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*Article*

# Genome-Wide Association Study for Yield and Yield-Related Traits in Chinese Spring Wheat

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**Abstract:** Wheat (*Triticum aestivum* L.) is one of the important grain crops that fulfill global food security requirements. Understanding the genetic basis of wheat yield and related traits is crucial for increasing yield through marker-assisted selection (MAS). In this study, a phenotypic analysis was conducted on the yield and related traits of 192 Chinese spring wheat genotypes in six field environments. Based on the 90K wheat SNP iSelect assay, a genome-wide association study (GWAS) identified 84 stable and significantly associated signals at 50 loci for 8 out of the 10 analyzed traits. These traits included grain yield (1), plant height (6), spike length (21), productive spikelet rate (12), kernel number per spikelet (1), kernel number per main spike (2), thousand kernel weight (5), and test weight (2). Seventy-one stable SNP markers were mapped to annotated genes, with 51 of them located in the coding sequences (CDSs) of 47 explanatory genes. Haplotype analysis revealed three blocks on chromosome 5A and two blocks on chromosome 5D associated with plant height (PH). Varieties with different haplotypes at these loci displayed a significant difference in plant height. The performance of traits was improved by increasing the number of superior alleles for productive spikelet rate and spike length. These results provided prospective alleles for controlling yield and yield composition in wheat breeding. These alleles could be used for marker-assisted selection to improve wheat yield.

**Keywords:** GWAS; haplotype analysis; wheat; yield; yield components

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## 1. Introduction

Wheat (*Triticum aestivum* L.) is a major cereal crop, meeting the global demand for food security [1–3]. The global wheat production for 2021–2022 is estimated to be over 778 million tons [4]. According to reports, wheat experiences an annual genetic gain of 1% [5]. However, in order to meet the demand of world population growth, the demand for wheat has been increasing by 1.7% annually [5]. In other words, by 2050, wheat production should increase by more than 50% compared to current levels in order to meet the demand of sustained population growth [5–7]. Accelerating the cultivation of high-yielding varieties is urgent.

Wheat yield is a complex polygenic genetic trait controlled by many small effect loci, with significant interactions between loci [8–10]. Due to its polygenic nature and the significant impact of environmental conditions, grain yield typically exhibits high genotype-environment interaction and low heritability [11]. This increases the challenge of improving

yield through phenotypic selection and hinders the progress of high-yield breeding [12]. Yield is primarily influenced by three factors: thousand kernel weight, kernel number per spike, and spike number per unit area [13–16]. It is also influenced by grain-related traits or yield components, such as ear weight and spike length [17]. Previous studies have found that the heritability of certain components is higher than that of grain yield itself [18–20]. Therefore, yield can be increased by improving yield components [21,22].

Through genome-wide association studies (GWASs) utilizing thousands to millions of data points generated by low-cost genotyping platforms [23], the genetic architecture of yield and yield components has been reported in much previous research [16,24–37]. Wheat has a planting history of over 4000 years in China and is widely cultivated in 10 major agricultural ecological regions, each with its own unique genetic characteristics [38,39]. This results in notable disparities in the objectives and criteria for enhancing wheat cultivars in these areas [40]. This study employed a GWAS approach with a 90K Illumina iSelect SNP array to analyze grain yield and its components in 192 different spring wheat genotypes. Studying and understanding the relationship between phenotype and genotype of yield and yield components will provide a valuable genetic resource for improving yield through marker-assisted selection methods.

## 2. Materials and Methods

### *2.1. Plant Materials and Field Trials*

The association panel consisted of 192 spring wheat genotypes, including varieties and breeding lines from various provinces in China. They were planted in Ershi, Shihezi, and Zhaosu, Xinjiang during the crop seasons of both 2012 and 2013. These environments were designated as 2012 Ershi (2012ES), 2012 Shihezi (2012SHZ), 2012 Zhaosu (2012ZS), 2013 Ershi (2013ES), 2013 Shihezi (2013SHZ), and 2013 Zhaosu (2013ZS). The field trial was conducted using a randomized complete block design with three replicates in each environment. Each block consisted of 10 rows, each 3 m long, with a row spacing of 25 cm and a plant spacing of 10 cm. The planting and harvesting dates, as well as experimental management, vary depending on the recommendations of each location in order to maximize yield potential. The key points of spring wheat planting technology are attached in the supplementary file.

### *2.2. Phenotype*

- Before harvesting, five main tillers from five randomly selected plants were chosen from the middle two rows of each plot to assess the following traits: plant height (PH), spike length (SL), spikelet number per spike (SNS), kernel number per spikelet (KNS), kernel number per main spike (KNMS), and kernel weight per main spike (KWMS).
- Productive spikelet rate (PSR) was calculated by dividing the number of productive spikelets by the total number of spikelets.
- After reaching full maturity, the grain yield (GY) was evaluated. All wheat plants in each cultivar's entire plot were harvested to measure the plot's yield. The results were then converted into yield per hectare (kg).
- The thousand-grain weight (TKW) was recorded by weighing 1000 grains in grams (g).
- Test weight (TW) was recorded by weighing one liter of grains in grams (g).

### *2.3. SNP Genotype*

The genomic DNA was extracted from 10-day-old seedlings using the CTAB procedure [41]. In 2015, genotyping of association groups was performed using the high-density wheat 90K Illumina iSelect SNP (Single Nucleotide Polymorphism) array by CapitalBio Technology company in Beijing (https://www.capitalbiotech.com/, accessed on 19 September 2023). According to the method described by Purcell et al. [42], all SNP markers with a call rate of less than 90% and a minor allele frequency (MAF) lower than 2% were excluded from the analysis for all genotypes. Determining the physical location of each SNP on wheat chromosomes, the SNP probe sequences were searched using BLAST

against the wheat genome assembly RefSeq v1.0 (https://wheat-urgi.versailles.inra.fr/Seq-Repository/Assemblies, accessed on 19 September 2023).

We provided detailed descriptions of the wheat population structure, principal component analysis (PCA), and SNP distribution on chromosomes in our earlier report [43].

