



Contents lists available at ScienceDirect

The Crop Journal

journal homepage: www.keaipublishing.com/en/journals/the-crop-journal/

Genetic sources and loci for wheat head blast resistance identified by genome-wide association analysis

Lei Wu^{a,1}, Xinyao He^{b,1}, Muhammad Rezaul Kabir^c, Krishna K. Roy^c, Md. Babul Anwar^c, Felix Marza^d, Yi He^a, Peng Jiang^a, Xu Zhang^{a,*}, Pawan K. Singh^{b,*}

^aCIMMYT-JAAS Joint Center for Wheat Diseases, Jiangsu Academy of Agricultural Sciences, Nanjing 210014, Jiangsu, China

^bInternational Maize and Wheat Improvement Center (CIMMYT), Apdo, Postal 6-641, 06600 Mexico D.F., Mexico

^cBangladesh Wheat and Maize Research Institute (BWMRI), Nashipur, Dinajpur 5200, Bangladesh

^dInstituto Nacional de Innovación Agropecuaria y Forestal (INIAF), La Paz, Bolivia

ARTICLE INFO

Article history:

Received 9 March 2021

Revised 24 June 2021

Accepted 24 July 2021

Available online xxxx

Keywords:

Magnaporthe oryzae pathotype *Triticum*

Host resistance

Wheat blast

GWAS

ABSTRACT

The emergence and spread of wheat blast caused by fungal pathogen *Magnaporthe oryzae* pathotype *Triticum* is a threat to global wheat production. The resistance level and genetic loci for blast resistance in Chinese germplasm remain unknown. A panel of 266 bread wheat accessions from China, CIMMYT-Mexico and other countries was screened for head blast resistance under 12 field experiments in Bolivia and Bangladesh. Subsequently, a genome-wide association study was performed to understand the genetic basis of wheat blast resistance. The average blast index of all the accessions was $53.7\% \pm 12.7\%$, and 10 accessions including Chinese accessions Yumai 10 and Yu 02321 showed moderate to high levels of blast resistance, accounting for only 3.8% in the panel. Fifty-eight significant SNPs clustered in a 28.9 Mb interval on the 2AS/2NS translocation region, explaining phenotypic variation between 10.0% and 35.0%. The frequency of the 2AS/2NS translocation in the Chinese accessions was as low as 4.5%. These results indicated that the 2NS fragment was the only major locus conferring resistance to wheat blast in this panel, and the resistant and moderately resistant lines identified could be deployed in breeding.

© 2021 Crop Science Society of China and Institute of Crop Science, CAAS. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co. Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Wheat blast caused by a fungal pathogen *Magnaporthe oryzae* pathotype *Triticum* (MoT) was first reported in Brazil in 1985, and it spread to the neighboring countries including eastern Bolivia, eastern Paraguay, and northern Argentina in the subsequent decades [1]. Severe outbreaks of wheat blast could cause up to 100% yield losses under favorable weather conditions [2,3], and affect the germination and nutritional quality of grains after harvest [4]. The wheat cropping area in some parts of Brazil dropped by 95% in 2016 mainly due to frequent blast epidemics [5]. In February 2016, explosive outbreak of wheat blast resulted in dramatic yield losses across eight districts in Bangladesh [6,7]. It was inferred that the pathogen isolates in Bangladesh came from South America based on genome sequencing results of field

isolates from different sources [8]. Recently, the occurrence of wheat blast has been reported in Zambia, Africa [9].

The intercontinental spread of wheat blast has aroused concern that it might become a global disease, which poses a great threat to wheat production and food security with the increasing wheat trade and climate change [1,3,5]. A weather-based model predicted that 40% of winter wheat production areas in USA were suitable for MoT propagation and the disease might outbreak in 25% of the country [10]. Currently, no wheat blast incidence has been reported in China, but there is a risk that the disease may occur in certain areas of southern China where agro-ecology conditions are conducive for the disease [11,12].

Breeding for wheat blast resistance is considered a sustainable and effective approach to control the disease, but few resistance genes are available. Among the designated MoT-specific resistance genes, *Rmg2* and *Rmg3* are temperature sensitive and effective only at the seedling stage [13], and *Rmg7* becomes ineffective at high temperature [14]. *Rmg8* combined with *RmgGR119* conferred resistance to MoT isolates from Brazil and Bangladesh at the head stage under laboratory conditions, indicating that the two genes might

* Corresponding authors.

E-mail addresses: xuzhang@jaas.ac.cn (X. Zhang), pk.singh@cgiar.org (P.K. Singh).

¹ These authors contributed equally to this study.

<https://doi.org/10.1016/j.cj.2021.07.007>

2214-5141/© 2021 Crop Science Society of China and Institute of Crop Science, CAAS. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co. Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

be promising in breeding program [15–18]. Three QTL associated with wheat blast on chromosomes 4A, 5A and 2B were identified from a Brazilian variety BR18-Terena, explaining 17.8%–19.6% of the phenotypic variation [19]. The 2AS/2NS translocation segment introduced from *Aegilops ventricosa* was a major locus for wheat blast resistance in field conditions [20]. Two co-dominant markers WGGB156 and WGGB159 linked to 2AS/2NS might be useful in marker assisted selection for wheat blast resistance [21]. More than 80% of accessions possessed the 2NS fragment in recent Kansas (USA) and CIMMYT wheat breeding materials, because this fragment was associated with multi-disease resistance and high yield potential [22–24]. Cruppe et al. [25] tested wheat blast resistance in over 780 wheat and wild-relative accessions under field and greenhouse conditions and found only four non-2NS spring wheat from CIMMYT that showed resistance to wheat blast. To date, the level and genetic loci for wheat blast resistance in Chinese wheat varieties remain unknown.

Recent advances in genotyping approaches based on single nucleotide polymorphisms (SNP) such as genotyping by sequencing (GBS) and high-density SNP chips enabled breeders to identify genomic loci responsible for important fungal diseases such as wheat blast [23], rust [26], tan spot [27], powdery mildew [28] and Fusarium head blight [29] through genome-wide association studies (GWAS) based on linkage disequilibrium (LD) analysis. In the current study, 266 wheat accessions including commercial varieties and breeding lines with worldwide origin were tested for wheat blast resistance under field conditions in Bolivia and Bangladesh, and GWAS was then performed using DArTSeq marker data to detect loci underlying wheat blast resistance.

2. Materials and methods

2.1. Plant materials

The panel used in this study involved 266 worldwide wheat accessions, including 132 Chinese accessions mainly from the Yellow and Huai River Valley Region and Middle-lower Yangtze Valley Region. The remaining accessions were composed of 71 from CIMMYT-Mexico, 41 from South America, 10 from North America, five each from Asia and Europe, and one each from Oceania and Africa (Table S1).

2.2. Wheat blast screening

The panel was evaluated during the 2018–2019 (denoted as 2019) and 2019–2020 (2020) cropping cycles in Quirusillas, Bolivia and Jashore, Bangladesh, and during the 2019 and 2020 cycles in Okinawa, Bolivia. In each cropping cycle, there were two sowings marked as ‘a’ and ‘b’ with an interval of around two weeks, to expose the materials to different environments. A mixture of aggressive MoT isolates including OKI1503, OKI1704, QUI1505, QUI1601, and QUI1612 was used as inoculum in Bolivia, and BHO17001, MEH17003, GOP17001.2, RAJ17001, CHU16001.3, and JES16001 were mixed to inoculate in Bangladesh. The spikes of each accession were sprayed with the inoculum at a concentration of 80,000 spores mL⁻¹ at anthesis and two days later. A field misting system was set to spray for 10 min every hour during daytime to maintain high humidity that is conducive for MoT infection. The total and infected numbers of spikelets for 10 spikes of each plot were recorded at the 14th or 21st days after the first inoculation, depending on disease progress, to calculate blast incidence and severity. Blast index was calculated with the formula: Index = incidence × severity, where “incidence” stands for the percentage of spike with blast symptom and “severity” for the averaged percentage of infected spikelets.

