QTL Mapping of Adult-Plant Resistance to Stripe Rust in Chinese Wheat Cultivar Chuanyu 16

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Abstract

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is a serious wheat fungal disease, causing significant annual yield losses worldwide. The Chinese wheat cultivar Chuanyu 16 has shown good adult-plant resistance (APR) to stripe rust in Sichuan province, a hotspot for stripe rust epidemics. Chuanyu 16 was crossed with Chuanyu 12 and Chuanmai 32. Two populations, each with 140 recombinant inbred lines (RILs), were developed by single-seed descent, and used for quantitative trait locus (QTL) mapping. Field trials were conducted in Chengdu and Yaan from 2005 to 2008, providing stripe rust reaction data for six environments. Seven hundred and thirty one simple sequence repeat (SSR) markers were screened for association with stripe rust reaction, initially through bulked segregant analysis (BSA). Three QTLs for stripe rust resistance derived from Chuanyu 16 were detected in the first cross. They were detected by inclusive composite interval mapping (ICIM) and designated *QYr.caas-1BL.1*, *QYr.caas-1BL.2* and *QYr.caas-2AS*. They explained 6.0 - 12.8%, 4.5 - 5.8% and 14.9 - 43.0%, respectively, of the phenotypic variance across environments. One digenic epistatic QTL between *QYr.caas-1BL.2* and *QYr.caas-2AS* explained 4.3 - 10.4% of the phenotypic variance. *QYr.caas-2AS* was also detected in Chuanmai 32/Chuanyu 16, explaining 27.9 - 57.2% of the phenotypic variance across six environments. This QTL showed a major effect against stripe rust in Chuanyu 16, and was located in a similar position to *Yr17*. Specific markers indicated the presence of a segment from chromosome 2N of *Triticum ventricosum* that carries *Yr17*. Despite the lack of evidence for *Yr17* in Chuanyu 16 based on pedigree, and inconsistencies in stripe rust response relative to a near-isogenic reference stock with the gene, we concluded that *QYr.caas-2AS* is *Yr17*. *QYr.caas-1BL.1* and *QYr.caas-1BL.2* showed minor effects for APR against stripe rust. *QYr.caas-1BL.1* is probably a new gene for APR to stripe rust.

Keywords: APR, Microsatellites, Quantitative trait locus, *Triticum aestivum*, Yellow rust

1. Introduction

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is a devastating wheat disease worldwide. Breeding and utilizing resistant wheat cultivars are the most economic and environmentally friendly way to control the disease (Line 2002; Chen 2005). Wheat rust resistance was conferred by race-specific major resistance or adult-plant resistance genes. The race-specific major gene resistance is usually effective at both the seedling and adult-plant stages, eliciting a hypersensitive response upon infection by a pathogen race possessing a corresponding virulence allele (McIntosh et al., 1995). When deployed in agriculture this type of resistance is overcome by virulent races. In contrast, adult-plant resistance, horizontal, slow-rusting or partial resistance is usually race non-specific, and expressed by increased latent period and reduced uredinial size, infection frequency and spore production (Caldwell 1968; Ohm and Shaner 1976; Parlevliet 1975). Wheat genotypes with this kind of resistance are usually susceptible at the seedling stage, and resistance develops as the plants approach the flowering stage and as temperatures increase. This kind of resistance is called adult-plant resistance (APR).

Several genetic analyses of APR show that resistance is conferred by the additive effects of a few genes (Singh and Rajaram 1994; Navabi et al., 2004; Singh et al., 2005). Epistatic effects of such genes have also been reported (Lin and Chen 2009; Lu et al., 2009). Field assessments at the adult plant stage in multiple environments are needed for genetic analysis of APR. To date, about 48 genes for stripe rust resistance are catalogued and 36 are temporarily designated. Among them, *Yr11-Yr14*, *Yr16*, *Yr18*, *Yr29*, *Yr30*, *Yr36*, *Yr39*, *Yr46* and *Yr48* are described as APR genes, but not all are race non-specific, whereas the others are race-specific major resistance genes (Chen 2005; McIntosh et al., 2010). About 77 QTLs for APR to stripe rust have been mapped on 17 of the 21 wheat chromosomes except for 1A, 1D, 3A and 7A (He et al. ,2011).

