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Genome-Wide Association Study for *Fusarium* Head Blight Resistance in Common Wheat from China

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Abstract: As a devastating wheat disease, *Fusarium* head blight (FHB) causes large losses in yield and quality. The purpose of this study was to detect the genetic loci for FHB resistance based on a genome-wide association study (GWAS) using two panels genotyped by the Wheat 660 K SNP array and Wheat 90 K SNP array. Phenotypic investigation results showed that 43.6–51.6% of the test varieties showed an infection type of more than 3, indicating that substantial improvement in the level of resistance was urgently required. GWAS detected 1264 SNPs associated with FHB response distributed on all wheat chromosomes. Fourteen QTL were stably detected in two environments. *gFHB-1B* (582.9~607.9 Mb on chromosome 1B) and *gFHB-5A* (577.9~596.5 Mb on 5A) were two novel resistance loci that were detected in two wheat panels. Haplotype analysis of both *gFHB-1B* and *gFHB-5A* indicated that varieties with *gFHB-1B_R* and *gFHB-5A_R* had consistently less FHB than varieties carrying a one or no resistance QTL. The application frequency of the FHB-resistant alleles gFHB-1B and gFHB-5A showed a gradually decreasing trend in FHB resistance breeding. This study identified new genetic loci for the control of FHB and provides useful information for marker-assisted selection in wheat FHB resistance.

Keywords: *Fusarium* head blight; genome-wide association study; resistance locus; haplotype analysis

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1. Introduction

Fusarium head blight (FHB), mainly caused by *Fusarium graminearum* but also other *Fusarium* species, is an important fungal disease of wheat [1]. Diseased grain is shriveled, reddish in color, and may contain the mycotoxin deoxynivalenol (DON) and other trichothecene toxins. Kernels with excessive DON pose a severe threat to human and animal health [2]. The disease is widespread worldwide, and outbreaks of the disease cause wheat yield losses of more than 50%, especially in China, France, India, Russia, and the United States [3]. Breeding and planting disease-resistant varieties is the most cost-effective and sustainable measure against FHB loss [4]. It is important to identify FHB-resistant germplasm in order to reduce losses caused by this disease.

The Chinese variety Sumai 3 is the best source of FHB resistance so far [5]. FHB resistance QTL have been reported on all wheat chromosomes, and molecular markers have been developed for most of the mapped QTL [6–8]. Seven FHB resistance loci have been officially named. *Fhb1* on 3B and *Fhb2* on 6B were derived from Sumai 3 [9,10]; *Fhb4* on 4B was detected in Wangshuibai [11]; *Fhb5* on 5A was reportedly present in both

Wangshuibai and Sumai 3 [12]; *Fhb3* on 7A, *Fhb6* on 1A, and *Fhb7* on 7D were from wild relatives of wheat, namely, *Leymus racemosus*, *Elymus tsukushiensis*, and *Thinopyrum ponticum*, respectively [13–15].

Fhb1 was identified in numerous studies [6,9,16–18] and was fine-mapped to a 1.1 Mb region in chromosome 3B [19]. Although *Fhb1* was identified as a pore-forming toxin-like (PFT) gene encoding a chimeric lectin [20], two other studies reported that *TaHRC*, encoding a putative histidine-rich calcium-binding protein, was the candidate gene [21,22]. Another cloned FHB resistance gene, *Fhb7*, encodes a glutathione S-transferase (GST) and confers broad resistance to *Fusarium* species by detoxifying trichothecenes through de-epoxidation [23]. Because of the low level of resistance conferred by an individual gene/QTL, it is therefore necessary to detect more FHB resistance genes/QTL that can be combined with those currently available in order to develop varieties with high levels of resistance.

Common wheat ($2n = 42$) is an allohexaploid (AABBDD) with a large genome (16 Gb), high sequence duplication between subgenomes, and an abundance of repetitive elements [24]. High-density wheat SNP arrays, such as the Wheat 90 K iSelect array [25], Wheat 660 K array [26], and 35 K Wheat Breeder's array [27], have played an important role in mapping the genetic loci underlying complex traits in wheat by genome-wide association studies (GWASs). These traits include reaction black point [28] and Fusarium crown rot [29]; the yield components plant height, kernel weight, kernel length, and peduncle length [30]; the quality traits hardness index, grain protein content, wet gluten content, and flour color [31]; and various metabolites [32].

The objectives of the present study were to survey FHB-resistance-related loci in two wheat panels GWAS in order to (1) identify new FHB resistance loci and (2) identify superior haplotypes of two new resistance QTL, and (3) the polymorphism information of all genes within the interval was used to conduct GWASs of candidate genes and screen candidate genes.

2. Materials and Methods

2.1. Plant Materials

A total of 406 Chinese wheat varieties were collected to investigate FHB response and divided into two panels depending on their released time. Panel I included 243 common wheat cultivars or advanced lines from the Huang-Huai valley, and these varieties were released after 2014 [29]. Panel II contained 163 wheat varieties from every province in China, after cultivation and domestication in the Yellow and Huai Valley of China, and these varieties were released before 2014 [30,31]. Both panels were planted at Jianyang in Fujian province (27.30° N, 118.2° E) during 2016–2017 cropping season and at Hangzhou in Zhejiang (30.3° N, 120.2° E) in 2021–2022 cropping season. Plants were grown with 10 cm spacing in 2 m rows with 23 cm between rows. Each population was planted in a randomized complete block design with two replicates and managed according to local practices.

