Assessment of Heterosis Based on Genetic Distance Estimated Using SNP in Common Wheat

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Abstract: This study assessed the genetic distance (GD) between parental genotypes using single nucleotide polymorphism (SNP) DNA markers and evaluated the correlation between GD and heterosis in common wheat. We examined the performance of parents and hybrids in a field experiment conducted in a randomized block design at a Shihezi location with three replications. Different traits such as the height of the parents and the F1 generation, number of harvested ears, number of grains per panicle, grain weight per panicle, 1000-grain weight, and grain yield were examined. Genotyping using a wheat 90K SNP chip determined the GD between the parents and analyzed the relationship between GD and heterotic performance of hybrids in wheat. Cluster analysis based on GD estimated using SNP chips divided the 20 elite parents into five groups which were almost consistent with the parental pedigree. Correlation analysis showed a significant association between GD and mid-parent heterosis (MPH) of 1000-grain weight. However, GD and high-parent heterosis (HPH) of 1000-grain weight showed no significant correlation. There was a weak correlation between GD and with spikelet number, harvested spikes, and yield at MPH or HPH. Hence, SNP analysis may be utilized in allocating wheat parents to heterotic groups. However, the correlation between SNP-based GD and hybrid performance still remains unclear.

Keywords: genetic distance; heterosis; single nucleotide polymorphism; heterosis prediction

1. Introduction

Wheat (*Triticum aestivum L.*) is the second largest food crop in China. The annual planting area is over 26.66 million hectares, accounting for 27% of the area of food crops; and the total output is more than 100 million tons, accounting for 22% of the output of food crops. Therefore, the continuous increases in the production of wheat and its stable production is a food security concern for China. However, pests and diseases are increasing with the warming of the global climate posing a threat to the safe production of wheat. Heterosis is a common phenomenon in nature. Plant breeders exploit heterosis as an effective genetic strategy to increase yield and stress resistance in wheat [1]. Freeman reported heterosis in wheat for the first time in 1919, where the F1 generation showed increased plant height when compared with their parents [2]. Wilson and Rose first discovered cytoplasmic male sterility and restoration in *Triticum timopheevi*, and utilized the three lines (male sterile line, maintainer line, and restorer line) to develop a wheat hybrid in 1962. Hybrid wheat research has made significant progress in understanding infertility mechanisms [3], the cloning of sterility genes [4], and research on reproduction technology [5] over the last three decades. However, wheat hybrids were not widely promoted and used around the world. The major constraint is to select elite parents to create a strong heterosis combination [6–8].

Traditionally, breeders estimated heterosis in wheat by observing progeny traits. These are often influenced by factors such as genetic relation of the parents and environmental conditions. Morphological observations also waste a lot of labor force and money. Therefore, some breeders have used the analysis of combining ability [9–12], and the heterosis group division [13,14] to improve the breeding efficiency of strong heterosis combination.

Molecular markers have been rapidly developed and widely used because they can accurately identify crop varieties and carry out marker-assisted breeding. A few studies have used molecular markers such as restriction fragment length polymorphism (RFLP), randomly amplified polymorphic DNA (RAPD), or simple sequence repeat (SSR) to estimate genetic diversity of wheat cultivars and lines [15–17]. However, the wheat genome is tremendous with many repeat sequences, and the assessment of wheat GD requires high-density molecular markers. SNP refers to a single-nucleotide mutation in the genome. The SNP marker was widely used due to cost effectiveness to assay a uniform distribution on chromosomes [18–20]. Presently, the rapid and high-throughput SNP genotyping platform offers opportunities to analyze genetic diversity [21], divided parents heterotic group [22], QTL mapping and heterosis prediction [23–25].