Sichuan province is a hotspot for stripe rust epidemics in China, and various new virulent races arose or emerged in this area. From previous reports (Wan et al., 2004, 2007), only *Yr5*, *Yr10*, *Yr15*, *Yr24* and *Yr26* confer resistance to the prevalent Chinese *Pst* race CYR 32. Cultivar Chuanyu 16 was released in 2002 with high resistance to stripe rust at the adult stage in the field. In the same year a widespread stripe rust epidemic affected about 6.6 million hectares of wheat, especially in Sichuan province. Most wheat cultivars with the widely used *Yr9* or Fan 6 resistance genes were affected by *Pst* races CYR 31 and CYR 32 (Wan et al., 2004). With the change in predominant races from CYR 30 to CYR 32 and CYR 33 over the past nine years, there was an increase in disease rating on cv. Chuanyu 16, but the increase was much less than on other genotypes with the so

called Fan 6 resistance. Cv. Chuanyu 16 has APR genes conferring moderate adult plant protection with stripe rust severity lower than 30% under average conditions and lower than 50% in severe epidemic conditions. With this level of resistance in combination with excellent agronomic traits, cv. Chuanyu 16 became a leading breeding parent in Sichuan. However, the chromosomal location and genetic effects of its APR genes remained unknown. The objective of this study was to identify the QTLs for APR to stripe rust in cv. Chuanyu 16 in a RIL population derived from a cross between cv. Chuanyu 16 and susceptible cultivar Chuanyu 12, and to validate the QTLs with a second RIL population derived from a cross between cv. Chuanmai 32 and cv. Chuanyu 16.

2. Materials and methods

2.1 Plant materials

Cv. Chuanyu 16, developed by the Chengdu Institute of Biology, Chinese Academy of Science, and released in Sichuan in 2002, is highly susceptible to *Pst* race CYR 32 at the seedling stage, and resistant to moderately resistant at the adult-plant stage, with stripe rust severity lower than 30% in normal epidemic years and lower than 50% in heavy epidemic years. Cv. Chuanyu 12, a 1B·1R line with *Yr9*, developed by the same institute and released in Sichuan in 1992, is highly susceptible to *Pst* races CYR 31 and CYR 32 at both the seedling and adult-plant stages, although it was originally resistant when released. Cv. Chuanmai 32, developed by the Crop Research Institute, Sichuan Academy of Agricultural Science and released in 2001, is moderately resistant to *Pst* races CYR 31 and CYR 32 at the adult plant stage, with stripe rust severity nearly 30%. One population of 140 F_7 RILs, derived from cv. Chuanyu 16/cv. Chuanyu 12, was used for QTL mapping, and a second population, also with 140 RILs, derived from cross cv. Chuanmai 32/cv. Chuanyu 16 was used for validating the QTLs and linked molecular markers.

2.2 Field trials and phenotypic characterization of stripe rust response

The two RIL populations were evaluated for stripe rust severity at sites near Chengdu in 2005, 2006, and 2007 and Yaan in 2006, 2007 and 2008 cropping seasons, providing data for six environments. Chengdu (103.85°E, 30.81°N) and Yaan (103.11°E, 29.95°N) are located about 150 Km apart in Sichuan. Chengdu is located in the central region of Sichuan basin where heavy stripe rust epidemics occurred every two or three years, while Yaan is in the southwestern region of Sichuan basin where heavy stripe rust epidemics occurred every year. The experimental plots were completely randomized with three replications in Chengdu 2005 and 2006, and two replications in Yaan 2006 and Chengdu 2007, and one replication in Yaan 2007 and 2008. Plots consisted of single rows 1.5 m in length and 30 cm between rows, with approximately 50 seeds sown in each row. The susceptible parent cv. Chuanyu 12 was included every tenth row as a susceptible check and as inoculum sources, and was also planted around the test area to ensure ample inoculum in spring.

Yaan is a hotspot for stripe rust epidemics. The field trials in the present work depended on natural epidemics at Yaan. In Chengdu, *Pst* race CYR 32 on seedlings of cv. Chuanyu 12 was introduced into the trial at the three-leaf stage in each season. Stripe rust severity after anthesis was recorded on line basis as visual estimates of percentage leaf area infected. Around April 15-20 in Chengdu and April 20-25 in Yaan, the stripe rust severity in the susceptible parent cv. Chuanyu 12 displayed between 85% and 100%. The data from readings at that time were the maximum disease severity (MDS).

