Epistatic interaction effect between chromosome 1BL (Yr29) and a novel locus on 2AL facilitating resistance to stripe rust in Chinese wheat Changwu 357-9

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Received: 11 November 2021 / Accepted: 18 May 2022 / Published online: 20 June 2022
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Abstract

Key message Four stable QTL for adult plant resistance were identified in wheat line Changwu 357-9, including a new QTL on 2AL showing significant interaction with Yr29 to reduce stripe rust severity.

Abstract Stripe rust (yellow rust) is a serious disease of bread wheat (Triticum aestivum L.) worldwide. Genetic resistance is considered the most economical, effective and environmentally friendly method to control the disease and to minimize the use of fungicides. The current study focused on characterizing the components of stripe rust resistance and understanding the interactions in Changwu 357-9 (CW357-9)/Avocet S RIL population. A genetic linkage map constructed using a new GenoBaits Wheat 16K Panel and the 660K SNP array had 5104 polymorphic SNP markers spanning 3533.11 cM. Four stable QTL, consistently identified across five environments, were detected on chromosome arms 1BL, 2AL, 3DS, and 6BS in Changwu357-9. The most effective QTL QYrCW357-1BL was Yr29. The 6BS QTL was identified as Yr78, which has been combined with the 1BL QTL in many wheat cultivars and breeding lines. The novel QTL on 2AL with moderate effect showed a stable and significant epistatic interaction with Yr29. The QTL on 3DL should be same as QYrsn.nwafu-3DL and enriches the overall stripe rust resistance gene pool for breeding. Polymorphisms of flanking AQP markers AX-110020417 (for QYrCW357-1BL), AX-110974948 (for QYrCW357-2AL), AX-109466386 (for QYrCW357-3DL), and AX-109995005 (for QYrCW357-6BS) were evaluated in a diversity panel including 225 wheat cultivars and breeding lines. These results suggested that these high-throughput markers could be used to introduce QYrCW357-1BL, QYrCW357-2AL, QYrCW357-3DL, and QYrCW357-6BS into commercial wheat cultivars. Combinations of these genes with other APR QTL should lead to higher levels of stripe rust resistance along with the beneficial effects of multi-disease resistance gene Yr29 on improving resistance to other diseases.

Abbreviations

ANOVA Analysis of variance
APR Adult plant resistance
AQP Allele-specific quantitative PCR

Communicated by Reem Aboukhaddour.

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Introduction

Wheat (*Triticum aestivum* L.) is a major cereal crop consumed widely throughout the world, and production is often constrained by diseases and pests causing substantial yield losses. Stripe rust (yellow rust) caused by *Puccinia striiformis* Westend. *f*. sp. *tritici* Eriks. occurs in almost all wheat-producing regions. This disease causes significant economic losses in terms of reduced grain production and additional costs associated with disease management (Hovmøller et al. 2010; McIntosh et al. 1995). The most profitable and environmentally friendly strategy for farmers to control wheat rusts in both developing and developed countries is to grow genetically resistant wheat varieties (Krattinger et al. 2009).

The application of genomic tools and development of genotyping platforms for wheat improvement have lagged behind other cereals such as rice and maize for a long period largely due to its allohexaploid nature (AABBDD genome), huge genome size (~17 Gb) and highly repetitive elements (>80%). Recent advances in sequencing technology, however, radically changed the landscape and provided opportunities to overcome these difficulties. Over the past few years, great progress was made in developing the reference genome assembly of polyploid wheat and its progenitors, including *T. urartu* (AA genome) (Ling et al. 2018), *Aegilops tauschii* (DD genome) (Jia et al. 2013; Luo et al. 2013, 2017; Zhao et al. 2017), and wild emmer wheat (*T. turgidum* ssp. *dicoccoides*) (AABB genome) (Avni et al. 2017). Subsequent exon capture sequencing and resequencing technologies now accelerate marker development and establish haplotypes associated with resistant and susceptible lines (Cobo et al. 2018; Krasileva et al. 2017; Hao et al. 2020). Single nucleotide polymorphisms (SNPs) as the most abundant and important type of DNA variation were used to develop several high-throughput SNP genotyping platforms such as the 9K, 16K, 35K, 55K, 90K, and 660K high-density SNP chips (Cavanagh et al. 2013; Wang et al. 2014; Jia and Zhao 2016; Qiao et al. 2022). A target sequencing (GBS) system with capture-in-solution (liquid chip) technology known as the wheat 16K SNP array with the advantage of greater power for detection of genetic diversity by linkage disequilibrium decay analysis and genome-wide association studies than the one-amplicon-one-SNP system was developed by a multiple single nucleotide polymorphism (mSNP) approach (Guo et al. 2021).