2.2. Index of FHB Response

The *F. graminearum* isolate FJX01 was used in this study. Spore suspensions were prepared using CMC medium and a diluted concentration of 10^5 spores mL^{-1}. Then, the spore suspension was sprayed at the early flowering stage (10% of spikes at anthesis). After inoculation, the nursery was mist-irrigated for 4 days. Total spikelets and number of symptomatic spikelets per spike were scored 21 days after infection and an average rate of 5 symptomatic spikelets was calculated for each variety in each replicate prior to conversion to a 1 to 4 type II response scale [33,34], where the averaged symptomatic spikelets rates were

1 = less than 0.25;
2 = 0.25–less than 0.5;
3 = 0.5–less than 0.75;

4 = 0.75–1 or entire spike dead.

Broad-sense heritability was calculated using the lme4 package in R software based on the mixed linear model [35].

2.3. Genotyping and Filtering

Panel I was genotyped using the Wheat 660 K SNP array [26,29], and genotyping was performed by Beijing CapitalBio Technology Company. Panel II was genotyped using the Wheat 90 K SNP array and genotyping was performed by Beijing Compass Technology & Investment Co. Ltd. [25,30,31]. Quality control was performed for SNP markers with minor allele frequency (MAF) > 0.05 and missing data < 20%. This pre-processing was examined by PLINK software [36]. Totals of 395,782 SNPs in Panel I and 41,561 SNPs in Panel II were used for final GWAS after quality control.

2.4. Genome-Wide Association Study

The population structures of Panel I and Panel II were evaluated using STRUCTURE software 2.3.4 with unlinked markers ($r^2 = 0$) [37], and population structures of Panel I and Panel II were shown in both reports by Sun et al. [30] and Yang et al. [29]. Panel I comprised ten subpopulations [29] and Panel II four subpopulations [30]. Principle component analysis (PCA) was performed by the GAPIT procedure using R software to assess the population structure [30]. GWAS of the present results was performed based on the mixed linear model (PCA+K) using GAPIT Version 3 package in *R* software [38]. The genome-wide significance threshold was determined by a uniform threshold of $1/n$ in Panel I and Panel II, where n was the effective number of independent SNPs calculated using Genetic type 1 Error Calculator (v0.2) [39]. However, this threshold filters out many real FHB resistance loci. Therefore, combined with the p-value of all SNPs in four replicates, a uniform suggestive genome-wide significance threshold (1.0×10^{-3} and 1.0×10^{-2} for Panel I and Panel II) was given.

2.5. Haplotype Analysis

Linkage disequilibrium and haplotype analysis of all SNPs associated with FHB response were performed with Haploview 4.2 software [40]. The significance of differences among haplotypes was based on t-tests ($p < 0.05$). Based on the large linkage disequilibria characteristic of wheat, we considered that two significant SNPs separated by more than 20 Mb represented different resistance loci.

2.6. Candidate Gene Identification

Using the Chinese Spring reference genome sequence RefSeq v1.1 [24], we normalized the physical locations of FHB-resistance-related QTL based on the closely linked markers. Then, candidate gene identification associated with high-confidence FHB resistance loci and candidate gene functional annotation was conducted using the genome assembly of the reference genome [24], EnsemblPlants and WheatOmics website [41]. The polymorphism information of these genes in the population was analyzed by exon capture sequencing of the genes in the candidate interval, and these polymorphic markers were added to the original wheat SNP array to conduct the GWAS of the candidate genes, and the possible candidate genes related to FHB resistance were screened.

3. Results

3.1. Distribution of FHB Responses in the Variety Panels

The correlation coefficients of FHB response among all 406 varieties ranged from 0.64 to 0.82 over the four replications (Figure 1A), and the broad-sense heritability of FHB resistance was 74.1%. The FHB responses of most varieties were 2 or 3 (Figure 1B). An analysis of mean FHB response in the four replicates indicated that 43.6–51.6% of varieties were susceptible (IT $\geq$ 3). Only 3.0–7.4% of varieties were of the highly resistant infection type (IT $\leq$ 1).

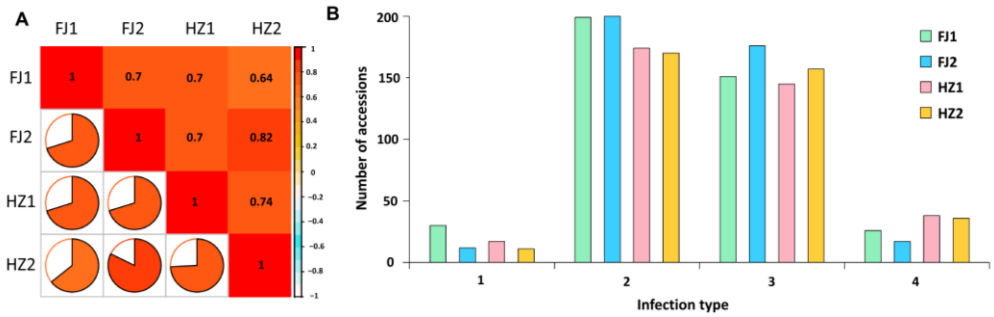

Figure 1. Frequencies of varieties with different infection types for FHB resistance response: (**A**) Correlation analysis of FHB response across four replications. (**B**) Frequencies of varieties in infection type classes. Note, FJ1, FJ2, HZ1, and HZ2 represent the first replicate in Fujian, the second replicate in Fujian, the first replicate in Hangzhou, and the second replicate in Hangzhou, respectively. The same below.

3.2. Genome-Wide Association Study of Wheat FHB Resistance

Separate GWASs performed on the two panels detected 1264 SNPs significantly associated with FHB response across the four replications, with phenotypic variation explained (PVE) ranging from 5.0% to 20.1% (Figure 2A,B; Table S1). They were mainly distributed on chromosomes 1A (79), 2A (114), 2B (93), 3A (181), 3B (61), 5A (94), 6A (66), 6B (62), and 7B (139) (Table S1).

