Mendelization and Molecular Mapping of a Large-effect QTL Conferring Durable Adult-plant Resistance to Stripe Rust in a Chinese Wheat Landrace 'Gaoxianguangtoumai'

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Research Article

Abstract

The Chinese wheat landrace 'Gaoxianguangtoumai' (GX) has exhibited a high degree of adult-plant resistance (APR) to stripe rust in field environments for more than a decade. To reveal the genetic basis for APR to stripe rust in GX, a set of 249 $F_{6:8}$ recombinant inbred lines (RILs) was developed from a cross between GX and the susceptible cultivar 'Taichung 29'. The parents and RILs were evaluated for disease severity at the adult-plant stage in field environments by artificial inoculation with the currently predominant Chinese *Puccinia striiformis* f. sp. *tritici* races during three cropping seasons, and genotyped using the Wheat 55K single-nucleotide polymorphism (SNP) array to construct a genetic map with 1,871 SNP markers. Two stable APR quantitative trait loci (QTL), *QYr.GX-2AS* and *QYr.GX-7DS* from GX, were detected on chromosomes 2AS and 7DS, which explained 15.5–27.0% and 9.6–15.6% of the total phenotypic variation, respectively. Compared with published genes and QTL, *QYr.GX-7DS* is likely *Yr18*, whereas *QYr.GX-2AS* is probably novel. Haplotype analysis revealed that *QYr.GX-2AS* is likely to be rare which present in 5.3% of the 325 surveyed Chinese wheat landraces. By analyzing a near-isogenic line population, *QYr.GX-2AS* was further mapped to an interval with a physical distance of about 1.37 Mb and co-segregated with a Kompetitive allele-specific PCR (KASP) marker. Furthermore, three tightly linked KASP markers were highly polymorphic among 109 Chinese wheat cultivars. The short physical interval and tightly linked KASP markers developed in this study will facilitate marker-assisted selection and map-based cloning of *QYr.GX-2AS*.

Key Message

QYr.GX-2AS, a novel adult-plant stripe rust resistance QTL on wheat chromosome 2AS derived from a Chinese landrace, behaves as a single Mendelian gene and provides more effective resistance than *Yr18.*

Introduction

Stripe rust (also known as yellow rust), caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is among the most harmful and widespread obligate pathogens of common wheat (*Triticum aestivum* L.) worldwide (Knott 1989; Wellings 2011). China has the largest stripe rust epidemic area in the world (Zeng and Luo 2006; Chen et al. 2014), and frequent epidemics have been reported (Han and Kang 2018). Since the 1950s, four severe epidemics of wheat stripe rust have occurred in China in 1950, 1964, 1990, and 2002, resulting in yield losses of 6.0, 3.2, 1.8, and 1.4 million tonnes, respectively (Li and Zeng 2000; Wan et al. 2004). The main cause of the outbreaks is the emergence of new virulent races that overcome the widely deployed resistance genes (Chen and Kang 2017). At present, CYR32 and CYR34 are the most virulent and predominant *Pst* races in China (Liu et al. 2017; Wang et al. 2018). Continuous improvement in the resistance of wheat cultivars to cope with evolving races of *Pst* is a high priority to control stripe rust (Manickavelu et al. 2016).

To date, more than 300 genes or quantitative trait loci (QTL) for stripe rust resistance on the 21 wheat chromosomes have been reported (Rosewarne et al. 2013; McIntosh et al. 2018). In general, these resistance genes and QTL can be classified into two major classes: all-stage resistance (ASR) and adult-plant resistance (APR). ASR usually confers complete resistance during all growth stages and is simple to select during breeding. However, most ASR genes are race specific and encode nucleotide-binding and leucine-rich repeat (NLR) proteins, and therefore are effective against only a subset of *Pst* races. With regard to the dynamic rust pathogen populations of the virulent races, only a small number of the characterized ASR genes, such as *Yr5* (Marchal et al. 2018), *Yr15* (Klymiuk et al. 2018), *Yr53* (Xu et al. 2013), *Yr61* (Zhou et al. 2014), *Yr65* (Cheng et al. 2014), and *Yr69* (Hou et al. 2016), are still widely effective against currently dominant *Pst* race groups in China (Sharma-Poudyal et al. 2013; Wu et al. 2018). In contrast, APR is effective starting at adult-plant growth stages and typically provides a degree of partial resistance, but it is usually non-race-specific and provides durable resistance to *Pst*. Of the three APR genes cloned to date, *Yr18* encodes a putative ATP-binding cassette transporter (Krattinger et al. 2009), *Yr36* encodes a kinase domain and a lipid-binding domain (Fu et al. 2009), and *Yr46* encodes a predicted hexose transporter (Moore et al. 2015). These genes represent different protein families compared with classical ASR genes (the NLR family) and provide unique mechanisms effective against a broader range of pathogens. As an example, *Yr18* has been globally used as a component of durable rust resistance in breeding programs and no evolution of increased virulence has been observed for

almost 100 years (Krattinger et al. 2009). To achieve a high degree of durable resistance, combining multiple APR genes into the same background has been considered as an important strategy for improvement of stripe rust resistance in wheat breeding.

Chinese wheat landraces are farmer-developed and maintained as traditional cultivars in China. These landraces harbor rich genetic diversity for stripe rust resistance. Numerous stripe rust genes or QTL have been identified, such as *Yr1* (Bansal et al. 2010), *Yr18* (Krattinger et al. 2009), *Yr81* (Gessese et al. 2019), *YrYL* (Wu et al. 2016), *YrBai* (Ma et al. 2015), *Yrqbc* (Cao et al. 2020), *QYr.caas-5AL* (Lan et al. 2010), *QYr.cau-6DL* (Zhang et al. 2017), *QYr.cau-2AL* (Wang et al. 2019a), *QYr.GTM-5DL* (Wu et al. 2020), and *QYr.AYH-5BL* (Long et al. 2021). Recently, our research program evaluated more than 1000 Chinese wheat landrace accessions collected from all ten agro-ecological zones (Zhou et al. 2017) for responses to stripe rust in the greenhouse and the field under inoculation with selected Chinese predominant races of *Pst* (Cheng et al. 2019; Long et al. 2019; Yao et al. 2019, 2020; Ye et al. 2019; Wang et al. 2021). Many resistant accessions of Chinese wheat landraces continually display APR to stripe rust in field environments, providing a novel resistance resource for the breeding of wheat cultivars with durable resistance to stripe rust. The novel APR genes require further research for identification, validation, and mendelization to facilitate their use in wheat breeding.

Gaoxianguangtoumai (GX) is a spring wheat landrace from Sichuan Province in southwest China, which is a regional center for oversummering and overwintering of the stripe rust pathogen. This landrace has exhibited a high degree of APR to stripe rust in field environments for more than a decade, but little information is available on the genetic basis of resistance in this landrace. The objectives of the present study were to (1) identify the QTL conferring APR to stripe rust in a recombinant inbred line (RIL) population developed from the cross between GX and a susceptible cultivar, 'Taichung 29' (TC 29), (2) validate and mendelize the novel QTL in a near-isogenic line (NIL) derived population, and (3) develop tightly linked Kompetitive allele-specific PCR (KASP) markers for use in marker-assisted selection in breeding programs.

