Enhanced Stripe Rust Resistance Obtained by Combining A Widely Dispersed, Stable QTL with Yr30 on Chromosome Arms 4BL And 3BS

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Research Article

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Abstract

Cultivars with durable resistance are the most popular means to control wheat stripe rust. Durable resistance can be achieved by stacking multiple adult-plant resistance (APR) genes that individually have relatively smaller effect. Chinese wheat cultivars Ruihua 520 (RH520) and Fengdecun 12 (FDC12) confer partial APR to stripe rust across environments. One hundred and seventy recombinant inbred lines from the cross RH520 × FDC12 were used to determine the genetic basis of resistance and identify genomic regions associated with stripe rust resistance. Genotyping was carried out using 55K SNP array and eight quantitative trait loci (QTL) were detected on chromosomes 2AL, 2DS, 3BS, 4BL, 5BL (2) and 7BL (2) by inclusive composite interval mapping. Only *QYr.nwafu-3BS* from RH520 and *QYr.nwafu-4BL.2* (named *YrFDC12* for convenience) from FDC12 were stable across the four testing environments. *QYr.nwafu-3BS* is likely the pleiotropic resistance gene *Sr2/Yr30*. *YrFDC12* was mapped in a 2.1 cM interval corresponding to 12 Mb and flanked by SNP markers *AX-111121224* and *AX-89518393*. Lines harboring both *Yr30* and *YrFDC12* displayed higher resistance than the parents and expressed pseudo-black chaff (PBC) controlled by two loci *Pbc1* and *PbcFDC12*, which were co-located with *Yr30* and *YrFDC12*, respectively. Both marker-based and pedigree-based kinship analyses revealed that *YrFDC12* was inherited from founder parent Zhou 8425B. Fifty-four other wheat cultivars shared the same haplotype of *YrFDC12* region. These results suggest an effective pyramiding strategy to acquire highly effective, durable stripe rust resistance in breeding.

Introduction

Wheat, is an old and important cereal crop grown worldwide providing nutrition and 20% of the energy required by humans globally. Security of wheat production encompasses a series of components, namely production, access (physical and economic), stability, and nutritional value (Savary et al. 2017). Stripe rust, caused by the fungus *Puccinia striiformis* f. sp. *tritici* (*Pst*), is one of the most important diseases of wheat (Hovmøller et al. 2010; McIntosh et al. 1995), and can cause devastating losses in yield and quality (Murray et al. 1995). Strategies suggested for managing rusts include host resistance, fungicides, cultural practices, biological control, and integrated disease management. Among them, developing and growing resistant cultivars based on host resistance is the most economic, effective and environment-friendly method (Chen 2005; Wellings 2011).

Rust resistance is generally classified into two types; race-specific and race non-specific. Race-specific resistance that often fits the description of “seedling or all-stage resistance” is usually conferred by major genes that cause hypersensitive response following recognition of pathogen effector molecules by host receptor molecules. The precise interaction of pathogen- and host-generated gene products is the basis of the gene-for-gene relationship as proposed by Flor in the 1950s (Flor 1971). This resistance type is often short-lived due to mutation for virulence, leading to re-assortment of virulence alleles carried by heterozygous avirulent genotypes of the pathogen (Mcdonald and Linde 2002), or through selection of previously rare, undetected pathogen variants, or by introduction of virulent variants from other geographic areas. In contrast, race non-specific resistance conferred by minor effect genes that

constrains the rate of disease development at post-seedling growth stages of plants and often referred to as “adult plant resistance (APR)” (Milus 1986; Chen 2013; Parlevliet 1985). Individual genes underlying this type of resistance have relatively small effects on disease response but often act additively in combination to reach near-immune levels effective across multiple environments (Singh et al. 2011). Some examples of well characterized stripe rust resistance genes of this type that have maintained effectiveness for long periods of time when in combinations include *Yr18* (Krattinger et al. 2009; Lagudah et al. 2006), *Yr29* (Singh et al. 2013), *Yr30* (Singh et al. 2000), *Yr36* (Fu et al. 2009) and *Yr46* (Moore et al. 2015; Herrera-Foessel et al. 2011), and in addition confer pleotropic effects on other diseases. Therefore, these genes are now being preferentially targeted by breeders to enhance multiple disease resistance.

Although more than 200 APR genes/QTL for stripe rust resistance are reported in the literature (Chen and Kang 2017; Bulli et al. 2016; Rosewarne et al. 2013), not all combinations are effective in improving the level of response largely due to epistatic effects. The choice of genes for stacking by breeders is often difficult as progress can be achieved when such minor genes act additively in enhancing the levels of resistance. In addition, breeder friendly markers can greatly facilitate both selection and stacking of APR genes.

Several genotyping platforms in the last few decades have greatly enhanced gene discovery and characterization studies, develop markers that can be used to assay for the presence of the genes in breeding germplasm and for pyramiding strategies. Single nucleotide polymorphisms (SNPs), the most common type of genetic variation in genomes, are currently preferred for QTL analysis. Next generation and high-throughput SNP-based genotyping technologies enable rapid marker development and map construction, further facilitating basic genetic research and advances in marker-assistant breeding (Rasheed et al. 2017). Several high-density, SNP chips and platforms such as Affymetrix Gene Chip, Illumina Bead Array, and kompetitive allele-specific polymerase chain reaction (KASP) and allele-specific quantitative PCR-based genotyping assay (AQP) are available for wheat genetic studies (Rasheed et al. 2016; Semagn et al. 2014). A series of high-throughput genotyping technologies, including the Wheat 9K (Cavanagh et al. 2013), 35K (Mu et al. 2019), 55K (Huang et al. 2019), 90K (Wang et al. 2014), 660K (Cui et al. 2017; Sun et al. 2020) and 820K SNP (Winfield et al. 2016) arrays, are commercially available. The Wheat55K SNP array developed by the Chinese Academy of Agricultural Sciences and synthesized by Affymetrix is a simplified version of the Wheat660K array (Affymetrix® Axiom® Wheat660). While keeping the high density and high efficiency advantages of the Wheat660K, the Wheat55K SNP array is economic and is therefore widely used in genetic research in wheat (Huang et al. 2019, 2020).