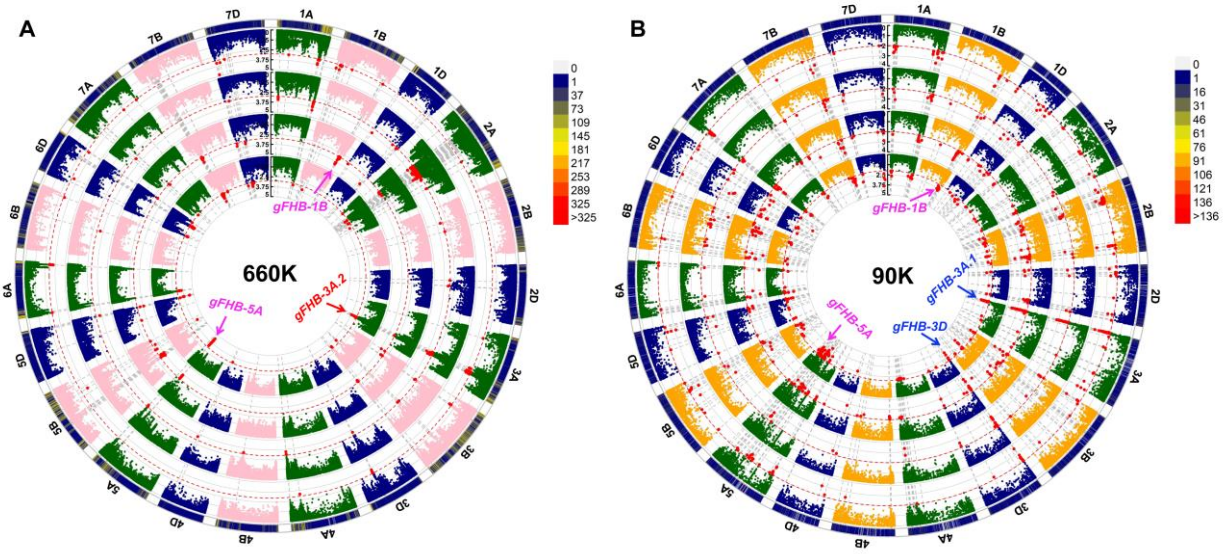

Figure 2. Manhattan circle plots for Panel I based on the Wheat 660 K SNP array (**A**) and Panel II based on the Wheat 90 K SNP array (**B**) across chromosomes. Note: Different letters around outermost ring (like 1A, 1B, 1D etc.) represent wheat chromosomes.

In Panel I, 638 SNPs were associated with FHB resistance with PVE of 5.0% to 11.8%, and these were mainly present in chromosomes 1A (44), 2A (101), 3A (119), 5A (43), 6A (52), and 7B (118) (Table S1). Using the physical position distribution of these SNPs, nine resistance loci were stably detected in at least two replicates in Panel I; they were, respectively, named *gFHB-1A.1* (3.4~46.2 Mb on chromosome 1A, average PVE 9.4%), *gFHB-1A.2* (527.2~534.3 Mb on 1A, average PVE 9.8%), *gFHB-1A.3* (579.4~591.3 Mb on 1A, average PVE 6.3%), *gFHB-1B* (582.9~607.9 Mb on 1B, average PVE 8.6%), *gFHB-3A.2* (539.7~570.8 Mb on 3A, average PVE 8.2%), *gFHB-3B* (3.3~14.3 Mb on 3B, average PVE 11.4%), *gFHB-5A* (577.9~596.5 Mb on 5A, average PVE 10.7%), *gFHB-5D* (524.8~565.7 Mb on 5D, average PVE 9.8%), and *gFHB-7B* (128.9~199.8 Mb on 7B, average PVE 9.4%) (Table 1).

Table 1. Fourteen FHB QTL detected by GWAS.

QTL	Marker Interval	Physical Position (Mb)	Physical Distance (Mb)	No. of Significant SNPs	PVE (%)	Average PVE (%)	Panels	No. Replications
gFHB-1A.1	tplb0025b13_2054~Kukri_c4900_2435	3.4~46.2	43	26	5.1~19.3	9.4	I & II	5
gFHB-1A.2	RAC875_rep_c120644_74~BS00009104_51	527.2~534.3	7.1	15	7.2~15.9	9.8	I & II	4
gFHB-1A.3	AX-110478077~AX-94942875	579.4~591.3	11.9	25	5.0~17.3	6.3	I & II	5
gFHB-1B	Kukri_c51864_225~AX-109320151	582.9~607.9	25	32	5.9~16.2	8.6	I & II	5
gFHB-2B	Tdurum_contig96648_102~BS00065136_51	694.1~704.0	9.9	27	7.3~18.2	12.5	II	4
gFHB-3A.1	Tdurum_contig76679_307~IAAV1155	1.3~14.9	13.5	57	8.1~19.7	13.8	II	4
gFHB-3A.2	AX-110433978~AX-109645516	539.7~570.8	31.1	100	5.0~9.7	8.2	I	4
gFHB-3B	Kukri_c64588_274~AX-110404403	3.3~14.3	11	12	6.1~17.8	11.4	I & II	5
gFHB-3D	Excalibur_c9485_707~Excalibur_c60530_113	0.8~9.7	9	21	7.9~19.7	14.3	Panel II	4
gFHB-5A	AX-89432740~Ku_c12469_983	577.9~596.5	18.6	33	8.8~13.4	10.7	I & II	5
gFHB-5D	AX-111388087~BobWhite_c31_2478	524.8~565.7	41	13	5.9~12.9	9.8	I & II	7
gFHB-6B	BS00003897_51~Kukri_c38732_546	132.1~151.1	19	13	8.8~16.9	12.1	II	4
gFHB-7A	BobWhite_c17904_259~Tdurum_contig30621_328	8.3~68.0	59.8	29	7.1~16.6	12.2	II	4
gFHB-7B	AX-109345488~Tdurum_contig10980_1229	128.9~199.8	70.9	114	5.8~10.4	8.4	I & II	5

Note: No. represented Number; PVE represented phenotypic variation explained.