Materials And Methods

Plant materials and races

The Chinese wheat landrace GX (accession number ZM7854 in National Germplasm Bank, China (NGBC) and AS1579 in Triticeae Research Institute, Sichuan Agricultural University) originating from Sichuan Province, was crossed (as the female parent) with the highly stripe rust susceptible wheat cultivar TC 29. In total, 249 $F_{6:8}$ RILs derived from a single F_1 seed were developed by single-seed descent. A NIL-derived population of 130 individuals (F_2), derived from a residual heterozygous line selected from the GX × TC 29 RIL population (F_8) carrying heterozygous segments covering the *QYr.GX-2AS* region, was used for validation of *QYr.GX-2AS*. A collection of 325 Chinese wheat landraces genotyped with the 55K single-nucleotide polymorphism (SNP) array was used for marker haplotype analysis (Zhou et al. 2017). A panel of 109 Sichuan wheat cultivars was used to determine the polymorphism of markers tightly linked with *QYr.GX-2AS*. The highly stripe rust susceptible wheat cultivars 'Mingxian 169', 'SY95-71', and 'Avocet S' (AvS) were used as susceptible controls in seedling and adult-plant tests throughout the study. The *Pst* races were kindly provided by the Plant Protection Institute of the Gansu Academy of Agricultural Sciences, Gansu, China.

Evaluation of resistance to stripe rust

Seedling tests to evaluate the stripe rust resistance of GX and TC 29 were conducted in a greenhouse using two prevalent Chinese *Pst* races (CYR32 and CYR34). Five plants of each line were sown in a plastic pot filled with nutrient soil and grown in a controlled environment in the greenhouse. Seedlings were inoculated at the two-leaf stage with each *Pst* race in accordance with the protocol of Hickey et al. (2012). Inoculated plants were placed in a dew chamber at 10 °C and 100% relative humidity for 24 h in the dark, and then moved to separate growth chambers at 15−16 °C with 12−14 h of light daily. When the susceptible check 'Mingxian 169' showed full sporulation, the infection type (IT) on the second leaf

(approximately 15–18 days after inoculation) was scored using a 0–9 scale (Line and Qayoum 1992). Plants with IT scores of 0 to 6 were considered resistant, whereas plants with IT scores of 7 to 9 were considered susceptible.

Assessments of adult-plant stripe rust responses were conducted at the Chongzhou Experimental Station (30°33'N, 103°39'E), Sichuan Agricultural University, Chengdu, China. The $F_{6:8}$ RIL population and the parental lines were evaluated for APR to stripe rust during the 2017–2018, 2018–2019, and 2019–2020 growing seasons (referred to as CZ2018, CZ2019, and CZ2020, respectively). The NIL-derived population (F_2) was evaluated for APR to stripe rust during the 2020–2021. In all tests, 20 seeds of each line were planted in rows 2 m in length and spaced 30 cm apart, with individual plants spaced 10 cm apart. The susceptible cultivar TC 29 was planted in every 20th row as a susceptible control. To provide inoculum for infection, the susceptible cultivars SY95-71 and AvS were planted around the perimeter of the experimental area as spreaders. Artificial inoculation was conducted using a mixture of currently predominant *Pst* races in China (comprising CYR32, CYR33, CYR34, G22-14, Su11-4, Su11-5, and Su11-7). Stripe rust response was first recorded by scoring the IT and disease severity (DS) when the susceptible checks SY95-71 and AvS showed more than 80% DS, and was followed by two additional evaluations at 7-day intervals (i.e., three evaluations in total) for three randomly selected individual plants. The IT was recorded based on the 0–9 scale of Line and Qayoum (1992). The DS was scored as the percentage infected leaf area (0, 5%, 10%, 20%, 40%, 60%, 80%, or 100%) in accordance with the Chinese National Standard, GB/T 15797-2011. The final DS (FDS) was used for phenotypic analysis.

Genotyping, linkage map construction, and QTL analysis

Genomic DNA was extracted from a single plant for each line of the wheat materials using the cetyltrimethylammonium bromide method (Stewart and Via 1993). The two parents (GX and TC 29) and the 117 RILs were genotyped using the Axiom® Wheat 55K SNP array (53,036 markers) by the China Golden Marker Biotechnology Company Ltd (Beijing, China). Monomorphic and SNP loci with a minor allele frequency less than 0.3 were excluded from further analysis (Ma et al. 2019). Polymorphic SNP markers were used to remove redundant markers in the binning step using the BIN function, with the parameters missing rate = 20% and distortion value = 0.01, implemented in QTL IciMapping v4.2 (Wang et al. 2019b). The binned markers were used for linkage map construction using the Kosambi mapping function (Kosambi 1944) with JoinMap v4.0 (Van Ooijen 2006). Mapping of QTL was performed using QTL IciMapping v4.2 based on inclusive composite interval mapping with the preset parameters Step = 1 cM, *p*-value for entering variables (PIN) = 0.001, and logarithm of the odds (LOD) = 2.5.

Haplotype analysis

Haplotype analysis was performed to identify haplotype variants for *QYr.GX-2AS* in a collection of 325 Chinese wheat landrace accessions (Zhou et al. 2017; Ye et al. 2019). The informative markers linked to *QYr.GX-2AS* were screened using the Wheat 55K or Wheat 660K SNP arrays in accordance with the method described by Long et al. (2021). The SNP genotype data and the phenotype data (FDS) were obtained from recently published studies (Cheng et al. 2019; Long et al. 2019; Yao et al. 2019, 2020; Ye et al. 2019; Wang et al. 2021). Haplotype variants were detected using Haploview v4.2 (http://www.broad.mit.edu/mpg/haploview/). The haplotypes detected in at least 10 accessions were considered to be major haplotypes. Boxplots were generated to display the average FDS of accessions carrying the different haplotypes. Haplotype data were combined with provenance information to examine the geographic distribution of the superior haplotypes in the 10 major agro-ecological production zones of Chinese wheat landraces.

Exome capture sequencing, development of KASP markers, and genetic mapping

Genomic DNA of the parents, GX and TC 29, was sequenced using the wheat exome capture sequencing protocol described by Dong et al. (2020). The sequence variants were identified using the variant calling pipeline GATK4 (Heldenbrand et al. 2019). The SNPs in the target region for *QYr.GX-2AS* detected by exome capture sequencing and the Wheat 55K array were converted to KASP markers using the PolyMarker online tool (Ramirez-Gonzalez et al. 2015). The KASP markers were used to screen the parents and NILs to confirm polymorphism before genotyping the NIL-derived population. The KASP assays were performed in 96-well format as 10 µL reactions containing 2 µL of 50–100 ng genomic DNA, 5 µL of HiGeno 2× Probe Mix B, 0.24 µM of each forward primer, 0.6 µM of the common reverse primer, and double distilled water to make up the volume to 10 µL. Each PCR was conducted using the BIO-RAD CFX96 qPCR system. Thermocycling was performed with a touchdown protocol: 95 °C for 10 min; 95 °C for 20 s and 61 °C (−0.6 °C per cycle) for 40 s for 10 cycles; and 95 °C for 20 s and 55 °C for 40 s for 38 cycles. Data analysis was performed manually using BIO-RAD CFX96 Manager 3.1.