Cultivars “Ruihua 520” (RH520) and “Fengdecun 12” (FDC12) are important lines used as parents in the breeding program of Jiangsu Ruihua Agricultural Science and Technology Co. Ltd in China. Both are susceptible at seedling stages to the prevalent races CYR32 and CYR34, but have expressed partial APR in the field since their release in 2014 and 2010, respectively. Recombinant inbred line (RIL) population combining these two sources (RH520 × FDC12) identified lines exhibiting transgressive segregation, some lines with near immunity and some showing high susceptibility. However, the genetic basis of the partial resistance in the both parent lines was unknown. The objectives of this study were to: 1) dissect

the genetic components of resistance in RH520 and FDC12; 2) identify superior recombinants that provide more effective protection and extend the level of durable resistance; and 3) develop tightly linked AQP markers that can facilitate MAS for the QTL associated with YR resistance.

Materials And Methods

Plant materials

A total of 226 $F_{5:7}$ RILs derived from a cross between RH520 (Zhengzhou 891/Qianfeng 1) and FDC12 (Zhoumai 16/Shanyou 225//Aikang 58) was used in QTL mapping (170 lines) and validation (56 lines). Mingxian169 (MX169), a susceptible Chinese landrace was grown as a disease spreader and cultivar Xiaoyan 22 (XY22) was used as the susceptible check.

Stripe rust evaluations

Seedling tests indicated that RH520 and FDC12 were susceptible to all test *Pst* races (Yu et al. 2020). For assessments of stripe rust reactions in the field 170 RILs and parents were planted at Yangling (YL) in Shaanxi province in 2018-2019 and 2019-2020, and at Jiangyou (JY) in Sichuan province in 2019-2020 and 2020-2021. Trials at Yangling were inoculated with a urediniospore mixture of CYR32 and CYR34 suspended in a light oil sprayed onto MX169 and XY22 in early March to initiate disease. Each plot consisted of a 1 m row sown with approximately 20 seeds and 25 cm row spacing. Two rows of highly susceptible cv. XY22 were planted after every 20 rows to ensure uniform disease development. A randomized complete block design with two replications was used in all experiments. Adult plant stripe rust reactions were determined by infection type (IT) and disease severity (DS). IT was recorded using a 0 to 9 scale ranging from complete immunity to high susceptibility (Line and Qayoum 1992); and disease severity was based on the modified Cobb Scale (Peterson et al. 1948). The first scoring was made when MX169 reached approximately 80% severity or more during the period 5–15 April at JY and 3–17 May at YL. IT and DS of homozygous lines were recorded as single values; and for segregating lines IT and DS were recorded as two or more values, but later averaged for each line. Disease assessments were made at least twice. The IT and final DS was used in subsequent analysis.

Phenotyping for pseudo-black chaff

Although pseudo-black chaff (PBC) was present in all environments, phenotyping was carried out only in 2021 at Yangling. The phenotype data for PBC was recorded at grain filling stage based on the presence of the black pigmentation around the stem internodes and glumes. A visual score of 0 or 1 scale was used, where 0 indicated no pigmentation and 1 indicated the presence of pigmentation.

Phenotypic data analysis

The frequency distributions of IT and DS of $F_{5:7}$ RILs across four environments were calculated using Excel 2016. Analysis of variance (ANOVA) and Pearson’s correlation coefficients among environments

were conducted using the “AOV” function in QTL IciMapping software 4.1 with the default parameters based on the IT and DS data (Meng et al. 2015). Broad-sense heritability (*h2 b*) was estimated as $h2\ b = \sigma2\ g/(\sigma2\ g + \sigma2\ ge/e + \sigma2\ \varepsilon/re)$, where $\sigma2\ g$, $\sigma2\ ge$ and $\sigma2\ r$ represented genotypic (line), genotype × environment and error variances, respectively, and *e* and *r* were the numbers of environments and replicates. Mean IT and DS data were used for subsequent QTL mapping.

SNP calling and clustering

Genomic DNA from single fresh leaf of each parent and RIL was extracted at the jointing stage using the CTAB protocol (Song et al. 1994) and the quality and quantity of DNA were assessed using a NanoDrop ND-1000 (Thermo Scientific, Wilmington, DE, USA). The wheat 55K SNP array improved by China Gold Marker (Beijing; http:// www.cgmb.com.cn) was used to genotype the parents and 170 RILs. SNP genotype calling and allele clustering was processed with the polyploid version of the Affymetrix Genotyping Console™ (AGC) software. SNPs were classified into six groups: (i) Poly High Resolution (PHR) SNPs that were polymorphic and co-dominant with a minimum of two samples containing the minor allele; (ii) no minor homozygote (NMH); these polymorphic and dominant SNPs had only two clusters, one being the heterozygote; (iii) mono high resolution (MHR) or monomorphic SNPs having only one cluster/allele; (iv) off-target variants (OTV) showing four clusters including one for a null allele; (v) call rate below threshold (CRBT) having all cluster properties above the threshold except for the call rate cut-of; and (vi) other type SNPs with one or more cluster properties below quality thresholds.

Linkage map construction and QTL analysis

The filtering criteria of SNP markers for linkage map construction were as follows: PHR/polymorphic, <10% missing values, major allele frequencies (MAF) ≤95%, and 1:1 segregation ratios confirmed by chi-squared tests ($P > 0.001$). A linkage map was constructed using QTL IciMapping V4.1 software and generated with Mapchart V2.3 (Meng et al. 2015; Voorrips 2002). Recombination fractions were converted to centiMorgans (cM) using the Kosambi function (Kosambi 1944). One marker was selected from each co-segregating marker group using the “BIN” function. Selected markers were used to construct the genetic map using the “MAP” function. To further narrow down the interval of target loci, 16 SNPs on chromosome 3BS and 76 SNPs on chromosome 4BL from 660K SNP array genotypes of RH520 and FDC12, were converted into AQP, respectively. A total of 13 AQP markers was used to genotype all 170 RILs to enrich the linkage map (Table S1). Inclusive composite interval mapping with the additive tool (ICIM-ADD) in IciMapping V4.1 was performed to detect QTL based on the phenotypic data including mean IT and DS scores, and PBC. Likelihood-of-odds (LOD) thresholds for declaring statistical significance were calculated by 1000 permutations at a p value ≤0.01. LOD significance thresholds estimated for each trait was 2.5. The phenotypic variances explained (PVE) by individual QTL and additive effects at the LOD peaks were also obtained. The physical positions in CS RefSeq v1.0 were obtained based on blast using flanking marker sequences for each QTL (http://wheatomics.sdau.edu.cn/). QTL were named according to the International Rules of Genetic Nomenclature (http://wheat.pw.usda. gov/ggpages/wgc/98/Intro.htm). Abbreviations ‘Yr’, ‘Pbc’ and

‘nwafu’ were adopted for ‘yellow (stripe) rust resistance’, ‘pseudo-black chaff’ and ‘Northwest A & F University’, respectively.