More than 80 permanently named stripe rust resistance (*R*) genes (*Yr1–Yr83*) and many QTLs have been mapped on all 21 wheat chromosomes (Li et al. 2020; McIntosh et al. 2017). These genes/QTL can be categorized as all-stage resistance (ASR) and adult plant resistance (APR) or high-temperature adult plant resistance (HTAPR) based on the growth stage at which they can be detected. ASR is often race-specific, qualitatively inherited and controlled by a single gene, whereas APR and HTAPR are more quantitative with individual genes having minor effectiveness, but when combined there are additive effects such that agronomically acceptable levels of resistance are achieved. The added advantage of this type of resistance is durability that is based on the thesis that the genes conferring this type of resistance are non-specific or that any erosion of effectiveness will be a gradual process rather than a ‘boom and bust’ characteristic of widespread use of single ASR genes (Chen 2005, 2013; Lagudah 2011; Chen and Line 1995), most recently evidenced in China with the emergence of the now-prevalent *Yr26*-virulent race group, including CYR34. This race group not only overcame *Yr26* but also possessed a wide array of virulence for other well-known ASR genes (Wu et al. 2020, 2021; Huang et al. 2021). Therefore, identification and characterization of APR or HTAPR genes will enrich the overall stripe rust resistance gene pool and thereby accelerate development of wheat cultivars with durable, high-level resistance that can also be combined with effective all-stage resistance (Chen 2013; Liu et al. 2018).

Changwu 131 and Changwu 134 developed by Dr. Zengji Liang (Agricultural and rural Bureau of Changwu County, Xianyang, China) have been commercial wheat cultivars in China for many years. Changwu 357-9 (CW357-9), one of those prefixed as “Changwu” derivatives, has shown a high level of resistance to stripe rust since its release in 1989. However, little was known about the genetic basis of the resistance to stripe rust in this line. The objectives of this study were to: (1) investigate the genetic basis of stripe rust resistance in Changwu 357-9 using a recombinant inbred line (RIL) population tested in multiple environments, (2) identify and map QTL in CW357-9 with significant additive and epistatic effects on resistance to stripe rust using the
wheat 16K SNP array, and (3) develop and validate AQP markers closely linked to three identified QTL.

Materials and methods

Plant materials

The 167 $F_3$-derived $F_6$ recombinant inbred line (RIL) population was derived from a cross of susceptible Avocet S (AvS) and resistant Changwu 357-9 (CW357-9). A panel of 225 Chinese wheat cultivars/breeding lines and $Yr$ gene carriers were evaluated for response to stripe rust across multiple field environments, and the data were used to determine the prevalence of resistance genes/QTL identified in CW357-9 based on flanking SNP markers (Zhou et al. 2021). The wheat cultivars Avocet S (AvS), Mingxian 169 (MX169), and Xiaoyan 22 (XY22) were used as susceptible controls.

Greenhouse evaluation

In previous studies, CW357-9 was tested in seedling with $Pst$ races CYR23, CYR29, CYR31, CYR32, CYR33, V26/CH4 2, V26/Gui22, Su11-4, Su11-5, and Su11-7, and it was susceptible to the currently predominant races CYR32, CYR33, and V26/Gui22 (Wu et al. 2016). In the present study, we used additional three potentially predominant races PST-Lab.1, PST-Lab.2, and PST-V26 collected from field and separated in our laboratory to identify the type of inheritance in CW357-9. The testing regime for seedlings and determination of virulence/avirulence characteristics of PST-Lab.1, PST-Lab.2, and PST-V26 were previously reported in Huang et al. (2021). Infection types (ITs) of all plants were recorded 18 to 21 days after inoculation when the symptoms were fully developed on the susceptible control (AvS and MX169), and based on a 0–9 scale as previously described (Line and Qayoum 1992). The records of IT data were repeated three times to ensure reliability.

Field experiments

The 167 $F_6$ RILs and parents for disease assessment were grown in five different environments including Jiangyou (JY) in Sichuan province and Yangling (YL) in Shaanxi province during 2017–2018 and 2018–2019, and Tianshui (TS) in Gansu province in 2018–2019, designated as 2018JY, 2018YL, 2019YL, and 2019TS, respectively. Lines carrying $Yr29$ (Pavon 76, Attila, and Avocet-Yr29) were included as checks. The locations in Sichuan and southern Gansu experience cool, wet weather that is ideal for natural stripe rust survival and spread. At each location, 30 seeds of each line were planted as 1-m single rows and a 30-cm row spacing with a mixture of MX169 and XY22 as susceptible spreaders sown after every 20 rows. Trials at Yangling were inoculated with a mixture of $Pst$ races PST-Lab.1, PST-Lab.2 and PST-V26 suspended in a light oil (1:300) sprayed onto MX169 and XY22 at flag leaf emergence. Two replicates of the RILs were planted in each environment. Stripe rust assessments on adult plants were made 5–25 April at Jiangyou (JY), 3–17 May at Yangling (YL), and 10–15 June at Tianshui (TS), when AvS and XY22 displayed 80% severity or more. Infection types (IT) using a 0 (resistant) to 9 (susceptible) scale (Line and Qayoum 1992) and disease severities (DS) based on the modified Cobb Scale (Peterson et al. 1948) were used to evaluate the adult plant responses to stripe rust. IT and DS of homozygous (not segregated) lines were recorded as single values, and for heterozygous (segregated) lines IT and DS were recorded as two or more values, but later not used in QTL detection. Disease assessment was made at least twice, and the highest IT and DS for each line were used for phenotypic and QTL analyses.