Polymorphic KASP markers were genotyped in the NIL-derived population of 130 individuals (F_2) for validation of *QYr.GX-2AS*. Linkage analysis was performed using JoinMap v4.0 (Kyazma BV, Wageningen, The Netherlands) (Van Ooijen 2006) with a LOD threshold of 3.0. The Kosambi map function (Kosambi 1944) was used to convert the recombination fractions to centi-Morgans. The linkage map was drawn using Mapdraw v2.1 (Liu and Meng 2003). In addition, to check the usefulness of the newly developed KASP markers for marker-assisted selection, three tightly linked markers for *QYr.GX-2AS* were further assessed in 109 wheat cultivars grown in Sichuan.

Data analyses

Best linear unbiased prediction (BLUP) values for each RIL, analysis of variance (ANOVA), Pearson's correlation coefficients, and broad-sense heritability (H^2) estimates were calculated using the "AOV" tool implemented in QTL IciMapping v4.2 (http://www.isbreeding.net) (Wang et al. 2019b). The goodness-of-fit of the observed rust response with the theoretical 3:1 ratio in the NIL-derived population (F_2) was performed using the chi-square (χ^2) test with Excel 2016 (Microsoft, Redmond, WA, USA). Student's *t*-tests ($P < 0.05$ and 0.01) were conducted with SPSS Statistics v17.0 (IBM Corp., Armonk, NY, USA) to evaluate the significance of differences between the two groups.

Results

Stripe rust response of the parents and RILs

Plants of GX were susceptible (IT = 8) to CYR32 and CYR34 at the seedling stage (Fig. 1a), but exhibited strong resistance (IT = 3, FDS < 10%) to mixed *Pst* races at the adult-plant stage in three crop seasons from 2018 to 2020 (Fig. 1b, Fig. 2, Table S1). These results indicated that GX showed non-race-specific APR to stripe rust. The frequency distributions of RILs for FDS were continuous with a pronounced skewness towards resistance, and the average FDS of RILs for GX × TC 29 was 12.5%–15.7% in the field tests, suggesting the presence of a large-effect QTL in the RIL population (Fig. 1c, Fig. 2, Table S1). Broad-sense heritability (H^2) was 96.7% for FDS in all tests (Table 1). Correlation coefficients (R^2) for FDS of the RILs among the different environments were significant ($P < 0.01$) and ranged from 0.82 to 0.95 (Table S2).

Table 1

The summary of final disease severity (FDS) data for the RILs population from the Gaoxianguangtoumai (GX) × Taichung 29 (TC 29) recorded in fields at Chongzhou in 2018-2020

Environments	Parents		RIL population				
	GX	TC 29	Min-max	Mean	SD	CV	H^2 (%)
CZ2018 (%)	5.0	80.0	0-100	14.0	25.2	1.8	
CZ2019 (%)	6.7	80.0	0-100	12.5	23.7	1.9	
CZ2020 (%)	5.0	80.0	0-100	15.7	27.0	1.7	
BLUP (%)	7.1	73.2	2.1-91.0	14.6	21.2	1.5	96.7

SD,standard deviation; CV,coefficient of variation; H^2,broad-sense heritability

Linkage map construction and QTL analysis

A total of 1,871 bin markers were used to construct the linkage map for the GX × TC 29 population (Table S3). The total length of the map covered 2,799.12 cM with an average interval of 1.50 cM between adjacent markers and spanned 911.04, 855.71, and 1,032.37 cM in the A, B, and D genomes, with a density of 1.34, 1.28, and 1.98 cM per marker, respectively (Table S3). The map consisted of 21 linkage groups defined with representatives from each of the 21 chromosomes.

Two major QTL conferring APR to stripe rust were detected from the resistant parent GX in each of the three field tests and BLUP data (Table 2, Fig. 3a, b). The most highly significant QTL, designated *QYr.GX-2AS*, was mapped to the short arm of chromosome 2AS and explained up to 27.0% of the phenotypic variation with a LOD score of 8.1 (Table 2, Fig. 3a). A second QTL, *QYr.GX-7DS*, was flanked by the SNP markers *AX-109379249* and *AX-110431109* on chromosome 7DS and overlapped with *Yr18*, and explained 9.6%−15.6% of the phenotypic variation in all trials and BLUP data (Table 2, Fig. 3b). We concluded that it was highly likely that *QYr.GX-7DS* corresponded to *Yr18*.

To determine the effects of the QTL, the RILs were divided into four groups based on the presence/absence of the most closely linked flanking markers of *QYr.GX-2AS* and *QYr.GX-7DS*. Clearly, the RILs that carried one of the QTL showed a lower FDS than those without any QTL (average FDS = 63.4%). In particular, the RILs carrying only *QYr.GX-2AS* showed only 9.3% of the average FDS, which was similar to the effect of both QTL in combination (average FDS = 7.1%) (Fig. 3c). This result indicated that *QYr.GX-2AS* had a large effect on stripe rust resistance and provided relatively stronger resistance than *QYr.GX-7DS*.

Table 2

Quantitative trait loci (QTL) for stripe rust resistance detected in the RILs population from the Gaoxianguangtoumai (GX) × Taichung 29 (TC 29) using final disease severity (FDS) data across three environments and BLUP values

QTL	Environment	Trait	Chromosome	LeftMarker	RightMarker	Distance (cM)	LOD	PVE (%)	Resistance source
QYr.GX-2AS	CZ2018	FDS	2AS	*AX-109957471*	*AX-110026721*	0.2	8.1	27.0	GX
	CZ2019			*AX-109957471*	*AX-110026721*	0.2	7.1	17.1	
	CZ2020			*AX-109957471*	*AX-110026721*	0.2	5.2	15.5	
	BLUP			*AX-109957471*	*AX-110026721*	0.2	7.7	21.8	
QYr.GX-7DS	CZ2018	FDS	7DS	*AX-109379249*	*AX-89737284*	9.6	3.3	9.6	GX
	CZ2019			*AX-110502471*	*AX-109303704*	9.6	6.6	15.6	
	CZ2020			*AX-109303704*	*AX-110431109*	9.6	4.9	13.6	
	BLUP			*AX-89737284*	*AX-89378255*	9.6	4.4	10.9	

Haplotype analysis of *QYr.GX-2AS*

To assess the distribution of *QYr.GX-2AS* among 325 Chinese wheat landraces, the favorable haplotype was identified by haplotype analysis and seven SNP markers tightly linked to *QYr.GX-2AS* were screened from the Wheat 55K or 660K SNP arrays (Fig. 4a, b, c). Eight major haplotypes ($n > 10$) were detected in the panel (Fig. 4a, b). GX and 15 other accessions clustered with Hap1 (Table S4), which showed a frequency of about 5.3% in the total population (Fig. 4a). Almost all accessions carrying Hap1, except one from Henan, were collected from Sichuan. The accessions carrying Hap1 showed 18.4% of the average FDS and thus were more strongly resistant to stripe rust than those accessions carrying other haplotypes (Hap2 = 37.2%, Hap3 = 24.1%, Hap4 = 47.7%, Hap5 = 21.5%, Hap6 = 39.0%, Hap7 = 27.0%, Hap8 = 47.6%) (Fig. 4c). These results revealed that the favorable haplotype of *QYr.GX-2AS* was Hap1, which was relatively rare among the Chinese wheat landraces.