Comparisons with previously reported *Yr* genes and QTL

To determine the relationships between loci identified in this study and previously reported *Yr* genes/QTL, we compared the relative physical and genetic distances of loci based on the IWGSC RefSeq v.1.0 and integrated linkage map consisting of SNP, DArT, SSR, STS, EST, RAPD and RFLP markers provided by Dr. Fa Cui (Ludong University in Shandong province; pers. comm.). The closest flanking markers were used to generate confidence intervals for previously reported *Pst* resistance genes/QTL in genetic populations. Significant markers were assumed to identify loci detected in genome-wide association studies (GWAS).

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A pedigree tree of FDC12 was constructed based on the information of pedigree and neighbor-joining tree. The genotype data for SNPs located in confidence intervals of target QTL were extracted from a diversity panel of 1,400 wheat accessions and used to perform phylogenetic analysis using MAGE 7. A neighbor-joining (NJ) tree was drawn using iTOL (https://itol.embl.de/). The resistance haplotype of FDC12 was tracked based on both pedigree and kinship analysis. Accessions grouped in same branch as FDC12 were considered to harbor the resistance haplotype.

Results

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Abbreviations

ADD, additive

ANOVA, analysis of variance

APR, adult plant resistance

AQP, allele-specific quantitative PCR

CIMMYT, International Maize and Wheat Improvement Center

cM, centiMorgans

CS, Chinese spring

DS, disease severity

EPI, epistasis

GWAS, genome-wide association analysis

h2 b, broad-sense heritability

ICIM, inclusive composite interval mapping

IT, infection type

IWGSC, International Wheat Genome Sequencing Consortium

KASP, kompetitive allele-specific polymerase chain reaction

LG, linkage group

LOD, likelihood-of-odds

MAF, major allele frequency

MAS, marker-assisted selection

NJ, neighbor-joining

PBC, pseudo-black chaff

PCR, polymerase chain reaction

PBC, pseudo-black chaff

Pst, *Puccinia striiformis* f. sp. *tritici*

QTL, quantitative trait loci

RIL, recombinant inbred lines

SNP, single nucleotide polymorphism

SSR, simple sequence repeat

YR, yellow rust

Declarations

Conflicts of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

Authors' contribution statement

SJ Liu and JH Wu designed and conducted the experiments, analyzed the data, and wrote the manuscript. YG Jin, ZH Xia, QD Zeng, and QL Wang participated in creation of the genetic populations and assisted in analysis of the SNP array data. XT Wang, YY Zhang, R Yu, S Huang, WJ Zheng, LY Qiao and MJ Xiang participated in greenhouse and field experiments and contributed to genotyping. RP Singh, S Bhavani and ZS Kang participated in revision of the manuscript. CF Wang, JH Wu and DJ Han conceived and directed the project and revised the manuscript.

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Tables

Table 1 Variance components for infection type (IT) and disease severity (DS) scores in a RIL population derived from the cross RH520 × FDC12 and tested across four environments

Sources of variation	IT				DS			
	Df	Mean square	F value	*P*-value	Df	Mean square	F value	*P*-value
RILs	169	36.9	20.3	<0.0001	169	7567.0	55.0	<0.0001
Environments	3	67.4	37.1	<0.0001	3	6077.3	45.0	<0.0001
Lines × Environments	506	4.1	2.3	<0.0001	506	557.9	4.1	<0.0001
Replicates	1	26.2	21.8	0.017	1	1504.8	10.24	0.134
Error	679	1.8			680	135.2		
h2 b	0.90				0.93			

Table 2 Correlation coefficients (*r*) of mean disease severity (DS) and infection type (IT) for the RH520 × FDC12 RIL population across four environments

Environment[a]	*r* values based on MDS (IT)[b]		
(location, year)	YL2019	YL2020	JY2020
YL2020	0.81 (0.75)		
JY2020	0.83 (0.72)	0.85 (0.79)	
JY2021	0.66 (0.51)	0.71 (0.66)	0.71 (0.61)

[a]YL, Yangling and JY, Jiangyou. 2019, 2020 and 2021 represent growing seasons 2018-2019, 2019–2020 and 2020-2021

[b]*r* values calculated for IT are shown in parenthesis. All *r* values were significant ($P < 0.001$).

Table 3 Quantitative trait loci (QTL) for pseudo-black chaff (PBC) and stripe rust resistance detected in the RH520 ×FDC12 RIL population using infection type (IT) and disease severity (DS) data across four environments

QTL, environments[a]	Flanking marker	Genetic position[b] (cM)	Physical interval[c] (Mb)	LOD[d]	PVE[e]	ADD[f]
QYr.nwafu-2AL						
20YL-IT	*AX-94417710- AX-111141805*	106	713.9-718.3	8.1	7.4	-0.8
20YL-DS	*AX-94417710- AX-111141805*	107	713.9-718.3	6.3	6.6	-8.0
21JY-DS	*AX-94417710- AX-111141805*	106	713.9-718.3	6.4	9.1	-9.7
QYr.nwafu-2DS						
20YL-IT	*AX-109525831- AX-111726271*	119	73.4-75.0	7.9	7.1	0.7
20JY-IT	*AX-109525831- AX-111726271*	119	73.4-75.0	3.8	5.9	0.5
21JY-IT	*AX-89563243- AX-111128536*	118	57.9-73.3	3.5	4.6	0.5
20JY-DS	*AX-110999397- AX-110483509*	120	75.7-79.7	3.3	4.7	6.7
21JY-DS	*AX-89563243- AX-111128536*	117	57.9-73.3	7.3	10.9	10.6
QYr.nwafu-3BS						
19YL-IT	*AX-110108039- AX-111197043*	1	4.3-9.1	13.4	30.7	-1.5
20YL-IT	*AX-110108039- AX-111197043*	1	4.3-9.1	16.5	36.5	-1.7
20JY-IT	*AX-110108039- AX-111197043*	1	4.3-9.1	9.7	23.0	-1.0
21JY-IT	*AX-110108039- AX-111197043*	0	4.3-9.1	9.7	23.2	-1.1
20YL-DS	*AX-110108039- AX-111197043*	1	4.3-9.1	17.5	38.0	-20.8
19YL-DS	*AX-110108039- AX-111197043*	0	4.3-9.1	13.5	30.9	-20.2
20YL-DS	*AX-110108039- AX-111197043*	1	4.3-9.1	17.5	38.0	-20.8
21JY-DS	*AX-110108039- AX-111197043*	0	4.3-9.1	12.8	29.4	-18.4
QYr.nwafu-4BL.2						