2.3. Statistical analysis

Best linear unbiased predictions (BLUPs) of blast index for each accession across different environments were estimated using R package “lme4” in order to combine analysis of variance across environments in a mixed linear model including genotype, environment and genotype-by-environment interaction as random factors [30]. The phenotypic data of Jash20a was used for phenotypic analysis but not for GWAS because of its low disease pressure and mostly non-significant correlation with other experiments. Broad sense heritability (H^2) was estimated following the formula described by He et al. [21]. Pearson’s correlation coefficients among environments were computed by R to test the consistency of blast responses across different environments [30]. Turkey’s mean comparison tests were performed among subgroups using R [30].

2.4. Genotyping

The GWAS panel was genotyped with the DArTSeq technology at the Genetic Analysis Service for Agriculture (SAGA) at CIMMYT, Mexico. The marker Ventriup-LN2 developed by Helguera et al. [31] was used to test whether an accession carried the 2AS/2NS fragment. Markers with more than 10% missing data or minor allele frequency less than 1% were eliminated, resulting in 18,436 high quality markers, of which 14,195 SNPs with known physical positions in Chinese Spring reference genome v.2.0 were used for population structure and LD analysis.

2.5. Population structure and estimation of LD

Population structure was analyzed using the Bayesian model-based clustering method in STRUCTURE v2.3.4 [32]. Five iterations for the hypothetical subpopulations (K value) from 1 to 8 were performed based on an admixture model with the same settings (100,000 Markov Chain Monte Carlo replications and 10,000 length of burn-in period). The software PLINK was used to calculate principal components of the population (PCA) and LD squared allele frequency correlation (r^2) estimated for all pairwise comparisons between SNPs in a distance of 10,000 kb [33]. The pairwise LD r^2 estimated from all the loci were plotted against the corresponding pairwise physical distances, and then a nonlinear regression was fitted in R. The critical r^2 value was determined as the 95th quantile for all r^2 values between unlinked SNPs. The intersection between the critical r^2 value and the regression line was used to estimate the average size for LD blocks in this panel. The software Haploview was used to calculate local pairwise LD and visualize the haplotype data [34].

2.6. Genome-wide association analysis

The kinship matrix (\mathbf{K} matrix) and \mathbf{Q} matrix were calculated by TASSEL v5.0 [35] and Structure v2.3.4, respectively. Genomic-wide association for wheat blast across environments was performed using software TASSEL v5.0 pipeline command line interface. No compression was applied and the P3D method was used to test for each trait-marker association, and \mathbf{K} and \mathbf{Q} matrices were used as covariates to remove the false positive results caused by population structure. The P -value threshold was determined with Bonferroni correction: $P = -\log_{10}(0.05/m)$, where m was the number of markers used in the analysis. The true position of significant SNPs was determined by LD estimation or sequence alignment with “Jagger” [36] and “Chinese Spring” [37] genome and SNPs that had multiple matches in genome sequence were excluded from further analysis. The sequences of all significant markers were aligned on the website of Triticeae Multi-omics Center (<http://>

wheatomics.sdau.edu.cn/blast/viroblast.php) using ViroBLAST program [38] with default parameters. In detail, the value of expect threshold was 10, the score of a nucleotide match was 2 and that of a mismatch was -3 , the costs to open and extend a gap was 5 and 2, respectively.

3. Results

3.1. Wheat blast screening

Broad variation was observed in wheat blast index across the 12 environments (Fig. 1). The average blast index of all accessions was $53.7\% \pm 12.7\%$, and there were 10 genotypes including Chinese accessions Yumai 10 and Yu 02321 that had a blast index less than 25.0% (Table 1), accounting for only 3.8% of the panel. Three Chinese accessions Ningmai 13, Shenhemai 1, and Zhoumai 24, none of which carried 2NS, showed tolerance to wheat blast with blast index between 25.0% and 35.0% (Table 1). About 30.5% (81 accessions) of the accessions had a blast index between 25.0% and 50.0%, while “PROINTA FEDERAL” showed the maximum index of 78.3%. No significant difference in blast index was observed among geographical regions ($P > 0.05$, Table S1), whereas significant difference was observed between 2AS and 2NS groups ($P < 0.01$, Fig. 2). Totally 23 2NS carriers were identified, exhibiting indices from 18.1% to 43.5%, with a grand mean index of 28.3%. Of the 132 Chinese accessions evaluated in the present study, 6 accessions had the 2AS/2NS translocation fragment including moderately resistant varieties Yumai 10 and Yu 02321 (Table S1). It is worth noting that over 20 non-2NS Chinese accessions had indices of less than 45.0%, including resistance sources for Fusarium head blight such as Ningmai 13 and Sumai 3 (Table S1).

Broad sense heritability (H^2) value for wheat blast resistance was estimated at 0.61 across environments. The wheat blast index in each environment had a large span from 16.8% to 80.7%. Experiments in Bolivia exhibited moderate correlations, whereas those in Bangladesh showed lower correlations, some of which were non-significant ($P < 0.01$, Fig. S1; Table S2).

3.2. Population structure and linkage disequilibrium

Population structure analysis indicated two subpopulations, which could be further divided into five groups 1A, 1B, 2A, 2B and 2C (Fig. 3a–c). The clustering of subpopulations mainly associated with geographical origins. Subpopulation 1 (130 accessions)

involved accessions mainly from CIMMYT, South America, North America, and Europe, while most accessions in subpopulation 2 (136 accessions) were from Asian countries including China, Japan and India (Table S1). Of the 23 accessions with 2NS, six were from China and 17 from CIMMYT (Table S1). Subpopulation 1 had a higher average wheat blast index (55.2%) than subpopulation 2 (52.3%). Among the groups, 1A had the highest mean blast index, followed by 2B, 1B, 2A, and 2C (Fig. 3d). The critical r^2 value was 0.12, which intersected the regression line of LD decay at a physical distance of 7.9 Mb in the whole genome, 9.1 Mb in A genome, 7.1 Mb in B genome and 8.0 Mb in D genome (Fig. S2).

3.3. Genome-wide association analysis

Marker-trait association (MTA) was performed to identify the loci responsible for wheat blast resistance using mixed linear model with **Q** and **K** matrix in TASSEL (Tables S3 and S4). A total of 68 MTAs were detected across the 11 environments, of which 58 significant SNPs clustered in a 28.9 Mb interval harboring the 2AS/2NS translocation region (Fig. 4a and c), explaining phenotypic variation between 9.4% and 28.5% (Table S5). This indicates the importance of the 2AS/2NS translocation in conditioning wheat blast resistance in the panel. Blocks based on local LD analysis were identified within the 2NS region (Fig. 4c), having different sizes and haplotypes (Fig. 4d). There were 10 significant SNPs with unknown physical position, which were not used in further analysis.

3.4. Favorable alleles for wheat blast resistance

The favorable alleles of each block on the 2AS/2NS fragment were identified (Fig. 5a–e). For each block, haplotypes Hap 3 and Hap 4 had lower blast index compared with other haplotypes ($P < 0.01$), indicating that these haplotypes were associated with 2NS conferring blast resistance. Frequency of the favorable allele of each haplotype was low in the panel, ranging from 2.4% to 5.5% (Fig. 4d).

4. Discussion

4.1. Limited genetic sources are available for wheat blast resistance

Identification and deployment of resistance varieties are essential to control wheat head blast and to avoid potential outbreak in disease-free regions. In earlier reports, USA cultivars Postrok, Jack-

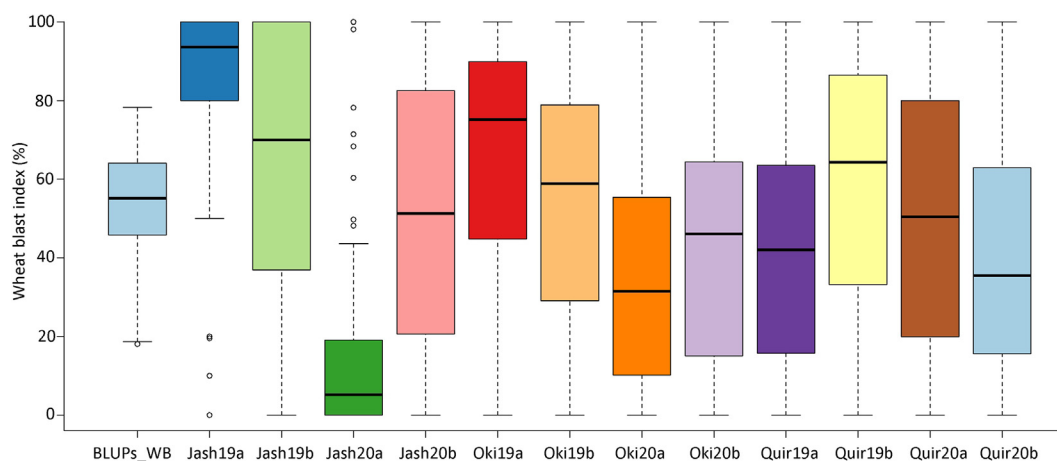


Fig. 1. Wheat blast evaluation across the 12 field experiments. Note: ‘Quir’ stands for Quirussillas, ‘Jash’ for Jashore, and ‘Oki’ for Okinawa, ‘19’ and ‘20’ for the 2018–2019 or 2019–2020 or 2020 cycle, respectively, and ‘a’ and ‘b’ for the first and second sowing, respectively. BLUP_WB stands for the best linear unbiased predictions (BLUPs) for wheat blast index across different experiments.