Validation and mapping of *QYr.GX-2AS*

To further validate and map the location of *QYr.GX-2AS*, the SNPs in the target region for *QYr.GX-2AS* identified by exome capture sequencing and the Wheat 55K array were selected for conversion to KASP markers. Eleven markers were confirmed to be polymorphic between GX and TC 29 (Table S5). Combined with the KASP markers for *QYr.GX-2AS*, a NIL-derived population of 130 individuals (F_2) for *QYr.GX-2AS* was developed from a residual heterozygous plant in the F_8 generation of RILs. No significant phenotypic differences were observed in the NIL-derived population, except for APR to stripe rust (Fig. 5a). With regard to stripe rust response in the field test, the F_2 plants of the NIL-derived population were clearly classifiable into 97 resistant (IT ≤ 6) and 33 susceptible (IT ≥ 7) individuals, which fits the expected ratio (3:1) for a single Mendelian factor (chi-square goodness-of-fit test, χ^2 = 0.01, P = 0.92) (Table S6). Using the newly developed eleven KASP markers (Table S6) to construct the genetic map, *QYr.GX-2AS* was localized to a 1.37 Mb interval between *KP2A_36.85* and *KP2A_38.22*, and co-segregated with the KASP marker *KP2A_37.09* (Fig. 5b).

Validation of KASP markers for marker-assisted selection

To check the specificity and polymorphism of the linked marker of *QYr.GX-2AS* for marker-assisted selection, a set of 109 Chinese wheat cultivars was tested with the markers *KP2A_36.85*, *KP2A_37.09*, and *KP2A_38.22* (Fig. S1, Table S7). Most of the lines amplified the susceptible-specific alleles in the three markers, which showed 85.3%, 99.1%, and 95.4% polymorphism, respectively, in the cultivars (Table S7). Thus, these KASP markers can be used as the specificity markers for marker-assisted selection of *QYr.GX-2AS* in the vast majority of Chinese wheat cultivars.

Discussion

Breeding for durable resistance to stripe rust has been among the highest priorities for wheat breeding in the last decade (Chen 2013). A large number of genes or QTL that confer various degrees of APR to stripe rust have been identified, but most only have minor effects on stripe rust response and are therefore difficult to use in breeding. Thus, identification of genes or QTL with a high degree of APR that are useful in breeding programs is required. The Chinese wheat landrace GX has displayed a high degree of APR to stripe rust in field environments for more than a decade in southwest China. The strong APR to stripe rust of GX is conferred by two QTL identified on chromosomes 2AS and 7DS, respectively. The QTL on 2AS (*QYr.GX-2AS*), being more effective than the QTL on 7DS (*Yr18*), had a large effect in the reduction of stripe rust severity at adult-plant stages, and thus shows great potential for use in breeding durable resistance to stripe rust in wheat.

QTL analysis is a useful procedure to reveal possible multiple loci when analyzing complex genetic traits, such as APR to stripe rust, in resistant germplasm. However, this procedure only allows approximate mapping of the QTL (Tanksley and Hewitt 1988) owing to the heterogeneity in genetic backgrounds. The confidence interval of many QTL spans a considerable genetic distance and, as a result, molecular markers for these QTL may not be reliably used in marker-assisted selection. As a strategy for accurate mapping of QTL in genetic analysis, NIL-derived populations that allow the conversion of a quantitative trait into a Mendelian factor have been widely used for fine mapping and cloning of many important QTL in wheat, such as *Yr18* (Krattinger et al. 2009), *Yr36* (Fu et al. 2009), *Fhb1* (Su et al. 2019), and *Fhb7* (Wang et al. 2020). In the present research, a NIL-derived population targeting *QYr.GX-2AS* was developed based on the method of heterogeneous inbred family analysis (Tuinstra et al. 1997). Members of this population were unambiguously classified as either resistant or susceptible and fitted the expected ratio (3:1) for a single Mendelian factor; thus, accurate mapping of the locus was possible. Analysis of the NIL population revealed that *QYr.GX-2AS*, flanked by *KP2A_36.85* and *KP2A_38.22*, was located in the interval 36.85 Mb to 38.22 Mb on chromosome 2AS. One KASP marker co-segregating with the targeted locus was successfully developed for marker-assisted selection.

Several genes that confer resistance to stripe rust have been identified on wheat chromosome 2AS, including *Yr17* (Bariana and McIntosh 1993), *Yr56* (McIntosh et al. 2014), *Yr69* (Hou et al. 2016), *YrR61* (Hao et al. 2011), and *YrSph* (Chen et al. 2012) (Fig. 6, Table S8). The genes *Yr17*, *Yr69*, and *YrSph* confer ASR to stripe rust. Although recent studies suggest that *Yr17* also confers APR to stripe rust in the field, *QYr.GX-2AS* is likely to differ from *Yr17* because accessions of the Chinese wheat landrace GX that lack the 2N alien segment carry *Yr17*. *Yr56* is a major gene conferring APR to stripe rust that was identified in the Australian durum wheat cultivar 'Wollaroi'. *Yr56* is flanked by *Xsun167* (*wPt-4197*) and *Xsun168* (*wPt-9104*) (McIntosh et al. 2014), which corresponds to the 'Chinese Spring' physical map region between 8.35 Mb and 14.28 Mb. *YrR61*, corresponding to the major-effect QTL *QYr.uga-2AS_26R61* conferring APR to stripe rust, was identified from the soft red winter wheat cultivar 'Pioneer' and is flanked by the markers *Xbarc124* (3.78 Mb) and *Xgwm359* (28.20 Mb) (Hao et al. 2011). Clearly, both *Yr56* and *YrR61* are located distant from *QYr.GX-2AS*. In addition, at least 20 QTL have been reported on chromosome 2AS, and most of them are located at a QTL hot-spot region in the distal end of 2AS (< 30 Mb) (Fig. 6). For example, *QYr.ufs-2A* (Agenbag et al. 2012), *QYrst.orr-2AS_Stephens* (Vazquez et al. 2012) and *QYr.sun-2A_Kukri* (Bariana et al. 2010) were all flanked by the basis of a common DArT marker *XwPt-0003*, which were nearly with the *QYrva.vt-2AS_VA00W-38* (Christopher et al. 2013) corresponds to the 'Chinese Spring' physical map region 29.94 Mb. *QYrtb.orz-2AS* (Vazquez et al. 2015) and *QYr.inra_2AS.1_Recital* (Dedryver et al. 2009) were located in 2AS close to marker *Xcfd36* (about 16.63 Mb) which are homologous to the *Yr17* introgression. The *QYr.ucw-2AS_PI610750* (Lowe et al. 2011), contributed by the synthetic derivative PI610750, is flanked by the *XwPt-3896* (13.14 Mb) and *Xwmc177* (33.70 Mb). *QYr.inra-*