19YL-IT	*AX-111121224-AX-89518393*	75	622.0-634.3	4.1	11.2	0.9
20YL-IT	*AX-111121224-AX-89518393*	75	622.0-634.3	5.5	13.7	1.1
20JY-IT	*AX-111121224-AX-89518393*	75	622.0-634.3	6.0	15.6	0.9
21JY-IT	*AX-111121224-AX-89518393*	75	622.0-634.3	4.7	12.4	0.9
19YL-DS	*AX-111121224-AX-89518393*	75	622.0-634.3	8.6	13.4	17.8
20YL-DS	*AX-111121224-AX-89518393*	75	622.0-634.3	8.4	14.0	16.2
20JY-DS	*AX-111121224-AX-89518393*	75	622.0-634.3	6.9	17.5	14.3
21JY-DS	*AX-111121224-AX-89518393*	75	622.0-634.3	4.2	11.5	11.8
QYr.nwafu-5BL.1						
19YL-IT	*AX-109900321-AX-109951695*	108	584.9-586.9	3.9	5.4	0.6
20YL-IT	*AX-111152749-AX-110508006*	109	585.8-595.6	7.1	6.3	0.7
20JY-DS	*AX-109900321-AX-109951695*	108	584.9-586.9	2.7	4.3	6.5
QYr.nwafu-5BL.2						
20JY-IT	*AX-109827342-AX-94987192*	138	661.2	5.7	9.0	0.6
21JY-IT	*AX-110399021-AX-109827342*	136	644.9-661.2	3.7	5.4	0.6
QYr.nwafu-7BL.1						
20YL-IT	*AX-110514055-AX-110498108*	64	363.2-478.1	4.6	4.1	-0.6
20JY-IT	*AX-110498108-AX-111236639*	65	478.1-486.9	4.2	7.0	-0.5
19YL-DS	*AX-110484893-AX-109930265*	68	504.7-605.1	3.3	4.6	-7.2
QYr.nwafu-7BL.2						
21JY-IT	*AX-111551132 - AX-109421983*	50	85.4-85.8	4.5	8.9	0.7

20JY-DS	*AX-111551132 - AX-109421983*	50	85.4-85.8	3.9	7.5	8.5
QPbc.nwafu-3BS	*AX-110108039- AX-111197043*	1	4.3-9.1	15.6	26.9	-0.24
QPbc.nwafu-7AL	*AX-94513729- AX-110505644*	81	797.4	3.1	3.6	0.28
QPbc.nwafu-5DS	*AX-109898339- AX-110415968*	21	295.5-303.4	4.1	4.8	-0.1

[a]YL, Yangling and JY, Jiangyou. 2019, 2020 and 2021 represent growing seasons 2018-2019, 2019–2020 and 2020-2021

[b]Peak position in centimorgans (cM) from the first linked marker of the relevant linkage group

[c]Physical location in mega base (Mb) from linked markers in wheat genome

[d]Logarithm of odds score

[e]Percentages of the phenotypic variation explained by individual QTL

[f]Additive effect of the allele. Negative signs indicate that the favorable allele is from RH520.

Table 4 The phenotype range and effect on IT and DS of 170 RH520 × FDC12 RILs in different groups based on their QTL status derived from flanking molecular markers

Group	Number	Mean-IT	Mean-DS	Effect		PBC
				IT	DS(%)	
None	3	7.3-7.5	85.0-96.7	/	/	No
3BS	3	7.0-8.5	70.0-93.3	/	/	No
4BL	10	7.7-8.6	82.5-94.5	/	/	No
X	25	6.5-6.9	63.6-70.1	0.4-1.0	14.9-33.1	No
3BS+X	20	5.5-6.6	43.3-63.4	0.7-2.0	21.6-53.4	No
4BL+X	39	5.6-6.4	51.0-61.7	0.9-1.9	23.3-45.7	No
3BS+4BL	4	3.5-4.3	13.8-25.0	3.0-4.0	60.0-82.9	Yes
3BS+4BL+X	45	1.5-3.5	6.6-13.5	3.8-6.0	71.5-90.1	Yes