### *2.4. Genome-Wide Association Study*

Marker-trait associations (MTAs) were estimated using the mixed linear model (MLM) implemented in TASSEL 5.0 [44]. The MLM method is a widely used approach in GWAS that takes into account the group structure (Q) and kinship matrix (K) as covariates (MLM: Q+K). This helps to minimize the possibility of obtaining false associations. The Q matrix was generated using Structure v2.3.4. The variance–covariance kinship matrix (K) reflects the relationships between individuals and was estimated using the scaled IBS method in TASSEL 5.0 [44]. To integrate the association results across various environments, the Bonferroni correction, $-\log10(20/47{,}362) \approx 3.37$, was calculated as a unified whole-genome significance threshold. The Bonferroni correction method is considered the most conservative method for selecting a threshold *P*-value because it assumes that every genetic variant tested is independent of the others. In order to avoid multiple significant associations within a single LD block, the support interval was determined to be 7 Mb, according to our earlier study [43].

### *2.5. Haplotype Analysis*

The haplotype analysis of significant SNP loci, where lines with different alleles exhibited significant phenotypic values ($p < 0.05$) in multiple environments, was performed using Haploview software version 4.2 [45]. The blocks were generated by Haploview based on confidence intervals provided by Gabriel et al. [46].

### *2.6. Candidate Genes*

The associated SNPs located within the candidate genes or intergenic regions were identified using the Chinese Spring annotation data. The protein function of candidate genes was predicted using the UniProt Protein Database (https://www.uniprot.org/, accessed on 19 September 2023) and Ensembl Plants (http://plants.ensembl.org/Triticum_aestivum/, accessed on 19 September 2023).

### *2.7. Statistical Analysis*

Descriptive statistics, Pearson's correlation coefficients (r) among yield and yield-related traits, and analysis of variance (ANOVA) were estimated using IBM SPSS Statistics 22 (https://www.ibm.com/support/pages/spss-statistics-220-available-download, accessed on 19 September 2023). The method for calculating broad-sense heritabilities ($h^2$) of yield and yield-related traits was described in our earlier report [43].

The average of the trait was calculated using the best linear unbiased predictor (BLUP) method [47,48] with the R package lme4 (version 1.1-33) [49].

The Manhattan and Q–Q diagrams were plotted using the R package CMplot (version 4.2.0), while the histogram of phenotypic effects of haplotypes was drawn in Origin 8.0.

## 3. Results

### *3.1. Phenotypic Assessment*

The coefficients of variation for yield and yield-related traits ranged from 1.63% for TW to 10.91% for SL, based on the BLUP value. The broad-sense heritability ($h^2$) estimates ranged from 0.24 to 0.89, with SL being the most heritable trait (0.89), followed by TKW (0.81), PSR (0.78), SNS (0.77), PH (0.76), TW (0.72), and KNMS (0.71); KNS (0.65), and GY (0.6) were moderately heritable, while KWMS was the least heritable trait (0.24, Table 1). The frequency distributions of BLUP values for yield and yield-related traits were all nearly symmetrically distributed (Figure S1). The analysis of variance results showed that almost all traits exhibited significant differences in genotypes, locations, and years (Table S2).

**Table 1.** Phenotypic variations and heritabilities of yield and yield-related traits based on BLUP value.

| Trait | Minimum | Maximum | Mean | SD | CV(%) | $h^2$ |
|---|---|---|---|---|---|---|
| GY | 2589.66 | 4251.07 | 3503.34 | 314.41 | 8.97 | 0.60 |
| PH | 75.46 | 107.88 | 90.17 | 6.11 | 6.77 | 0.76 |
| SL | 6.17 | 13.49 | 9.70 | 1.06 | 10.91 | 0.89 |
| SNS | 15.55 | 20.32 | 18.19 | 0.85 | 4.69 | 0.77 |
| PSR | 84.46 | 95.90 | 91.91 | 1.80 | 1.96 | 0.78 |
| KNS | 3.11 | 4.31 | 3.70 | 0.22 | 5.89 | 0.65 |
| KNMS | 31.72 | 54.34 | 42.65 | 3.74 | 8.77 | 0.71 |
| KWMS | 31.72 | 54.34 | 42.65 | 3.74 | 8.77 | 0.24 |
| TKW | 35.45 | 50.32 | 41.98 | 2.71 | 6.45 | 0.81 |
| TW | 711.40 | 792.09 | 761.21 | 12.42 | 1.63 | 0.72 |

GY, grain yield; PH, plant height; SL, spike length; SNS, spikelet number of spike; PSR, productive spikelet rate; KNS, kernel number per spikelet; KNMS, kernel number per main spike; KWMS, kernel weight per main spike; TKW, thousand kernel weight; TW, test weight; SD, standard deviation; CV, coefficient of variations; $h^2$, broad-sense heritability.

Correlation analysis was conducted among yield and yield-related traits based on the BLUP values across six environments, and many correlations were found (Table 2). GY showed a highly significant and positive correlation with PSR, KNS, KNMS, KWMS, TKW, and TW (0.35 **, 0.34 **, 0.40 **, 0.44 **, 0.60 **, and 0.45 **, respectively), while it was extremely and negatively correlated with PH (−0.22 **). PH showed a highly positive correlation with SNS (0.24 **), while it exhibited a highly negative correlation with PSR and KNS (−0.34 ** and −0.46 **, respectively) and a significant negative correlation with KNMS (−0.15 *). There were strong correlations, either positive or negative, among the yield components. For example, SL showed a significantly positive correlation with SNS, KNMS, and KWMS (0.24 **, 0.27 **, and 0.33 **, respectively); SNS had a significantly negative correlation with PSR and TKW (−0.22 ** and −0.21 **, respectively).