2A_CampRemy from Camp Remy (Mallard et al. 2005) is located by the *Xgwm382a* and *Xgwm359* (about 28.20 Mb). *QYrzv.swust-2AS* (Zhou et al. 2021) flanked by *IWB7877* and *IWB72720* is derived from the wild emmer wheat (*T. dicoccoides*) accession Zavitan, corresponding to the 'Chinese Spring' physical map region between 5.25 Mb and 5.33 Mb. Similarly, the other QTL identified by GWAS are located in different regions from *QYr.GX-2AS* on chromosome 2AS, expect for a minor locus *QYr.wsu-2A.1_IWA2526* (about 36.63 Mb). Hence, the large-effect QTL *QYr.GX-2AS* identified in the present study is unlikely to be the previously reported QTL.

According to gene annotation information in IWGSC RefSeq v1.1, 16 predicted genes are located in the candidate region for *QYr.GX-2AS* (Fig. 5c, Table S9). None of these genes is a classic NBS-LRR resistance gene. In addition, no annotations accorded with the protein types encoded by the APR genes *Yr18* (ABC transporter), *Yr36* (kinase-START), and *Yr48* (hexose transporter), implying that the candidate gene for *QYr.GX-2AS* might differ from known stripe rust resistance genes. Combined with exon sequencing data, eight predicted genes showed non-synonymous variants between GX and 'Chinese Spring' in exon regions, including a RING/U-box, ascorbate peroxidase, glycosyltransferases, and F-box family protein, that may be involved in disease resistance. For confirmation of the candidate gene and cloning of *QYr.GX-2AS*, fine mapping to narrow the candidate interval will be performed using a large NIL-derived population in future work.

Declarations

Funding

Conflicts of interest

The authors declare that they have no competing interests.

Availability of data and material

The datasets supporting the conclusions of this study are included in this article and its supplementary information files. The raw sequence data have been submitted to GenBank under Bioproject no. PRJNA734801. The materials, including the resistant Chinese wheat landrace 'Gaoxiangguangtoumai' (GX), used in this study are deposited at Triticeae Research Institute, Sichuan Agricultural University and National Germplasm Bank, China (NGBC).

Code availability

Not applicable.

Authors' contributions

YQW and FYL carried out the experiment, analyzed the data, and drafted the manuscript; FNG, FJY, LL, XYZ, LYD, YW and HL carried out the phenotypic evaluation; WL, QTJ, YMW, JM, PFQ, MD and YLZ provided resources and technique guidance; HYK, YFJ and GYC designed and carried out the experiment, formulated the questions, analysed the data and revised the manuscript. All authors have reviewed and approved the final manuscript.

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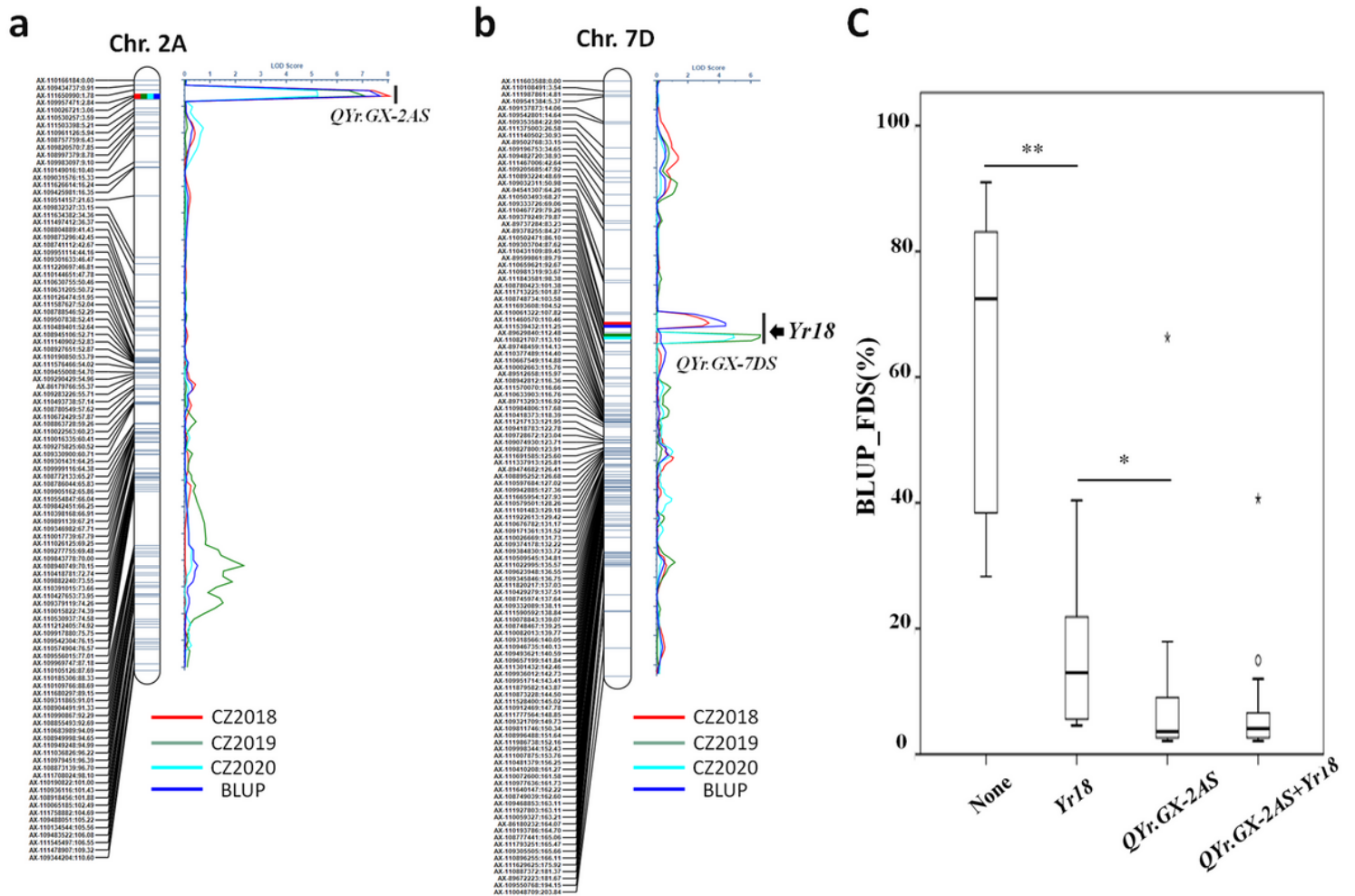
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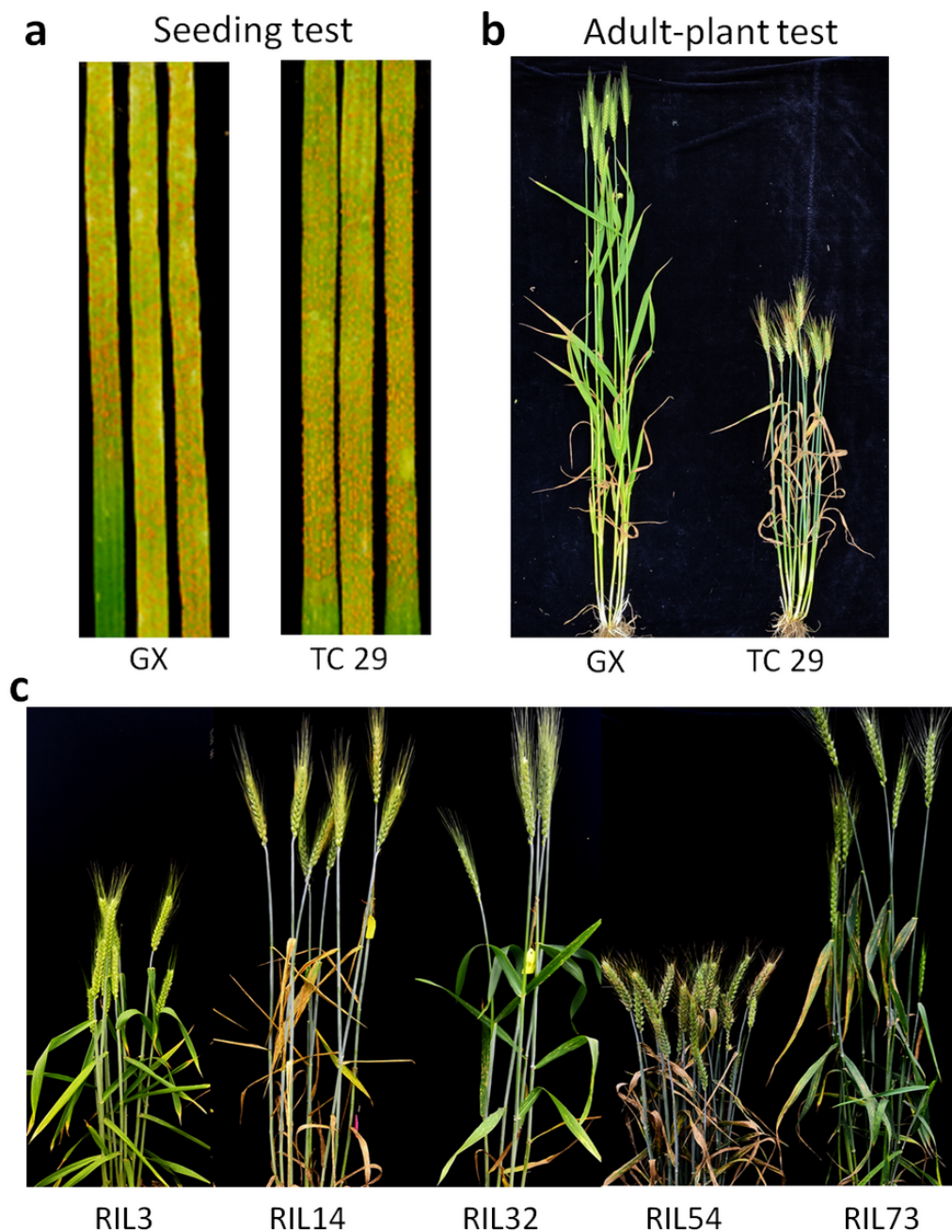
Figure 1

