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ORIGINAL ARTICLE

Genetic architecture of wheat stripe rust resistance revealed by combining QTL mapping using SNP-based genetic maps and bulked segregant analysis

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Abstract

Key message **A major stripe rust resistance QTL was mapped to a 0.4 centimorgan (cM) genetic region on the long arm of chromosome 7B, using combined genome-wide linkage mapping and bulk segregant analysis.**

Abstract The German winter wheat cv. Centrum has displayed high levels of adult plant stripe rust resistance (APR) in field environments for many years. Here, we used the combined genome-wide linkage mapping and pool-extreme genotyping to characterize the APR resistance. One hundred and fifty-one $F_{2:7}$ recombinant inbred lines derived from a cross between susceptible landrace Mingxian 169 and Centrum were evaluated for stripe rust resistance in multiple environments and genotyped by the wheat 35K single nucleotide polymorphism (SNP) array. Three stable quantitative trait loci (QTL) were identified using QTL analysis across five field environments. To saturate the major QTL, the wheat 660K SNP array was also used to genotype bulked extremes. A major QTL named *QYrcen.nwafu-7BL* from Centrum was mapped in a 0.4 cM genetic interval flanking by *AX-94556751* and *AX-110366788* across a 2 Mb physical genomic region, explaining 19.39-42.81% of the total phenotypic variation. It is likely a previously uncharacterized QTL based on pedigree analysis, reaction response, genotyping data and map comparison. The SNP markers closely linked with *QYrcen.nwafu-7BL* were converted to KASP markers and validated in a subset of 120 wheat lines. A 211 F_2 breeding population from a cross of an elite cultivar Xinong 979 with Centrum were developed for marker-based selection. Three selected lines with desirable agronomic traits and the positive alleles of both KASP markers showed acceptable resistance which should be used as resistance donors in wheat breeding programs. The other QTL *QYrcen.nwafu-1AL* and *QYrcen.nwafu-4AL* with additive effects could enhance the level of resistance conferred by *QYrcen.nwafu-7BL*.

Introduction

Stripe rust (yellow rust), caused by *Puccinia striiformis* Westend. f. sp. *tritici* Erikss. (*Pst*), is one of the most damaging diseases of bread wheat (*Triticum aestivum*) (McIntosh et al. 1995; Wellings 2011). The disease is especially destructive in regions with a mild winter under cool and wet conditions during late spring and early summer, such as the Sichuan basin and southern Gansu in China (Zeng and

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Jingmei Mu and Shuo Huang have contributed equally to this work.

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Luo 2006). Historically in China, race changes caused seven nationwide epidemics and subsequently led to major cultivar replacements (Wan et al. 2007). In recent years, stripe rust occurred annually in regions growing 4.2 million ha wheat and caused heavy grain yield losses in the southwestern and northwestern China (He et al. 2011). The most recent epidemic was caused by the emerging CYR34 race group with virulence to *Yr26* (Bai et al. 2017; McIntosh et al. 2018), which circumvents resistance in large number of wheat cultivars and breeding lines (Han et al. 2015; Wu et al. 2018; Zeng et al. 2015).

Effective fungicides have been developed to control stripe rust, but may be restricted by management and financial factors (Chen 2014). Growing resistant cultivars is an economical and environmentally sound method to prevent the disease. Resistance to stripe rust can be distinguished into all-stage resistance (ASR) and adult plant resistance (APR) based on growth stages when resistance expresses (Chen 2005). As ASR is effective throughout the whole growth stages and mostly provides complete protection, this type of resistance is more attractive to farmers and also widely used by breeders (Ellis et al. 2014; Singh et al. 2014). However, ASR is mostly race specific and often easily overcome by new pathogen races (Chen 2013; McDonald and Linde 2002). In contract, APR expressed mostly at post-seedling stages and was generally controlled by qualitatively inherited genes. APR controlled by a single gene or quantitative trait locus (QTL) usually provides partial control against all races. Mainly due to its non-race specificity, APR is usually durable and has become more and more preferred by breeders (Chen 2013; Singh et al. 2010). APR genes generally act additively and provide adequate levels of durable resistance when present in combination with 4–5 this type of resistance genes (Singh et al. 2005). Examples of *Yr18*, *Yr29* and *Yr46*, which confer partial resistance, combining 2–4 minor genes, have provided effective resistance to stripe rust in many wheat cultivars grown in China and other countries (Herrera-Foessel et al. 2014; Lan et al. 2015; Ren et al. 2017).

Although combining APR genes for high levels of resistance may be achieved through field selection, breeding programs rely more and more on marker-assisted selection (MAS) using closely linked molecular markers. High-throughput genotyping in hexaploid wheat has been made possible in recent years through the advent of SNP arrays including 9K and 90K chips from Illumina (Cavanagh et al. 2013; Wang et al. 2014), 660K (Cui et al. 2017) and 820K chips from Affimetrix (Winfield et al. 2012), and the subsequent development of kompetitive allele-specific PCR (KASP) assays (Rasheed et al. 2016; Semagn et al. 2013). Despite these high-density nature of these arrays, 9K and 90K iSelect chips did not provide enough coverage in the D genome to detect SNP variation, and these high-throughput arrays are not amenable and cost-effective for breeders (Wang et al. 2014; Cavanagh et al. 2013). To avoid these limitations, we have utilized a 'Wheat Breeders Array' which includes 35,143 informative markers and provides a large number of genome-wide polymorphic and codominant markers for genotyping, reducing required computational load and promoting rapid identification of SNPs. This array is more suitable for gene mining and target breeding (Allen et al. 2017).