Table 1
Genotypes with wheat blast index less than 35% across the 12 experiments.

CIMMYT GID	Name/Pedigree	Origin	Subgroup	2NS	WB index (%)
1396801	CANINDE #1	CIMMYT	1B	Yes	18.1
7806808	BORLAUG100 F2014	CIMMYT	1B	Yes	18.6
5307520	CHIBIA//PRLII/CM65531/3/MISR 2	CIMMYT	1B	Yes	20.6
8750829	Yumai 10	China	2A	Yes	23.3
8750828	Yu 02321	China	2A	Yes	23.5
4754362	MUTUS	CIMMYT	1B	Yes	23.5
6174949	QUELEA	CIMMYT	1B	Yes	24.1
12725	MILAN	CIMMYT	1B	Yes	24.8
6176054	VALK	CIMMYT	1B	Yes	24.8
4754187	HUIRIVIS #1	CIMMYT	1B	Yes	24.9
6279648	KRICHAUFF/2*PASTOR/4/CROC_1/AE.SQUARROSA(224)//2*OPATA/3/2*RAC655/5/PARUS/PASTOR	CIMMYT	1B	Yes	27.0
6176474	KACHU #1//PI 610750/SASIA/3/KACHU	CIMMYT	1B	Yes	27.1
6418272	ATTILA/3*BCN*2//BAV92/3/HEILO/4/CHIBIA//PRLII/CM65531/3/MISR 2	CIMMYT	1B	Yes	27.3
6175409	WAXBILL	CIMMYT	1B	Yes	27.9
8750732	Emai 19	China	2A	Yes	30.6
8750771	Ningmai 13	China	2C	No	32.2
5794268	NG8201/KAUZ/4/SHA7//PRL/VEE#6/3/FASAN/5/MILAN/KAUZ/6/ACHYUTA/7/PBW343*2/KUKUNA	CIMMYT	1B	Yes	32.4
8750792	Shenmai 1	China	2A	No	33.2
282484	BUCK AUSTRAL	Argentina	1A	No	33.5
8750841	Zhoumai 98165	China	2C	Yes	33.6
4319982	MURGA	CIMMYT	1B	Yes	34.2
8750840	Zhoumai 24	China	2C	No	34.3

Note: Subgroup information was based on the structure and PCA data, and the 2AS/2NS translocation was diagnosed by the marker *Ventriup-LN2*.

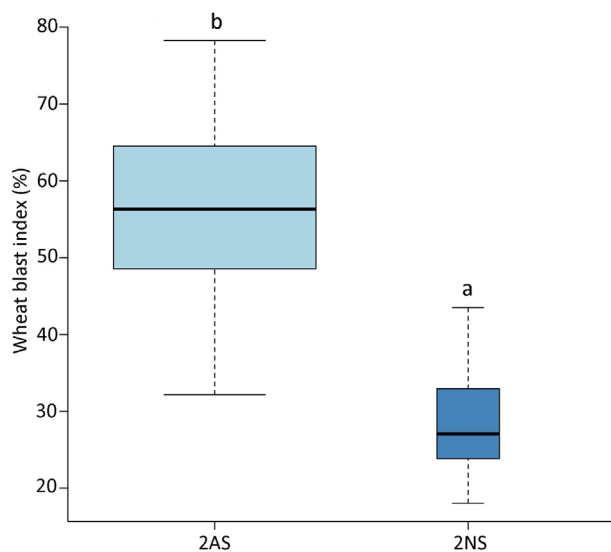


Fig. 2. Wheat blast index distribution patterns in 2AS and 2NS accessions. "a" and "b" indicate significant difference at $P < 0.01$.

Pot, Overley, Jagalene, Jagger, and Santa Fe showed less than 3% severity, all of which are 2NS carriers [39], and *de novo* reassembly sequence of the 2NS segment in Jagger has recently been released [22]. In our study, 10 accessions were found to have a blast index less than 25.0%, including Chinese accessions Yumai 10 and Yu 02321, and genotyping results indicated that all these accessions carried the 2NS fragment, whereas non-2NS resistant accession was not identified. Other 2NS carriers Emai 9, Zhoumai 98165, Zheng 9405, and Mianmai 37 showed tolerance to wheat blast with blast indices ranging from 30.6% to 43.5%. The frequency of 2NS fragment in Chinese accessions assayed was as low as 4.5%, in agreement with the fact that 2AS/2NS translocation has not been widely utilized in breeding programs in China [11,40]. However, its frequency in CIMMYT genotypes was higher at 23.9%, in accordance with the moderate frequency of 2NS in CIMMYT materials released between 1990s to early 2010s [22–23]. It is noteworthy that the frequency has increased to around 90% in CIMMYT

materials released after 2015, due to its contribution to rust resistance and yield advantage [22–24]. In accordance with previous research, our results also showed that not all 2NS accessions showed a high resistance to wheat blast (Table S1), indicative of background effect in functioning of 2NS translocation. Wheat blast resistance based on single gene (2NS translocation) is risky more so as the breakdown or erosion of 2NS resistance to wheat blast has been reported in Paraguay, Bolivia and Brazil due to the emergence of more aggressive MoT isolates [1,25]. The search for non-2NS sources might help address this problem. Four non-2NS breeding lines from CIMMYT were reported to have a good resistance to wheat blast [25]; but recent results indicated that they could still be heavily infected under high disease pressure [41], implying that the non-2NS resistance identified so far is not as good as the 2NS resistance. Nevertheless, these non-2NS sources are valuable for breeding, as well as the ones identified in this study, which could be used to identify novel resistance gene(s)/QTL for durable resistance to wheat blast [25].

The 2NS fragment was the only major and stable resistance locus from our GWAS analysis. It is worth pointing out that the frequency of favorable haplotype blocks in our panel was low due to the low frequency of allelic variation in our population or/and low marker density used in the analysis. The blocks detected in this paper on 2NS were distributed in the entire translocation segment, and there was no significant difference in the effects of different blocks. Normally it is believed that no recombination happens between the homoeologous regions of 2NS and 2AS [22], and the blocks might have been caused by the influences from bread wheat alleles on 2AS or genotyping errors; but rare recombination events between 2NS and 2AS might have also been involved, as suggested in a few previous studies [21,42,43]. Although, we cannot completely rule out the possibility that these studies might also have genotyping inaccuracies. The Gao et al. [22] study has shown that there could be recombination in the 2NS-adjacent region (33–40 Mb on 2AS of the hexaploid wheat genotype VPM1). It is thus critical to also distinguish recombination events within 2NS and those in the adjacent 2AS region (likely to be the block 5 of this study at 29 Mb in CS corresponding to around 40 Mb in Jagger) in future studies.