Stripe rust response of the resistant parent Gaoxianguangtoumai (GX) and susceptible parent Taichung 29 (TC 29) with CYR34 at the seedling stage (a) and mixture Pst at the adult-plant stage (b); Stripe rust response of the randomly selected RILs of lines in the field (c).
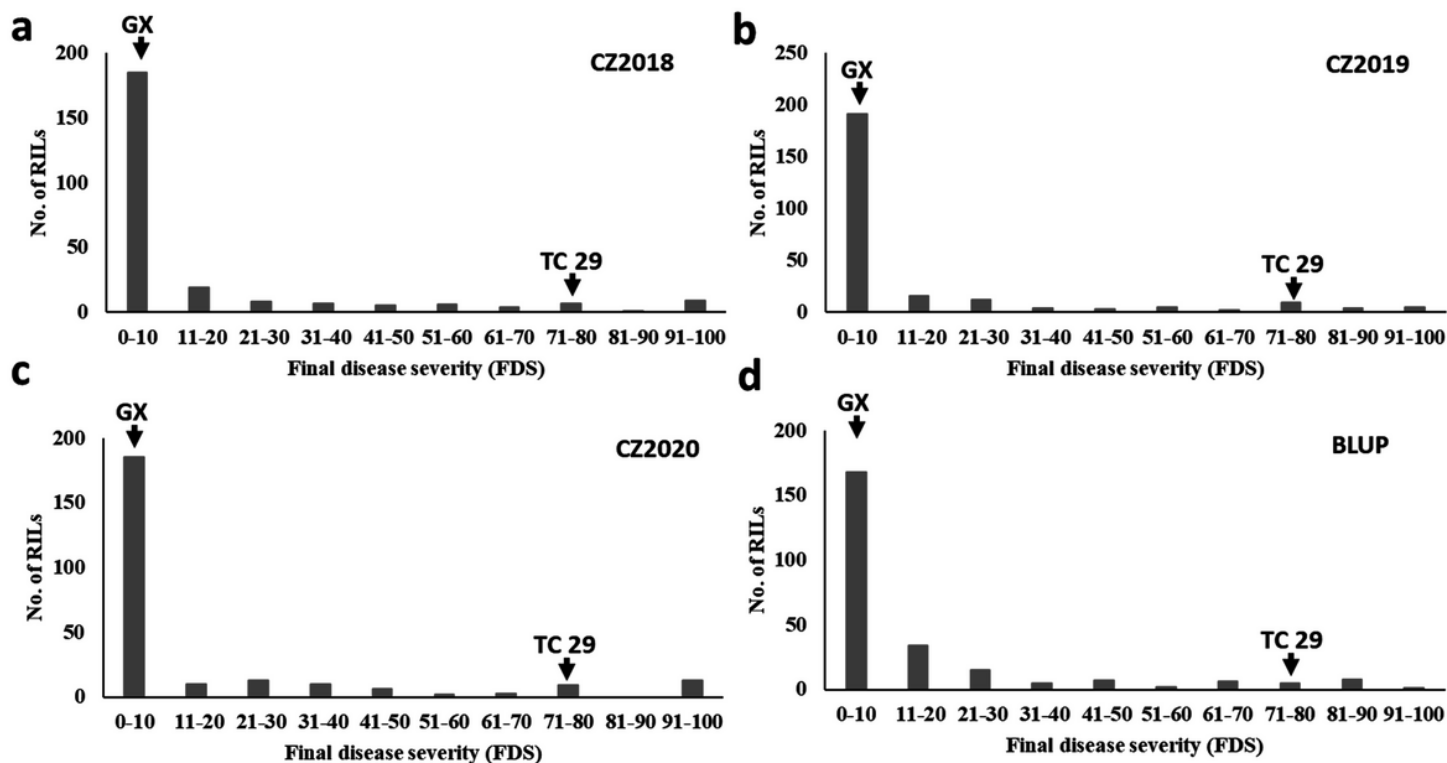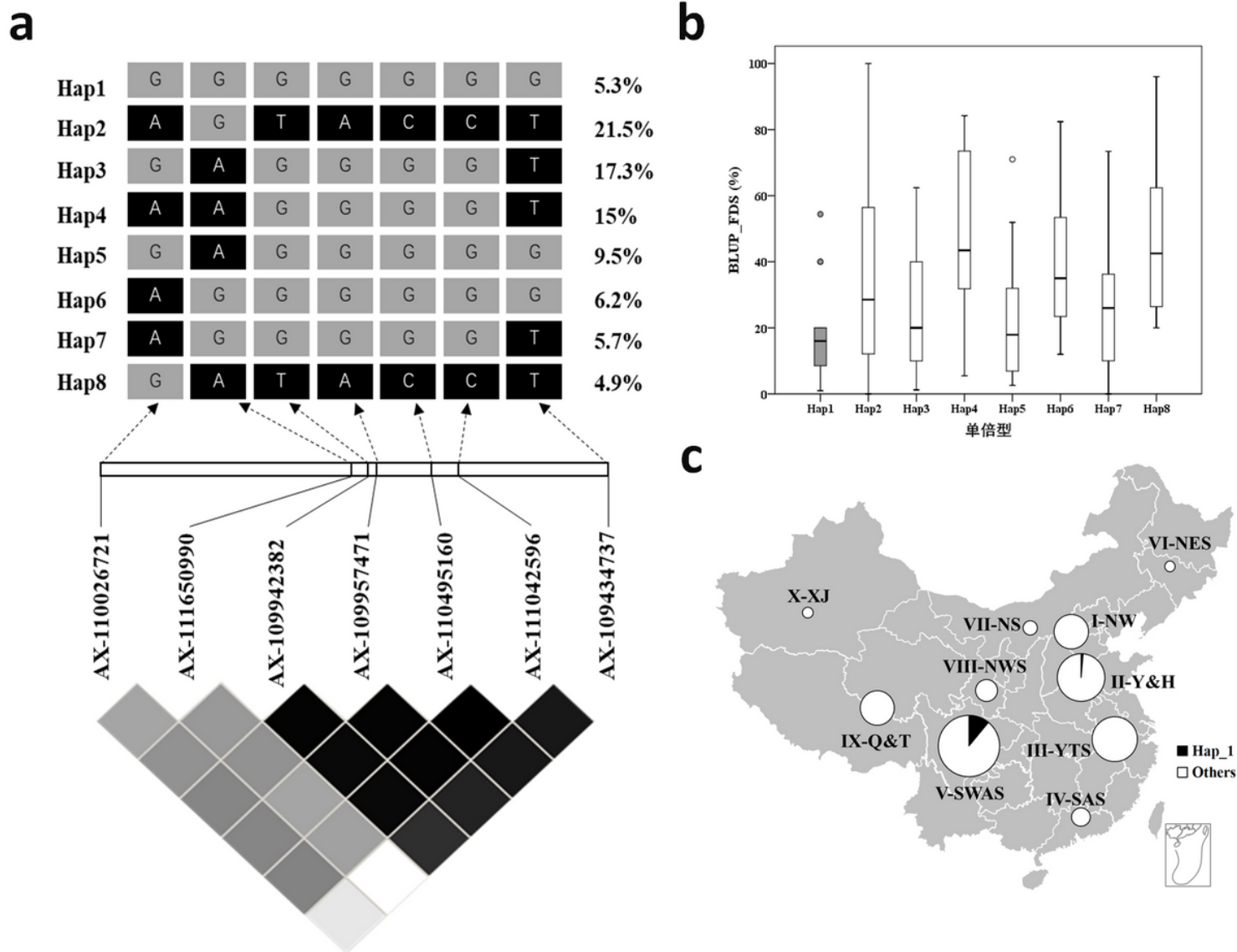
Figure 2