Phenotypic analysis

ANOVA of the mean IT and DS for the RILs in each environment was undertaken to determine the effects of genotype ($G$), environment ($E$), and $G \times E$ interaction. Pearson’s correlation coefficient ($r$) analysis and ANOVA were conducted using the “AOV” function in QTL IciMapping software 4.1 with the default parameters (Meng et al. 2015). Broad-sense heritabilities ($h^2_b$) of resistance were based on the equation

$$h^2_b = \frac{\sigma^2_g}{\sigma^2_g + \sigma^2_e + \sigma^2_{ge} + \sigma^2_{re}},$$

where $\sigma^2_g$, $\sigma^2_e$, and $\sigma^2_{ge}$ represent the genotypic, environmental, and genetic by environmental variances, respectively, and $\sigma^2_{re}$ the error variance. In addition, the mean phenotypic values for all five environments were used to evaluate the genetic effects and find the best confidence region for each QTL (Mu et al. 2019).

SNP calling and clustering

Genomic DNA were extracted from pools of 10–15 plants from each parent and RIL at the jointing stage using the CTAB protocol (Clarke 2009), and DNA quality was assessed using a NanoDrop ND-1000 (Thermo Scientific, Wilmington, DE, USA). The RILs and parents were genotyped by a new wheat 16K SNP array from Mol Breeding (Shijiazhuang in Hebei province; http://www.molbreeding.com). The wheat 660K SNP array from CapitalBio Corporation (Beijing; http://www.capitalbio.com) was used to genotype the two parents. The distribution of SNPs from the 16K array is shown in Table S1. The procedure for marker clustering was described in Huang et al. (2021).
Linkage map construction and QTL analysis

A Chi-squared (χ2) test for goodness of fit to a 1:1 segregation ratio was performed for each SNP before processing by including those <10% missing values and major allele frequencies (MAF) ≤ 95%. One marker was selected from each co-segregating marker group using the “BIN” function in IciMapping V4.2 software. The selected markers were used to generate the genetic map using the “MAP” function in IciMapping V4.2 software and drawn in Mapchart V2.3 (Meng et al. 2015; Voorrips 2002). Combining the calculated value by 1000 permutations at a probability of 0.01, the logarithm of odds (LOD) score to determine significant QTL was 6.8 in all five environments. Recombination fractions were converted to cM using the Kosambi function (Kosambi 1943). The phenotypic data including IT, DS, and mean values from all environments were used to identify the QTL. Inclusive composite interval mapping with the additive tool (ICIM-ADD) in IciMapping V4.2 was performed to detect QTL. The phenotypic variances explained (PVE) by individual QTL and additive effects at the LOD peaks were also obtained. Due to low marker density, some QTL mapped in potentially large regions. To further narrow down the flanking intervals of target loci, significant SNPs from 660K SNP array were converted into allelic specific quantitative PCR (AQD) markers by JasonGen Biological Technology Co., Ltd (Beijing; http://www.jasongen.com) to genotype the RIL population.

Epistasis

Genotyped SNP markers associated with stripe rust resistance across five environments, were used for pairwise interaction analysis in Network version 2.1 (Yang et al. 2008). QTL effects were evaluated by the mixed linear model (MLM) approach. A ‘‘2D genome scan’’ option was used to map epistatic QTL with or without single-locus effects. additive × additive (A*A) epistatic effects of mapped using the ‘‘map epistasis’’ function. F values were used to control the error rate by permutation tests.

Results

Genetic linkage map

Of the 20,995 SNPs, 5104 (24.4%) showed polymorphism between the parents. By using the “BIN” function in QTL IciMapping 4.2, redundant polymorphic SNPs were removed showing >10% missing data and distorted segregation. Finally, 841 SNPs were chosen to construct the genetic linkage map; they were distributed in 22 linkage groups spanning 3533.11 cM. The A, B, and D genomes included 290 (34.48%), 374 (44.47%), and 177 (21.05%) markers covering lengths of 1268.96, 1356.53, and 1012.27 cM with average marker intervals of 4.38, 3.63, and 5.72 cM, respectively. Only chromosome 2D had two linkage groups; the other chromosomes were each represented by a single linkage group (Table S1).