The German wheat cultivar 'Centrum' (Hussar/Konsul//Lambros) was introduced into China in the 1990s and has shown a high level of APR against stripe rust despite the several changes in predominant *Pst* races. It also exhibited moderate resistance to Fusarium head blight (Badea et al. 2008) and high resistance to powdery mildew (Nematollahi et al. 2008), therefore an excellent multi-resistant wheat germplasm. In addition, it is semidwarf and of good adaptability. Thus, investigating the genetic basis of resistance in Centrum is important for developing new resistant cultivars with higher yields and adaptation. A recombinant inbred line (RIL) population was developed from a cross of Centrum with the susceptible Chinese landrace Mingxian 169 (MX169). Meanwhile, a F_2 breeding population was developed from Xinong 979 × Centrum, as Xinong 979 has many desirable agronomical traits and has been a major cultivar grown in several provinces of China. The objective of this study was to (1) identify QTL conferring APR against stripe rust using combined genome-wide SNP scanning and pool-extreme genotyping; (2) validate the polymorphism of the linked KASP markers for marker-assisted selection; and (3) select progeny lines with the resistance QTL and other agronomic traits.

Materials and methods

Plant materials

Centrum was crossed with Mingxian 169, a Chinese landrace highly susceptible to most Chinese stripe rust races at both seedling and adult plant stages. A total of 151 $F_{2:7}$ RILs were developed from MX169 × Centrum using the single-seed descent method. Centrum was highly susceptible to prevalent *Pst* races CYR32 and CYR33 at the seedling stage tested under controlled conditions, whereas it has been highly resistant at the adult plant stage in fields. An F_2 population was developed from cross Xinong 979 × Centrum to incorporate the Centrum stripe rust resistance into an adapted wheat background, as Xinong 979 is a widely grown wheat cultivar, but susceptible to stripe rust. MX169 and Xiaoyan 22 were used as susceptible controls. Wheat lines carrying *Yr2*, *Yr6*, *Yr39*, *Yr52*, *Yr59*, *YrC591*, *YrZh84* and *Yr79* on chromosome 7BL were included to test for response

to stripe rust for comparison with Centrum. A subset of 120 wheat accessions, comprised of 59 breeding lines, 60 genetic stocks and 1 cultivar, were used for marker tests. Their phenotypes against stripe rust have previously been summarized in Han et al. (2012).

Greenhouse trials

Seedling test was conducted under greenhouse conditions to characterize the stripe rust reaction of Centrum and to compare the wheat genotypes previously reported to have stripe rust resistance genes on chromosomal 7B, including lines Kalyansona (*Yr2*), Heinese Kolben (*Yr6*), Alpowa (*Yr39*), PI 183527 (*Yr52*), PI 178759 (*Yr59*), C591(*Yr67*), PI182103(*Yr79*) and Zhou 8425B (*YrZh84*). Ten seeds of each accession were sown per pot (9×9×9 cm). At the two-leaf stage, the seedlings (14 days after sowing) were inoculated with urediniospores of each race mixed with talc at an approximate ratio of 1:20 (urediniospores: talc). Inoculated plants were incubated in darkness in a dew chamber at 10 °C for 24 h and then transferred to a greenhouse at 17 ± 2 °C and photoperiod of 16-h light (10,000 lx) and 8-h darkness. Infection types (IT) were recorded using a 0–9 scale when the susceptible check (MX169) showed full sporulation (about 15 d after inoculation). Plants with ITs 0–3 were considered high resistant, 4–6 were moderate resistant, 7 were moderate susceptible and 8–9 were highly susceptible (Line and Qayoum 1992). In order to confirm and clarify ITs of the entries, all tests were repeated three times.

Field trials

The $F_{2:7}$ RILs and their parents were evaluated for APR to stripe rust in fields in Yangling of Shaanxi province and Tianshui of Gansu province in 2016 and 2017 and in Jiangyou of Sichuan province in 2017. Field trials were conducted in randomized complete blocks with two replicates at each location. Each plot consisted of a single row with 1.0 m length and 25 cm between rows. Approximately 10 seeds were sown in each row. Every twentieth row was planted with the highly susceptible control Xiaoyan 22. To increase inoculum, highly susceptible cultivar MX169 was planted to surround the experimental nursery. The field of Yangling was artificially inoculated with a mixture of races CYR32 and CYR33 in 2016 and CYR32, CYR33 and CYR34 in 2017 in late March after the emergence of flag leaves. The fields in Tianshui and Jiangyou were tested under natural infection because both locations are in the hotspot regions of stripe rust. Infection type (IT) based on the 0–9 scale (Line and Qayoum 1992) and disease severity (leaf areas infected, DS; modified Cobb scale, Peterson et al. 1948) of each parent or RIL was scored when the susceptible check MX169 had 80% or more DS values, 8–10 April at Jiangyou, 1–10 May at Yangling and 7–10 June at Tianshui.

Statistical analysis for the phenotypic data

The IT and DS data from each environment were used for analysis of variance (ANOVA) and subsequent QTL mapping. ANOVA and computation of correlation coefficients were performed using SAS V9.0 (SAS Institute Inc., Cary, NC). The contributions of lines (RILs) and environments were evaluated using PROC MIXED, where lines were treated as fixed effects, and environment, line × environment interaction and replicates nested in environments were all treated as random. The information in the ANOVA table was used to calculate broad-sense heritability (h_b^2) for stripe rust resistance: $h_b^2 = \sigma g^2/(\sigma g^2 + \sigma ge^2/r + \sigma \varepsilon^2/re)$, where σg^2, σge^2 and $\sigma \varepsilon^2$ were estimated for genotypic (line), genotype × environment interaction and residual error variances, respectively, and e and r were the numbers of environments and replicates per environment.

Genotyping of the mapping population

Genomic DNA was extracted from fresh F_6-derived wheat leaves of each line using the sodium dodecyl sulfonate (SDS) method (Song et al. 1994). All 151 lines and their parents were genotyped with 35K array by Capital Bio Corporation (Beijing, China; http://www.capitalbio.com) using the Affymetrix GeneTitan® system according to the procedure described by Affymetrix (Axiom® 2.0 Assay for 384 samples P/N 703154 Rev. 2). Allele calling was carried out using the Affymetrix proprietary software package Axiom Analysis Suite, following the Axiom® Best Practices Genotyping Workflow (http://media.affymetrix.com/support/downloads/manuals/axiom_genotyping_solution_analysis_guide.pdf). Markers with more than 20% missing data were removed, and markers were binned based on their pattern of segregation using the 'bin' function in QTL IciMapping V4.1 (Meng et al. 2015; Wang 2009). Following binning, linkage groups were ordered and then all markers which displayed a unique pattern of segregation and did not previously fall into a bin were iteratively added into each linkage group. Additionally, markers were tested for significant segregation distortion using a Chi-square test. Markers with the P value below 0.01 of the Chi-square test statistic were removed before creating the genetic map.