In Panel II, 678 significant SNPs were associated with FHB resistance with PVE of 7.3% to 20.1%, and these SNPs were mainly distributed on wheat chromosomes 2B (91), 3A (76), 5A (69), and 6B (60) (Table S1). A total of 13 FHB resistance loci were detected in this panel (Table 1). Among them, eight FHB resistance loci (*gFHB-1A.1*, *gFHB-1A.2*, *gFHB-1A.3*, *gFHB-1B*, *gFHB-3B*, *gFHB-5A*, *gFHB-5D*, and *gFHB-7B*) were simultaneously detected in both Panel I and Panel II. *gFHB-1B* and *gFHB-5A*, as stable FHB resistance loci detected in both panels, were chosen as high-confidence FHB resistance loci for further analysis (Figure 3).

Figure 3. Chromosomal locations of significant SNPs associated with five stable FHB resistance loci (*gFHB-1B*, *gFHB-3A.1*, *gFHB-3A.2*, *gFHB-3D*, and *gFHB-5A*). (**A**–**D**) represent the physical position of all significant SNPs detected on chromosomes 1A, 3A, 3D and 5A by GWAS in Panel I and Panel II. Note: The red marker name indicates the marker from the wheat 660K SNP array; The blue marker name indicates the marker from the wheat 90K SNP array. The red locus name indicate the locus detected by panel I; the blue locus names indicate the locus detected by panel II; the pink locus names indicate the locus detected by Panel I and Panel II.

3.3. Haplotype Analysis of High-Confidence FHB Resistance Loci *gFHB-1B* and *gFHB-5A*

There were 14 significant SNPs for *gFHB-1B* in a 10.9 Mb block with high linkage disequilibrium (LD) in Panel I (Figure 4A). There were two frequent haplotypes for this block (Figure 4B). Varieties carrying *Hap1* (IT 2.4–2.7) expressed significantly higher resistance than those carrying *Hap2* (IT 3.1–3.3) across the four replications (Figure 4C). In Panel II, there were 12 significant SNPs for *gFHB-1B* located in a 21.6 Mb block with a high LD (Figure 4D). Five main haplotypes were detected for this block (Figure 4E). Varieties carrying *Hap1*/*Hap2*/*Hap3* (2.1–2.2) showed significantly higher FHB resistance than those carrying *Hap4*/*Hap5* (2.4–2.6) over the four replications (Figure 4F). Therefore, *Hap1* in Panel I and *Hap1*/*Hap2*/*Hap3* in Panel II were superior haplotypes (*Hap_1B_R*) for FHB resistance conferred by the *gFHB-1B* QTL.