Phenotypic evaluation

The CW357-9 seedlings were resistant (IT 3-4) to PST-Lab.1 and PST-Lab.2, but susceptible (IT 8-9) to PST-V26. CW357-9 was highly resistant (IT 1-2, DS ≤ 5%) at the adult plant stage in the field, whereas AvS was highly susceptible (IT 8-9) in all experiments. Based on these results, CW357-9 possessed both seedling resistance to two potentially predominant races PST-Lab.1 and PST-Lab.2 and APR in the field. In the seedling test, all the RILs and two parents were phenotyped by PST-Lab.1 to identified ASR. In the field experiments, both IT and DS data for RILs showed continuous distributions (Fig. 1), indicating that resistance in CW357-9 was quantitatively inherited. Pearson’s correlation coefficients of pairwise comparisons of IT and DS ranged from 0.60–0.85 and 0.58–0.88 (P < 0.001) (Table 1), respectively. Broad-sense heritabilities for both IT and DS were 0.92 (Table 2). P values in the ANOVA for IT and DS were highly significant (P < 0.0001) for RILs, environments, and line × environment interactions. Lack of significant variation between the replicates suggested that genetically controlled resistance was the main source of phenotypic variation in the RIL population (Table 2). These results indicated that the QTL conferring resistance was effective in the five environments.

Additive QTL for stripe rust resistance

Two QTL for seedling resistance to race PST-Lab.1 were detected on chromosomes arms 2BL and 4DL, but did not confer resistance in field, indicating that isolate PST-V26 was prevalent in field experiments. Both IT and DS data from the field environments were used to detect QTL at the adult plant stage. Four consistent QTL on chromosome arms 1BL, 2AL, 3DL, and 6BS, designated as QYrCW357-1BL, QYrCW357-2AL, QYrCW357-3DL, and QYrCW357-6BS, respectively, were identified in all five environments using the ICIM method in QTL IciMapping 4.2. All detected QTL were derived from the resistant parent CW357-9 (Table 3; Fig. 2a, b). QYrCW357-1BL with the largest effect was closely linked to markers AX-110020417 and 16k-16852 and explained 19.8–28.8% and 23.9–29.1% of variation in IT and DS, respectively (Table 3; Fig. 2a). QYrCW357-2AL located in a 3 cM interval spanned by markers 16k-4252 and 16k-4207 explained 4.0–10.0% and 5.8–12.9% of the phenotypic variation in IT and DS, respectively, across environments.
QYrCW357-6BS, linked to 16k-15955 and AX-109914318, explained 2.8–8.1% (IT) and 2.6–8.3% (DS) of the phenotypic variances, respectively. QTL on 3DL, flanked by 16k-9333 and 16k-9526, explained 2.8–8.1% and 9.1–16.4% of the variation in IT and DS, respectively. All QTL had additive effects (Table 3).

Epistatic interaction detected by QTL Network version 2.1

Significant epistatic interactions were detected across all field traits using QTL Network version 2.1. Two different intervals on 1BL and 2AL corresponding to the markers

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**Table 1** Correlation coefficients ($r$) for stripe rust infection type (IT) and disease severity (DS) in the AvS × CW357-9 RIL population tested in five field environments

| Environment | r value based on IT (DS) $^b$ |
|-------------|-------------------------------|
|             | 2018YL | 2018JY | 2019JY | 2019YL |
| 2018JY      | 0.70 (0.72) | – | – | – |
| 2019JY      | 0.85 (0.88) | 0.73 (0.80) | – | – |
| 2019Y1      | 0.71 (0.70) | 0.67 (0.63) | 0.69 (0.67) | – |
| 2019TS      | 0.61 (0.61) | 0.76 (0.75) | 0.60 (0.58) | 0.67 (0.63) |

$^a$YL, TS, and JY are abbreviations for Yangling, Tianshui, and Jiangyou, respectively

$^b$All $r$ values were significant at $P=0.001$

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**Table 2** Analysis of variance (ANOVA) for stripe rust infection type (IT) and disease severity (DS) data for the AvS × CW357-9 RIL population evaluated at Yangling and Jiangyou in 2017 and 2018 and Tianshui in 2018

| Source of variation | IT | | | | DS | | | |
|---------------------|---|---|---|---|---|---|---|---|
| df | Mean square | F value | P-value | df | Mean square | F value | P-value |
| RILs | 166 | 38.8 | 39.3 | <0.0001 | 166 | 6850.3 | 54.3 | <0.0001 |
| Replicates | 1 | 6.8 | 6.9 | | 1 | 1872.6 | 14.8 | |
| Environments | 4 | 217.8 | 220.9 | <0.0001 | 4 | 37,363.6 | 296.2 | <0.0001 |
| Line × environment | 660 | 3.1 | 3.1 | <0.0001 | 660 | 561.9 | 4.5 | <0.0001 |
| Error | 662 | 0.99 | | | 662 | 126.1 | | |
| h$^2b$ | 0.92 | | | | 0.92 | | | |
Table 3  Summary of stripe rust APR QTL detected in the A\textsc{v}S\times\textsc{cW}357-9 RIL population using IciMapping 4.1