Combined bulked segregant analysis using the 660K SNP array

To obtain closer SNP markers and saturate the targeted QTL, bulk segregant analysis (BSA) was performed to identify markers polymorphic between the resistant parent Centrum

and susceptible parent MX169 and between the resistant DNA (R-bulk) and susceptible DNA (S-bulk) bulks. Equal amounts of DNA from 10 homozygous resistant (IT 1, DS ≤ 5) $F_{2:7}$ RILs were pooled to prepare the R-bulk and those of 10 homozygous susceptible (IT 9, DS ≥ 90) RILs in all environments pooled to prepare the S-bulk. The bulks, along with the parental DNA samples, were genotyped with the 660K SNP array. Polymorphic SNPs associated with resistance in BSA were localized to chromosomes based on the high-density 660K genetic maps (Cui et al. 2017).

Genetic linkage map construction and QTL analysis

The genotypic data for SNP markers were used to construct genetic linkage maps using software QTL IciMapping V4.1, and maps were made by MapChart V2.3 (Voorrips 2002). Map distances (in centimorgans, cM) were calculated based on the Kosambi mapping function (Kosambi 1943).

The walking speed chosen for QTL mapping was 1.0 cM, with $P = 0.001$ in stepwise regression. Based on 1000 permutations at a probability of 0.01, the phenotypic variance explained (PVE) by a single QTL was determined also using QTL IciMapping V4.1. In this study, the genotype of Centrum was defined as B, and that of MX169 as A. Thus, the allele from Centrum reduced stripe rust IT and DS when the additive effect was positive. QTL detected in at least two environments were included in the results.

Marker validation

KASP markers converted from SNP markers linked to *QYr-cen.nwafu-7BL* were validated in a subset of 120 wheat lines. The F_2 plants from Xinong 979 × Centrum selected with desirable agronomical traits in the nursery field of Tianshui were used for marker-assisted selection.

Results

Phenotypic evaluation

Disease severity (DS) of Centrum was consistently 1%, with IT = 1 when tested under field conditions, whereas MX169 displayed 100% severity with IT = 9 in all environments (Fig. 1). The IT and DS values of the 151 individual RILs were continuously distributed from 1 to 9, and 1.0–100.0%, indicating quantitative variation (Fig. 2). The broad-sense heritability of IT and DS was 0.94 and 0.93, respectively. ANOVA of IT and DS revealed significant differences ($P < 0.0001$) among RILs, environments, and line × environment interactions (Table 1). No significant variation was detected among replications within experiments, and lines were the main significant sources of

Fig. 1 Graphic display of stripe rust response of the parents MX169 and Centrum at the adult plant in the field

phenotypic variation based on the high heritability. The IT and DS had correlation 0.61–0.82 on IT and 0.63–0.81 on DS, 0.71–0.92 between IT and DS, $P < 0.001$ across environments (Table 2), indicating the IT and DS data were highly correlated at five environments. These results suggested that the expression of APR was consistent across environments and QTL controlling APR had a very large effect on reducing stripe rust severity.

Genetic linkage map

The parental lines and 151 RILs were genotyped with the 35K SNP array, 6099 of 35,143 SNP loci showed polymorphism between the parents. Among polymorphic SNPs, 437 were removed due to more than 10% missing data or severe segregation distortion ($P < 0.001$). The remaining 5662 SNPs fell into 1595 bins (4067 were redundant) that were used to construct genetic linkage map. The 1595 markers were distributed in 25 linkage groups spanning a total length 3066 cM. The A, B and D genomes included 635 (39.8%), 806 (50.5%) and 154 (9.7%) markers covering lengths of 1268.1, 1232.4 and 565.64 cM with average marker intervals of 2.0, 1.5 and 3.7 cM, respectively. Chromosomes 1A, 1B,1D, 2A, 2B, 3A, 3B, 4A, 4B, 4D, 5A,5B, 5D, 6A, 6D, 7A, 7B and 7D each had single linkage group; chromosomes 2D, 3D, 5B and 6B each had two linkage groups (Table S1).