Frequency distributions of the final disease severity (FDS) for the RIL population derived from Gaoxianguangtoumai (GX) × Taichung 29 (TC 29) at Chongzhou in 2018 (a), 2019 (b), 2020 (c) and BLUP values (d).
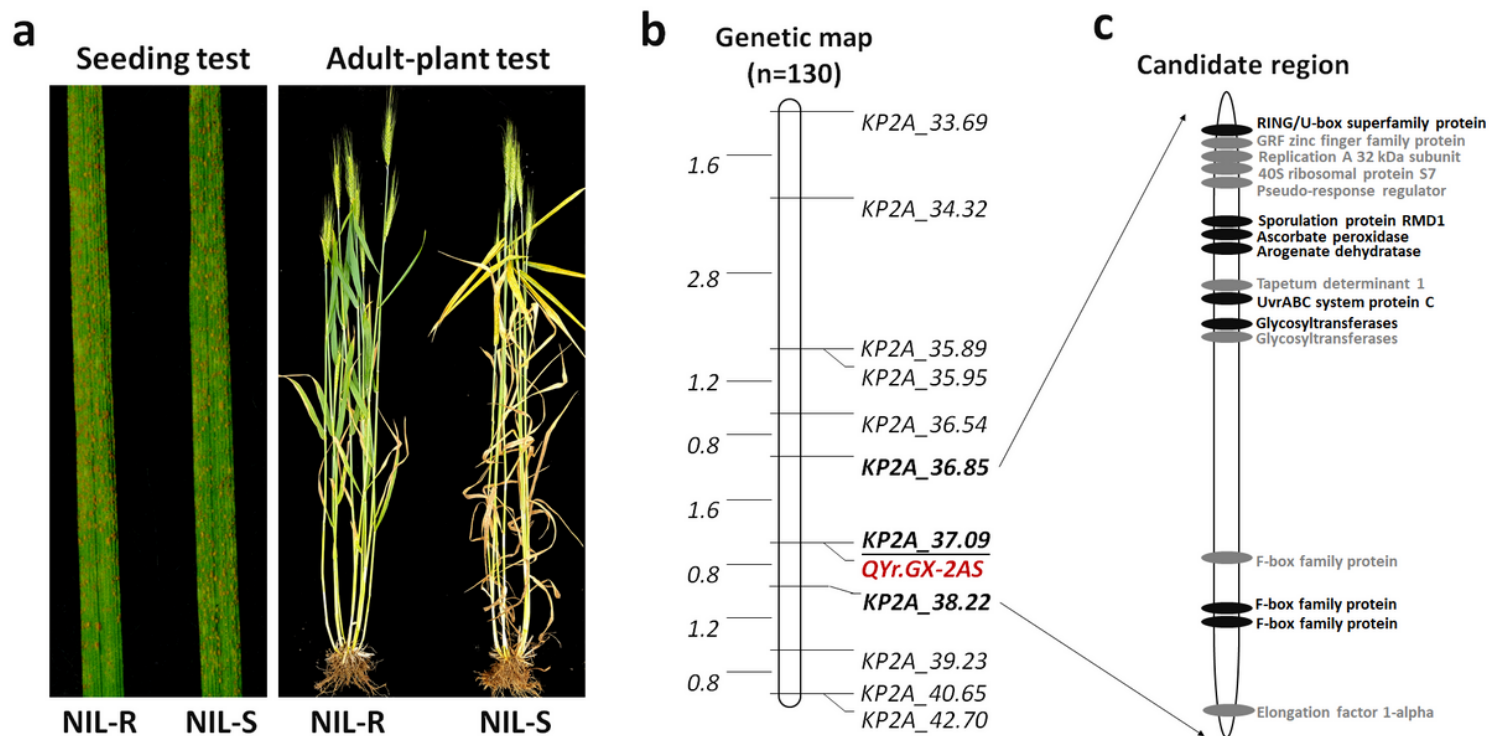
Figure 3