| QTL           | Environment | Marker interval | Genetic position | LODb | PVEc | Addd |
|---------------|-------------|----------------|------------------|------|------|------|
| QYrCW357-JBL  | 2018YL-IT   | AX-110020417    | 16k-16852        | 152  | 10.5 | 25.7 |
|               | 2018YL-DS   | AX-110020417    | 16k-16852        | 153  | 10.6 | 25.8 |
|               | 2018Y-IT    | AX-110020417    | 16k-16852        | 153  | 12.1 | 28.8 |
|               | 2018Y-DS    | AX-110020417    | 16k-16852        | 153  | 10.2 | 24.9 |
|               | 2019YL-IT   | AX-110020417    | 16k-16852        | 153  | 9.8  | 24.3 |
|               | 2019YL-DS   | AX-110020417    | 16k-16852        | 153  | 12.4 | 29.1 |
|               | 2019Y-IT    | AX-110020417    | 16k-16852        | 153  | 8.0  | 19.8 |
|               | 2019Y-DS    | AX-110020417    | 16k-16852        | 153  | 9.8  | 23.9 |
|               | 2019TS-IT   | AX-110020417    | 16k-16852        | 153  | 9.8  | 24.5 |
|               | 2019TS-DS   | AX-110020417    | 16k-16852        | 153  | 10.9 | 26.4 |
| IT_mean       | AX-110020417| 16k-16852        | 153              | 11.4 | 27.5 | 1.0  |
| DS_mean       | AX-110020417| 16k-16852        | 153              | 11.8 | 27.9 | 13.7 |
| QYrCW357-2AL  | 2018YL-IT   | AX-110020417    | 16k-9514         | 22   | 2.5  | 3.3  |
|               | 2018YL-DS   | AX-110020417    | 16k-9514         | 22   | 3.6  | 5.4  |
|               | 2018Y-IT    | AX-110020417    | 16k-9514         | 22   | 4.0  | 4.2  |
|               | 2018Y-DS    | AX-110020417    | 16k-9514         | 22   | 3.7  | 4.6  |
|               | 2019YL-IT   | AX-110020417    | 16k-9514         | 22   | 6.0  | 8.1  |
|               | 2019YL-DS   | AX-110020417    | 16k-9514         | 22   | 6.1  | 8.3  |
|               | 2019Y-IT    | AX-110020417    | 16k-9514         | 22   | 4.2  | 4.6  |
|               | 2019Y-DS    | AX-110020417    | 16k-9514         | 22   | 3.7  | 3.8  |
|               | 2019TS-IT   | AX-110020417    | 16k-9514         | 22   | 4.2  | 3.2  |
|               | 2019TS-DS   | AX-110020417    | 16k-9514         | 22   | 4.9  | 5.4  |
| IT_mean       | AX-110020417| 16k-9514         | 22               | 4.7  | 3.8  |
| DS_mean       | AX-110020417| 16k-9514         | 22               | 4.4  | 3.9  |
| QYrCW357-3DL  | 2018YL-IT   | AX-110020417    | 16k-15955        | 51   | 9.2  | 11.6 |
|               | 2018YL-DS   | AX-110020417    | 16k-15955        | 51   | 8.9  | 11.0 |
|               | 2018Y-IT    | AX-110020417    | 16k-15955        | 51   | 9.2  | 11.6 |
|               | 2018Y-DS    | AX-110020417    | 16k-15955        | 51   | 8.9  | 11.0 |
|               | 2019YL-IT   | AX-110020417    | 16k-15955        | 51   | 7.0  | 7.9  |
|               | 2019YL-DS   | AX-110020417    | 16k-15955        | 51   | 4.4  | 3.4  |
|               | 2019Y-IT    | AX-110020417    | 16k-15955        | 51   | 7.7  | 9.2  |
|               | 2019Y-DS    | AX-110020417    | 16k-15955        | 51   | 10.2 | 10.4 |
| IT_mean       | AX-110020417| 16k-15955        | 51               | 10.0 | 9.3  |
| DS_mean       | AX-110020417| 16k-15955        | 51               | 10.6 | 11.7 |

*a* YL, TS, and JY are abbreviations for Yangling, Tianshui, and Jiangyou, respectively; Mean, average data from five environments

*b* LOD, logarithm of odds score

*c* PVE, percentage of phenotypic variance explained by individual QTL

*d* Add, additive effect of resistance allele. A negative value indicates that the resistance allele is from CW357-9

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AX-110020417-16k-16852 (QYrCW357-1BL or Yr29) and 16k-4252-AX-110974948 (QYrCW357-2AL) showed an estimated additive by additive interaction (A*A) effects of 0.24–0.34 and 3.24–4.50 in IT and DS, respectively (Table 4). The QTL on 1BL and 2AL showed a significant epistatic interaction for reduced stripe rust severity, whereas the presence of the 3DL and 6BS QTL were not detected for epistatic effects.