Studies have shown that statistically significant but low correlations exist between the different estimates of genetic diversity and F1 performance or MPH for grain yield and other related traits [26]. Many scientists have accurately predicted the hybrid performance in maize using GD based on SSR and the SNP molecular marker [27]. However, fewer studies have analyzed the relationship between GD and wheat heterosis. The present study used 20 elite wheat cultivars and lines to construct incomplete double-crossing populations, and investigated yield and heterosis of five yield-related traits. It involved genotyping using wheat 90K SNP array (Illumina) to estimate the GD between parents. We further analyzed the relationship between GD and heterosis, and discussed the application potential of wheat 90K SNP array in selecting strong crosses of hybrid wheat.

2. Materials and Methods

2.1. Experimental Material

A set of 20 winter wheat cultivars and lines were selected for this study from different ecological regions, representing a wide range of genetic backgrounds. This included 15 elite varieties (lines) from Huanghuai area and Xinjiang local, China. The five AL-type restorer lines were produced by the Institute of Crop Research, Xinjiang Academy of Agri-Reclamation Science (XAARS), China.

2.2. Field Trial

The test was conducted at Xinjiang Academy of Agri-Reclamation Sciences during 2016–2017 growing season. The 20 elite parents were crossed in a half-diallel mating design to produce 100 hybrids and a total of 120 entries were grown. The field trials used a randomized complete block design with three replications. Plots consisted of five rows each, 1.5 m long with a row spacing of 0.25 m. Plant density was approximately 2.7×10^6 plants ha^{-1}.

2.3. Character Investigation and Data Collection

Ten plant heights were measured from the ground level to the tip of the spikes at maturity in each plot. After harvesting, other agronomic traits including grain yield, number of spikelets per hectare, number of kernels per spike, weight of kernels per spike, and 1000-grain weights were determined. Grain yield data were collected from the middle row of each plot to reduce the effects of competition among parents, checks, and crosses.

Formulas for calculating the mid-parent heterosis (MPH) and the high-parent heterosis (HPH) were as follows:

MPH% = (F1 value − parent mean)/parent mean × 100;

HPH % = (F1 value − high parent)/high parent × 100, where F1 is hybrid performance, and high parent was the higher yielding. MPH and HPH were tested for significance with an ordinary *t*-test. Combining ability analysis was estimated according to Kalhoro et al. [10].

2.4. DNA Extraction and SNP Genotyping

The parental DNA was extracted from plant tissue following the standard extraction protocol for genomic DNA using the Tiangen kit (Tiangen Biotech, Beijing, China). Quality and quantity of the extracted DNA were analyzed according to the whole genome sample delivery request. The specific requirements were as follows: (1) DNA concentration greater than 50 ng μL^{-1}; (2) total DNA greater than 1 μg; and (3) 260/280 absorbance ratio between 1.7 and 2.1. DNA samples were sent to Beijing Compass Biotechnology Co., Ltd. for SNP genotyping. The chip test procedure was performed on an Infinium HD SNP chip (Illumina Inc.). The steps were as follows: (1) DNA quantification; (2) DNA amplification; (3) DNA fragmentation; (4) fragmented DNA precipitation and resuspension; (5) DNA and chip hybridization; (6) single base extension and staining; (7) chip scanning; and (8) data analysis.

2.5. Quality Control of SNP Data

The SNP array showed a detection rate between 0.975 and 0.985 (average of 0.98) with SNP markers with deletion rates between 0 and 1 (average of 0.042). We excluded and used the remaining (4799) SNPs based on removal rate and minor allele frequency, with removal rate greater than 10% and a minor allele frequency (MAF) less than 0.01.

2.6. Statistical Analysis

Yield and yield-related data were analyzed using SPSS version 22.0. SNP array data were processed using the genotyping module within GenomeStudio version 2.0 (Illumina). This included standardization, clustering, and genotyping of the raw data. Genetic distance was analyzed using MEGA version 5.05. The correlation analysis among the genetic distance and heterosis was analyzed using SPSS version 22.0.