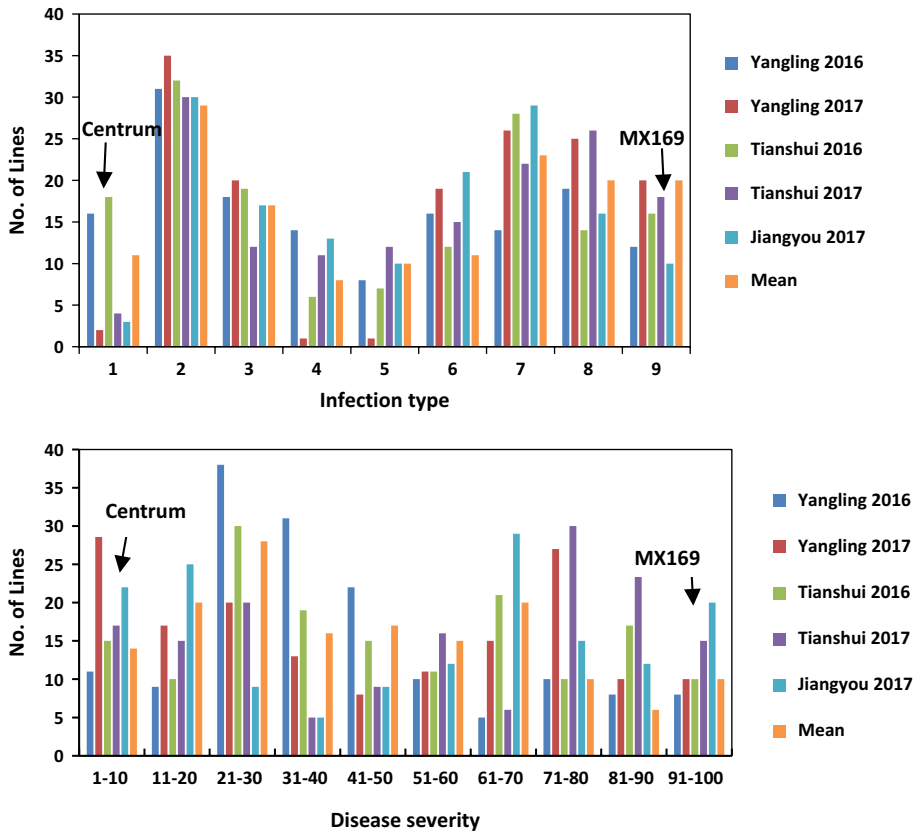


Fig. 2 Frequency distributions of MX169 × Centrum recombinant inbred lines for stripe rust infection type (IT) and disease severity (DS) in field trials at Yangling during 2015–2016 (Yangling 2016), 2016–2017 (Yangling 2017), at Tianshui 2015–2016 (Tianshui 2016) and 2016–2017 (Tianshui 2017), and at Jiangyou 2016–2017 (Jiangyou 2017)

Table 1 Analysis of variance and estimate of broad-sense heritability of infection type (IT) and disease severity (DS) among RILs from MX169 × Centrum tested in artificial and natural infection of *Puccinia striiformis* f. sp. tritici at Yangling, Tianshui and Jiangyou in 2016 and in 2017

Source of variation	IT				DS			
	df	Mean square	*F* value	*P*	*df*	Mean square	*F* value	*P*
Line	150	48.44	83.31	< 0.0001	150	4740.5	60.27	< 0.0001
Replicates/environment	5	5.64	9.71		5	2783.78	35.39	
Environments	4	230.84	397.06	< 0.0001	4	77,377.27	983.78	< 0.0001
Line × environments	600	3.11	5.35	< 0.0001	600	358.55	4.56	< 0.0001
Error	750	0.58			747	78.65		
h_b^2	0.94				0.93			

Table 2 Correlation coefficients (*r*) of infection type (IT) and disease severity (DS) of the RILS from MX169 × Centrum across five environments

Environments	Yangling 2016	Yangling 2017	Tianshui 2016	Tianshui 2017	Jiangyou 2017
Yangling 2016	1				
Yangling 2017	0.81 (0.81)[a]	1			
Tianshui 2016	0.85 (0.78)	0.79 (0.69)	1		
Tianshui 2017	0.63 (0.61)	0.65 (0.70)	0.69 (0.64)	1	
Jiangyou 2017	0.80 (0.78)	0.80 (0.82)	0.81 (0.71)	0.70 (0.74)	1

[a] *r* values based on IT data are given in parentheses. All *r* values were significant at $P = 0.001$

QTL of APR to stripe rust

The QTL were detected using IT and DS data from all environments considered to be stable. Stable QTL were identified on chromosomes (chr) 1AL, 4AL and 7BL and designated as *QYrcen.nwafu-1AL*, *QYrcen.nwafu-4AL* and *QYrcen.nwafu-7BL*, respectively. All detected QTL were derived from the resistant parent Centrum using ICIM analysis. *QYrcen.nwafu-7BL* explained 26.1–42.8% of IT and 19.3–33.4% of DS on phenotypic variation, effective

across all environments. This QTL was identified from Centrum and located within a 0.4-cM interval between markers *AX-94556751* and *AX-110366788* on the long arm of chromosome 7B. *QYrcen.nwafu-1AL* located in an interval of 5.0 cM between *AX-94488258* and *AX-94458040* on chromosome 1AL. It explained 10.7–15.9% of IT and 9.6–16.1% of DS of phenotypic variation in all five environments. *QYrcen.nwafu-4AL*, flanked by markers *AX-94695204* and *AX-94996273* on chromosome 4AL with a genetic distance of 1.82 cM, explained 10.3-15.9% on IT and 12.5–18.4% on DS of the phenotypic variation in all environments (Table 3, Fig. 3a).

Table 3 QTL detected in the MX169×Centrum RIL population with infection type (IT) and disease severity (DS) under artificial condition Yangling and natural condition Tianshui and Jiangyou in 2016 and in 2017

QTL	Environment	Position (cM)	Marker interval	Data	LOD[a]	ADD[b]	PVE[c]
QYrcen.nwafu-7BL	Yangling 2016	311	AX-94556751- AX-110366788	IT[d]	17.9	1.7	42.8
				DS[e]	11.7	10.1	30.9
	Yangling 2017			IT	12.7	1.2	33.3
				DS	17.0	16.1	33.4
	Tianshui 2016			IT	17.4	1.1	32.7
				DS	7.9	7.7	15.3
	Tianshui 2017			IT	9.2	0.8	26.1
				DS	10.2	11.1	19.3
	Jiangyou 2017			IT	8.5	1.4	28.9
				DS	10.7	12.6	23.4
	Mean			IT	12.8	0.7	36.4
				DS	9.7	7.9	27.2
QYrcen.nwafu-1AL	Yangling 2016	92	AX-94488258-AX-94458040	IT	5.9	0.6	10.7
				DS	8.0	0.6	9.6
	Yangling 2017			IT	6.0	5.1	12.9
				DS	8.9	5.1	16.1
	Tianshui 2016			IT	7.0	0.9	11.3
				DS	7.2	0.6	15.4
	Tianshui 2017			IT	6.1	3.5	15.3
				DS	6.9	5.9	14.3
	Jiangyou 2017			IT	6.9	0.5	15.9
				DS	8.1	0.9	11.2
	Mean			IT	7.3	1.2	15.4
				DS	8.0	3.9	14.2
QYrcen.nwafu-4AL	Yangling 2016	6	AX-94695204-AX-94996273	IT	5.1	4.7	11.4
				DS	6.9	5.7	18.4
	Yangling 2017			IT	5.2	5.9	15.9
				DS	6.8	5.4	15.6
	Tianshui 2016			IT	8.5	9.7	10.3
				DS	8.1	8.7	12.5
	Tianshui 2017			IT	4.8	3.8	14.4
				DS	7.4	10.3	12.9
	Jiangyou 2017			IT	8.3	10.9	11.8
				DS	8.9	11.2	10.6
	Mean			IT	9.9	0.6	12.6
				DS	7.5	6.7	12.6