Table 4  Epistatic interaction between the locus on 1BL and 2AL identified by QTL Network version 2.1

| Traits     | QTL1a                   | Flanking interval       | QTL2b                   | Flanking interval       | A1*A2c effect |
|------------|-------------------------|-------------------------|-------------------------|-------------------------|---------------|
| 2018YL-IT  | QYrCW357-1BL (Yr29)     | AX-110020417-16k-16852  | QYrCW357-2AL            | 16k-4252-AX-110974948   | 0.26**        |
| 2018YL-DS  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   | 3.55**                  |
| 2018YJ-IT  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   | 0.24*         |
| 2018YJ-DS  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   | 3.24*         |
| 2019YL-IT  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   | 0.34**        |
| 2019YL-DS  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   | 3.98**        |
| 2019YJ-IT  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   | 0.34*         |
| 2019YJ-DS  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   | 4.50**        |
| 2019TS-IT  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   | 3.64*         |
| 2019TS-DS  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   | 0.25*         |
| IT_mean    | AX-110020417-16k-16852  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   | 4.08**        |
| DS_mean    | AX-110020417-16k-16852  | AX-110020417-16k-16852  | AX-110020417-16k-16852  | 16k-4252-AX-110974948   |               |

*P<0.005; **P<0.001

aFirst QTL and interval of a pair of interacting QTL

bSecond QTL and interval of a pair of interacting QTL

cA1*A2 is the additive × additive interaction or epistatic effect across different environments
QTL combinations and interaction

In order to investigate the effects of QTL combinations, RILs were classified into five genotypic groups based on all field tests (Table S2). RILs with all four QTLs \( QYrCW357-1BL, QYrCW357-2AL, QYrCW357-3DL, \) and \( QYrCW357-6BS \) were more resistant (lower IT and DS) than all others, displaying resistance similar to CW357-9 (Fig. 3a, b; Table S2). Among these genes, the combination of \( QYrCW357-1BL \) and \( QYrCW357-2AL \) showed the most significant effect in reducing stripe rust severity (Fig. 3c, d). RILs with none of the four stable QTLs had mean IT and DS values of 8.2 and 88.6%, respectively; RILs with only one QTL (1BL or 2AL) had mean values of 6.9 and 71.0% for the 1BL locus (similar to Avocet-\( Yr29 \) in Table S3) and 7.2 and 76.1% for 2AL, respectively (Fig. 3c, d). The group combining \( QYrCW357-1BL \) and \( QYrCW357-2AL \), with mean IT and DS of 4.6 and 36.0%, respectively, showed significant effect in reducing IT and DS (Fig. 3c–f).

Polymorphisms of AQP markers for stripe rust resistance in wheat genotypes

To determine the robustness of identified markers for stripe rust resistance in CW357-9, genotyping of the 225-accession panel for polymorphic AQP markers \( AX-110020417, AX-110974948, AX-109466386 \) and \( AX-109995005 \) represented for \( QYrCW357-1BL, QYrCW357-2AL, QYrCW357-3DL, \) and \( QYrCW357-6BS, \) respectively, suggested these markers were significantly associated with the DS scores of the wheat panel (Table S4). The genotyping assays generated three groups for different combination, enabled by testing the user-friendly markers for validation of both epistatic and additive effects (Fig. 4). Wheat lines with both \( QYrCW357-1BL \) (or \( Yr29 \)) and \( QYrCW357-2AL \) were on the average more resistant than lines without them, but some accessions containing the QTL were highly susceptible, indicating that the effects of the two QTL alone could be influenced by recombination between markers, genetic background, and environment. However, wheat lines combining all four loci had the lowest average DS in Yangling and Tianshui (Fig. 4). Sequences for the AQP markers \( AX-110020417, \)
AX-110974948, AX-109466386, and AX-109914318 are provided in Table S4.

**Discussion**

There is now strong evidence that pyramiding multiple partially effective resistance genes with additive or positive interaction in a single wheat cultivar can lead to more durable resistance than a single highly effective all-stage resistance gene (Huang et al. 2019). The data also suggest that the level of resistance required to protect yield potential and to prevent significant disease spread will require about four genes (Huang et al. 2019, 2021; Zeng et al. 2019). In addition, the numbers of epistatic interactions are frequently larger than the number of additive QTL, and the importance and number of epistatic interactions in terms of both the number of loci involved and effects may be greater than the additive QTL (Malmberg et al. 2005; Liu et al. 2022). CW357-9 is such a wheat genotype combining four partial APR QTL with both epistatic and additive effects and has maintained highly resistance for more than ten years in China.