3. Results and Analysis

3.1. Estimation of Genetic Distance and Clustering of Parents

Among the 20 parents, the GD between Xiaoyan 54 and Xindong 36 was the smallest (0.008), the GD between Yannong 19 and Xindong 41 was the largest (0.276), and the GD between all parents consisted of a range from 0.008 to 0.276, with an average of 0.212. The GD between restorer lines consisted of range from 0.078 to 0.189 (Table 1). Based on cluster analysis, the 20 parents were divided into five main groups as follows: group I was the four restorer lines, Xinjiang local varieties (lines) were divided into group II and III according to cultivars (lines) origin, group IV was the new variety in the North China winter wheat region, and group V was the new variety (line) in the Huanghuai wheat region. The results showed that the grouping was almost consistent with the actual pedigree (Figure 1).

Table 1. Genetic distance estimation between parents using SNP molecular markers.

GD	XD33	XD36	KD002	XD41	BM38	KM1	GY8901	XY54	XD51	08(153)	XD52	AR144-1	AR2-4	09AR2	12AR2	AR20-2	05(65)	XY22	PB717
XD36	0.061																		
KD002	0.059	0.047																	
XD41	0.019	0.059	0.062																
BM38	0.066	0.074	0.067	0.069															
KM1	0.073	0.058	0.064	0.071	0.067														
GY8901	0.070	0.070	0.067	0.072	0.065	0.069													
XY54	0.060	0.002	0.046	0.059	0.073	0.057	0.069												
XD51	0.067	0.052	0.055	0.063	0.067	0.063	0.064	0.051											
08(153)	0.058	0.057	0.038	0.058	0.063	0.068	0.067	0.056	0.060										
XD52	0.069	0.055	0.049	0.067	0.072	0.050	0.077	0.054	0.058	0.059									
AR144-1	0.064	0.070	0.060	0.068	0.073	0.076	0.070	0.069	0.074	0.067	0.076								
AR2-4	0.064	0.053	0.035	0.067	0.072	0.066	0.068	0.052	0.059	0.056	0.053	0.030							
09AR2	0.064	0.056	0.043	0.067	0.071	0.070	0.068	0.055	0.063	0.059	0.058	0.025	0.013						
12AR2	0.066	0.061	0.048	0.065	0.070	0.072	0.070	0.059	0.064	0.060	0.056	0.053	0.042	0.047					
AR20-2	0.073	0.075	0.075	0.075	0.076	0.071	0.079	0.074	0.080	0.078	0.070	0.036	0.060	0.053	0.066				
05(65)	0.029	0.064	0.061	0.043	0.068	0.071	0.071	0.064	0.066	0.058	0.071	0.068	0.064	0.067	0.065	0.080			
XY22	0.079	0.084	0.082	0.079	0.079	0.065	0.078	0.083	0.083	0.077	0.070	0.072	0.074	0.073	0.075	0.065	0.079		
PB717	0.071	0.073	0.068	0.071	0.061	0.055	0.080	0.072	0.074	0.062	0.056	0.075	0.068	0.071	0.074	0.066	0.073	0.067	
YN19	0.075	0.072	0.069	0.076	0.074	0.080	0.080	0.071	0.071	0.067	0.074	0.073	0.070	0.071	0.071	0.059	0.076	0.074	0.070