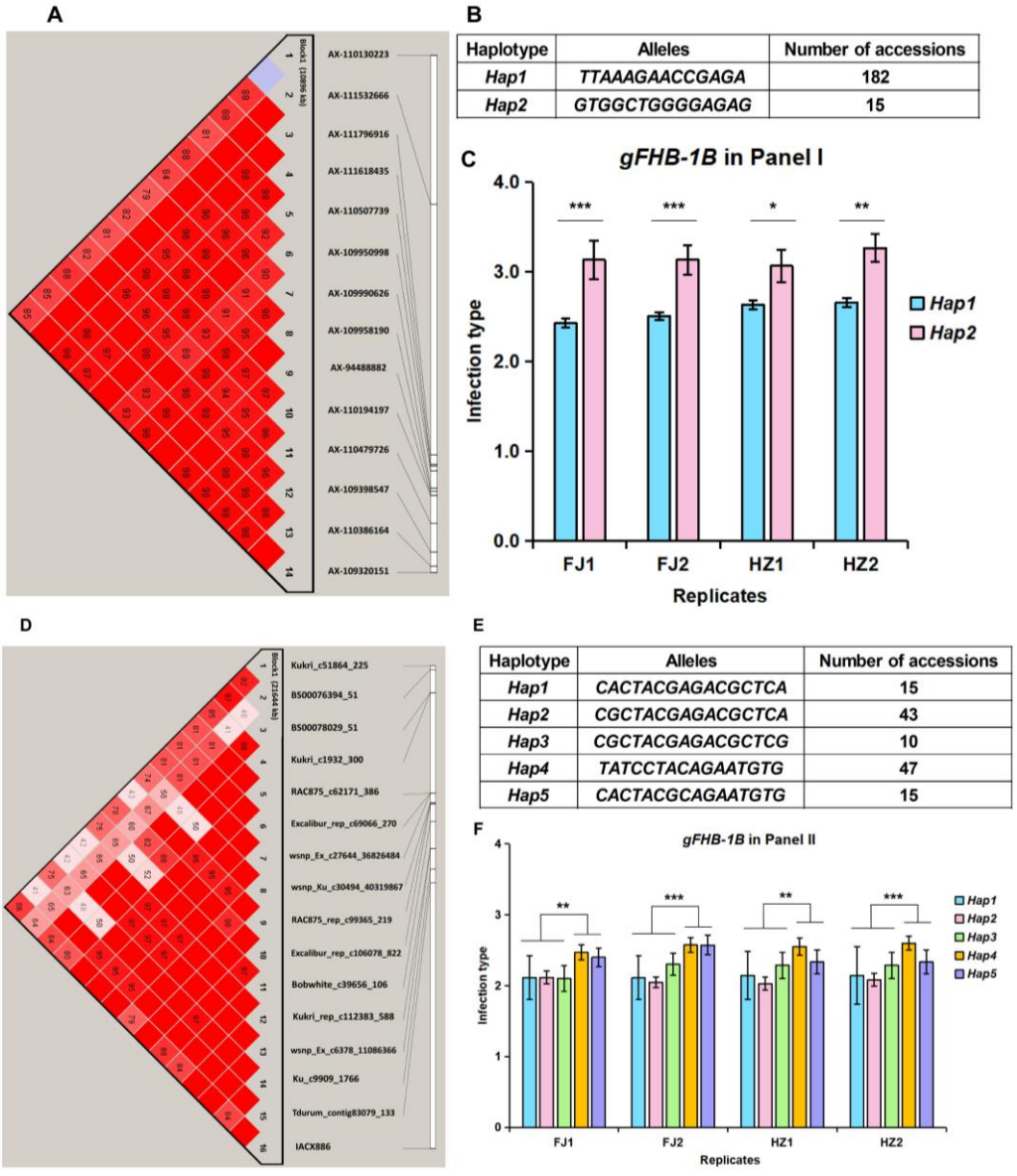

Figure 4. Haplotype analysis of significant SNPs in *gFHB-1B*: (**A**) LD heatmap of significant SNPs in the region of *gFHB-1B* in Panel I. (**B**) Two majority haplotypes in Panel I. (**C**) Mean infection types for haplotypes in Panel I. (**D**) LD heatmap of the significant SNPs in the region of *gFHB-1B* in Panel II. (**E**) Five major haplotypes of *gFHB-1B* detected in Panel II. (**F**) Mean infection types produced by Panel II varieties with different haplotypes. Data are means ± S.E., * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

There were 22 SNPs associated with *gFHB-5A* located in a 10.8 Mb block with high LD in Panel I (Figure 5A). There were three main haplotypes for this block (Figure 5B). Varieties carrying *Hap1*/*Hap2* (IT 2.5–2.8) had significantly higher resistance than those carrying *Hap3* (3.2–3.4) across the four replications (Figure 5C). For Panel II, there were nine significant SNPs located in a 14.1 Mb block (Figure 5D). Among varieties with the four most frequent haplotypes in this block (Figure 5E), those carrying *Hap1*/*Hap2* (IT 2.1–2.2) showed higher resistance than the group carrying *Hap3*/*Hap4* (2.5–2.6) (Figure 5F). Therefore, varieties with *Hap1*/*Hap2* in Panel I and *Hap1*/*Hap2* in Panel II were superior haplotypes (*Hap_5A_R*) at the *gFHB-5A* locus.