**Table 2.** Phenotypic correlations (r) of the yield and yield components for the Chinese spring wheat association mapping panel.

| Trait | GY | PH | SL | SNS | PSR | KNS | KNMS | KWMS | TKW |
|---|---|---|---|---|---|---|---|---|---|
| PH | −0.22 ** | | | | | | | | |
| SL | 0.13 | 0.08 | | | | | | | |
| SNS | −0.13 | 0.24 ** | 0.24 ** | | | | | | |
| PSR | 0.35 ** | −0.34 ** | −0.14 * | −0.22 ** | | | | | |
| KNS | 0.34 ** | −0.46 ** | 0.14 | −0.06 | 0.27 ** | | | | |
| KNMS | 0.40 ** | −0.15 * | 0.27 ** | 0.37 ** | 0.26 ** | 0.64 ** | | | |
| KWMS | 0.44 ** | −0.12 | 0.33 ** | 0.23 ** | 0.21 ** | 0.59 ** | 0.81 ** | | |
| TKW | 0.60 ** | −0.13 | 0.09 | −0.21 ** | 0.12 | 0.12 | 0.01 | 0.35 ** | |
| TW | 0.45 ** | −0.08 | 0.15 * | −0.16 * | 0.13 | 0.08 | −0.03 | 0.00 | 0.34 ** |

GY, grain yield; PH, plant height; SL, spike length; SNS, spikelet number of spike; PSR, productive spikelet rate; KNS, kernel number per spikelet; KNMS, kernel number per main spike; KWMS, kernel weight per main spike; TKW, thousand kernel weight; TW, test weight. "*" and "**" indicate significant differences at $p < 0.01$ and $p < 0.05$, respectively.

### 3.2. Genome-Wide Association Study and Annotations

After filtering out low-quality SNPs, there were 47,362 SNPs available for GWAS analysis. Based on the Manhattan and Q–Q plots of BLUP values, we identified 176 significant SNP markers associated with 9 out of the 10 analyzed traits at 118 loci (Figure S2; Table S3). These loci included 4, 6, 64, 3, 20, 8, 3, 6, and 4 loci associated with GY, PH, SL, SNS, PSR, KNS, KNMS, TKW, and TW, respectively. The associated loci were distributed across all chromosomes except chromosome 4D, and the explained phenotypic variation ($R^2$) ranged from 6.16% to 15.39% (Table S3). The phenotypic variation explained refers to the ability of allelic variations to affect the phenotype. The data were analyzed separately for each environment, and SNP markers that were consistently detected in at least two individual

environments (including BLUP, which is considered an environment) were considered stable. A total of 84 significant SNP markers were identified at 50 loci for 8 out of the 10 analyzed traits. These traits included GY (1), PH (6), SL (21), PSR (12), KNS (1), KNMS (2), TKW (5), and TW (2). The markers were located on all chromosomes except for 1B, 3D, and 4D (Table 3). Candidate gene prediction was conducted on these SNP markers, and 70 of them were successfully mapped to annotated genes. Among these, 51 SNP markers were found in the coding sequences (CDSs) of 47 annotated genes, which were identified as candidate genes (Table S4). Those stable SNP markers also underwent haplotype analysis and cumulative effects analysis.

**Table 3.** Significant single-nucleotide polymorphisms (SNPs) for yield and yield-related traits identified by genome-wide association analysis in multi-environment.

| Trait | Environment | SNP | Chromosome | Position (bp) |
|---|---|---|---|---|
| GY | E2, E7 | *BS00109912_51* | chr7A | 653,949 |
| PH | E1, E5 | *RAC875_rep_c112729_702* | chr7D | 8,344,704 |
| | E5, E6 | *Kukri_c31479_147* | chr5A | 569,989,461 |
| | E4, E5 | *BS00081949_51* | chr7A | 734,538,957 |
| | E5, E7 | *wsnp_Ex_c621_1231444* | chr5A | 591,156,150 |
| | E3, E5, E7 | *RAC875_rep_c109969_119* | chr5A | 593,332,277 |
| | E3, E4, E5 | *wsnp_Ex_c2185_4094843* | chr5A | 593,173,030 |
| | | *wsnp_Ex_c44164_50292954* | chr5A | 593,334,252 |
| | | *wsnp_Ex_rep_c109532_92292121* | chr5A | 595,037,357 |
| | | *BobWhite_c15758_79* | chr5A | 595,372,995 |
| | | *Excalibur_c24051_502* | chr5D | 473,342,851 |
| | | *GENE-2794_70* | chr5D | 473,794,273 |
| | | *BS00066447_51* | chr5D | 473,795,001 |
| | | *wsnp_RFL_Contig2265_1693968* | chr5D | 473,796,494 |
| | E3, E5 | *Excalibur_c31769_793* | chr5A | 592,636,579 |
| | | *Tdurum_contig29286_319* | chr5B | 585,001,363 |
| SL | E2, E7 | *RAC875_c37934_285* | chr1A | 20,977,423 |
| | | *IACX596* | chr2A | 165,849,288 |
| | | *Tdurum_contig31037_205* | chr3A | 571,407,364 |
| | | *Tdurum_contig11714_304* | chr3A | 585,937,902 |
| | | *Tdurum_contig42087_1941* | chr4A | 277,890,095 |
| | | *Ku_c9559_737* | chr5A | 8,243,302 |
| | | *wsnp_Ku_c9559_15999945* | chr5A | 8,243,340 |
| | | *Excalibur_c36501_188* | chr5A | 9,325,567 |
| | | *Tdurum_contig10759_260* | chr5A | 573,813,835 |
| | | *BS00109922_51* | chr6A | 4,678,762 |
| | | *Excalibur_c37700_1016* | chr7A | 314,410,710 |
| | | *wsnp_Ex_c7907_13427724* | chr6B | 118,967,499 |
| | | *Kukri_c30551_400* | chr6B | 223,257,837 |
| | | *Tdurum_contig35251_485* | chr6B | 226,361,465 |
| | | *Excalibur_c36650_1557* | chr6B | 226,362,930 |
| | | *CAP11_c763_391* | chr6B | 228,242,555 |
| | | *Tdurum_contig45585_432* | chr7B | 700,818,624 |
| | | *Tdurum_contig17062_665* | chr7B | 700,827,651 |
| | | *Excalibur_c22642_90* | chr1D | 20,056,978 |
| | | *BobWhite_c13718_682* | chr5D | 543,058,038 |
| | | *D_GBB4FNX01C3F21_57* | chr6D | 471,002,720 |