Note: GD = Genetic distance; XD33 = Xindong33; XD36 = Xindong36; KD002 = Kendong002; XD41 = Xindong41; BM38 = Baomai38; KM1 = Kemai1; GY8901 = Gaoyou8901; XY54 = Xiaoyan54; XD51 = Xindong51; 08(153) = 2008(153); XD52 = Xindong52; AR144-1 = 99AR144-1; AR2-4 = 09AR2-4; 09AR2 = 09AR2; 12AR2 = 2012AR2; AR20-2 = 09AR20-2; 05(65) = 2005(65); XY22 = Xiaoyan22; PB717 = Pubing717; YN19 = Yannong19.
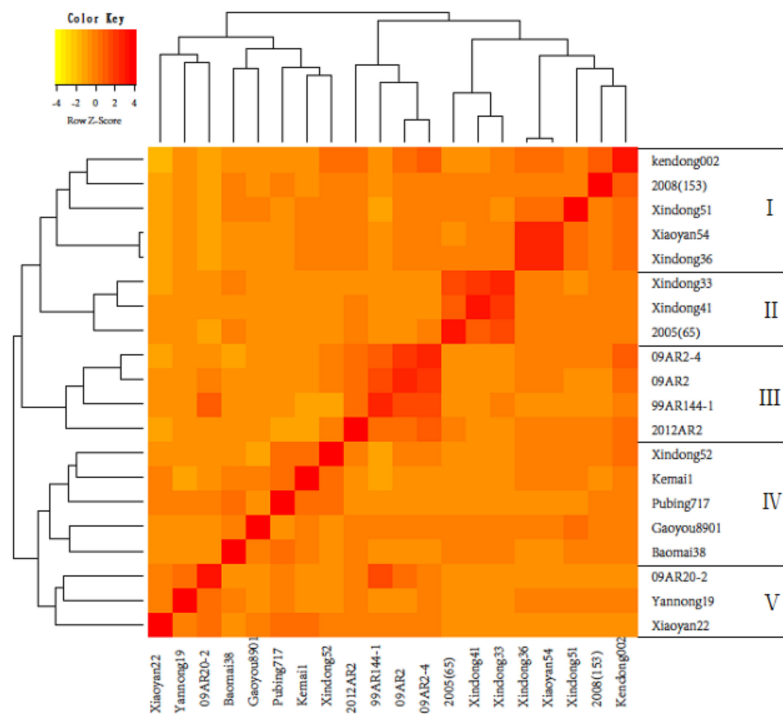
Figure 1. Cluster analysis of 20 elite parents.

3.2. Yield Performance of Parents and F1 Hybrids

The yield performance and general combining ability of the parents and their F1 hybrids are shown in Table 2. The results showed that the grain yield of F1 generation ranged from 468.0 g to 1279.5 g, and the average yield of 100 hybrid combinations was 909.0 g. Among all hybrid combinations, 10 combinations showed 20% greater yield than the all hybrids combined average and 18 combinations showed 10%–20% greater yield than all the combination average. The combination Pubing 717 × Xindong 41 produced a grain yield of 1279.5 g, which was 40.76% above average and the combination 09AR2 × 09AR20-2 produced a grain yield of 468.0 g, which was 48.51% below average.

Table 2. Yield performance and general combining ability of F1 hybrid combinations.

Yield	XD52	XD41	AR144-1	08(153)	GY8901	05(65)	AR20-2	YN19	BM38	XY22	Female GCA
PB717	981.00	1279.50	1030.00	953.30	1142.00	1069.50	1147.00	1073.70	900.00	1000.50	148.69
KD002	1184.00	1161.00	1163.50	953.00	882.00	1120.00	985.00	785.00	1005.50	1079.30	122.87
KM1	1220.00	1066.00	866.30	1019.30	958.00	933.00	1152.70	880.00	981.30	1048.50	103.55
XY54	1036.00	874.00	875.00	872.00	995.70	911.00	927.00	946.30	988.70	1035.00	37.11
XD36	1020.70	887.30	913.30	968.70	892.30	898.70	1097.00	884.00	776.30	1003.00	25.17
XD33	948.00	1029.00	974.50	1068.00	931.00	1002.70	696.00	1113.50	899.00	652.00	22.41
XD51	837.00	878.00	1026.50	894.50	984.00	782.50	729.00	866.50	977.00	977.00	−13.76
12AR2	978.70	967.70	895.30	861.30	766.00	777.70	934.00	890.50	835.70	483.70	−69.90
AR2-4	860.70	812.50	849.50	638.00	830.00	870.70	687.00	787.00	689.30	471.70	−159.32
09AR2	911.70	854.70	746.30	773.30	565.30	530.00	468.00	574.70	635.00	862.00	−216.86
Male GCA	89.23	72.42	25.47	−8.41	−17.96	−18.97	−26.28	−28.43	−39.77	−47.28	

Note: GCA = general combining ability.