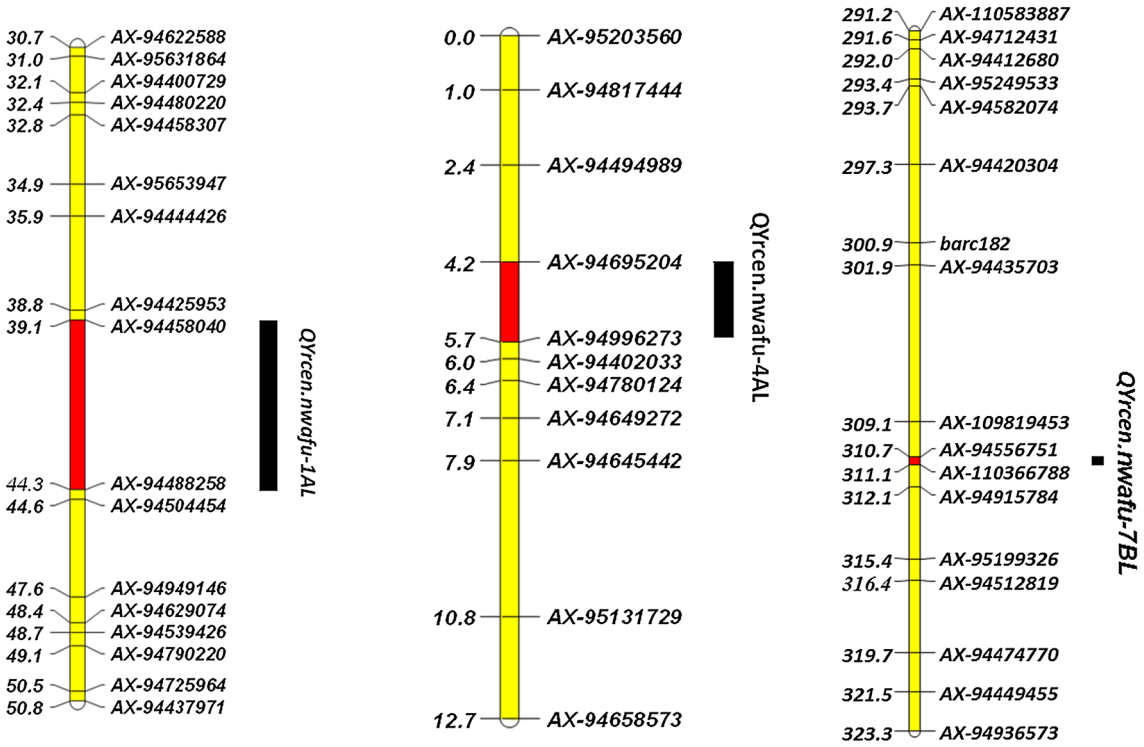
[a]LOD, logarithm of odds score

[b]Add, additive effect of resistance allele

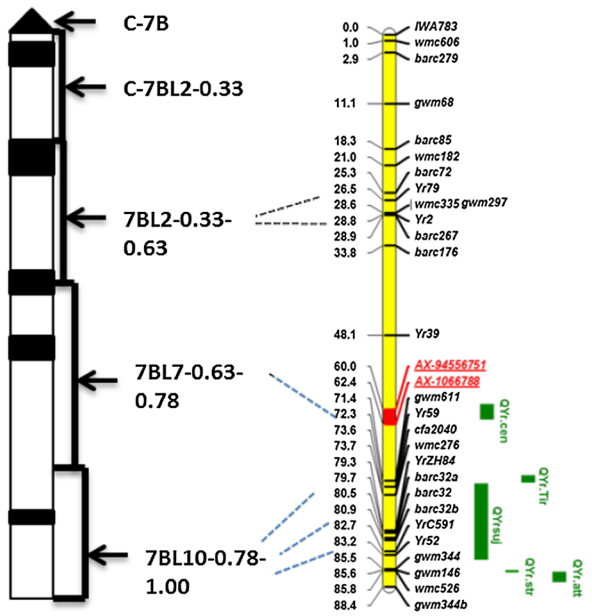
[c]PVE, percentage of the phenotypic variance explained by individual QTL

[d]IT, infection type

[e]DS, disease severity



a Genetic map of RILs from MX169 x Centrum



b Deletion Bin map of 7BL

c Consesus map of 7BL

Fig. 3 **a** Genetic map of RILs from the cross of MX169 and Centrum. **b** Deletion bin map of wheat chromosome 7BL. **c** Identified QTL (red bar with underlined font and red region on chromosome 7B) in this study and previously mapped Pst resistance QTLs (green bars) were positioned based on integrated genetic maps (Maccaferri et al. 2015; Fa Cui, personal communication) (color figure online)

Combined BSA with 660K SNP array

To saturate marker density in the major QTL region, we combined BSA with 660K SNP arrays. Approximately 4177 SNPs were polymorphic between the DNA bulks; 643, 431 and 500 of these were located on chromosomes 1A, 4A and 7B, respectively, whereas the others were distributed across other chromosomes (Fig. S1). The proportion of SNPs common between bulks and parents on chromosome 7B was the highest; the numbers of markers on chromosomes 1A and 4A were also relatively high (Fig. S1). These genomic regions were consistent with the results of genome-wide QTL mapping. Based on the physical positions of polymorphic SNP loci from the 660K SNP array on 7B, 36 chromosome-specific SNP, which covered a 9 Mb (from 709 to 718 Mb) genomic region encompassing the *QYrcen.nwafu-7BL* locus, were selected for conversion to KASP markers and then screened on the parents and bulks to confirm polymorphisms before being genotyped on the entire population; 6 successfully distinguished the contrasting parents and bulks and finally were used to construct the high-density map of 7B. The procedure of SNP conversion to KASP markers and selective KASP assays followed Wu et al. (2018), and the sequences of flanked markers of *QYrcen.nwafu-7BL* are shown in Table 4.