**Table 3.** *Cont.*

| Trait | Environment | SNP | Chromosome | Position (bp) |
|---|---|---|---|---|
| | E4, E5 | *Excalibur_c56319_61* | chr7A | 661,962,199 |
| | | *RAC875_c525_1372* | chr7B | 750,086,340 |
| | | *RAC875_c104604_381* | chr2D | 637,425,446 |
| | | *D_contig37514_120* | chr7D | 568,950,209 |
| | | *tplb0049k01_89* | chr7D | 569,717,896 |
| | | *Kukri_c22576_148* | chr7D | 570,647,452 |
| | | *tplb0041e14_1096* | chr7D | 570,648,425 |
| | | *Excalibur_c7895_385* | chr7D | 570,665,966 |
| | | *D_GBB4FNX02ILZW2_114* | chr7D | 570,825,150 |
| | | *BobWhite_c11549_468* | chr7D | 571,196,430 |
| | | *Kukri_c101311_72* | chr7D | 571,255,045 |
| | | *Kukri_c61816_202* | chr7D | 571,260,010 |
| | | *D_contig25474_188* | chr7D | 571,717,776 |
| | | *Excalibur_c16804_1108* | chr7D | 572,735,439 |
| | | *tplb0057p21_1365* | chr7D | 573,433,563 |
| | | *tplb0057p21_1042* | chr7D | 573,434,059 |
| | E4, E6 | *BobWhite_c22580_115* | chr4B | 604,051,170 |
| | E3, E4 | *tplb0032k20_90* | chr7D | 16,153,942 |
| PSR | E1, E7 | *wsnp_Ex_c11827_18986376* | chr2A | 733,922,282 |
| | E2, E7 | *Kukri_c24962_123* | chr1A | 998,1126 |
| | | *BobWhite_c23632_322* | chr1A | 539,762,811 |
| | | *RAC875_rep_c102485_468* | chr2A | 758,397,306 |
| | | *Ra_c108749_837* | chr4A | 70,798,652 |
| | | *wsnp_Ex_rep_c66426_64644630* | chr4A | 70,813,286 |
| | | *wsnp_Ku_c49919_55679171* | chr4A | 71,253,251 |
| | | *BobWhite_c35402_66* | chr4A | 614,241,032 |
| | | *BS00045284_51* | chr5A | 109,342,918 |
| | | *BS00080365_51* | chr7A | 537,058,999 |
| | | *BobWhite_c19554_544* | chr2B | 637,574,105 |
| | | *RAC875_c6921_1276* | chr3B | 556,682,737 |
| | | *Excalibur_c49685_207* | chr7B | 744,260,654 |
| | | *Kukri_c36429_687* | chr5D | 329,195,114 |
| KNS | E4, E7 | *Kukri_c56494_585* | chr6A | 425,737,504 |
| KNMS | E2, E7 | *Tdurum_contig35492_150* | chr2B | 647,109,508 |
| | E2, E6 | *Tdurum_contig4885_1307* | chr7A | 68,049,240 |
| | | *Tdurum_contig4885_1833* | chr7A | 68,049,666 |
| TKW | E2, E7 | *RAC875_rep_c105041_121* | chr7A | 92,892,087 |
| | | *Ex_c6196_971* | chr7A | 92,892,096 |
| | | *Excalibur_c6196_668* | chr7A | 92,892,399 |
| | | *RFL_Contig2200_1024* | chr7A | 93,036,212 |
| | | *wsnp_Ex_c20062_29096408* | chr7A | 93,077,341 |
| | | *Tdurum_contig13784_824* | chr5B | 451,179,330 |
| | | *RAC875_rep_c105584_237* | chr7B | 43,881,084 |
| | | *Kukri_c20975_765* | chr7D | 101,580,773 |
| | | *Tdurum_contig49575_1237* | chr7D | 621,647,564 |
| TW | E2, E3 | *IAAV3049* | chr1D | 384,511,578 |
| | E2, E7 | *GENE-1389_396* | chr2D | 109,700,911 |

E1, 2012_ES; E2, 2012_SHZ; E3, 2012_ZS; E4, 2013_ES; E5, 2013_SHZ; E6, 2013_ZS, which represent 2012 and 2013 cropping seasons in Er'shi (ES), Shihezi (SHZ), and Zhaosu (ZS), respectively; E7, BLUP, best linear unbiased predictor of yield and yield components in 192 wheat cultivars during two cropping seasons across three environments. GY, grain yield; PH, plant height; SL, spike length; PSR, productive spikelet rate; KNS, kernel number per spikelet; KNMS, kernel number per main spike; TKW, thousand kernel weight; TW, test weight.

### 3.3. Haplotype Analysis

To investigate the influence of various genotypes on yield and yield-related traits, stable SNPs were chosen to categorize the population according to their genotypes. Then, *t*-tests were performed to determine the significance of genotype effects on specific traits (Table S5). Five SNPs (*wsnp_Ex_c621_1231444, RAC875_rep_c109969_119, wsnp_Ex_c2185_4094843, wsnp_Ex_c44164_50292954, Excalibur_c31769_793*) at one locus on chromosome 5A and four SNPs (*Excalibur_c24051_502, GENE-2794_70, BS00066447_51, wsnp_RFL_Contig2265_1693968*) at one locus on chromosome 5D showed significant differences ($p < 0.05$) in PH values between the two allele cultivars in at least five environments (Tables 3 and S5). This indicates that these loci have a significant impact on phenotypic variation. Haplotype analysis for these two loci identified three blocks in the 591–598 Mb interval on chromosome 5A and two blocks in the 470–477 Mb interval on chromosome 5D, respectively (Table S6). To facilitate the description of haplotype effects, haplotypes with positive and negative effects were referred to as "superior haplotypes" and "inferior haplotypes", respectively. Comparison between accessions with superior haplotypes and those with inferior haplotypes showed significant differences in PH values ($p < 0.05$) in at least five environments (Figures 1 and 2).