3.3. Correlation of Yield-Related Traits between Parents and F1 Hybrids

Correlation analysis of yield and five yield-related traits of parents and F1 generation showed a significant positive association between grain number per spike and grain weight per ear and plot yield ($p > 0.05$, $r = 0.78, 0.63$) (Table 3). Grain weight per spike and plot yield was positively correlated ($p < 0.05$, $r = 0.63$). However, 1000-grain weight was negatively correlated with grain number per spike and plot yield ($p < 0.05$, $r = −0.50, −0.15$). We also analyzed the correlation of yield and yield-related traits for the selected 28 strong heterosis combinations. The results showed a significant positive

correlation between number of harvested spikes and yield of the plot ($p > 0.05$, $r = 0.65$), between number of grains per spike and grain weight per ear ($p > 0.05$, $r = 0.63$), and between grain weight per spike and 1000-grain weight ($p > 0.05$, $r = 0.54$). The number of harvested spikes was negatively correlated with grain weight per panicle ($p < 0.05$, $r = -0.74$).

Table 3. Heterosis of yield-related traits and yield in F1 hybrids.

	Harvest of Spikelets	Grain Number per Spike	Grain Weight per Spike	1000-Grain Weight	Yield
Harvest of spikelets	1.00	−0.16	−0.43	−0.36	0.42
Grain number per spike		1.00	0.78	−0.50	0.63
Grain weight per spike			1.00	0.14	0.63
1000-grain weight				1.00	−0.15
Yield					1.00

3.4. Analysis of Mid-Parent and High-Parent Heterosis of Yield in F1 Generation

MPH of the 10 female parents ranged from −18.67 to 20.42 and HPH ranged from −24.18 to 12.82. MPH of the 10 male parents ranged from −11.07 to 13.30 and HPH ranged from −21.17 to 5.06. For the 100 combinations, MPH ranged from −47.47 to 45.43. Meanwhile, 19 combinations showed a MPH of more than 20%, of which 16 showed more than 10% to 20%. HPH ranged from −50.84 to 32.54. Here, nine combinations showed a HPH of more than 20%, accounting for 9% of the hybrid combinations; 14 combinations showed more than 10% to 20%, accounting for 14% of the hybrid combinations. The combination Kendong 002 × Xiaoyan 22 showed the largest heterosis of 45.43% and a HPH of 27.73%. The combination Kendong 002 × 2005(65) showed the highest HPH of 32.54 and a MPH of 36.81% (Table 4). Both mid-parent and high-parent heterosis of eight hybrid combinations exceeded 20%.

Table 4. Mid and high-parental heterosis in F1 hybrid yield.