Additive interactions between detected resistance loci

To determine the additive effects of the QTL, the flanking markers for each QTL were used to determine the presence of parental alleles in the RIL. These genotypes were grouped into six groups based on the combination of potential QTL. The lines with three QTL had mean IT value of 1.5 and DS value of 14.3% across the six environments, which were similar to those of the resistant parent. Lines with two QTL had a mean IT value of 3.9–4.2 and DS value of 45.3–49.8%. RILs with only 1A or 4A QTL had mean IT of 6.2–7.0 and DS of 70.1–74.2%. RILs with 7B QTL had a mean IT of 4.6 and DS of 53.2%. Lines with no QTL had mean IT 8.5 and DS 90.1%, similar to the susceptible parent. Grouping was performed using the 'BIP' tool in IciMapping 4.1 software (Fig. 4).

Evaluation of KASP markers for *QYrcen.nwafu-7BL*

A set of 120 wheat genotypes including 2 lines with a stripe rust resistance gene or QTL on 7BL and 118 wheat cultivars and breeding lines were used together with Centrum and MX169 to evaluate the robustness of KASP markers linked with *QYrcen.nwafu-7BL* (Table S2). None of the genotypes had both flanking markers *AX-94556751* and *AX-110366788* from wheat 660K SNP array, indicating that these genotypes do not have the 7BL QTL and the combination of both markers could be used for marker-assisted selection of *QYrcen.nwafu-7BL*.

In order to validate the adaptability of KASP markers to selection for *QYrcen.nwafu-7BL*, the 211 $F_{2:3}$ population from the cross Xinong 979 × Centrum was genotyped and phenotyped. According to the presence/absence of homozygous flanking markers to surmise the target QTL, three lines with desirable agronomic traits were selected to carry positive alleles associated with resistance to stripe rust (IT 3, DS 40–50%).

Discussion

Stripe rust pathogen is able to produce new races through mutation, somatic recombination and sexual recombination which may lead to large-scale epidemics (Tang et al. 2018). Especially in recent years, the emerging and spread of *Yr26*-virulent races with broad virulence spectrum has become a main threat in China (Han et al. 2015; McIntosh et al. 2018). Centrum was chosen for this study because it has retained a high resistance level over many years (Wang et al. 2010). Using phenotypic data and genetic maps, the APR to stripe rust in Centrum was largely attributed to one major and two minor QTL with additive effects and was consistently identified by ICIM analysis across five environments.

Table 4 Primer sequences of KASP markers developed based on SNP markers with close linkages to stripe rust resistance quantitative trait loci

SNP name	QTL name	Primer sequence (5′–3′)
AX-94556751_A	*QYrcen.nwafu-7BL*	GAAGGTGACCAAGTTCATGCTttccaAgcattttgCcagtgaagG
AX-94556751_B	*QYrcen.nwafu-7BL*	GAAGGTCGGAGTCAACGGATTttccaAgcattttgCcagtgaagA
AX-94556751_C	*QYrcen.nwafu-7BL*	tgatatgaaAgCTtgcagatgtaaC
AX-110366788_A	*QYrcen.nwafu-7BL*	GAAGGTGACCAAGTTCATGCTaGgGtatgGtgtacGtgtgT
AX-110366788_B	*QYrcen.nwafu-7BL*	GAAGGTCGGAGTCAACGGATTaGgGtatgGtgtacGtgtgC
AX-110366788_C	*QYrcen.nwafu-7BL*	ATGcaTtGCagGTaGCCTaA

KASP markers: A, primers with the added FAM adapter; B, primers with the added HEX adapter; and C, common primers