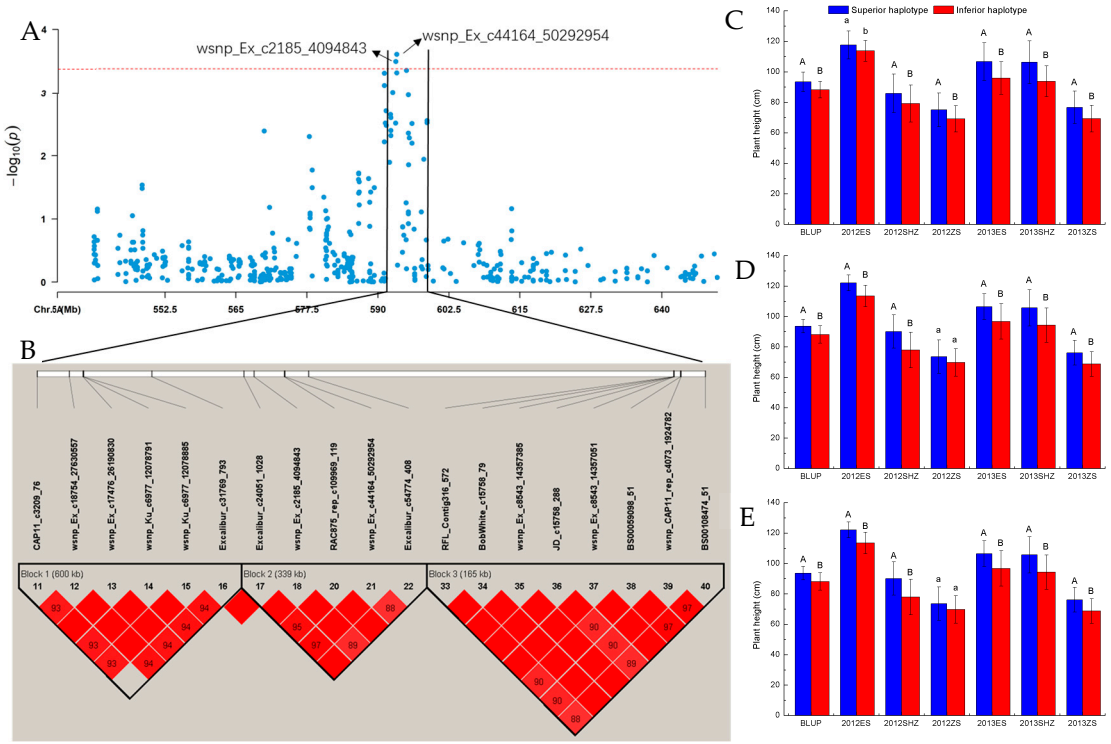


**Figure 1.** Haplotype analysis. (**A**) Local Manhattan plot. (**B**) Haplotype analysis of multi-environment significant SNPs associated with plant height on chromosome 5A. (**C**–**E**) Phenotypic effects of haplotypes in blocks 1, 2, and 3, respectively; different lowercase letters indicate significant differences at $p < 0.05$. 2012_ES, 2012_SHZ, 2012_ZS, 2013_ES, 2013_SHZ, and 2013_ZS represent the cropping seasons in Er'shi (ES), Shihezi (SHZ), and Zhaosu (ZS) for the years 2012 and 2013, respectively; E7, BLUP represents the best linear unbiased predictor of plant height in 192 wheat cultivars during two cropping seasons across three environments. Different uppercase and lowercase letters indicate significant differences at $p < 0.01$ and $p < 0.05$, respectively.

