RIL) population derived from M and B (unpublished results; Table 5) and from the literature that are associated with these regions (Zanke *et al*. 2014a, b; Zegeye *et al*. 2014;

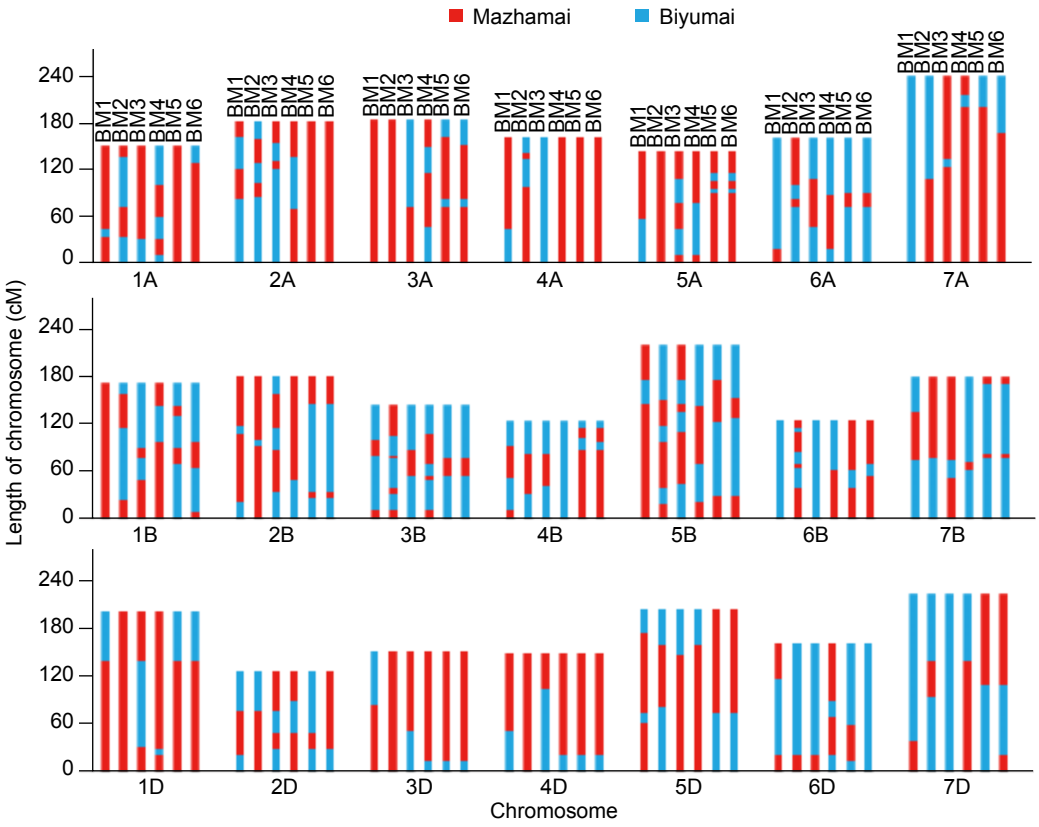

Fig. 3 Genotypic map of BM1–6 based on 8 331 single nucleotide polymorphisms (SNPs). Blue block indicate alleles inherited from Biyumai (B), red block indicates allele inherited from Mazhamai (M).

Table 4 Number and origin of alleles and genomic regions specific to BM1–6

Sibling lines	No. of specific allele			No. of specific genomic regions		
	Total	M	B	Total	M	B
BM1	409	91	318	11	4	7
BM2	402	173	229	8	6	2
BM3	728	91	637	17	4	13
BM4	724	328	396	13	5	8
BM5	117	96	21	3	2	1
BM6	8	8	0			
BM1–4	291	244	47	10	7	3

Kertho *et al*. 2015; Lopes *et al*. 2015; Naruoka *et al*. 2015; Sukumaran *et al*. 2015; Wu *et al*. 2015). Seven of the 11 BM1-specific regions are associated with QTLs for TGW, PH, ETN, SL, SNS, GNS, HD, and Yr or Lr (Table 5). Four pleiotropic regions, BM1.R1, BM1.R5, BM1.R7, and BM1.R11, harbor QTL2, QTL23, QTL29, and QTL33, respectively (Table 5). The favorable alleles of QTL2 and QTL33 that increase TGW and PH are derived from M and B, respectively. BM1.R1 and BM1.R11 harbor both of these alleles, which is consistent with the relatively high TGW and PH of BM1 (Tables 2 and 5). Nine of the 13 BM4-specific regions are associated with QTLs for yield-related traits (GNS, ETN, SNS, PH, and SL) and for yellow rust and leaf rust (Table 5). BM4 harbors alleles that increase GNS on BM4.R8, BM4.R9, and BM4.R10, and alleles that decrease PH on BM4.R11 and BM4.R1, which is consistent with the relatively short PH of BM4 (Table 2). Three BM4-specific regions (BM4.R8, BM4.R10, and BM4.R13) are associated with HD, which may explain the broad adaptability of BM4 (Tables 2 and 5). In addition, 8 of 10 specific regions that are common to BM1 and BM4 but not found in the other four sibling lines are associated with yield components and harbor favorable alleles that could increase TGW and ETN, which might explain the higher TGW of BM1 and BM4 compared with the other lines. The association of pleiotropic regions with favorable QTLs could explain why BM1 is a widely planted cultivar and BM4 is a founder parent.