Figures

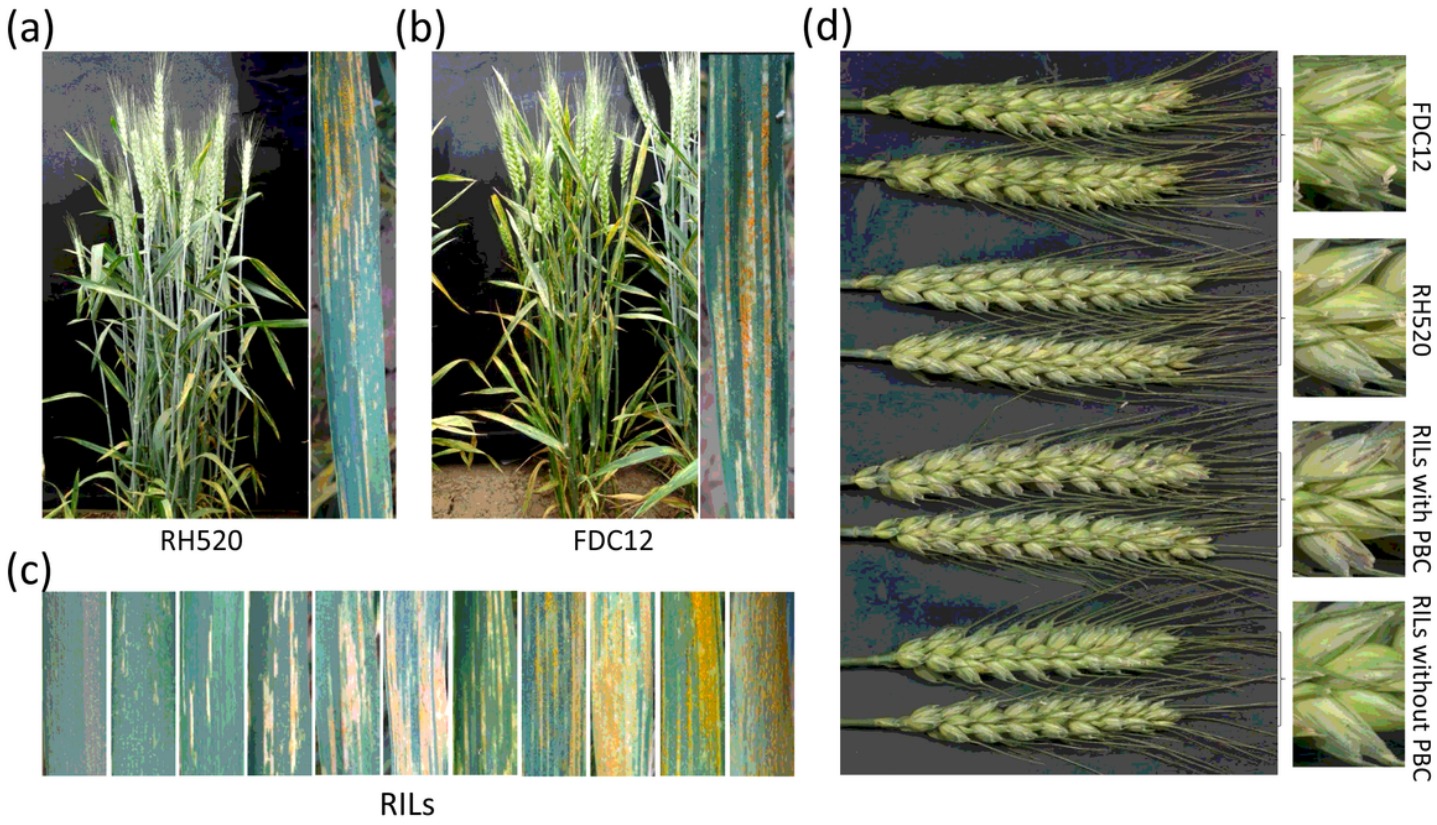

Figure 1

Adult-plant stripe rust reaction and pseudo-black chaff (PBC) scores for FDC12, RH520 and RILs

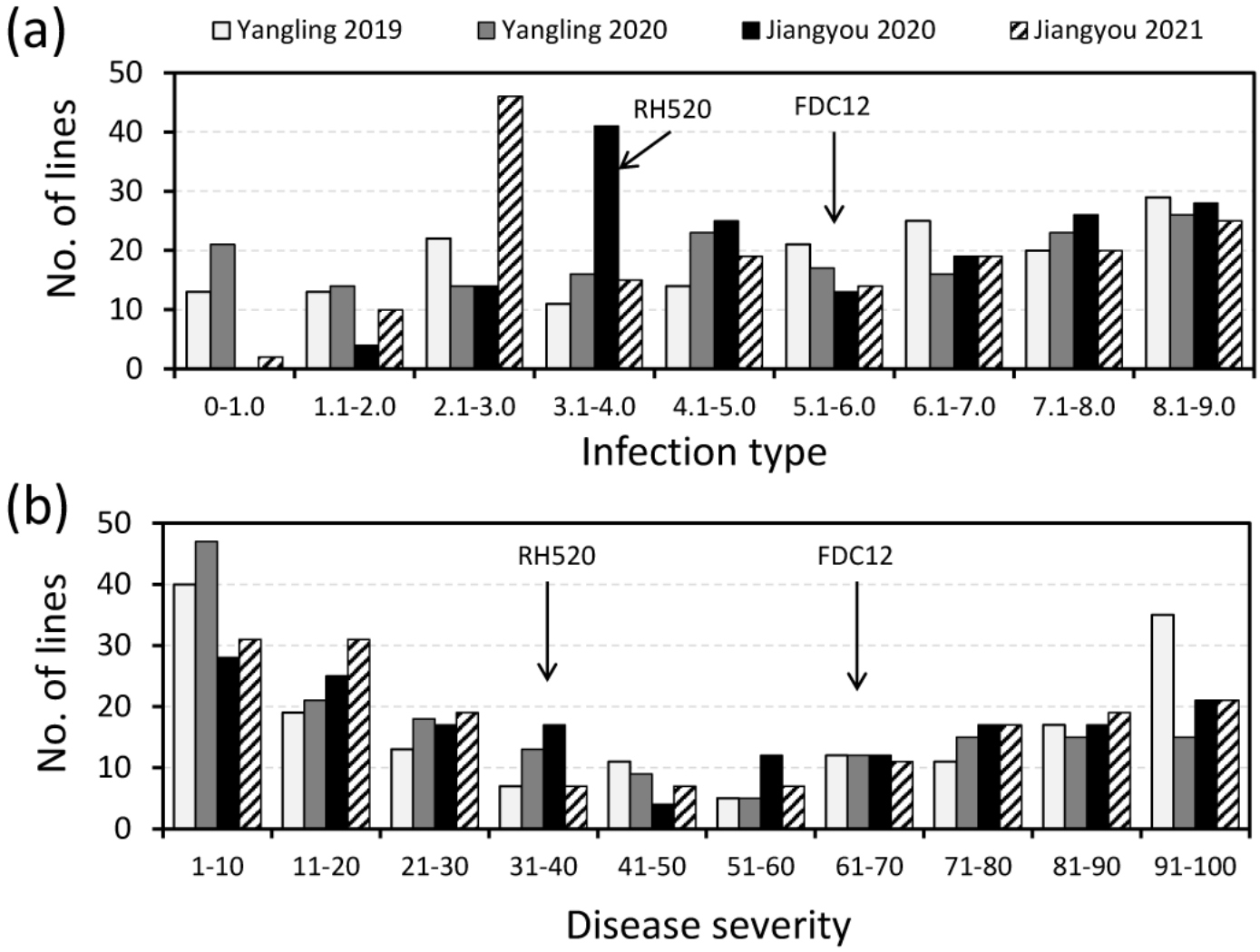

Figure 2

Frequency distributions of mean infection types (IT) and disease severities (DS) for 170 RILs from cross RH520 × FDC12 evaluated at Yangling and Jiangyou (a, b). Values for parents RH520 and FDC12 are indicated by arrows