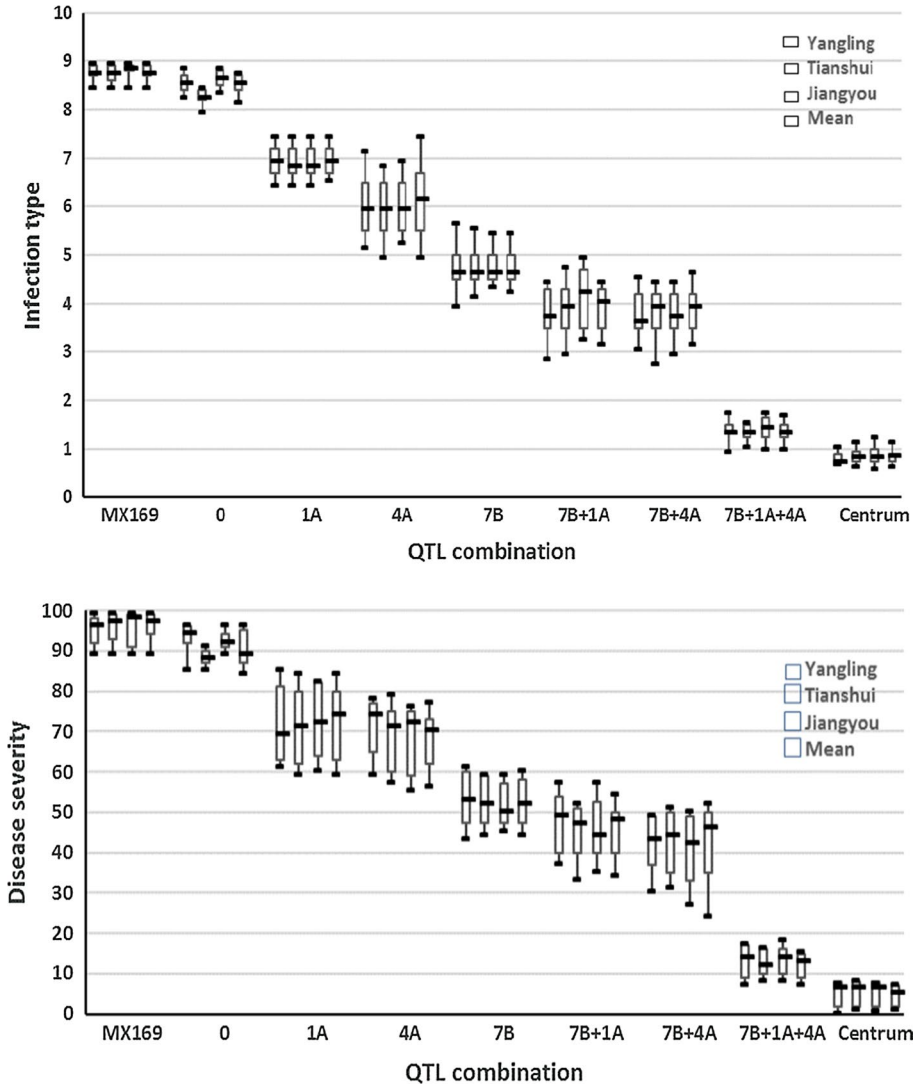


Fig. 4 Effects of QTL combinations on stripe rust scores illustrated by mean infection type and disease severity scores of RILs from the MX169 × Centrum population at combined environments. The box plots (the minimums and maximums are black dots, medians are crosses, the first quartile and the third are boxes) for infection type and disease severity associated with the identified QTL and their combination

Comparison of QTL with previously reported genes

QYrcen.nwafu-7BL

In this study, we mapped *QYrcen.nwafu-7BL* flanked by *AX-94556751* and *AX-110366788*, explaining 26.1–42.8% of IT and 19.3–33.4% of DS of the total phenotypic variation across all the environments. Previous studies reported some *Yr* genes on 7BL including *Yr2* (Lin et al. 2004), *Yr6* (Li and Niu 2007), *Yr39* (Lin and Chen 2007), *Yr52* (Ren et al. 2012a), *Yr59* (Zhou et al. 2014), *YrZH84* (Li et al. 2006), *Yr67* (Xu et al. 2014) and *Yr79* (Feng et al. 2018). Several QTL was also mapped to 7BL, including *QYr.nsw-7B* (Imtiaz et al. 2004), *QYr-7BL* in wheat variety strongfield (Singh et al. 2013), *QYr.caas-7B.1* in wheat cultivar Neixiang 188 (Yao et al. 2009), *QYr.csiro-7BL* (Rosewarne et al. 2008) *QYr.caas-7BL.1* and *QYr.caas-7BL.2* (Ren et al. 2012b) and two QTL from a genome-wide associate study (GWAS) (Bulli et al. 2016). To determine their relationships with *QYrcen.nwafu-7BL*, RIL-140 (*QYrcen.nwafu-7BL*), Kalyansona (*Yr2*), Heinese Kolben (*Yr6*), Alpowa (*Yr39*), PI 183527 (*Yr52*), PI178759 (*Yr59*), C591 (*Yr67*), PI182103 (*Yr79*) and Zhou 8425B (*YrZH84*) were tested at seedlings under the low temperature in the greenhouse with races CYR32, CYR33 and CYR34, and at adult plant stage in the fields with mixed races CYR32 and CYR34, with the exception that PI182103 (*Yr79*) was not tested at the adult plant stage. In the seedling test, all eight varieties were susceptible (ITs 7–9) to the three races, indicating they had APR except for C591 (resistant to CYR32, IT 2) and Zhou 8425B (resistant to CYR32 and CYR33, IT 1, 2, respectively). In the field tests, the nine varieties displayed different response: Kalyansona and Heinese Kolben were completely susceptible (IT = 8, DS = 90–100%). Alpowa has low infection type (IT = 2–3) and high disease severity (DS = 50–80%), and C591 and Zhou 8425B were susceptible (IT = 8, DS = 60–80%). PI 183527, PI 178759 and PI 182103 were resistant (IT = 2)

with short necrotic stripes and no uredinia. In contrast, RIL-140 that carried only *QYrcen.nwafu-7BL* was moderately resistant (IT = 4–5, DS = 40–50%; Table S4). The phenotypic data indicated that the 7BL QTL in Centrum is likely a different gene. KASP markers linked to *QYrcen.nwafu-7BL* were assayed on wheat varieties Alpowa, PI 183527, PI 178759 and Zhou 8425B, but these lines had only one of both KASP marker alleles in Centrum, and the KASP allele at *AX-94556751* in Centrum was unique (Table S5). In addition, twelve SSR markers *Xbarc176, Xgwm577, Xgwm611, Xgwm146, Xbarc182, cfa2040, Xbarc32, Xwmc557, Xgwm131, Xgwm43, Xbarc32 and Xwmc335* linked with previously reported genes/QTL on chromosome 7BL were evaluated on MX169, Centrum and the developed R and S bulks of RILs. All SSR markers were not polymorphic in MX169 and Centrum except *Xbarc182*. *QYrcen.nwafu-7BL* can be also distinguished from *Yr52* by the marker *Xbarc182*, which was reported to be proximal to the *Yr52* (Ren et al. 2012a), whereas it was mapped distal of *QYrcen.nwafu-7BL*. There were also several QTL located on 7BL. Ren et al. (2012b) identified two QTL flanked separately by *XwPt8106-Xbarc176* and *Xgwm577-XwPt-4300* on common wheat SHA3/CBRD. Imtiaz et al. (2004) identified a QTL *QYr.nsw-7B* closely linked to *Xgwm611* in Tiritea. Singh et al. (2013) identified a QTL linked to *Xgwm146* on 7B in durum wheat Strongfield. However, all of these markers were not polymorphic between MX169 and Centrum (Table S6). Feng et al. (2018) reported that the *Yr* genes on chromosome 7BL can be separated into two groups. The first group consisting of *Yr2*, *Yr6*, *Yr39*, and *Yr79* is clustered in a more proximal chromosome region between SSR markers *Xbarc72* and *Xgwm517*. The second group consisting of *Yr67* (*YrC591*), *YrZH84*, *Yr52* and *Yr59* are clustered in a more distal region between SSR markers *Xgwm577* and *Xwmc526*. But *QYrcen.nwafu-7BL* was not in both groups based on an integrated genetic map (Fig. 3c, Bulli et al. 2016). When compared to these genes in deletion bin map (Sourdille et al. 2004), the genes in first group were likely on 7BL2-0.33-0.63; the second ones were likely on 7BL10-0.78-1.00; however, *QYrcen.nwafu-7BL* was likely located on 7BL7-0.63-0.78 (Fig. 3b).