As reported in several studies, alleles or genomic regions specific to founder parents can harbor QTLs or genes for important traits, and those alleles or regions are transmitted to the progeny (Lee *et al*. 2004; Borojevic and Borojcvic 2005b; Li *et al*. 2012; Zhou *et al*. 2012; Jia *et al*. 2013; Xiao *et al*. 2014). In the present study, 9 of 13 BM4-specific regions were found to be associated with QTLs for multiple traits of interest. In future work, we will detect variation in

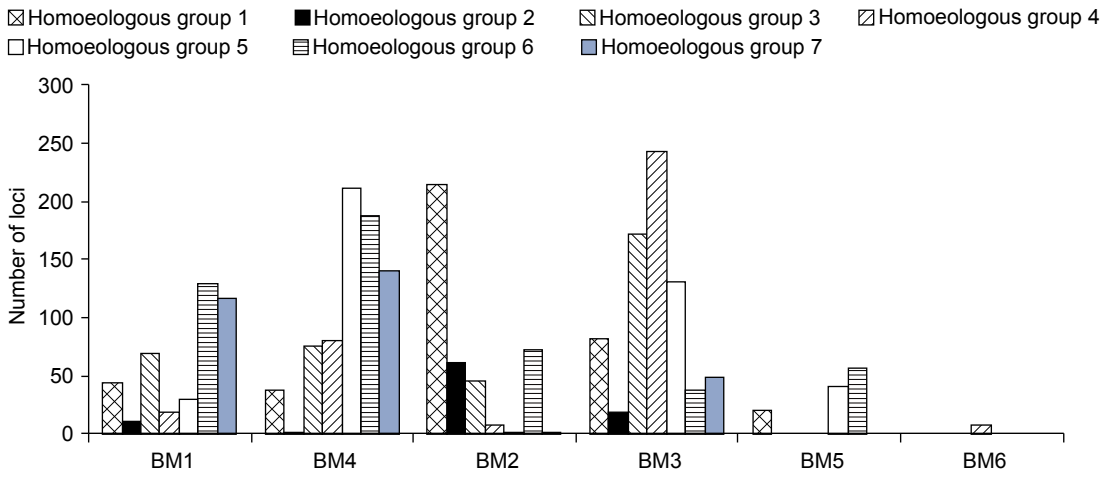

Fig. 4 Distribution of genomic alleles specific to six sibling lines (BM 1–6) on the seven wheat homoeologous groups.

Table 5 Genomic regions specific to BM1, BM4, and BM1 and 4 and important traits associated with these regions

ID	Chr.[1)]	Number of SNPs	Interval (cM)	Length (cM)	Allele origin	Associated QTL[2)*]	Reported QTL/Gene[3)]
BM1.R1	1B	40	[95.1, 114.1]	19.01	M	QTL2–TGW (M, 1.16), PH (M, 2.59)	GL (Wu *et al.* 2015), PH (Zanke *et al.* 2014b)
BM1.R2	2A	8	[148.8, 151.3]	2.50	B		
BM1.R3	3D	61	[141.8, 149.8]	8.01	B		
BM1.R4	4B	5	[84.8, 87.0]	2.23	M	QTL19–SNS (M, 0.45)	PH (Zanke *et al.* 2014b)
BM1.R5	5B	13	[29.1, 38.3]	9.17	M	QTL23–ETN (B, 1.22), SL (B, 0.3)	TGW (Wu *et al.* 2015), GT (Wu *et al.* 2015), HD (Zanke *et al.* 2014a)
BM1.R6	6A	9	[3.4, 6.4]	3.00	M		
BM1.R7	6A	115	[77.9, 80.7]	2.84	B	QTL29–SNS (M, 0.49), GNS (M, 1.72), PH (M, 2.19)	TGW (Sukumaran *et al.* 2015) PH (Zanke *et al.* 2014b) Yr/Lr (Kertho *et al.* 2015)
BM1.R8	7A	27	[33.2, 36.1]	2.81	B	QTL32–SNS (M, 0.82)	PH (Zanke *et al.* 2014b)
BM1.R9	7A	53	[42.1, 52.4]	10.27	B		PH (Zanke *et al.* 2014b)
BM1.R10	7A	11	[59.1, 64.6]	5.52	B		
BM1.R11	7A	18	[113.3, 115.3]	1.98	B	QTL33–TGW (B, 0.85), PH (B, 3.92)	
BM4.R1	1A	19	[56.4, 65.4]	9.04	B		
BM4.R2	1D	8	[21.8, 28.2]	6.41	B		Yr (Naruoka *et al.* 2015)
BM4.R3	3A	42	[13.5, 31.2]	17.69	B		
BM4.R4	3B	5	[9.7, 11.9]	2.18	M		
BM4.R5	3B	9	[99.4, 102.5]	3.11	M	QTL14–ETN (M, 1.4)	
BM4.R6	4B	23	[54.6, 63.0]	4.16	B	QTL18–GNS (M, 1.77)	
BM4.R7	4B	57	[71.3, 79.7]	8.45	B	QTL19–SNS (M, 0.45)	PH (Zanke *et al.* 2014b), Maturity (Sukumaran *et al.* 2015), *Rht*-B1&*Rht*-D1 (Lopes *et al.* 2015)
BM4.R8	5A	193	[52.1, 70.3]	18.19	B	QTL21–GNS (B, 4.22), SL (B, 0.89)	PH (Zanke *et al.* 2014a), HD (Zanke *et al.* 2014a), Lr (Kertho *et al.* 2015)
BM4.R9	5B	8	[142.6, 144.3]	1.65	B	QTL26–GNS (B, 1.46)	
BM4.R10	6A	103	[19.2, 43.1]	23.86	M	QTL33–SNS (M, 0.49), PH (M, 2.19), GNS (M, 1.72)	HD (Zanke *et al.* 2014a)
BM4.R11	6B	69	[57.0, 67.2]	6.44	M	QTL30–PH (B, 8.76)	GW (Wu *et al.* 2015), GT (Wu *et al.* 2015), PH (Zanke *et al.* 2014b), Yr (Maccaferri *et al.* 2015)