Cultivars (Lines)		XD52	XD41	AR144-1	08(153)	GY8901	05(65)	AR20-2	YN19	BM38	XY22
PB717	MPH	−5.00	30.36	7.14	−12.35	25.24	17.16	15.55	19.34	−0.89	19.63
	HPH	−9.72	23.82	−0.30	−16.52	10.52	3.50	11.00	3.87	−12.90	−3.18
KD002	MPH	22.59	30.84	34.17	−4.07	7.87	36.81	9.63	−2.54	23.52	45.43
	HPH	8.96	24.88	30.83	−16.50	4.38	32.54	3.47	−7.10	18.99	27.73
KM1	MPH	22.26	15.98	−1.43	−0.60	12.75	9.68	23.88	5.07	15.94	35.44
	HPH	12.27	14.66	−4.69	−10.74	5.39	2.64	21.34	−3.20	7.95	15.35
XY54	MPH	7.89	−0.87	1.57	−11.72	22.62	12.05	3.83	18.31	22.31	40.53
	HPH	−4.67	−0.59	−1.61	−23.64	19.43	9.27	−2.60	13.51	18.59	24.15
XD36	MPH	4.29	−1.43	3.78	−3.74	7.44	8.08	20.37	8.02	−6.11	32.84
	HPH	−6.07	−4.56	2.69	−15.17	2.48	3.22	15.23	1.53	−10.83	15.19
XD33	MPH	−3.20	14.23	10.65	6.06	12.01	20.49	−23.68	35.96	8.64	−13.72
	HPH	−12.76	10.68	9.52	−6.48	6.77	14.98	−26.89	27.69	3.09	−25.23
XD51	MPH	−15.32	−3.51	15.36	−11.97	8.13	−6.99	−20.86	4.63	16.77	27.74
	HPH	−22.97	−1.38	15.29	−21.67	5.84	−12.11	−23.42	−2.67	15.29	9.73
12AR2	MPH	−3.05	3.94	−1.70	−16.95	−11.07	−9.91	−0.87	4.87	−2.56	−38.45
	HPH	−9.93	3.79	−3.97	−24.58	−17.84	−16.58	−1.89	−4.48	−10.36	−0.48
AR 2-4	MPH	−8.01	−5.21	1.49	−33.77	5.39	10.42	−20.88	1.51	−12.06	−33.75
	HPH	−20.79	−12.60	−4.47	−44.13	5.02	9.89	−27.84	−5.18	−12.15	−39.88
09AR2	MPH	−4.86	−2.85	−13.15	−21.57	−30.22	−34.66	−47.47	−27.98	−21.26	17.33
	HPH	−16.10	−8.06	−16.08	−32.28	−31.89	−36.14	−50.84	−30.76	−23.49	3.85

3.5. Correlation between Genetic Distance and Hybrid Performance

We selected 10 hybrid combinations with yield heterosis of 20% over the average for the correlation analysis. The results showed that the plot yield variation ranged from 1113.5 g to 1279.5 g, the MPH variation ranged from 20.69 to 36.81, the female general combining ability ranged from 22.41 to 148.69, and the male general combining ability ranged from −28.43 to 89.23. The special combining ability of the 10 strong heterosis combinations ranged from 56.75 to 210.52. According to the results of the cluster, we found that among strong heterosis combinations that cross type was mostly IV × II (V) and I × III (II) (Table 5). Therefore, we infer that group I and IV (as the female parent crosses with other groups of parents) tend to produce some strong heterosis combinations.

Table 5. Relationship between group division and strong combination yield, MPH, GCA and SCA.

	Plot Yield (g)	MPH (%)	GCA (♀), (♂)	SCA	SNP Clustering Combination Type
Pubing717 × Xindong41	1279.5	30.36	148.69, 72.42	149.66	IV × III
Pubing717 × Gaoyou8901	1142.0	25.24	148.69, −17.96	102.26	IV ×V
Pubing717 × 09AR20-2	1149.0	20.69	148.69, −26.28	115.58	IV × II
Kemai1 × Xindong52	1220.0	22.26	103.55, 89.23	118.26	IV × I
Kemai1 × 09AR20-2	1152.7	23.88	103.55, −26.28	166.47	IV × II
Kendong002 × 99AR144-1	1163.5	34.17	122.87, 25.47	106.20	I × II
Kendong002 × Xindong41	1161.0	30.84	122.87, 72.42	56.75	I × III
Kendong002 × 2005 (65)	1120.0	36.81	122.87, −18.97	107.14	I × III
Kendong002 × Xindong52	1184.0	22.59	122.87, 89.23	62.94	I × I
Xindong33 × Yannong19	1113.5	35.96	22.41, −28.43	210.52	III × V

Note: MPH = Mid-parent heterosis; GCA = general combining ability; SCA = special combining ability

Correlation analysis proved a significant association ($p > 0.05$) between GD based on SNP and MPH of 1000-grain weight. However, HPH of 1000-grain weight did not show a significant correlation ($p < 0.05$) (Table 6). Additionally, analysis showed weak correlations ($p < 0.05$) with mid-parent and high-parent heterosis of grain number per spike, harvested spikes, and plot yield.