**Four stable QTL for APR in CW357-9**

QYrCW357-1BL with the largest effect on APR, spanned by the markers AX-110020417 and 16k-16852, was mapped on chromosome arm 1BL (Table 3; Fig. 2a). Yr29, the only designated Yr gene on 1BL, closely linked to, and commonly identified by, marker csLV46G22 has been mapped in many studies (William et al. 2003; Cobo et al. 2018; Kolmer et al. 2012; Lan et al. 2014, 2015; Ponce-Molina et al. 2018; Rosewarne et al. 2012). This
multi-pathogen resistance allele \((Lr46/Yr29/Pm39/Sr58/Ltn2)\) was widely used in CIMMYT germplasm (Singh et al. 2013; Lan et al. 2015; Kolmer et al. 2015; Rosewarne et al. 2006, 2008). Genotyping of CW357-9 and \(Yr29\) carriers (Pavon 76, Attila, AVSYr29NIL) with the PCR makers \(AX-110020417\) and \(cslLV46G22\) showed that CW357-9 and \(Yr29\) shared an allele that differed from AvS. CW357-9 also showed leaf tip necrosis in our field (Fig. 1a). Thus, \(QYrCW357-9\) also likely to be \(Yr29\).

The second QTL \(QYrCW357-2AL\) conferring APR explained 4.0–12.9% of the phenotypic variation in IT and DS was flanked by markers \(I6k-4252\) and \(AX-110974948\) (Table 3; Fig. 2b). Many genes for APR were previously mapped on chromosome arm 2AL, including \(QYr.caas-2AL\) in Zhong 892 (Liu et al. 2015), \(QYr.qin.nwafu-2AL\) in QN142 (Zeng et al. 2019), and \(Yrxy2\) in Xiaoyan 54 (Zhou et al. 2011) closely linked to the markers \(IWB11764, AX-94895021,\) and \(Xqwm794\), respectively. Two additional QTL closely linked to markers \(IWA7339\) and \(IWA544\), respectively, were detected by genome-wide association analysis (GWAS) (Fig. 5a and b, Table S3). Based on the integrated genetic map (Bulli et al. 2016) (F. Cui, personal communication) and physical map in IWGSC RefSeq v1.0 (IWGSC 2018) (Fig. 5, Table S5), the QTL on 2AL was presented in the different location with previous QTL, indicating that \(QYrCW357-2AL\) appeared to be a new stripe rust resistance gene.

\(QYrCW357-3DL\) with minor effects was detected on 3DL (Table 3). In a previous study, \(QYrsn.nwafu-3DL\) in Shaannong 33 flanked by \(AX-109466386\) (180,398,197) and \(AX-110284733\) (414,838,337) was mapped in a similar physical region based on IWGSC RefSeq v1.0 (Huang et al. 2021; IWGSC 2018). Genotyping of \(QYrsn.nwafu-3DL\)-linked AQP marker \(AX-109466386\) showed that CW357-9 and Shaannong 33 had the same allele that differed from AvS. In addition, similar level of explanation was found for PVE. Based on the integrated map (Huang et al. 2021), these results indicated that \(QYrCW357-3DL\) and \(QYrsn.nwafu-3DL\) should be same and different from other QTL genes in the region.

Dong et al. (2017) mapped \(QYr.ucw-6B\) (\(Yr78\)) close to the marker \(IWA7257\). Several studies confirmed that \(QYrsn.nwafu-6BS\) in Shaannong 33, \(QYr.wgp-6B.1\) in Stephens, \(QYr.sun-6BS\) in Janz, and \(QYrMa.wgp-6BS\) in Madsen were \(Yr78\) (Huang et al. 2021; Dong et al. 2017; Liu et al. 2018). In our study, \(QYrCW357-6BS\), flanked by the markers \(I6k-15955\) and \(AX-109914318\), explained 6.6–11.7% of the phenotypic variation in IT and DS (Table 3). Genotyping result of CW357-9, Shaannong 33, Stephens, Madsen, and AvS with the marker \(IWA7257\) (\(Yr78\)) showed that CW357-9, Shaannong 33, Stephens, and Madsen presented different alleles with AvS, suggesting that \(QYrCW357-6BS\) likely to be same with \(Yr78\).