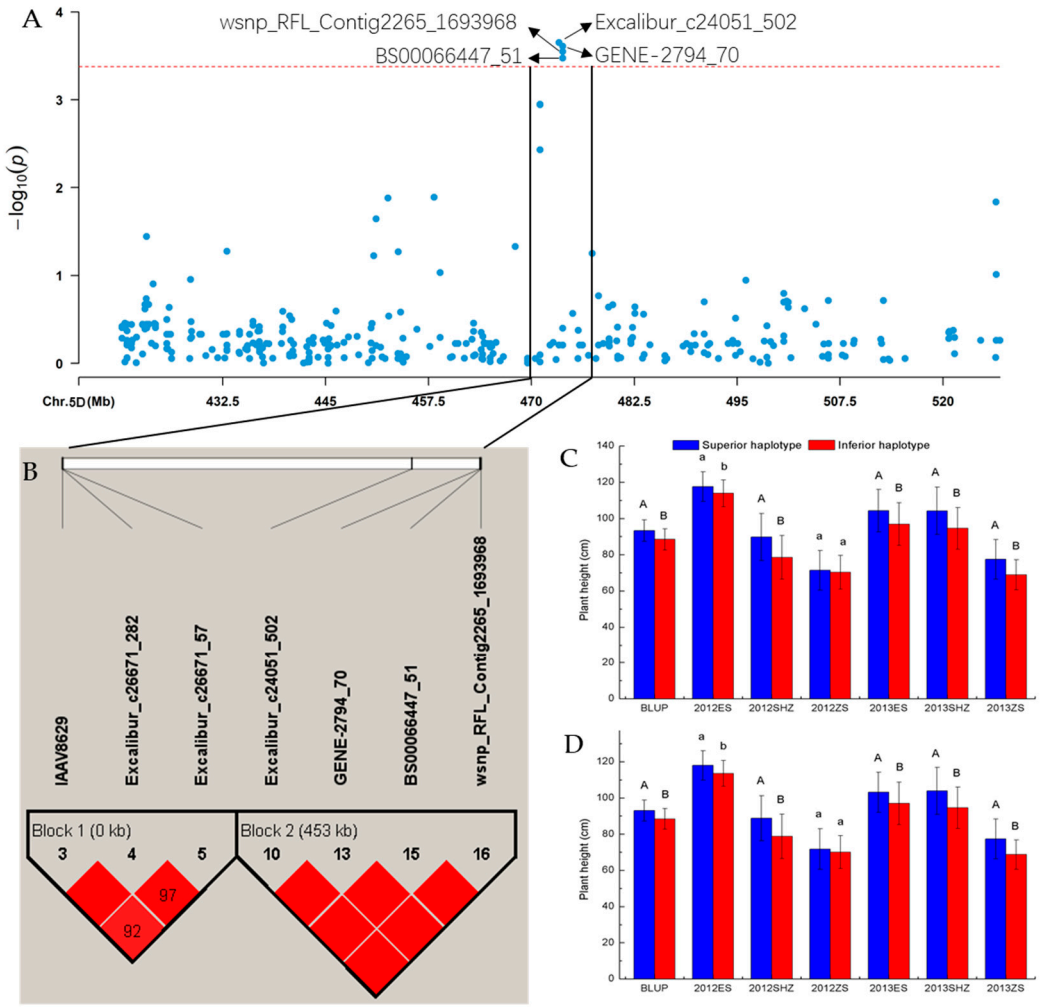


**Figure 2.** Haplotype analysis. (**A**) Local Manhattan plot. (**B**) Haplotype analysis of multi-environment significant SNPs associated with plant height on chromosome 5D. (**C**,**D**) Phenotypic effects of haplotypes in blocks 1 and 2, respectively, different lowercase letters indicate significant differences at $p < 0.05$. 2012_ES, 2012_SHZ, 2012_ZS, 2013_ES, 2013_SHZ, and 2013_ZS represent the cropping seasons in Er'shi (ES), Shihezi (SHZ), and Zhaosu (ZS) for the years 2012 and 2013, respectively; E7, BLUP represents the best linear unbiased predictor of plant height in 192 wheat cultivars during two cropping seasons across three environments. Different uppercase and lowercase letters indicate significant differences at $p < 0.01$ and $p < 0.05$, respectively.

### *3.4. Cumulative Effect Analysis*

Stable SNPs associated with a specific phenotype that were clustered in different loci and phenotype values of cultivars with different alleles showed significant differences ($p < 0.05$) in at least two environments (Tables 3 and S5). We estimated the cumulative effects of favorable alleles. The cultivars with a higher number of superior alleles exhibited improved phenotypic traits. The correlation coefficients between the number of superior alleles and the productive spikelet rate and spike length were 0.8896 and 0.8353, respectively (Figure 3).

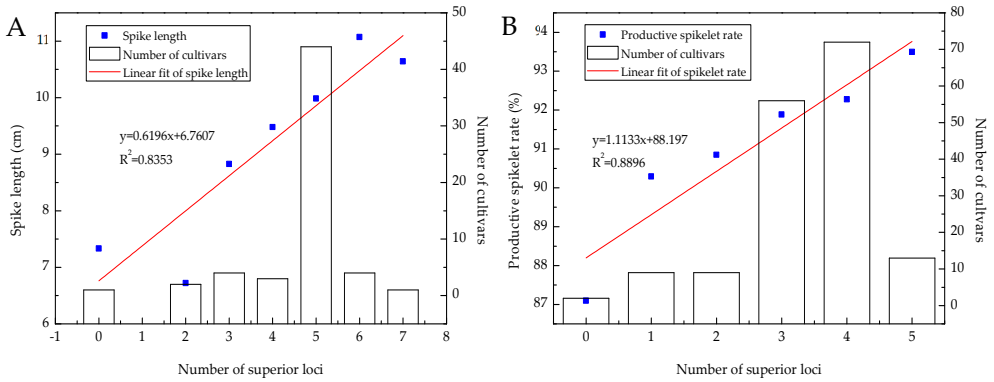


**Figure 3.** Cumulative effects of favorable alleles on spike length (**A**) and productive spikelet rate (**B**) in the GWAS population.

## 4. Discussion

### *4.1. Traits Analysis*

Grain yield improvement is one of the most challenging objectives in wheat breeding. Wheat grain yield is the ultimate result of plant growth and development, which is determined by several factors, including spike number per unit area, kernel number per spike, and thousand kernel weight [50], but is also influenced by other yield-related traits, such as plant height and spike length [51]. In the present study, grain yield was significantly associated with PH, PSR, KNS, KNMS, KWMS, TKW, and TW, consistent with previous studies [51,52], indicating that enhancing these traits could be a viable strategy for improving grain yield. Grain yield is controlled by numerous genes that have a lesser effect on wheat [50]. It is also intensely impacted by environmental factors and crop management practices, including abiotic stress tolerance, biotic resistance, adaptation to various soils, and climate changes [35,53,54]. The broad-sense heritability of GY in the present research was 0.6. This value indicates the proportion of phenotypic variation that can be attributed to genetic factors. It was observed that all yield-related traits had higher heritability than GY, except for KWMS. Therefore, these yield-related traits can be selected to improve GY in breeding programs due to their more accurate measurement and greater repeatability across different environments compared to overall yield [13,20,21]. Considerable phenotypic variation (CV) among the accessions and high broad-sense heritabilities were found across the environments for yield and yield-related traits in this study (Table 1, Figure S1), implying that the population was well-suited for GWAS to identify the genetic basis of yield and related traits [52].

### *4.2. Marker-Trait Associations*

A total of 50 loci for yield and yield-related traits were repeatedly identified across environments in this study that were distributed on all chromosomes, except for chromosome 4D. QTLs influencing grain yield and yield components were found on chromosome 4D in other studies [55,56], while they were not detected in this research. The reason may be that chromosome 4D contains a lower marker density, there was no separation for trait differences related to that chromosome, or the influence of a locus was too small to detect [51]. Those stable loci that were identified across multiple environments are discussed in detail in the present study because they are typically the preferred loci for further fine-mapping, map-based cloning, and marker-assisted selection (MAS) in the future [35].

#### 4.2.1. Association for GY

Only one significant and stable MTA for GY was detected on chromosome 7A at 653,949 bp in the present study. To our knowledge, there has not been a report on a locus mapped in this region that is related to controlling variation for GY. However, MTAs for GY on chromosomes 1A, 2A, 5A, 6A, 2B, 3B, 4B, 5B, 7B, and 2D, which were reported in

other studies [28,57–59], were not detected in our research. The annotation conducted on this SNP showed that it was mapped in the CDS of a gene that had not been reported (*TraesCS7A02G000936*). This discovery may lead to the identification of a new gene that regulates wheat yield.