The 2NS fragment contains an abundance of nucleotide-binding domain leucine-rich repeat (NLR) genes, ABC transporter genes and

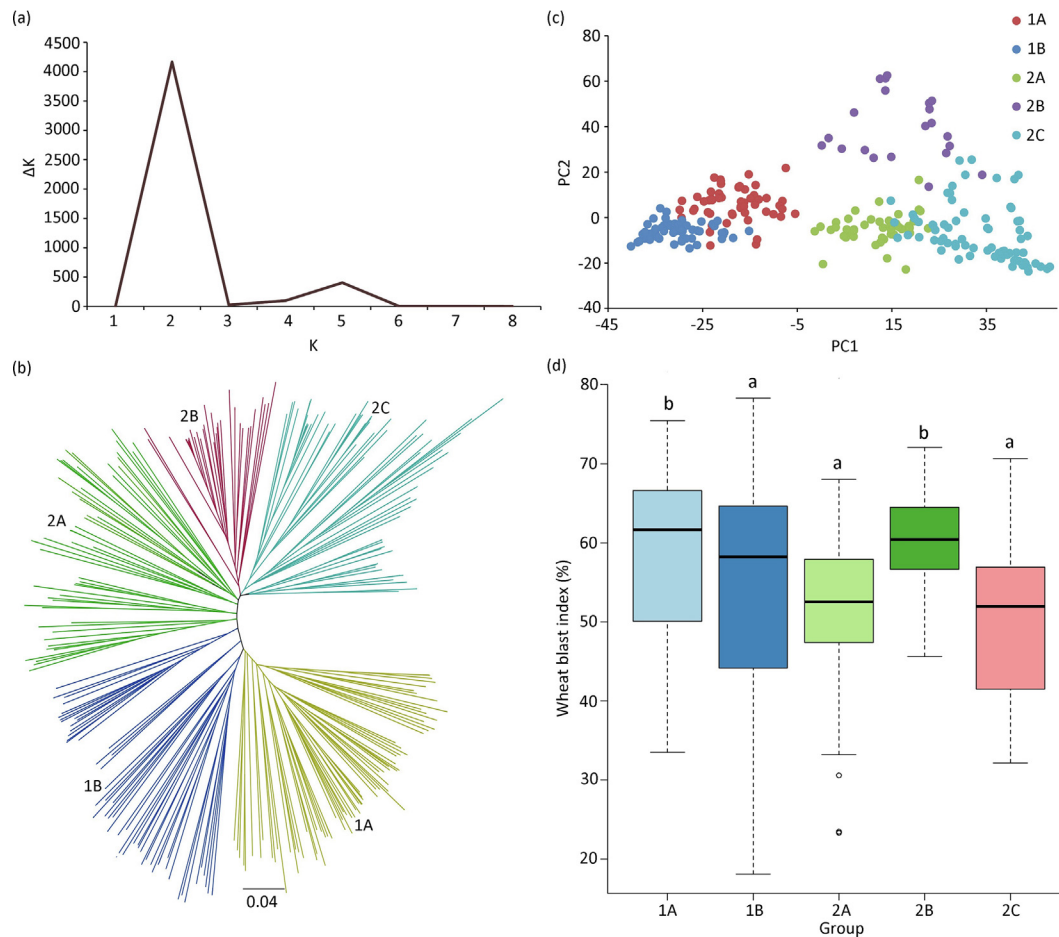


Fig. 3. Kinship and population structure of the 266 accessions. (a) Number of sub-population inferred from structure analysis. (b) Neighbor-joining tree based on genotypic data. (c) Groups estimated by principal component analysis. (d) Distribution patterns of wheat blast index in different groups. “a” and “b” indicate significant difference at $P < 0.01$.

cytochrome P450 genes that were potentially involved in disease resistance [22]. Considering that the 2NS fragment confers resistance to rusts [31,44], nematodes [44,45] and wheat blast [2,20,23,24], it might have one or more genes involved in a shared pathway for biological stress response. Cloning of the underlying gene for wheat blast resistance is critical for better understanding the resistance mechanism and for development of functional markers. To achieve this goal, targeted mutation and sequence capture technologies could be used. And if recombination does happen within the 2AS/2NS translocation region, it will serve as an additional tool for the fine mapping and cloning work.

4.2. Future strategies in preventing wheat blast outbreak in China

The emergence and spread of wheat blast made us realize that it is becoming a globally important disease; though, MoT isolates causing wheat blast has not been reported in China. It is recommended that strict quarantine measures be taken on wheat or other small grains imported from wheat blast endemic areas, because infected seeds can spread the pathogens over long dis-

tances. According to a very recent study, some *M. oryzae* pathotype *Oryzae* (MoO) isolates were able to cause typical blast symptoms on spikes of certain wheat genotypes at high temperature under laboratory conditions, indicating that MoO could increase the risk for wheat blast outbreak in wheat–rice rotation areas in China [46]. It should be alerted on the potential host jump of MoO from rice to wheat, considering that a similar host jump happened in South America, which directly caused the emergence of wheat blast [47]. The *M. oryzae* pathotype *Lolium* (MoL) is also capable of inciting blast on wheat spikes under field or laboratory conditions in USA [48,49]. In China, MoL is also present [50], but its geographical distribution is largely unknown. Therefore, an urgent need is to investigate the distribution of MoL in various wheat cropping regions in China, and to perform risk assessment on those regions based on local climatic data. A predictive and warning system based on climatic data has been developed in Brazil [51] and Bangladesh [52] to forecast wheat blast epidemic, enabling plant protective officials to make strategic decisions for disease control. This work is important and valuable for preemptive prevention strategies against wheat blast in China, just as wheat blast in Ban-