\(Yr29\) and \(Yr78\) are frequently combined in Chinese wheat germplasm

Combinations of \(QYrCW357-1BL\) (\(Yr29\)) on chromosome arm 1BL and \(QYrCW357-6BS\) (\(Yr78\)) on 6BS were detected in several Shaanxi wheat cultivars, including Qinnong 142 (Zeng et al. 2019), Shaannong 33 (Huang et al. 2021), and Xinong3517 (Huang unpublished data). These cultivars were highly resistant in the field at Shaanxi, Gansu, and Sichuan provinces, which are hotspot regions for over-season survival of \(Pst\) and have frequent occurrence of stripe rust. In this study, most carrier varieties with \(Yr29\) and \(Yr78\) were from Sichuan (12, 21.4%), Henan (9, 16.1%), and Shandong (8, 14.3%). Similar results reported in Huang et al. (2021) indicate varieties carrying \(Yr29\) and \(Yr78\) are common in these provinces.

Gene–gene interaction contributing to stripe rust resistance

A method of MAS based on QTLs with epistatic effects was proposed (Liu et al. 2003). Changwu 357–9 with desirable agronomic traits and a high level of durable resistance to stripe rust can be used as a parent for marker-assisted breeding for favorable epistatic interactions. Based on the epistatic analysis of field IT and DS, \(QYrCW357-1BL\) (or \(Yr29\)) and \(QYrCW357-2AL\) showed a significant interaction (Table 4, Fig. 2). \(Yr29\) is present in many wheat cultivars around the world and has remained effective for more than 60 years (Cobo et al. 2017). The novel locus on chromosome arm 2AL interacted with \(Yr29\) and other genes to confer an acceptable level of resistance to stripe rust in Chinese wheat Changwu 357–9 (Fig. 2c–f, Table S2). Based on genotyping of the flanking AQP markers, these results suggested that these markers can be used for developing new cultivars with high-level of durable resistance to stripe rust (Table S4). In addition, further exploration may provide insight for understanding the interactions observed between \(QYrCW357-1BL\) or \(Yr29\) and \(QYrCW357-2AL\) in this study as well as functional mechanisms that contribute to this resistance gene network.

Conclusion

\(CW357-9\) with durable resistance to stripe rust for more than a decade carries a 4-gene combination of APR genes, including \(Yr29\), \(Yr78\), \(QYrCW357-2AL\), and \(QYrCW357-3DL\) with additive and epistatic effects. The QTL on chromosome arms 2AL and 3DL were novel. The key points from
this work were: (1) \textit{QYrCW357-2AL} and \textit{QYrCW357-3DL} can be selected to enrich the overall stripe rust resistance gene pool for breeding; (2) the combination of \textit{Yr78} and \textit{Yr29} is frequent among wheat cultivars and breeding lines in China; and (3) the discovery of favorable epistatic interaction between \textit{Yr29} and \textit{QYrCW357-2AL}. Finally, CW357-9 not only represents a useful breeding parent but the markers developed here can be potentially used in MAS to develop new cultivars with potentially durable resistance. Field trials in disease nurseries will still be required to determine that lines with the selected resistance gene combination confer an acceptable level of protection from stripe rust.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00122-022-04133-9.

**Acknowledgements** The authors are grateful to Prof. R.A. McIntosh, Plant Breeding Institute, University of Sydney, for language editing and proofreading of the draft manuscript. This study was supported financially by National Key R&D Program of China (2021YFD1401000 and 2021YFD1200600), International Cooperation and Exchange of the National Natural Science Foundation of China (31961430191), National Science Foundation for Young Scientists in China (31901494 and 31901869), National Natural Science Foundation of China (31971890), China Postdoctoral Science Foundation funding (2021M702698), and National “111 plan” (BP0719026).

**Author contribution statement** SH designed and conducted the experiments, analyzed the data, and wrote the manuscript. YBZ, HR, XL, XZ, CLZ, QDZ, and QLW participated in creation of the genetic population and revised the manuscript. YBZ, HR, XL, XZ, CLZ, QDZ, and QLW participated in genotyping. RPS, SB, and ZSK participated in revision and assisted in analysis of the SNP array data. YBZ, HR, ZYZ, EL, XZ, QDZ, and QLW participated in analysis of the data, and wrote the manuscript. YBZ, HR, XL, XZ, CLZ, QDZ, and QLW contributed to genotyping. RPS, SB, and ZSK participated in revision and proofreading of the draft manuscript. This study was funded by the Department of Plant Protection and Exchange of the National Natural Science Foundation of China (31961430191), National Science Foundation for Young Scientists in China (31901494 and 31901869), National Natural Science Foundation of China (31971890), China Postdoctoral Science Foundation funding (2021M702698), and National “111 plan” (BP0719026).

**Funding** This study was funded by the Department of Plant Protection at the University of Northwest A&F.

**Data availability** All data, models, or code generated or used during the study are available from the corresponding author by request.

**Declarations**

**Conflict of interest** The authors declare that they have no conflict of interest.

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