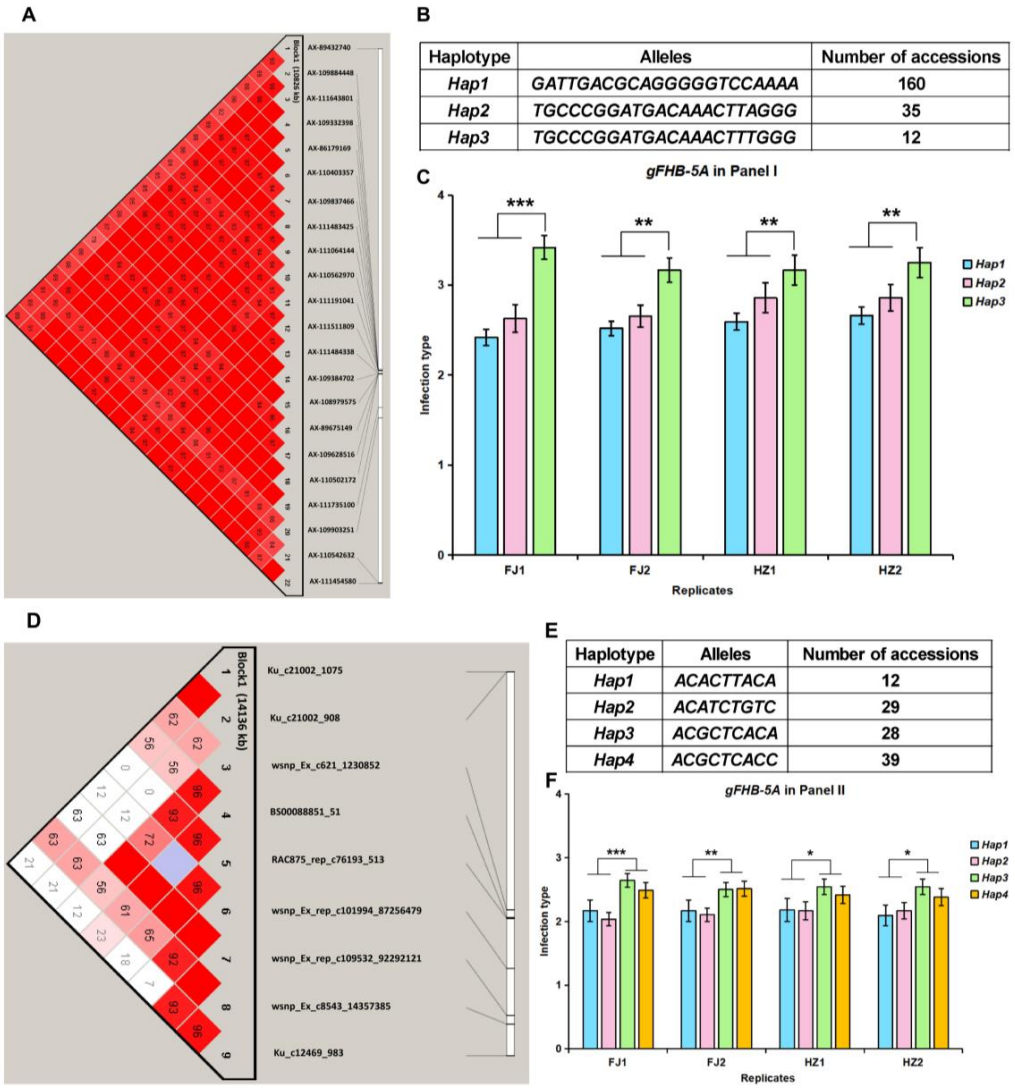

Figure 5. Haplotype analysis of significant SNPs in *gFHB-5A* l: (**A**) LD heatmap of SNPs in the region of *gFHB-5A* in Panel I. (**B**) Three main haplotypes at *gFHB-5A* in Panel I. (**C**) Comparison of mean infection types for different haplotypes in Panel I. (**D**) LD heatmap of SNPs in the region of *gFHB-5A* in Panel II. (**E**) Four majority haplotypes of *gFHB-5A* in Panel II. (**F**) Analysis of mean infection types for haplotypes in Panel II. Data are means ± S.E., * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Varieties combining *gFHB-1B_R* and *gFHB-5A_R* had consistently less FHB than varieties carrying a one or no resistance QTL (Figure 6).

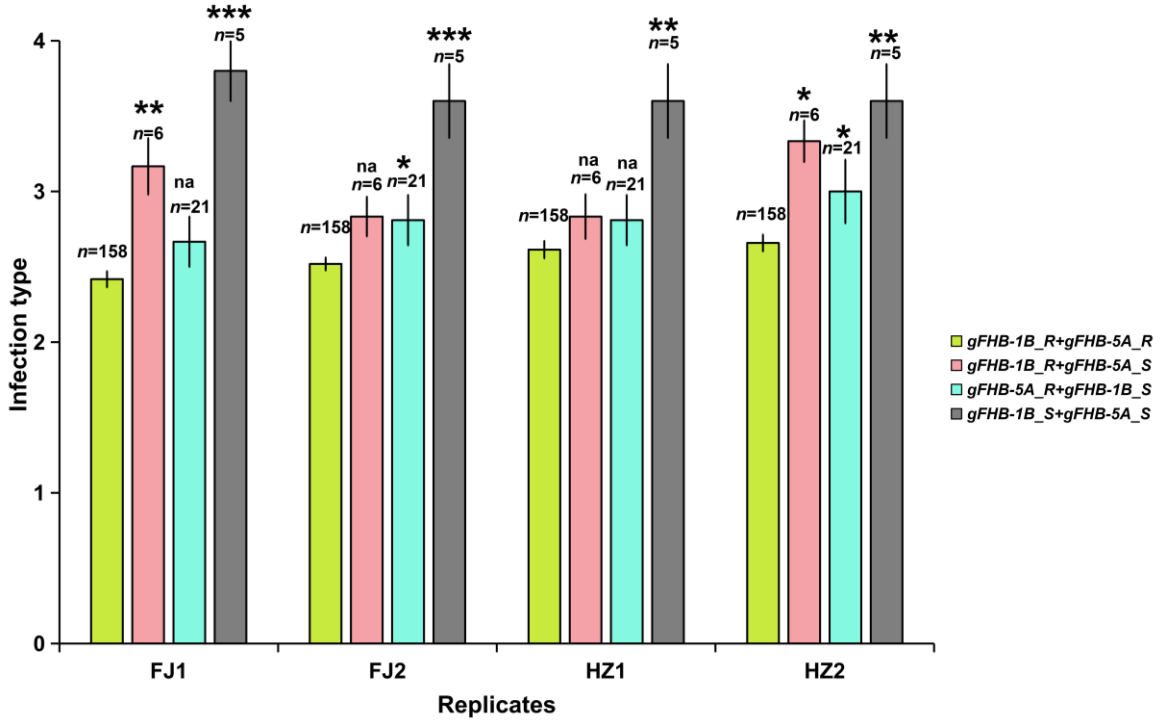

Figure 6. Effects of combining *gFHB-1B* and *gFHB-5A* haplotypes. Data are means ± S.E., * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, na $p > 0.05$, compared to *gFHB-1B_R+gFHB-5A_R*.

3.4. Prediction of Candidate Genes

By integrating haplotype results for all significant SNPs in both panels, the *gFHB-1B* candidate region was narrowed to a 7.6 Mb interval (597.0~604.6 Mb) containing 85 high-confidence annotated genes (https://plants.ensembl.org/Triticum_aestivum/Tools/Blast, accessed on 14 April 2023). We amplified and sequenced 85 candidate genes in 406 varieties. According to the sequencing results, polymorphism analysis was conducted, and the polymorphisms of these genes were added back to the original wheat SNP array for GWAS of the candidate genes. Then, only TraesCS1B02G374300_604562060 with *p*-values of 6.4×10^{-4} and 8.5×10^{-4} in the region of TraesCS1B02G374300 was detected to be significantly associated with FHB response in at least two replicates in Panel I (Table S2). As a consequence, TraesCS1B02G374300, encoding a MYB-related transcription factor, was considered as the candidate gene for *gFHB-1B*.