Table 6. Correlation between GD and MPH and HPH of yield and yield related traits.

Trait	Correlation Coefficient	Trait	Correlation Coefficient
Kernels per spike MPH	−0.012	Spike number per acreage MPH	−0.257
Kernels per spike HPH	−0.198	Spike number per acreage HPH	−0.203
Thousand seed weight MPH	0.399 *	Yield per acreage MPH	0.371
Thousand seed weight HPH	0.365	Yield per acreage HPH	0.208

Note: GD = genetic distance; * Indicates significance at 0.05 levels. MPH: Mid-parent heterosis; HPH: High-parent heterosis.

4. Discussion

The main target of hybrid crop breeding is to identify parents with high genetic diversity [28] that have a high proportion of selected strong heterosis cross in F1 generation. Previous studies have shown that genetic diversity for 26 microsatellite loci varied from 0.43 to 0.94 with an average of 0.77 in 998 bread wheat cultivars [16]. The average genetic diversity based on AFLP (0.502) and SSR (0.503) markers were similar in Iranian bread wheat [15]. In this study, we estimated the GD from 0.008 to 0.276 with an average distance of 0.212. This agrees well with published results that found average polymorphism information content of 0.18 among 20 US elite wheat cultivars using SNP marker [29]. Compared to the previous studies on common wheat, this level of GD is low. Generally, polymorphism information content for SNPs ranged from 0.04 to 0.50 in wheat [30]. Because SNP markers are mainly bi-allelic, the GD cannot exceed 0.50 [31]. Furthermore, SNP density ranges from one per 370 bp to one per 540 bp in the wheat genome [30]. Therefore, SNP markers have good genome-wide coverage compared to traditional molecular markers and are more efficient in GD analysis in wheat cultivars [32]. In this study, cluster analysis results showed the elite 20 parents were divided into five groups. The grouping generated by SNP data showed a certain agreement with the pedigree. Amongst them, Xiaoyan 54 and Xindong 36, Xindong 51, 2008 (153), and Dongdong 002 were classified into one group, of which Xindong 36, Xindong 51, 2008 (153) and Kendong 002 were all from the same origin of breeding, the Xinjiang Academy of Agricultural Sciences. Looking at the pedigree of Xiaoyan 54, we see that they have no same parents with the other four varieties (lines). 09AR20-2 and the other four restorer lines were not assigned in the group, but get together with the wheat varieties in the northern wheat region. Looking at the pedigree, one of the parents of 09AR20-2 was a Jimai 26 from Hebei province, North China. Therefore, carrying out wheat groupings by pedigrees has certain limitations. For this reason, SNP markers are not only more accurate, but also improve efficiency in terms of wheat genetic distance analysis.

The major aim in hybrid breeding is the exploitation of heterosis. Few studies have used GD to estimated F1 hybrid yield for improving the breeding efficiency on wheat heterosis utilization. However, the correlation between GD and heterosis was still unclear. Previous studies have shown significant correlation between GD and heterosis for the quality character such as water absorption, dough development [33] and grain weight in wheat [34]. However, in our study, the results demonstrated that GDs were not significantly correlated with heterosis effects for all the analyzed traits. However, a positive significant correlation was found between MPH and GD for 1000-grain weight. A similar analysis was reported by Liu et al. [14]. Therefore, we inferred that the relationship between GD and hybrid performance is variable. The first reason depends on the genetic materials used in the study. The second reason is that the relative amount of heterosis also depends on environmental factors. These inference results are consistent with the results of Zhang et al. [35] and Dreisigacker et al. [36].

5. Conclusions

In the current study, we concluded that the SNP chip was an effective tool for the evaluation of wheat GD, and GD between all parents was in the range from 0.008 to 0.276. A SNP chip can also be used as a potential tool grouping the parents. The relationship between GD and hybrid performance showed no significant correlation. To accurately predict heterosis of wheat based on GD, further research is required.

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