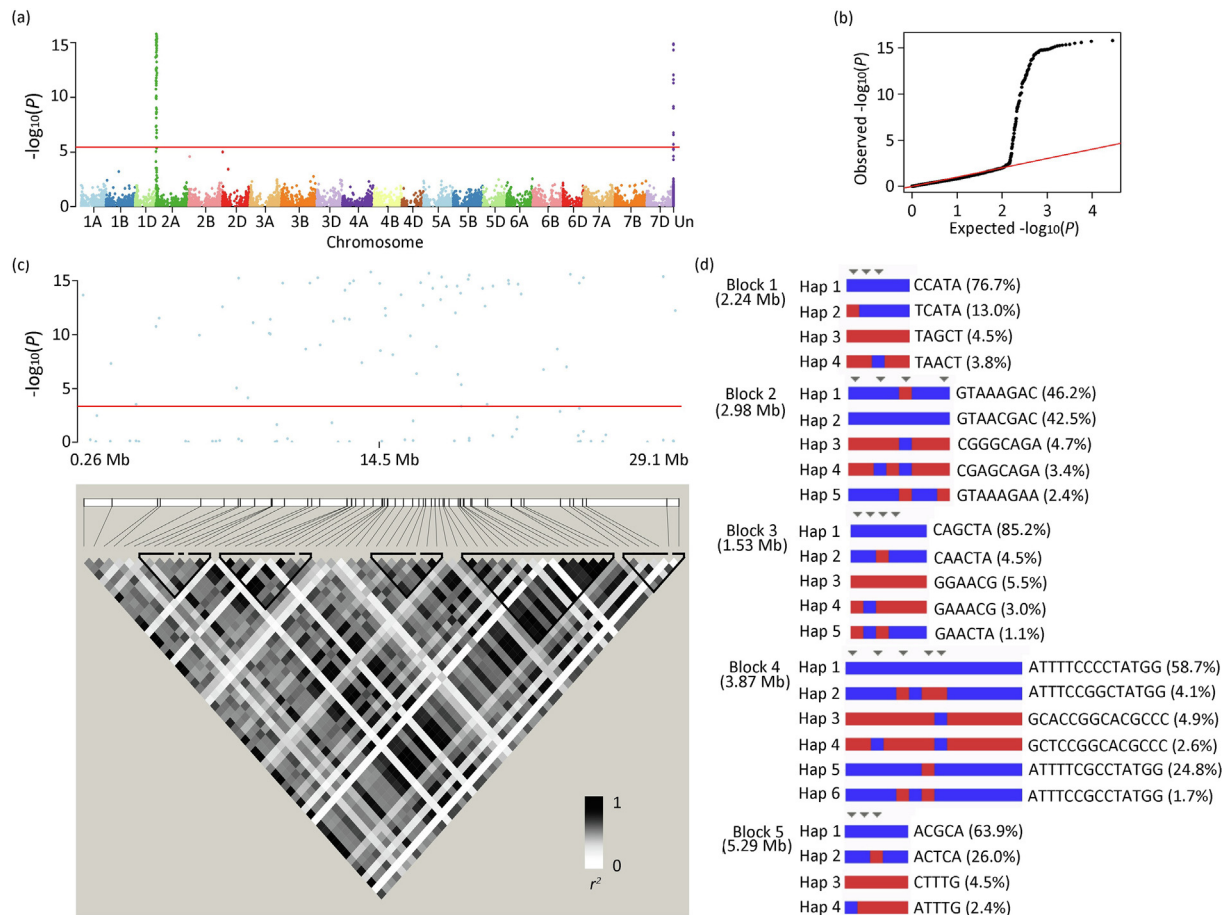


Fig. 4. GWAS results for wheat blast resistance and haplotype blocks analysis on the 2AS/2NS translocation region. (a) Manhattan and (b) Q-Q plots showing SNPs associated with WB resistance. (c) Manhattan plots on the 2AS/2NS translocation region and the five haplotype blocks. (d) Haplotypes of the five haplotype blocks on 2AS/2NS and their frequencies. The SNPs marked with gray triangle had the largest r^2 . Note: BLUP values for wheat blast index across all experiments except Jash20a were used in the analysis. Un stands for markers with unknown physical location.

gladesh was predicted by researchers before its outbreak in 2016 [53]. The frequency of 2NS fragment was extremely low in Chinese wheat as reported in this study, and no other resistant sources were available. Therefore, it is also recommended that breeders use the 2NS fragment in potential wheat blast vulnerable areas in China.

CRediT authorship contribution statement

Lei Wu: Data curation, Formal analysis, Visualization, Writing - original draft. **Xinyao He:** Data curation, Formal analysis, Investigation, Writing - review & editing. **Muhammad Rezaul Kabir:** Investigation, Writing - review & editing. **Krishna K. Roy:** Investigation, Writing - review & editing. **Md. Babul Anwar:** Investigation, Writing - review & editing. **Felix Marza:** Investigation, Writing - review & editing. **Yi He:** Visualization, Validation, Writing - review & editing. **Peng Jiang:** Visualization, Validation, Writing -

review & editing. **Xu Zhang:** Conceptualization, Project administration, Supervision, Writing - review & editing. **Pawan K. Singh:** Conceptualization, Project administration, Supervision, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors received financial support through the CGIAR Research Program on WHEAT and the National Natural Science Foundation of China (31561143004). Technical support from Jose Asister, Jhonny Villagomez, Roberto Butron, and Francisco Lopez

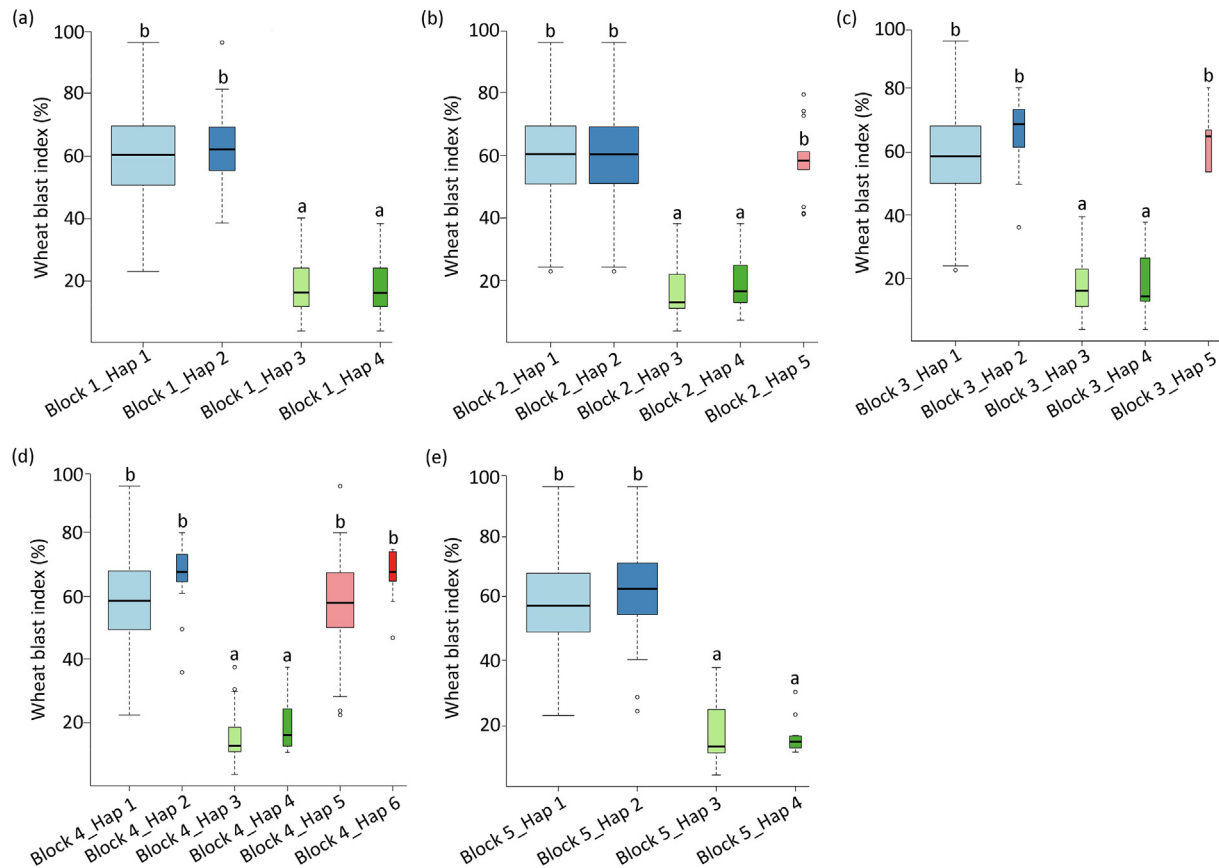


Fig. 5. Allelic effects of the five haplotype blocks on the 2AS/2NS translocation region. “a” and “b” indicate significant difference at $P < 0.01$.

in field trials in Bolivia, Tanusree Roy and Rokshana Begum in field trials in Bangladesh is highly acknowledged.

Appendix A. Supplementary data

Supplementary data for this article can be found online at <https://doi.org/10.1016/j.cj.2021.07.007>.