#### 4.2.2. Association for PH

Our study identified five genomic regions associated with plant height in two or more of the six environments, distributed on chromosomes 5A, 5B, 5D, 7A, and 7D. Four SNP loci were co-located with the loci detected in earlier studies [13,28,60]. We did not discover any associations with PH on chromosomes 1A, 2B, 2D, 3B, 4B, 4D, 6A, and 6B, as reported in earlier research [28,60,61]. This suggests that the frequency of dwarfing genes in our germplasm was too low. In bread wheat, at least 17 out of the 21 chromosomes contain genes that regulate plant height [62–64]. So far, 24 height-related *Rht* genes (*Rht1-Rht24*) have been designated and cataloged in wheat [65]. PH is highly heritable and primarily controlled by *Rht-B1* and *Rht-D1* genes [62,64,66], which are the primary semi-dwarf genes discovered in North American spring wheat germplasm [67], located on the short arms of chromosomes 4B and 4D, respectively [68], whereas our work did not find any MTAs near the Rht-B1 and Rht-D1 genes. This may have been because there was no North American germplasm in our population. As found in our study, Edae et al. [26] did not find any *Rht* gene associated with PH in the WAMI (wheat association mapping initiative) population.

Wheat dwarf genes are either insensitive to gibberellic acid or responsive to gibberellic acid [60]. However, our associations did not correspond to those genes. In the present study, we mapped 15 stable SNPs for PH to 14 annotated genes. Among these, eight SNPs were found within the CDSs of genes, making them potential candidates for further investigation (Table S4). Interestingly, two SNPs on 5A and three SNPs on 5D were located in the same gene, *TraesCS5A02G400400*, which encodes Alpha-N-acetylglucosaminidase. Alpha-N-acetylglucosaminidase (NAGLU) is a crucial enzyme required for the degradation of glycosaminoglycans heparan sulfate, as reported in previous animal studies [69,70].

Due to the observation of a specific set of alleles on a single chromosome, haplotypes are inherited together, and the opportunity for contemporary recombination is minimal [71]. Constructing haplotypes between adjacent SNPs on chromosomes is an alternative approach to enhance the power of GWAS. GWAS combined with haplotype analysis outperforms single-marker-based analysis in terms of statistical significance (better *p*-values) and the estimation of allele effects, as shown in previous studies on wheat and other crops [32,72–74]. The haplotype analysis conducted on markers showed that different alleles had a highly significant impact on PH in five or more of the six environments. The average PH of the varieties carrying the superior haplotypes was significantly higher than that of varieties carrying inferior alleles in five out of six environments ($p < 0.05$; Figures 2 and 3). These loci can be considered for improving cultivars for PH in future breeding programs.

#### 4.2.3. Association with SL

Nineteen stable QTLs for SL were mapped on chromosomes 1A, 2A, 3A, 4A, 5A (2), 6A, 7A (2), 4B, 6B (2), 7B, 1D, 2D, 5D, 6D, and 7D (2). Similar associations have been found in other studies on the components of grain yield [13,75,76]. QTLs controlling SL on chromosome 5B, which was previously reported by Marza et al. [75], were not identified in this study. In contrast, QTLs on chromosomes 2A (165 Mb), 3A (571–585 Mb), 4A (277 Mb), 7A (314 Mb), 6B (118 and 223–228 Mb), and 7B (700 Mb) were consistently detected and explained a higher percentage of phenotypic variation in this study, which has never been reported before [30,77], indicating that they may represent new QTLs.

Among the 39 identified MTAs for SL, 29 were located within coding genes. Two functional genes identified in the present study were found to have a significant association with the development of SL. Auxin response factor ARF17, identified by the SNP marker *D_contig37514_120*, was found to be associated with SL in this study. A similar

finding was reported in a recent study on rapeseed, which found that ARF17 plays a crucial role in pod length development [78]. Glutathione transferase was identified by the SNP marker *tplb0032k20_90*. It plays a crucial role in the growth and development of plants in vivo and in shoot regeneration in vitro [79]. Additionally, it is involved in combating various biotic and abiotic stresses, including heavy metals, oxidative stress, cold stress, drought stress, and salt stress [80,81]. Other functional genes were also identified, including *TraesCS5A02G376100*, which was identified by the SNP marker *Tdurum_contig10759_260* and encodes RECA1, a protein involved in homologous recombination repair and organellar development [82]. *TraesCS7B02G433300* was identified by the SNP marker *Tdurum_contig45585_432*, which encodes OS9. The OS9 protein has various roles, such as participating in the transport of ER-to-Golgi [83] and regulating the Na-K-2Cl co-transporter in endoplasmic reticulum-associated degradation [84]. AVT6E was identified by the SNP marker *D_contig37514_120*, which is an amino acid transporter mainly accumulated in the endoplasmic reticulum but also partially localized in the vacuolar membrane [85]. PHIP1 was identified by the SNP marker *Excalibur_c22642_90*, which represents a plant-specific RNA-binding protein and is associated with the formation of the cell plate during cytokinesis [86]. The annotated unknown functional genes may be new genes related to SL and should be given more attention in the future.

#### 4.2.4. Association with PSR

Fourteen MTAs were detected for PSR on chromosomes 1A, 2A, 4A, 5A, 2B, 3B, 7B, and 5D. Among them, four MTAs (1A (9Mb), 4A, 3B, 7B) have been reported in previous studies [30,77], while the others were novel. Annotation was conducted on these SNPs, and nine known genes were identified. The SNP *wsnp_Ex_c11827_18986376* was located in the CDS region of *TraesCS2A02G505800*, which encodes Nicotinamide adenine dinucleotide phosphate (NADPH)-cytochrome P450 reductase (CPR). This enzyme is crucial for transferring electrons from NADPH to cytochrome P450 monooxygenases [87]. SNP *wsnp_Ku_c49919_55679171* was located in the CDS region of *TraesCS4A02G072800*, which encodes TOC34 (translocase of chloroplast). TOC34 serves as a receptor for proteins that contain a chloroplast-targeting signal [88].