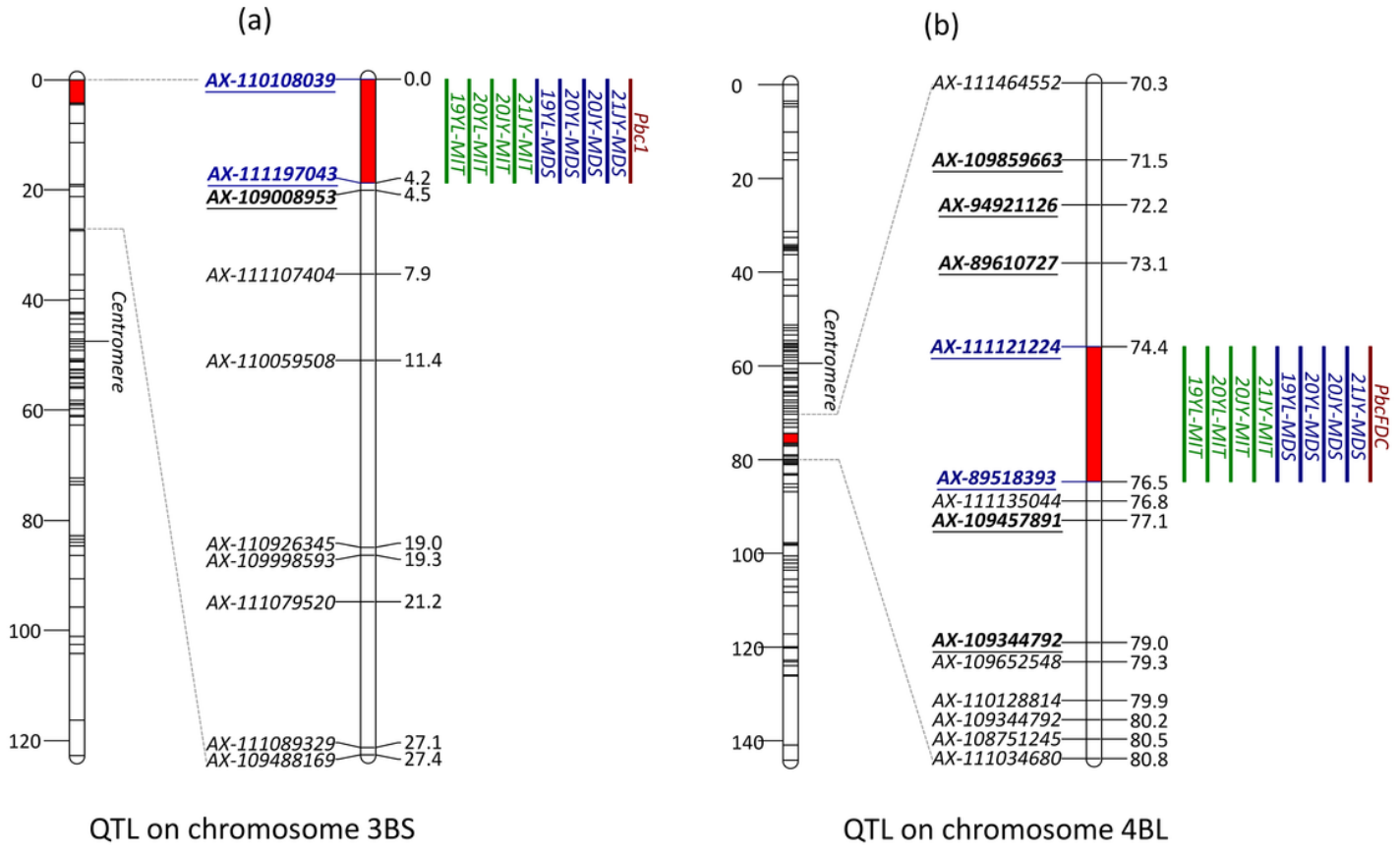

Figure 3

Graphical display of positions of quantitative trait loci (QTL) for stripe rust resistance across all environments. QTL were identified by inclusive composite interval mapping (ICIM). The QTL detected by mean infection type (IT), disease severity (DS) and pseudo-black chaff (PBC) scores are shown in green, blue and brown, respectively. Markers flanking the QTL are in blue and confidence interval of QTL are in red. AQP markers are indicated by bold and underline.