References

- [1] P.C. Ceresini, V.L. Castroagudín, F. Rodrigues, J.A. Rios, C. Eduardo Aucique-Pérez, S.I. Moreira, E. Alves, D. Croll, J.L.N. Maciel, Wheat blast: past, present, and future, *Annu. Rev. Phytopathol.* 56 (2018) 427–456.
- [2] C.D. Cruz, B. Valent, Wheat blast disease: danger on the move, *Trop. Plant Pathol.* 42 (2017) 210–222.
- [3] M.A. Sadat, J. Choi, Wheat blast: A new fungal inhabitant to Bangladesh threatening world wheat production, *Plant Pathol. J.* 33 (2017) 103–108.
- [4] M.Z. Surovy, N.U. Mahmud, P. Bhattacharjee, M.S. Hossain, M.S. Meheeb, M. Rahman, B.C. Majumdar, D.R. Gupta, T. Islam, Modulation of nutritional and biochemical properties of wheat grains infected by blast fungus *Magnaporthe oryzae* *Triticum* pathotype, *Front. Microbiol.* 11 (2020) 1174.
- [5] P.C. Ceresini, V.L. Castroagudín, F. Rodrigues, J.A. Rios, C.E. Aucique-Pérez, S.I. Moreira, D. Croll, E. Alves, G. de Carvalho, J.L.N. Maciel, B.A. McDonald, Wheat blast: from its origins in South America to its emergence as a global threat, *Mol. Plant Pathol.* 20 (2019) 155–172.
- [6] M.T. Islam, K.H. Kim, J. Choi, Wheat blast in Bangladesh: the current situation and future impacts, *Plant Pathol. J.* 35 (2019) 1–10.
- [7] P.K. Malaker, N.C. Barma, T.P. Tewari, W.J. Collis, E. Duveiller, P.K. Singh, A.K. Joshi, R.P. Singh, H.J. Braun, G.L. Peterson, First report of wheat blast caused by *Magnaporthe oryzae* pathotype *Triticum* in Bangladesh, *Plant Dis.* 100 (2016) 2330.
- [8] M.T. Islam, D. Croll, P. Gladieux, D.M. Soanes, A. Persoons, P. Bhattacharjee, M.S. Hossain, D.R. Gupta, M.M. Rahman, M.G. Mahboob, N. Cook, M.U. Salam, M.Z. Surovy, V.B. Sancho, J.L. Maciel, A. Nhanijúnior, V.L. Castroagudín, J.T. Reges, P. C. Ceresini, S. Ravel, R. Kellner, E. Fournier, D. Tharreau, M.H. Lebrun, B.A. McDonald, T. Stitt, D. Swan, N.J. Talbot, D.G. Saunders, J. Win, S. Kamoun, Emergence of wheat blast in Bangladesh was caused by a South American lineage of *Magnaporthe oryzae*, *BMC Biol.* 14 (2016) 84.
- [9] B. Tembo, R.M. Mulenga, S. Sichilima, K. M'Siska, M. Mwale, P.C. Chikoti, P.K. Singh, X. He, K.F. Pedley, G.L. Peterson, R.P. Singh, H.J. Braun, Detection and characterization of fungus (*Magnaporthe oryzae* pathotype *Triticum*) causing wheat blast disease on rain-fed grown wheat (*Triticum aestivum* L.) in Zambia, *PLoS ONE* 15 (2020) e0238724.
- [10] C.D. Cruz, R.D. Magarey, D.N. Christie, G.A. Fowler, J.M. Fernandes, W.W. Bockus, B. Valent, J.P. Stack, Climate suitability for *Magnaporthe oryzae* *Triticum* pathotype in the United States, *Plant Dis.* 100 (2016) 1979–1987.
- [11] X. He, Y. Hao, Y. Zhou, Z. He, Progress and perspective in wheat blast research, *Acta Agron. Sin.* 43 (2017) 1105–1114 (in Chinese with English abstract).
- [12] X. Cao, L. Chen, Y. Zhou, X. Duan, Potential distribution of *Magnaporthe grisea* in China and the world, prediated by MaxEnt, *Plant Protect.* 37 (2011) 80–83.
- [13] S.W. Zhan, S. Mayama, Y. Tosa, Identification of two genes for resistance to *Triticum* isolates of *Magnaporthe oryzae* in wheat, *Genome* 51 (2008) 216–221.
- [14] A.G. Tagle, I. Chuma, Y. Tosa, *Rmg7*, a new gene for resistance to *Triticum* isolates of *Pyricularia oryzae* identified in tetraploid wheat, *Phytopathology* 105 (2015) 495–499.
- [15] V.L. Anh, N.T. Anh, A.G. Tagle, T.T.P. Vy, Y. Inoue, S. Takumi, I. Chuma, Y. Tosa, *Rmg8*, a new gene for resistance to *Triticum* isolates of *Pyricularia oryzae* in hexaploid wheat, *Phytopathology* 105 (2015) 1568–1572.
- [16] V.L. Anh, Y. Inoue, S. Asuke, T.T.P. Vy, N.T. Anh, S. Wang, I. Chuma, Y. Tosa, *Rmg8* and *Rmg7*, wheat genes for resistance to the wheat blast fungus, recognize the same avirulence gene *AVR-Rmg8*, *Mol. Plant Pathol.* 19 (2018) 1252–1256.
- [17] J.T. Horo, S. Asuke, T.T.P. Vy, Y. Tosa, Effectiveness of the wheat blast resistance gene *Rmg8* in Bangladesh suggested by distribution of an *AVR-Rmg8* allele in the *Pyricularia oryzae* population, *Phytopathology* 110 (2020) 1802–1807.
- [18] S. Wang, S. Asuke, T.T.P. Vy, Y. Inoue, I. Chuma, J. Win, K. Kato, Y. Tosa, A new resistance gene in combination with *Rmg8* confers strong resistance against *Triticum* isolates of *Pyricularia oryzae* in a common wheat landrace, *Phytopathology* 108 (2018) 1299–1306.
- [19] R. Goddard, A. Steed, C. Chinoy, J.R. Ferreira, P.L. Scheeren, J.L.N. Maciel, E. Caierão, G.A.M. Torres, L. Consoli, F.M. Santana, J.M.C. Fernandes, J. Simmonds, C. Uauy, J. Cockram, P. Nicholson, Dissecting the genetic basis of wheat blast resistance in the Brazilian wheat cultivar BR 18-Terena, *BMC Plant Biol.* 20 (2020) 398.
- [20] C.D. Cruz, G.L. Peterson, W.W. Bockus, P. Kankanala, J. Dubcovsky, K.W. Jordan, E. Akhunov, F. Chumley, F.D. Baldelomar, B. Valent, The 2NS translocation from *Aegilops ventricosa* confers resistance to the *Triticum* pathotype of *Magnaporthe oryzae*, *Crop Sci.* 56 (2016) 990–1000.