#### 4.2.5. Association with KNMS

KNMS in wheat is a critical factor that limits yield improvement [50]. More than 100 QTLs for KNMS have been detected, scattered across all 21 chromosomes in wheat [50,51,89–93]. Three MTAs for KNMS were identified in the current study and were found to be distributed on 2B (1) and 7A (2), These MTAs were also reported in earlier studies [94], in which MTAs were analyzed using unconditional and conditional QTL mapping on a doubled haploid (DH) population consisting of 168 lines. *Tdurum_contig35492_150* was located in the CDS region of *TraesCS2B02G453400*, which encodes a protein containing the CUE (coupling of ubiquitin conjugation to ER degradation) domain. According to reports, some proteins containing the CUE domain are associated with cell apoptosis in yeast and mammalian species [94,95]. The *SPL35* gene encodes a novel CUE domain-containing protein that plays a role in regulating cell death and defense response in rice [96]. Whether or not this gene is involved in regulating KNMS is worth exploring in the future.

#### 4.2.6. Association with TKW

TKW is one of the main components contributing to wheat yield and gradually increases during this period. QTLs for TKW have been discovered on all wheat chromosomes except 1A [89,90,94,97,98]. In the present study, five stable QTLs for TKW were detected on chromosomes 7A, 5B, 7B, and 7D (2), which is consistent with some previous investigations [59,99,100]. Annotation was conducted on these loci, and five known functional genes were identified. *TraesCS7B02G044200* was identified by *RAC875_rep_c105584_237*, which encodes Acyl-coenzyme A oxidase. This enzyme plays a crucial role in the biosynthesis of jasmonic acid in plant peroxisomes [101]. The annotated gene *TraesCS7D02G526100*

encodes a protein containing the KIX_2 domain. This protein possesses a highly conserved, independently folded triple helix bundle that serves as a docking site for transcription factors, enabling promoter activation and target specificity during gene regulation [102].

#### 4.2.7. Association with TW

The TW of grains is an important factor in grading and trade because it is typically an indicator of quality and, consequently, impacts prices [103]. Two stable SNPs for TW were identified on chromosomes 1D and 2D. To our knowledge, there has yet to be a report on TW. The annotated gene *TraesCS5B02G029100* encodes phosphatidate phosphatase, an enzyme that catalyzes the dephosphorylation of phosphatidate to produce diacylglycerol. This enzyme plays a crucial role in regulating phospholipid and triacylglycerol metabolism [104].

In short, this article identified 84 stable SNP markers that were significantly associated with yield and yield-related traits. Among them, 1 was associated with GY, 15 were associated with PH, 39 were associated with SL, 14 were associated with PSR, 1 was associated with KNS, 3 were associated with KNMS, 9 were associated with TKW, and 2 were associated with TW. Based on these significant SNP markers, we further identified 47 candidate genes associated with yield and yield components, as well as 5 haplotypes linked to PH. Those SNP markers, candidate genes, and superior haplotypes may be used in marker-assisted selection for wheat breeding programs.

#### 4.2.8. Cumulative Effect Analysis of Super Alleles

By comparing the average phenotypic values of varieties carrying the same alleles in the association panel, the superior allele for each QTL region was determined [105]. The first SNP was selected if multiple SNPs significantly associated with the trait were identified within one QTL. In order to declare significant SNPs associated with a QTL, the support interval was set as 7 Mb [43,106]. There were seven favorable alleles for SL and five favorable alleles for PSR in the present study. Varieties with a higher number of favorable alleles demonstrated better phenotypic values (Figure 3). The number of varieties with five superior alleles for SL and four superior alleles for PSR was the largest, indicating that breeders selected these alleles. Similar results have been obtained in recent investigations on other crop species [30]. This suggests that yield can be increased in the future by accumulating a greater number of superior alleles, and the superior alleles identified in our research will be used in the future.

## 5. Conclusions

In this study, an association population consisting of 192 varieties was genotyped using the 90K wheat SNP iSelect assay, and their yield and nine yield-related traits were phenotyped in six different environments. GWAS, based on BLUP, detected 176 significant associations at 118 SNP loci across 20 chromosomes. Eighty-four associations at 51 loci were detected in two or more environments. Haplotype analysis identified three blocks on chromosome 5A and two blocks on chromosome 5D for plant height (PH). Varieties with different haplotypes at these loci exhibited a significant difference in plant height. The phenotypic traits depended on the number of alleles to increase the phenotypic value. These results provide valuable information for the future utilization of marker-assisted selection to enhance wheat yield.

**Supplementary Materials:** The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/agronomy13112784/s1: Table S1: The names and origins of the 192 entries in the association panel; Table S2: Analysis of variance for yield and yield components of Chinese spring wheat; Table S3: Significant SNPs associated with yield and yield-related traits by genome-wide association study based on BLUP values; Table S4: Candidate genes identified by genome-wide association study; Table S5: *P*-values of *t*-tests for the efficacy of different alleles on yield-related traits; Table S6: Haplotypes with different alleles in the blocks; Figure S1: Frequency distributions of BLUP values of yield and yield-related traits in 192 spring wheat cultivars. GY, grain yield; PH, plant height; SL, spike length; SNS, spikelet number of spike; PSR, productive

spikelet rate; KNS, kernel number per spikelet; KNMS, kernel number per main spike; KWMS, kernel weight per main spike; TKW, thousand kernel weight; TW, test weight; Figure S2: Manhattan and quantile-quantile (Q-Q) plots for yield and yield-related traits identified by genome-wide association analysis based on BLUP values. Horizontal line represents the significance threshold by which markers were considered associated with a trait (≈3.37). A, grain yield (GY); B, plant height (PH); C, spike length (SL); D, spikelet number of spike (SNS); E, productive spikelet rate (PSR); F, kernel number per spikelet (KNS); G, kernel number per main spike (KNMS); H, kernel weight per main spike (KWMS); I, thousand kernel weight (TKW); J, test weight (TW).

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