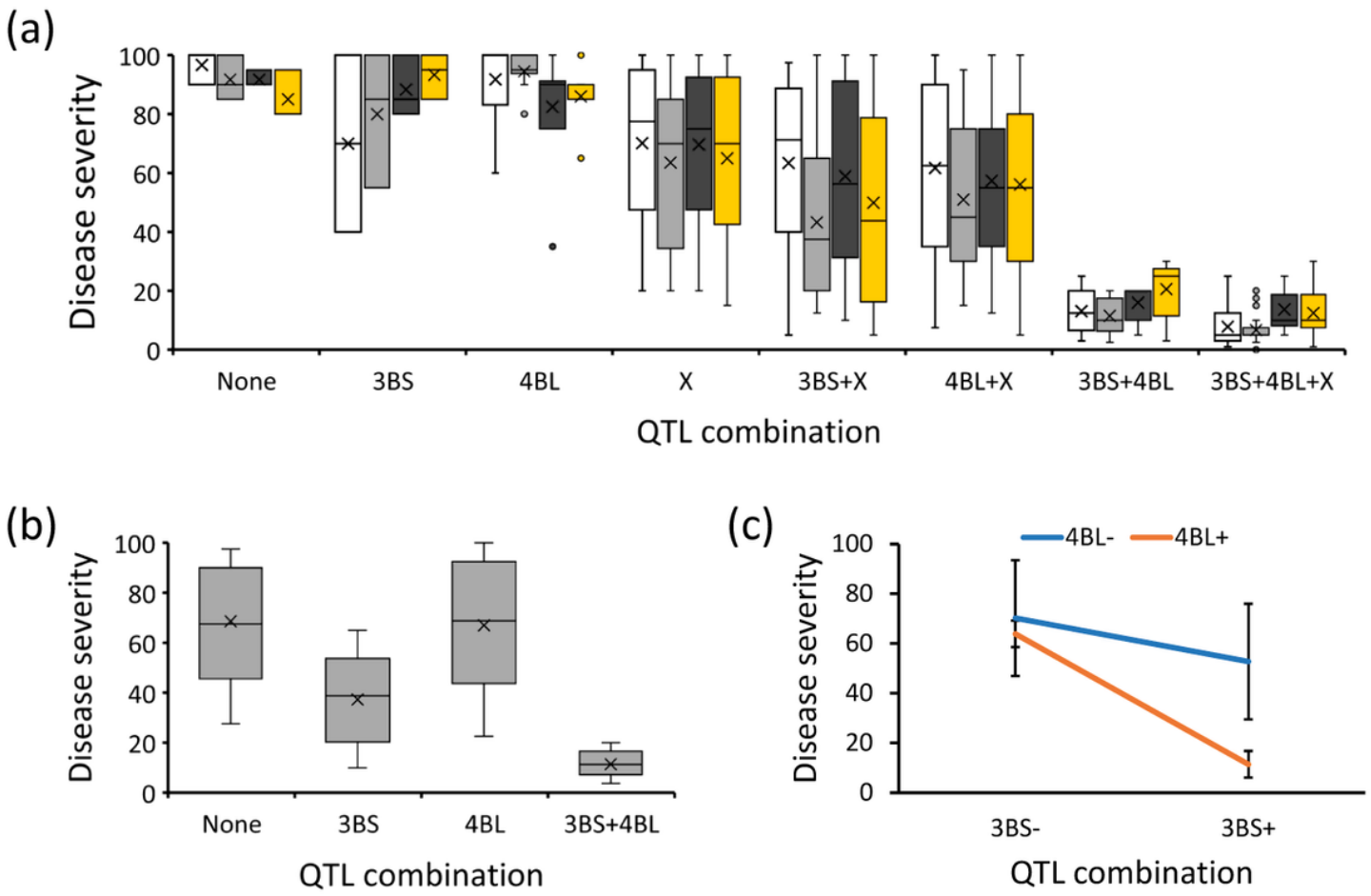

Figure 4

Effects of quantitative trait loci (QTL) combinations on final disease severity (DS) scores. (a) Effects of QTL combinations on reducing disease severity; (b) Validation of the combined effect of Yr30 and YrFDC12 in an additional 58 RILs. (c) Interaction model of Yr30 and YrFDC12. Box plots (minima and maxima are black dots, medians are crosses, and the first and third quartiles are boxes) for b, maximum disease severity (DS) associated with the identified QTL and combinations. X-axis refers to different groups of QTL combinations and Y-axis refers to DS levels. Details of the groups are in Supplementary Table S3