- [21] X. He, M.R. Kabir, K.K. Roy, M.B. Anwar, K. Xu, F. Marza, F. Odilbekov, A. Chawade, E. Duveiller, E. Huttner, P.K. Singh, QTL mapping for field resistance to wheat blast in the Caninde#1/Alondra population, *Theor. Appl. Genet.* 133 (2020) 2673–2683.
- [22] L. Gao, D.H. Koo, P. Juliana, T. Rife, D. Singh, C. Lemes da Silva, T. Lux, K.M. Dorn, M. Chinesmith, P. Silva, X. Wang, M. Spannagl, C. Monat, B. Friebe, B. Steuernagel, G.J. Muehlbauer, S. Walkowiak, C. Pozniak, R. Singh, N. Stein, M. Mascher, A. Fritz, J. Poland, The *Aegilops ventricosa* 2N(v)S segment in bread wheat: cytology, genomics and breeding, *Theor. Appl. Genet.* 134 (2020) 529–542.
- [23] P. Juliana, X. He, M.R. Kabir, K.K. Roy, M.B. Anwar, F. Marza, J. Poland, S. Shrestha, R.P. Singh, P.K. Singh, Genome-wide association mapping for wheat blast resistance in CIMMYT's international screening nurseries evaluated in Bolivia and Bangladesh, *Sci. Rep.* 10 (2020) 15972.
- [24] P. Juliana, J. Poland, J. Huerta-Espino, S. Shrestha, J. Crossa, L. Crespo-Herrera, F. H. Toledo, V. Govindan, S. Mondal, U. Kumar, S. Bhavani, P.K. Singh, M.S. Randhawa, X. He, C. Guzman, S. Dreisigacker, M.N. Rouse, Y. Jin, P. Pérez-Rodríguez, O.A. Montesinos-López, D. Singh, M. Mokhlesur Rahman, F. Marza, R.P. Singh, Improving grain yield, stress resilience and quality of bread wheat using large-scale genomics, *Nat. Genet.* 51 (2019) 1530–1539.
- [25] G. Cruppe, C.D. Cruz, G. Peterson, K. Pedley, M. Asif, A. Fritz, L. Calderon, C. Lemes da Silva, T. Todd, P. Kuhnem, P.K. Singh, R.P. Singh, H.J. Braun, N.C.D. Barma, B. Valent, Novel sources of wheat head blast resistance in modern breeding lines and wheat wild relatives, *Plant Dis.* 104 (2020) 35–43.
- [26] D. Kumar, A. Kumar, V. Chhokar, O.P. Gangwar, S.C. Bhardwaj, M. Sivasamy, S. V.S. Prasad, T.L. Prakasha, H. Khan, R. Singh, P. Sharma, S. Sheoran, M.A. Iqbal, S. Jaiswal, U.B. Angadi, G. Singh, A. Rai, G.P. Singh, D. Kumar, R. Tiwari, Genome-wide association studies in diverse spring wheat panel for stripe, stem, and leaf rust resistance, *Front. Plant Sci.* 11 (2020) 748.
- [27] P.K. Singh, J. Crossa, E. Duveiller, R.P. Singh, A. Djurlie, Association mapping for resistance to tan spot induced by *Pyrenophora tritici-repentis* race 1 in CIMMYT's historical bread wheat set, *Euphytica* 207 (2016) 515–525.
- [28] Y. Kang, K. Barry, F. Cao, M. Zhou, Genome-wide association mapping for adult resistance to powdery mildew in common wheat, *Mol. Biol. Rep.* 47 (2020) 1241–1256.
- [29] L. Wu, Y. Zhang, Y. He, P. Jiang, X. Zhang, H. Ma, Genome-wide association mapping of resistance to Fusarium head blight spread and deoxynivalenol accumulation in Chinese elite wheat germplasm, *Phytopathology* 109 (2019) 1208–1216.
- [30] R Core Team, R: A Language and Environment for Statistical Computing, Vienna, Austria, 2011.
- [31] M. Helguera, I. Khan, J. Kolmer, D. Lijavetzky, L. Zhong-qi, J. Dubcovsky, PCR assays for the cluster of rust resistance genes and their use to develop isogenic hard red spring wheat lines, *Crop Sci.* 43 (2003) 1839–1847.
- [32] J.K. Pritchard, M. Stephens, P. Donnelly, Inference of population structure using multilocus genotype data, *Genetics* 155 (2000) 945–959.
- [33] C.C. Chang, C.C. Chow, L.C. Tellier, S. Vattikuti, S.M. Purcell, J.J. Lee, Second-generation PLINK: rising to the challenge of larger and richer datasets, *GigaScience* 4 (2015) 7.
- [34] J.C. Barrett, B. Fry, J. Maller, M.J. Daly, Haploview: analysis and visualization of LD and haplotype maps, *Bioinformatics* 21 (2005) 263–265.
- [35] P.J. Bradbury, Z. Zhang, D.E. Kroon, T.M. Casstevens, Y. Ramdoss, E.S. Buckler, TASSEL: software for association mapping of complex traits in diverse samples, *Bioinformatics* 23 (2007) 2633–2635.
- [36] S. Walkowiak, L. Gao, C. Monat, G. Haberer, M.T. Kassa, J. Brinton, R.H. Ramirez-Gonzalez, M.C. Kolodziej, E. Delorean, D. Thambugala, V. Klymiuk, B. Byrns, H. Gundlach, V. Bandi, J.N. Siri, K. Nielsen, C. Aquino, A. Himmelbach, D. Copetti, T. Ban, L. Venturini, M. Bevan, B. Clavijo, D.H. Koo, J. Ens, K. Wiebe, A. N'Diaye, A. K. Fritz, C. Gutwin, A. Fiebig, C. Fosker, B.X. Fu, G.G. Accinelli, K.A. Gardner, N. Fradley, J. Gutierrez-Gonzalez, G. Halstead-Nussloch, M. Hatakeyama, C.S. Koh, J. Deek, A.C. Costamagna, P. Foebert, D. Heavens, H. Kanamori, K. Kawaura, F. Kobayashi, K. Krasileva, T. Kuo, N. McKenzie, K. Murata, Y. Nabeka, T. Paape, S. Padmarasu, L. Percival-Alwyn, S. Kagale, U. Scholz, J. Sese, P. Juliana, R. Singh, R. Shimizu-Inatsugi, D. Swarbreck, J. Cockram, H. Budak, T. Tameshige, T. Tanaka, H. Tsuji, J. Wright, J. Wu, B. Steuernagel, I. Small, S. Cloutier, G. Keeble-Gagnère, G. Muehlbauer, J. Tibbits, S. Nasuda, J. Melonek, P.J. Hucl, A.G. Sharpe, M. Clark, E. Legg, A. Bharti, P. Langridge, A. Hall, C. Uauy, M. Mascher, S.G. Krattinger, H. Handa, K.K. Shimizu, A. Distelfeld, K. Chalmers, B. Keller, K.F.X. Mayer, J. Poland, N. Stein, C.A. McCartney, M. Spannagl, T. Wicker, C.J. Pozniak, Multiple wheat genomes reveal global variation in modern breeding, *Nature* 588 (2020) 277–283.
- [37] R. IWGSC, K. Appels, C. Eversole, B. Feuillet, J. Keller, N. Rogers, C.J. Stein, N. Pozniak, F. Stein, A. Choulet, K. Distelfeld, J. Eversole, J. Poland, G. Rogers, A.G. Ronen, C. Sharpe, G. Pozniak, N. Ronen, O. Stein, K. Barad, F. Baruch, G. Choulet, M. Keeble-Gagnère, A.G. Mascher, G. Sharpe, A.A. Ben-Zvi, N. Josselin, M. Stein, A. Mascher, F. Himmelbach, G. Choulet, M. Keeble-Gagnère, J. Mascher, F. Rogers, J. Balfourier, M. Gutierrez-Gonzalez, A.A. Hayden, C. Josselin, G. Koh, R. K. Muehlbauer, E. Pasam, C.J. Paux, P. Pozniak, A.G. Rigault, J. Sharpe, V. Tibbits, F. Tiwari, G. Choulet, M. Keeble-Gagnère, A.A. Mascher, J. Josselin, M. Rogers, F. Spannagl, D. Choulet, H. Lang, G. Gundlach, G. Haberer, K.F.X. Keeble-Gagnère, D. Mayer, E. Ormanbekova, V. Paux, H. Prade, T. Šimková, F. Wicker, M. Choulet, D. Spannagl, H. Swarbreck, M. Rimbart, N. Felder, H. Guilhot, G. Gundlach, G. Haberer, J. Kaithakottil, D. Keilwagen, P. Lang, T. Leroy, K.F.X. Lux, S. Mayer, L. Twardziok, R. Venturini, H. Appels, F. Rimbart, A. Choulet, G. Juhász, F. Keeble-Gagnère, M. Choulet, D. Spannagl, M. Lang, G. Abrouk, G. Haberer, K.F.X. Keeble-Gagnère, T. Mayer, F. Wicker, T. Choulet, H. Wicker, D. Gundlach, M. Lang, D. Spannagl, M. Lang, R. Spannagl, I. Appels, C. Fischer, P. Uauy, R.H. Borrill, R. Ramirez-Gonzalez, D. Appels, S. Arnaud, B. Chalabi, F. Chalhouh, A. Choulet, R. Cory, M.W. Datla, M. Davey, J. Hayden, D. Jacobs, S.J. Lang, M. Robinson, B. Spannagl, J. Steuernagel, V. Tibbits, F. van Tiwari, B.B.H. Ex, C.J. Wulff, S.J. Pozniak, A.G. Robinson, A. Sharpe, M. Cory, E. Benhamed, A. Paux, L. Bendahmane, D. Concia, J. Latrasse, J. Rogers, M. Jacobs, R. Alaux, J. Appels, A. Bartoš, H. Bellec, J. Berges, C. Doležel, Z. Feuillet, B. Frenkel, A. Gill, T. Korol, O.A. Letellier, H. Olsen, K. Šimková, M. Singh, E. van