By integrating the haplotype analysis results from the two panels for all significant SNPs in the *gFHB-5A* QTL, the candidate region of this locus was narrowed to a 6.4 Mb interval (582.4~588.8 Mb) containing 80 high-confidence annotated genes. We amplified and sequenced 80 candidate genes in 406 varieties. According to the sequencing results, polymorphism analysis was conducted and the polymorphisms of these genes were added back to the original wheat SNP array for GWASs of the candidate genes. In Panel I, two polymorphic markers (TraesCS5A02G385600_583570621 and TraesCS5A02G385600_583570633) within TraesCS5A02G385600 were detected to be significantly associated with FHB response in at least two replicates (Table S2). In Panel II, five polymorphic markers (TraesCS5A02G386500_584060887, TraesCS5A02G386500_584060909, TraesCS5A02G386500_584060919, TraesCS5A02G387000_584507296, and TraesCS5A02G389800_585434071) within TraesCS5A02G386500, TraesCS5A02G387000, and TraesCS5A02G389800 were detected to be significantly associated with FHB response in at least two replicates (Table S2). As a consequence, TraesCS5A02G385600 encoding a late embryogenesis abundant D-like protein, TraesCS5A02G386500 encoding a myosin family protein, TraesCS5A02G387000 encoding a receptor-like kinase, and TraesCS5A02G389800 encoding a tetratricopeptide repeat protein were considered as the candidate genes for *gFHB-5A*.

3.5. Distribution of Resistance Alleles for gFHB-1B and gFHB-5A in the Huang-Huai Valley

Among Panel I varieties, which were developed after 2014, 80.3% and 74.9% carried alleles *Hap_1B_R* or *Hap_5A_R*, indicating that these genes were widely present in the Huang-Huai valley (Figure 7A). Based on the released years of varieties, Panel II varieties were divided into three periods based on time release, i.e., pre-1980, 1980–2000, and 2000–2014. The frequencies of *Hap_1B_R* during those periods were 63.6%, 54.9%, and 50.0%, respectively (Figure 7B), and the corresponding frequencies for *Hap_5A_R* were 50.0%, 39.0%, and 32.4%, a clear decline over time (Figure 7B). It is suggested that the application frequency of the FHB-resistant alleles *gFHB-1B* and *gFHB-5A* showed a gradually decreasing trend in FHB resistance breeding, and breeders should pay more attention to their application value in future FHB wheat breeding.

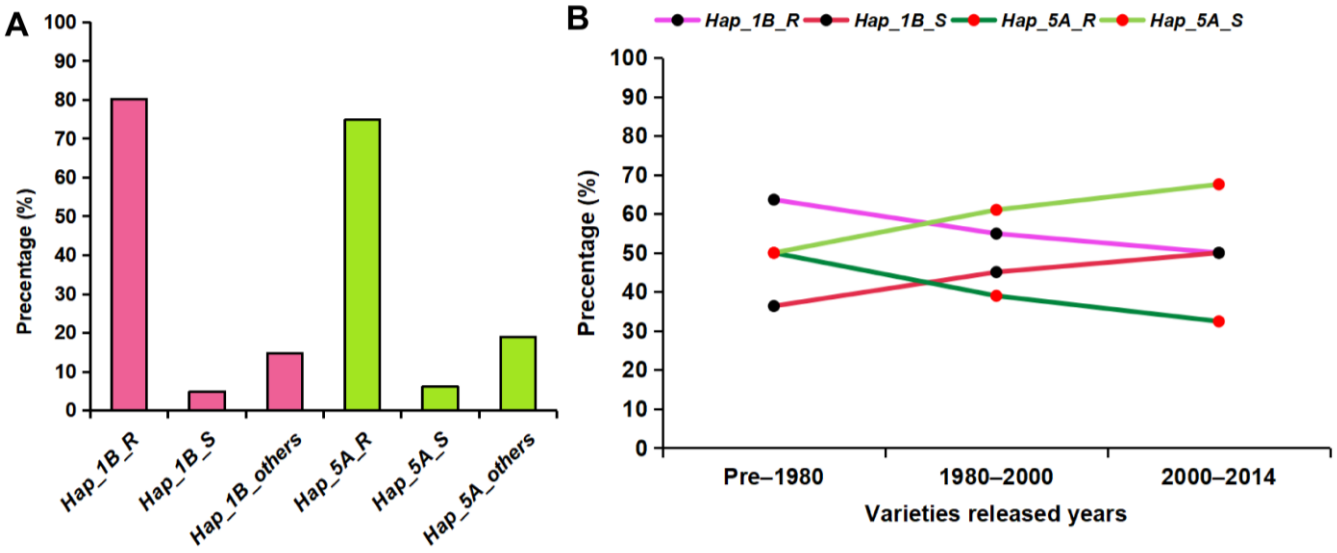

Figure 7. (**A**) Percentages of resistance alleles at the *gFHB-1B* and *gFHB-5A* QTL in Panel I. (**B**) Percentages of resistance alleles at the *gFHB-1B* and *gFHB-5A* QTL in Panel II varieties released pre-1980, 1980–2000, and 2000–2014.

4. Discussion

FHB is a major threat for wheat yield and quality. Many researchers are working on the screening of FHB-resistant germplasm. Because FHB is easily affected by the external environment, the germplasm resources screened by researchers are finite [42]. Here, we used two panels totaling 406 wheat varieties to represent genetic diversity in Chinese germplasm resources in GWASs and genotyped them with the commonly used Wheat 660 K and 90 K SNP arrays. Among 14 FHB resistance QTL detected in this study, 9 were detected by the 660 K SNP array and 13 were detected by the 90 K SNP array. By normalizing the physical locations of the markers, eight FHB resistance loci were detected by both SNP arrays. It becomes apparent that when two chips are used simultaneously to map a trait, the reliability and stability of loci can be mutually verified. The significant SNPs detected by the 660 K array were more concentrated in distribution than those detected by the 90 K array, as evidenced by the SNP discovery in the region of *gFHB-5A*.

Hundreds of QTL for FHB resistance have been detected across all 21 wheat chromosomes [43]. Here, 14 FHB-resistance-related QTL were located by GWAS; among them, 8 loci were stably detected in two variety panels. By analyzing the genotype of FHB resistance loci carried by the varieties, we found that Yanmai 888, Jimai23, Changnong339-5-1, Mianyang 86-11, Beijing 841, Zhengmai9023, and Youmai4 carried at least four resistance alleles showing FHB resistance of infection type 1. This is of great value in breeding FHB-resistant varieties by gene polymerization of large dominant FHB resistant loci such as *Fhb1-Fhb7* and novel small-effect FHB resistant loci.