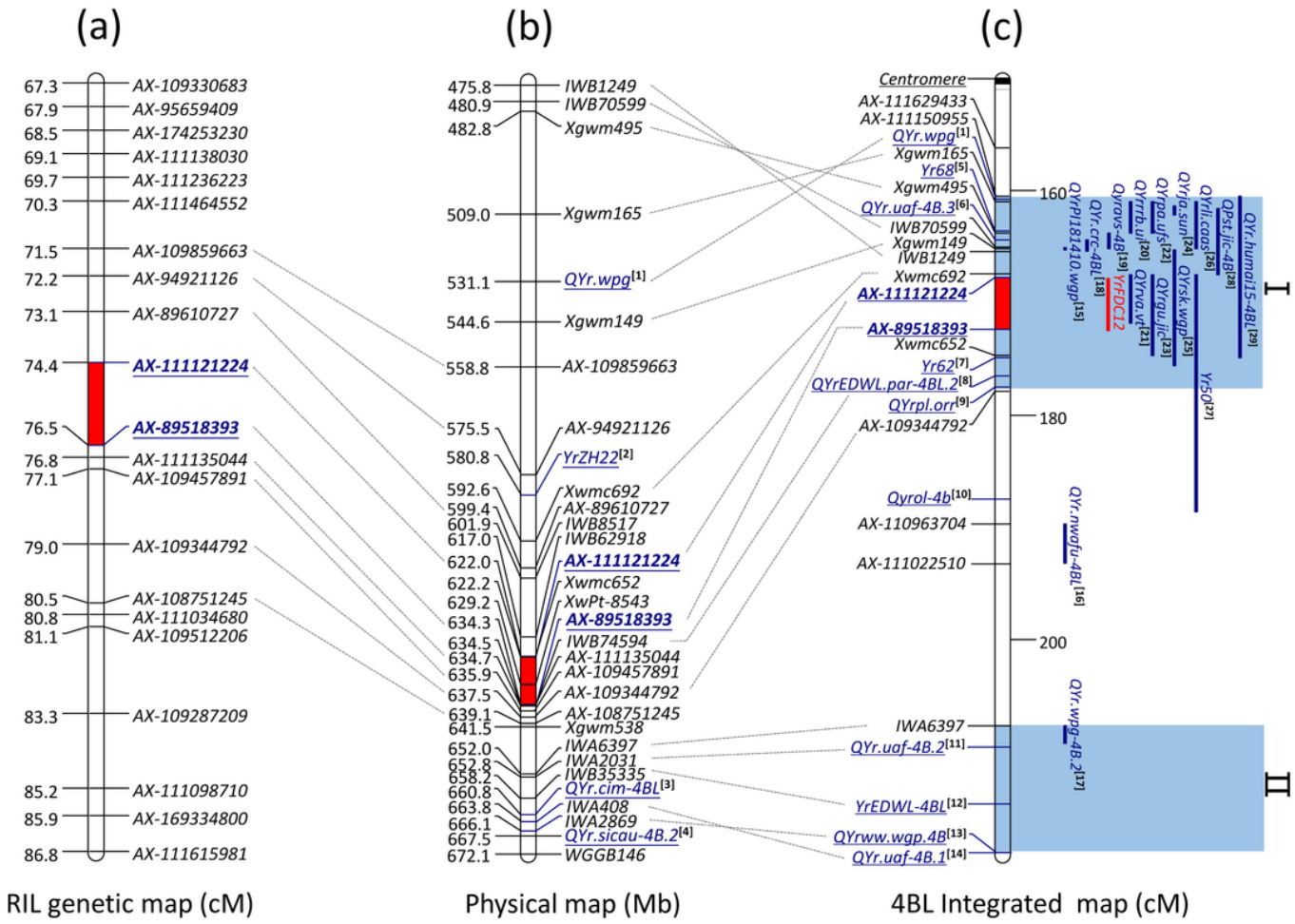

Figure 5

Location of YrFDC12 on chromosome 4BL. (a) Genetic linkage map of YrFDC12 based on data from 170 RILs. Markers flanking the QTL are in blue and in underlined bold font. (b) Physical map of chromosome 4BL constructed using polymorphic markers from the genetic linkage map and markers linked to the other reported genes/QTL on 4BL. (c) Identified QTL (red bar and underlined font) in this study and previously mapped Pst resistance genes and QTL (blue bars or marked in blue) were positioned based on integrated genetic maps provided by Prof. Cui Fa. Confidence intervals of QTL are indicated with blue lines. Red region on chromosome 4BL represents YrFDC12. Two slightly blue regions (I, II) represent two resistance-gene-rich clusters on chromosome arm 4BL. References: [1] Naruoka et al. 2015;[2] Wang et al. 2017;[3] Yuan et al. 2019;[4] Li et al. 2019;[5] Chen and Kang et al. 2017;[6] Habib et al. 2020;[7] Lu et al. 2014;[8] Liu et al. 2017;[9] Vazquez et al. 2012;[10] Suenaga et al. 2003;[11] Habib et al. 2020;[12] Liu et al. 2017;[13] Mu et al. 2020;[14] Habib et al. 2020;[15] Liu et al. 2020;[16] Wu et al. 2018;[17] Naruoka et al. 2015;[18] Rosa et al. 2019;[19] William et al. 2006;[20] Chen et al.2012;[21] Christopher et al. 2013;[22] Agenbag et al. 2012;[23] Melichar et al. 2008;[24] Zwart et al.2010;[25] Liu et al. 2019;[26] Lu et al.2009; [27] Liu et al. 2013;[28] Jagger et al.2011;[29] Yuan et al. 2018.

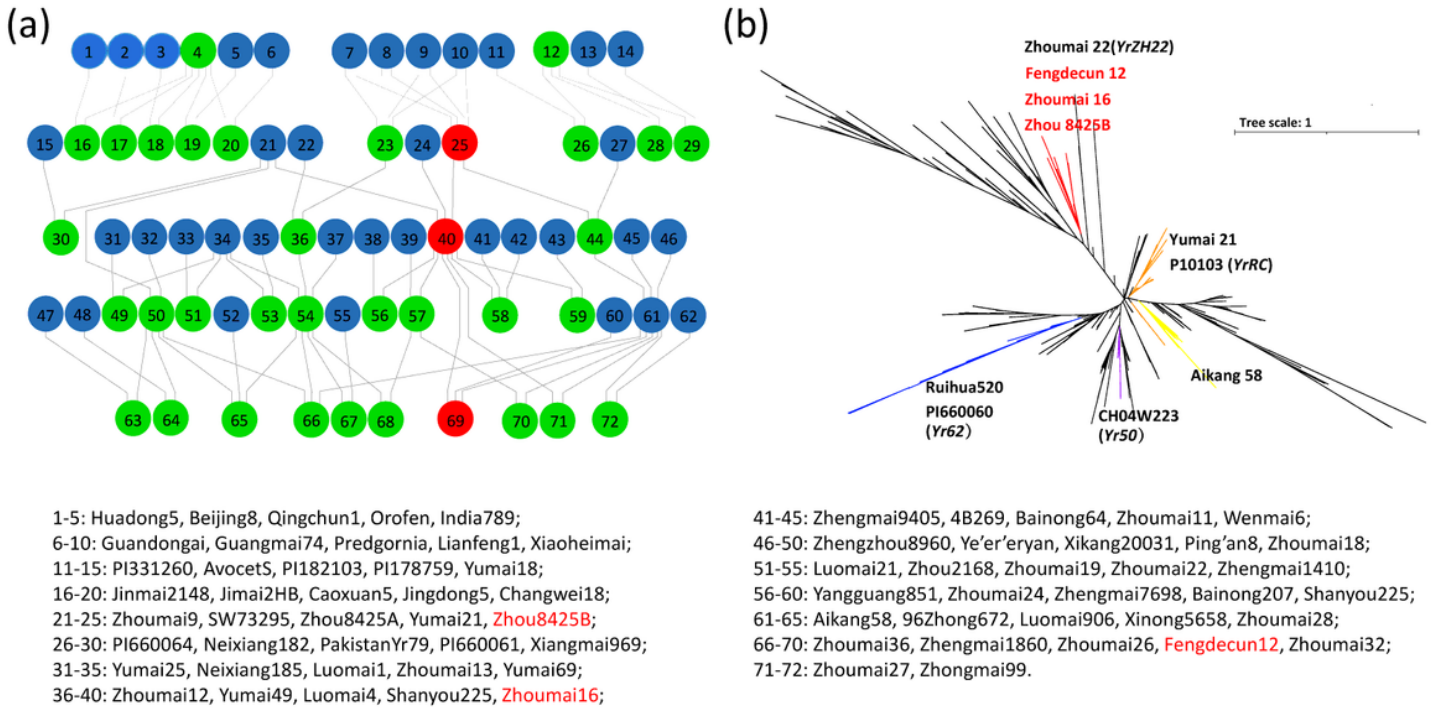

Figure 6

The donor lines of favorable allele of YrFDC12. (a) Pedigree information of FDC12, (b) phylogenetic tree of the candidate YrFDC12 region among 1,400 accessions including the parents of FDC12. Details of results based on Wheat660K SNP markers are in Supplementary Table S5. Red, green and blue represent the donor genotypes of YrFDC12 in Fengdecun12 (FDC12), lines sharing the same haplotype as FDC12 in the region of YrFDC12, and lines carrying the adverse allele or not identified in candidate region of YrFDC12.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Fig.S1.pptx
- SupplymentaryTable1.xlsx
- SupplymentaryTable2.xlsx
- SupplymentaryTable3.xlsx
- SupplymentaryTable4.xlsx
- SupplymentaryTable5.xlsx