der Valárik, S. Vossen, S. Vautrin, A. Weining, Z. Korol, T. Frenkel, V. Fahima, D. Glikson, J. Raats, V. Rogers, B. Tiwari, E. Gill, J. Paux, J. Poland, J. Doležel, H. Čihalíková, H. Šimková, J. Toegelová, P. Vrána, B. Sourdille, R. Darrier, M. Appels, D. Spannagl, I. Lang, D. Fischer, V. Ormanbekova, D. Prade, L. Barabaschi, P. Cattivelli, S. Hernandez, H. Galvez, B. Budak, J.D.G. Steuernagel, K. Jones, B.B.H. Witek, G. Wulff, I. Yu, J. Small, R. Melonek, A. Zhou, T. Juhász, R. Belova, O.A. Appels, K. Olsen, R. Kanyuka, K. King, S. Nilsen, C.J. Walkowiak, R. Pozniak, R. Cuthbert, R. Datla, K. Knox, D. Wiebe, A. Xiang, T. Rohde, J. Golds, J. Doležel, J. Čížková, H. Tibbits, B.A. Budak, S. Akpınar, G. Biyiklioglu, J. Muehlbauer, L. Poland, J. Gao, A. Gutierrez-Gonzalez, J. N'Diaye, H. Doležel, J. Šimková, M. Čihalíková, J. Kubaláková, J. Šafář, H. Vrána, A. Berges, S. Bellec, M. Vautrin, F. Alaux, A.F. Alfama, R. Adam-Blondon, C. Flores, T. Guerche, M. Letellier, H. Loaec, C.J. Quesneville, A.G. Pozniak, S. Sharpe, H. Walkowiak, J. Budak, J. Condie, C. Ens, R. Koh, Y. Maclachlan, T. Tan, F. Wicker, E. Choulet, A. Paux, J.M. Alberti, F. Aury, V. Balfourier, A. Barbe, C. Couloux, K. Cruaud, S. Labadie, P. Mangenot, B. Wincker, G. Gill, M. Kaur, S. Luo, K. Sehgal, P. Singh, O.P. Chhuneja, S. Gupta, P. Jindal, P. Kaur, P. Malik, B. Sharma, N.K. Yadav, J. Singh, C. Khurana, P. Chaudhary, V. Khurana, A. Kumar, S. Mahato, A. Mathur, N. Sevanti, R.S. Sharma, J. Tomar, J. Rogers, M. Jacobs, A. Alaux, H. Bellec, J. Berges, C. Doležel, Z. Feuillet, B. Frenkel, A. Gill, E. van der Korol, S. Vossen, B. Vautrin, G. Gill, M. Kaur, S. Luo, J. Sehgal, K. Bartoš, O. Holušová, M.D. Plihal, D. Clark, G. Heavens, J. Kettleborough, M. Wright, M. Valárik, B. Abrouk, K. Balcárková, Y. Holušová, M. Hu, E. Luo, N. Salina, K. Ravin, A. Skryabin, V. Beletsky, A. Kadnikov, M. Mardanov, A. Nesterov, E. Rakitin, H. Sergeeva, H. Handa, S. Kanamori, F. Katagiri, S. Kobayashi, T. Nasuda, J. Tanaka, R. Wu, M. Appels, G. Hayden, P. Keeble-Gagnère, J. Rigault, O.A. Tibbits, T. Olsen, F. Belova, M. Cattonaro, K. Jiumeng, K.F.X. Kugler, M. Mayer, S. Pfeifer, X. Sandve, B. Xun, H. Zhan, M. Šimková, J. Abrouk, P.E. Batley, D. Bayer, S. Edwards, H. Hayashi, Z. Toegelová, P. Tulpová, S. Visendi, L. Weining, X. Cui, K. Du, X. Feng, W. Nie, L. Tong, P. Wang, H. Borrill, S. Gundlach, G. Galvez, D. Kaithakottil, T. Lang, M. Lux, D. Mascher, V. Ormanbekova, R.H. Prade, M. Ramirez-Gonzalez, N. Spannagl, C. Stein, L. Uauy, N. Venturini, R. Stein, K. Appels, J. Eversole, P. Rogers, L. Borrill, F. Cattivelli, P. Choulet, K. Hernandez, D. Kanyuka, M. Lang, K. Mascher, E. Nilsen, C.J. Paux, R.H. Pozniak, H. Ramirez-Gonzalez, I. Šimková, M. Small, D. Swarbreck, Spannagl, C. Uauy, Shifting the limits in wheat research and breeding using a fully annotated reference genome, *Science* 361 (2018) eaar7191.
- [38] W. Deng, D.C. Nickle, G.H. Learn, B. Maust, J.I. Mullins, ViroBLAST: a stand-alone BLAST web server for flexible queries of multiple databases and user's datasets, *Bioinformatics* 23 (2007) 2334–2336.
- [39] C.D. Cruz, W.W. Bockus, J.P. Stack, X. Tang, B. Valent, K.F. Pedley, G.L. Peterson, Preliminary assessment of resistance among U.S. wheat cultivars to the *Triticum* pathotype of *Magnaporthe oryzae*, *Plant Dis.* 96 (2012) 1501–1505.
- [40] W. Xue, X. Xu, J. Mu, Q. Wang, J. Wu, L. Huang, Z. Kang, D. Han, Evaluation of stripe rust resistance and genes in Chinese elite wheat varieties, *J. Triticeae Crops* 34 (2014) 1054–1060 (in Chinese with English abstract).
- [41] X. He, P. Juliana, M.R. Kabir, K.K. Roy, R. Islam, F. Marza, G. Peterson, G.P. Singh, A. Chawade, A.K. Joshi, R.P. Singh, P.K. Singh, Screening and mapping for head blast resistance in a panel of CIMMYT and South Asian bread wheat germplasm, *Front. Genet.* 12 (2021) 679162.
- [42] S. Xue, J.A. Kolmer, S. Wang, L. Yan, Mapping of leaf rust resistance genes and molecular characterization of the 2NS/2AS translocation in the wheat cultivar jagger, *G3-Genes Genomes Genet.* 8 (2018) 2059–2065.
- [43] J.R. Ferreira, G. Torres, L. Consoli, G.A. Camilotti, S. Scagliusi, A.N. Hani, C. Turchetto, C.C. Deuner, R. Goddard, P. Nicholson, Quantitative trait loci conferring blast resistance in hexaploid wheat at adult plant stage, *Plant Pathol.* 70 (2020) 100–109.
- [44] A.M. Tanguy, O. Coriton, P. Abélard, F. Dedryver, J. Jahier, Structure of *Aegilops ventricosa* chromosome 6Nv, the donor of wheat genes *Yr17*, *Lr37*, *Sr38*, and *Cre5*, *Genome* 48 (2005) 541–546.
- [45] V.M. Williamson, V. Thomas, H. Ferris, J. Dubcovsky, An *Aegilops ventricosa* translocation confers resistance against root-knot nematodes to common wheat, *Crop Sci.* 53 (2013) 1412–1418.
- [46] S. Wang, J. Wang, Z. Zhang, Z. Hao, X. Zhu, Y. Wang, F. Lin, G. Sun, The risk of wheat blast in rice-wheat-co-planting regions in China: MoO strains of *Pyricularia oryzae* cause typical symptom and host reaction on both wheat leaves and spikes, *Phytopathology* (2021), <https://doi.org/10.1094/PHYTO-10-20-0470-R>.
- [47] Y. Inoue, T.T.P. Vy, K. Yoshida, H. Asano, C. Mitsuoaka, S. Asuke, V.L. Anh, C.J.R. Cumagun, I. Chuma, R. Terauchi, K. Kato, T. Mitchell, B. Valent, M. Farman, Y. Tosa, Evolution of the wheat blast fungus through functional losses in a host specificity determinant, *Science* 357 (2017) 80–83.
- [48] M. Farman, G. Peterson, L. Chen, J. Starnes, B. Valent, P. Bachi, L. Murdock, D. Hershman, K. Pedley, J.M. Fernandes, J. Bavarecos, The *Lolium* pathotype of *Magnaporthe oryzae* recovered from a single blasted wheat plant in the United States, *Plant Dis.* 101 (2017) 684–692.
- [49] K.B. Mills, L.V. Madden, P.A.O. Paul, Quantifying the effects of temperature and relative humidity on the development of wheat blast incited by the *Lolium* pathotype of *Magnaporthe oryzae*, *Plant Dis.* 104 (2020) 2622–2633.

- [50] J. Zhang, Y. Zhao, Z. Han, M. Zhao, Identification and control of turf gray leaf spot, *Acta Agrestia Sin.* 25 (2017) 442–444 (in Chinese with English abstract).
- [51] J.M.C. Fernandes, M. Nicolau, W. Pavan, C.A. Hölbig, M. Karrei, F. de Vargas, J.L. B. Bavaresco, A.T. Lazzaretti, R.Y. Tsukahara, A weather-based model for predicting early season inoculum build-up and spike infection by the wheat blast pathogen, *Trop. Plant Pathol.* 42 (2017) 230–237.
- [52] K.H. Kim, E.D. Choi, Retrospective study on the seasonal forecast-based disease intervention of the wheat blast outbreaks in Bangladesh, *Front. Plant Sci.* 11 (2020) 570381.
- [53] E. Duveiller, D. Hodson, K. Sonder, A.V. Tiedermann, An international perspective on wheat blast, *Phytopathology* 101 (2011) S220.