To prove the novelty of the loci, we compared the physical distance of the FHB-resistance-related markers detected in this study with linked markers detected in previous studies. Notably, *Fhb1*, a major-effect QTL in the Asian variety Sumai 3, detected in many previous studies was reported to encode a putative histidine-rich calcium-binding protein, and a deletion spanning its start codon resulted in FHB resistance [20–22]. In the present study, the physical position of *gFHB-3B* (3.3~14.3 Mb) overlapped the regions of *Qfhb.nmbu.3B.1* (7–9 Mb), *high-confidence meta QTL-1* (*hcmQTL-29*: 3~8 Mb), and *hcmQTL-30* (7~9 Mb). We speculated that *gFHB-3B* might be *Fhb1* [43,44].

We detected three FHB resistance QTL on 1A. The physical position of *gFHB-1A.1* (3.4~46.2 Mb) was in the same region as *Qfhb.nmbu.1A.1* (3.1~13.3 on 1A) and *high-confidence meta QTL-1* (*hcmQTL-1*: 28~38 Mb) previously reported by Nannuru et al. [44] and Zheng et al. [43]. *Qfhb.nmbu.1A.2* (520~590 Mb) was reported by Nannuru et al. [44], whereas the physical interval of *gFHB-1A.2* 527.2~534.3 Mb and that of *gFHB-1A.3* was 579.4~591.3 Mb in a similar location to *hcmQTL-4* (577~584 Mb) [43]. This last gene was predicted to be *TraesCS1A02G428400*, annotated as a tryptophan synthase alpha chain. We speculate that *gFHB-1A.1*, *gFHB-1A.2*, and *gFHB-1A.3* are the same as reported in previous studies, although candidate genes are currently unconfirmed.

Multiple FHB disease resistance QTL located on chromosome 1B were identified by previous studies, such as *QFHB.vt-1B.1* (476.3~476.9 Mb), *QFHB.vt-1B.2* (330.2~341.9 Mb), *hcmQTL-5* (208~223 Mb), *hcmQTL-6* (530~546 Mb), *hcmQTL-7* (562~572 Mb), and *hcmQTL-8* (637~642 Mb) [43,45] In addition, *QFhb-1BL.1* (326.0 Mb) and *QFhb-1BL.2* (327.0 Mb) were detected by GWAS using a panel of 236 elite soft red winter wheat (SRWW) lines (Ghimire et al., 2022). Petersen et al. [46] identified *Qfhb.nc-1B.4* and mapped the QTL flanked by the markers IWB31692 (658.5 Mb) and IWB9040 (676.8 Mb). The *gFHB-1B* (582.9~607.9 Mb) identified in this study is located between the published *hcmQTL-7* and *hcmQTL-8*, and whether these three loci indicate the same locus needs further research.

Additionally, *gFHB-2B*, *gFHB-3A.2*, *gFHB-3D*, *gFHB-5D*, *gFHB-6B*, *gFHB-7A*, and *gFHB-7B* could correspond to the previously reported *hcmQTL-17* at 689~704 Mb on chromosome 2B [43,47], *QFhb.hbass-3AL* in Jingzhou 66 at 530.9~617.6 Mb [48], *QFhs.fal-3DS* from Arina at 6.75~7.09 Mb [43,49], *gFHB-5A* (577.9~596.5 Mb) located between *hcmQTL-46* (464~472 Mb) and *hcmQTL-47* (644~662 Mb) [43], *Qfhs.ksu-5DL1* from Chokwang at 430.04~676.71 Mb [43,50], *hcmQTL-62* from Sumai3 and durum variety DT707 at 147~154 Mb on 6B [16,43,51], *hcmQTL-66* from RL4137 at 37~49 M on 7A [43,52], and *hcmQTL-73* from Dream at 143~163 Mb on chromosome 7B [43,53]. Among the QTL reported on 3A, the closest location to *gFHB-3A.1* (1.3~14.9 Mb) is *hcmQTL-23* (15~21 Mb) [43], others were more distal [43].

Since no previously reported QTL overlapped *gFHB-1B*, *gFHB-3A.1*, or *gFHB-5A*, these resistance loci are probably novel. High-confidence FHB resistance loci *gFHB-1B* and *gFHB-5A* were subjected to further analysis. The GWAS analysis of candidate genes was performed again based on the polymorphic amplification of candidate genes, and five potential resistance candidate genes were predicted.

FHB disease resistance in wheat is a complex quantitative trait. Most varieties show variable levels of partial resistance. Marker-assisted selection to combine various QTL is the most economic and effective route to reduce yield losses. Here, 14 FHB resistance loci were detected and three of them are probably novel. Favorable haplotypes that should improve the level of FHB resistance were detected. Five potential resistance candidate genes were predicted for *gFHB-1B* and *gFHB-5A*, respectively, combined with a haplotype analysis of two panels and genome-wide association analysis of candidate genes. In conclusion, this study found some favorable alleles and new FHB QTL through the genome-wide association study of FHB resistance loci, which enhanced gene diversification and enriched the FHB resistance gene pool, which has important theoretical significance for resisting the possible FHB epidemic in future production. It also provides important marker information for marker-assisted selection breeding.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/agronomy13071712/s1, Table S1: Details of 1264 SNPs associated with FHB response detected by the current genome-wide association studies (GWAS), Table S2: Details of SNPs associated with FHB response detected by genome-wide association study (GWAS) after adding the polymorphism of candidate genes.

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