(Continued on next page)

Table 5 (Continued from preceding page)

ID	Chr.[1)]	Number of SNPs	Interval (cM)	Length (cM)	Allele origin	Associated QTL[2)*]	Reported QTL/Gene[3)]
BM4.R12	6D	4	[20.4, 26.9]	6.49	B		
BM4.R13	7B	136	[64.9, 82.9]	18.02	M	QTL36–PH (B, 2.41)	GL (Wu *et al.* 2015), HD (Zanke *et al.* 2014a), Yr (Maccaferri *et al.* 2015)
BM1-4.R1	1A	13	[50.7, 51.9]	1.28	B		
BM1-4.R2	1B	53	[43.7, 60.6]	16.96	M	QTL2–TGW (M, 1.16), PH (M, 2.59)	HD (Zanke *et al.* 2014a), Yr (Zegeye *et al.* 2014; Kertho *et al.* 2015, Naruoka *et al.* 2015)
BM1-4.R3	2B	54	[95.8, 99.2]	3.33	M		PH (Zanke *et al.* 2014b), Yr (Maccaferri *et al.* 2015)
BM1-4.R4	3B	30	[85.0, 97.6]	12.59	M	QTL14–ETN (M, 1.4)	
BM1-4.R5	5A	17	[49.0, 51.4]	2.42	B		PH (Zanke *et al.* 2014b), HD (Zanke *et al.* 2014a), TGW (Wu *et al.* 2015), Yr (Zegeye *et al.* 2014)
BM1-4.R6	5B	8	[112.4, 116.1]	3.74	M	QTL25–PH (B, 3.09)	HD (Zanke *et al.* 2014a), HD (Lopes *et al.* 2015)
BM1-4.R7	6D	27	[133.5, 134.8]	1.25	M		HD (Zanke *et al.* 2014a)
BM1-4.R8	6D	5	[155.6, 160.4]	4.86	M		
BM1-4.R9	7B	5	[167.6, 171.1]	3.55	B	QTL37–ETN (B, 1.51)	PH (Zanke *et al.* 2014b), HD (Zanke *et al.* 2014a)
BM1-4.R10	7D	24	[22.8, 32.2]	9.31	M		PH (Zanke *et al.* 2014b)

[1)] Chr., chromosome.
[2)] TGW, thousand grain weight; PH, plant height; SNS, spikelet number per spike; ETN, effective tiller number; GNS, grain number per spike; SL, spike length.
[3)] GL, grain length; GT, grain thickness; HD, heading date; Yr, stripe rust; and Lr, leaf rust; GW, grain width.
*, unpublished results.

these regions in BM4 derivative lines to assess the genetic contributions of the founder parent to the performance of progeny and the potential value of these regions for further improvement in breeding.

5. Conclusion

Phenotypic and genomic comparisons indicated that both the widely planted cultivar BM1 and the founder parent BM4 were superior to other sibling lines based on performance and have specific alleles and regions that differ from these other lines and are found to associate with favorable QTLs. Furthermore, BM4 has more genetic diversity than BM1 based on the number of specific alleles, regions and recombination breakpoints. Our work illustrates that the combination of phenotypic and SNP genotyping analyses is useful for revealing the genomic characteristics speicifc to and shared by elite common wheat lines derived from the parents, though the resolution needs to be improved through using a higher number of polymorphic SNPs or by performing additional complementary experiments.

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Appendix associated with this paper can be available on http://www.ChinaAgriSci.com/V2/En/appendix.htm

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