In addition, the origins of these wheat genotypes were considered when determining the gene relationships. Centrum is a winter wheat from Germany. However, PI 178759 with *Yr59* is a spring wheat from Iraq. Zhou 8425B is a Chinese winter wheat, and PI 183527 is a spring wheat from India. PI 182103 is a spring wheat originally from Pakistan. Wheat variety C591 is originally from India. Other wheat genotypes carrying minor-effect QTL also have origins different from Centrum. Therefore, *QYrcen.nwafu-7BL* is likely a novel QTL for stripe rust resistance. Allelic tests are needed to test the hypothesis and determine the genetic distances between the genes.

QYrcen.nwafu-1AL

QYrcen.nwafu-1AL from Centrum and flanked by *AX-94488258* and *AX-94458040* explained 4.6-6.1% of the phenotype variance across all the environments. To date, three QTL have been reported on chromosome 1AL. Hard red winter wheat TAM 112 (Basnet et al. 2014) was identified to have a minor QTL on chromosome 1AL spanning a genetic distance of 6 cM in the marker region of *Xwpt5167-Xwpt666616-Xwpt732616*. Ren et al. (2012b) identified a minor QTL contributed by Naxos, flanked by *Xwpt0164* and *Xbarc213*. Ramburan et al. (2004) identified an APR QTL in Kariega on chromosome 1A, designated as *QYr.sgi-1A*. These QTL were inconsistently detected across environments. As different kinds of flanking markers were used in these studies, the relationships among these QTL are still uncertain.

QYrcen.nwafu-4AL

QYrcen.nwafu-4AL was also from Centrum, and it was detected in all environments. The linked markers *AX-94695204*, *AX-94996273* and *AX-94402033* mapped the QTL to the long arm of chromosome 4A within 2 cM. So far, there are two permanently named genes for stripe rust reported on 4AL, namely *Yr51* and *Yr60*. *Yr51*, originated from an Australian wheat landrace AUS27858, confers all-stage resistance (Randhawa et al. 2013). *Yr60*, identified in cultivar Almop, also confers all-stage resistance (Herrera-Foessel et al. 2015). Thus, both were ASR genes. Additionally, *Yr60* co-segregates with SSR marker *Xwmc776* and *Yr51* flanked by marker Sun104, which were not detected in the present study. Based on pedigree origin, resistance type and linkage marker, *QYrXY.nwafu-4AL* appears to be different with both *Yr51* and *Yr60*. 12 QTL have been identified on chromosome 4AL. *QYr.sgi-4A.1*, identified as a major QTL in the wheat cultivar Kariega, was only 4.3 cM away from *Yr51* (Ramburan et al. 2004). QTL designated *QYrid.ui-4A* reported in the germplasm IDO444 was identified as HTAP resistance gene. It was also located on the region of *QYr.sgi-4A.1* (Chen et al. 2012). *QYrst.orr-4AL* detected in the cultivar Stephens was not stable in field test (Vazquez et al. 2012). *QYrns.orz-4AL* with a minor effect, detected in wheat line 'NSA-980995' (Limagrain, UK), has a minor effect to reduce stripe rust (Vazquez et al. 2015). *QYren.orz-4AL*, came from Einstein (Limagrain, UK), was also identified in just one environment with minor effect (Vazquez et al. 2015). Flanking markers of *QYrid.ui-4A*, *QYr.orr-4AL*, *QYrns.orz-4AL* and *QYren.orz-4AL* fall into this chromosomal bin 4AL4-0.80-1.00, which is the same as *Yr51* (Chen

et al. 2012; Vazquez et al. 2012, 2015). Therefore, *QYrXY.nwafu-4AL* was probably different with these QTL based on marker location. Further studies are required for concise location and confirmation of relationships with previously reported genes/QTL.

Marker-assisted selection for *QYrcen.nwafu-7BL*

QYrcen.nwafu-7BL was stably expressed across all environments with a large effect to reduce stripe rust. The large effect of this QTL makes it useful for breeding wheat cultivars with adequate resistance to stripe rust. In this study, wheat lines with *QYrcen.nwafu-7BL* were selected using KASP markers *AX-94556751* and *AX-110366788* in the population of Xinong 979 × Centrum. Xinong 979, developed by Professor Hui Wang (College of Agronomy, Northwest A&F University, China), has been grown in China over one million hectares, but this cultivar is susceptible to current predominant *Pst* races in China. Xinong 979 was chosen as a recipient parent to transfer stripe rust resistance QTL. Based on our results, the KASP markers linked to *QYrcen.nwafu-7BL* were reliable for MAS. These selected lines and KASP markers can be directly applied by breeders in wheat breeding programs.

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Author contribution statement JMM conducted the experiments, analyzed the data and wrote the manuscript. SH, QLW and JHW assisted in analyzing the data. QLW, QDZ and DJH identified the resistant parental line, made the cross and participated in field experiments. SH, MFD, SJL and SZY participated in field experiments and contributed to genotyping. DJ Han and ZS Kang conceived and directed the project and revised the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

Ethical standards I declare on behalf of my co-authors that the work described is original, previously unpublished research and not under consideration for publication elsewhere. The experiments in this study comply with the current laws of China.

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