QTL conferring adult plant stripe rust resistance detected by inclusive composite interval mapping (ICIM) in the RILs population from Gaoxianguangtoumai (GX) × Taichung 29 (TC 29). Graphical displays of QTL (a) QYr.GX-2AS and (b) QYr.GX-7DS detected on chromosome 2A and 7D based on the final disease severity (FDS) from three field trials and BLUP data. The box plots for final disease severity (FDS) based on the BLUP data associated with the two loci (QYr.GX-2AS and Yr18) and their combination in the Gaoxianguangtoumai (GX) × Taichung 29 (TC 29) RIL population (c).
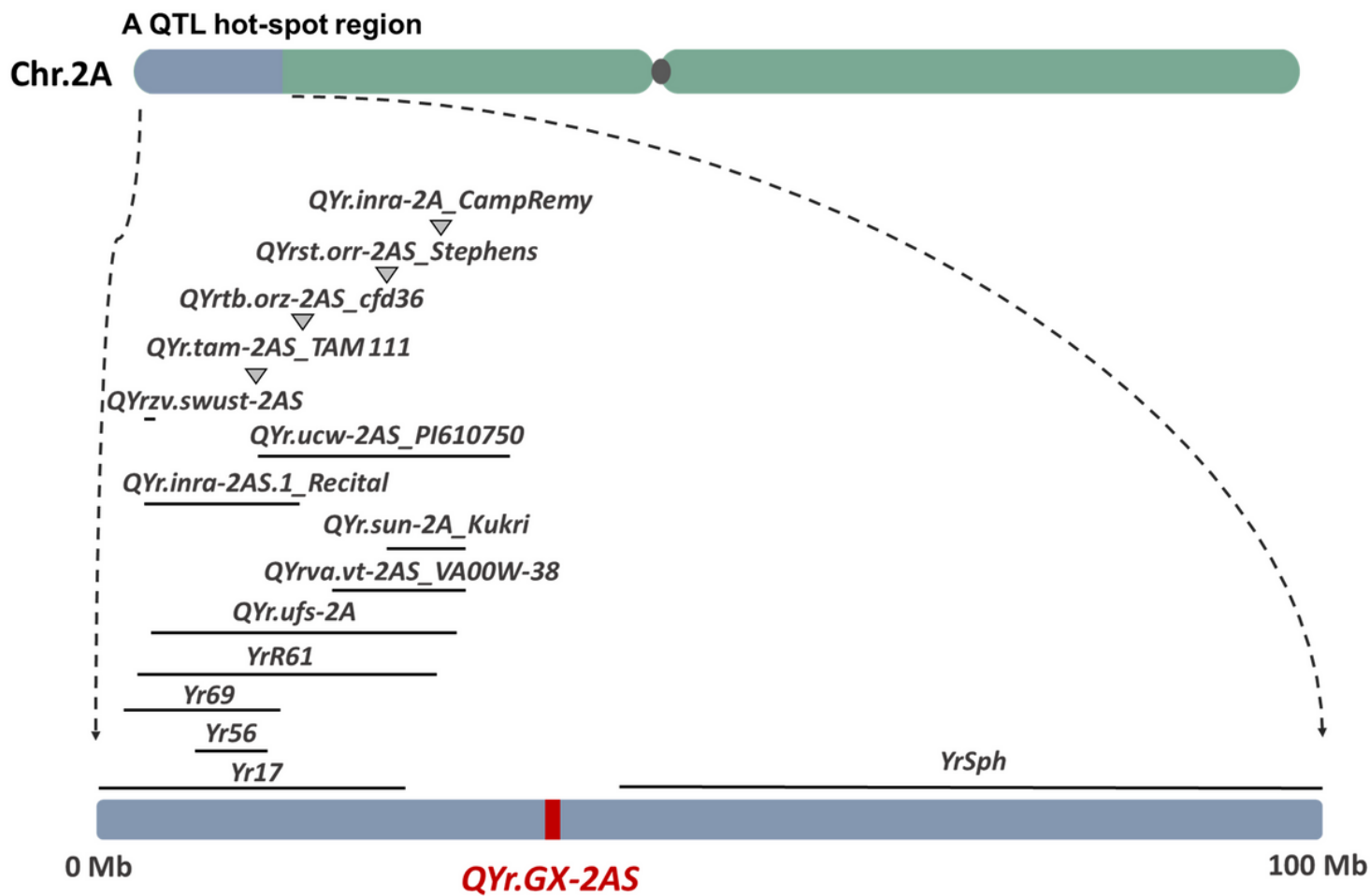
Figure 4

Haplotype analysis of QYr.GX-2AS associated with stripe rust resistance in 325 Chinese wheat landraces. (a) LD heatmap surrounding QYr.GX-2AS. The number on the right shows the distribution frequency of 8 haplotypes in these Chinese wheat landraces. (b) Boxplot displays the mean final disease severity of the accessions carrying different haplotypes. (c) Frequencies of resistance allele of QYr.GX-2AS in Chinese wheat landraces in ten major agro-ecological production zones of China.

Figure 5

Stripe rust response of the near-isogenic lines with mixture Pst at the adult-plant stage in the field (a), genetic map of chromosomes 2AS showing locations of stripe rust resistance genes QYr.GX-2AS based on the NIL-derived population (b), predicted genes in IWGSC RefSeq v1.1, highlight in black showed non-synonymous variants between Gaoxianguangtoumai (GX) and Chinese Spring in the exon regions (c).

Figure 6

Comparison of QYr.GX-2AS with previously identified genes/QTL (from biparental population) for resistance to stripe rust based on the reference genome of bread wheat (IWGSC, RefSeq v1.0).

Supplementary Files

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