2.3 Statistical analysis

The SAS statistical package (SAS Institute, Cary, NC, USA) was used to conduct an analysis of variance (ANOVA) for estimating genetic and environmental effects of lines, environments and line×environment interactions using data from Chengdu 2005, 2006 and 2007, and Yaan 2006 in which two or three replications were carried out in the field trials. The ANOVA results were used to estimate the heritability (h^2) calculated by the formula $h^2 = V_l/(V_l+V_{le}+V_e)$, where V_l, V_{le} and V_e are the variance component estimates of lines, line×environment interaction and environments (Basford et al. 2004, Yang. 2007), respectively. As replications were not the same in the field trial every year, the variance components (V_l, V_{le} and V_e) were estimated by REML model in SAS software. Phenotypic correlation coefficients among different environments for MDS were calculated on a mean basis using the Microsoft Excel analytical tool.

2.4 Molecular marker analysis

The CTAB method (Sharp et al., 1988) was used to extract genomic DNA from young leaves of the parents and F_7 RILs. SSR analysis, including PCR, polyacrylamide gel electrophoresis and gel staining, followed Li et al. (2006) and Bassam et al. (1991). Cv. Chuanyu 16, cv. Chuanyu 12 and two bulks were screened with 731 SSR markers, including 561 pairs of primers from the Beltsville Agriculture Research Center (BARC) (Song et al.,

2002), 114 pairs of primers from Gatersleben Wheat Microsatellite (GWM) (Röder et al., 1998), 38 pairs of primers from Wheat Microsatellite Consortium (WMC) (Gupta et al., 2003), 12 pairs of primers from the Clermont Ferrand D-genome (CFD) set (Guyomarc'h et al., 2002), 5 pairs of primers from the Clermont Ferrand A-genome (CFA) set (Sourdille et al., 2004) and *Xcewm32* (Zhu et al., 2010). Two markers linked with *Yr17*, VENTRIUP-LN2 and CAPS marker URIC-LN2-*Dpn*Ⅱ (Helguara et al., 2003), were also used.

2.5 Bulked segregant analysis

Based on averaged disease severities from six environments, five lines with the highest levels of resistance were selected to make a resistant bulk and five with the highest levels of susceptibility were used to make a susceptible bulk. After adjusting DNA concentrations, equal amounts of DNA from each line were mixed to make the respective bulks. SSRs were selected to genotype the 10 most resistant and 10 most susceptible lines, respectively, when the same patterns of SSR polymorphism were observed between the resistant and susceptible parents, and between the resistant and susceptible bulks. Those SSRs showing linkage with stripe rust reaction were used to genotype the entire population. Additional markers for enriching the chromosomal regions linked to resistance genes were selected from published wheat consensus maps (http://www.shigen.nig.ac.jp/wheat; http://wheat.pw.usda.gov; Somers et al. 2004) and tested for polymorphism between the parents and between bulks. Those showing polymorphism were also used to genotype the entire population for linkage analysis.

2.6 Map construction and QTL detection

QTL mapping was based on the averaged MDS in each environment, and also the averaged data across all environments. Software IciMapping 3.0 was employed for construction of a genetic linkage map (Wang et al 2010). Map distances between markers were calculated using the Kosambi (1944) mapping function. The positions of detected QTLs and digenic interactions between non-allelic QTLs were determined by inclusive composite interval mapping (ICIM) using IciMapping 3.0 (Li et al. 2007, 2008). A logarithm of odds (LOD) of 2.0 was set to declare significance of QTLs. Each QTL was represented by a 20-centimorgan (cM) interval with the local LOD maximum as central point. QTL with overlapping 20 cM intervals from different environments were considered to be the same. QTL effects were estimated as the proportion of phenotypic variance explained (PVE) by the QTL. The chromosomal assignments of the linkage group were based on published wheat maps (Somers et al. 2004), Graingenes (http://wheat.pw.usda.gov) and the Komugi integrated wheat consensus maps (http://www.shigen.nig.ac.jp/wheat).

2.7 Validation of QTLs and their linked molecular markers

The 33 markers linked to QTLs identified in the cv. Chuanyu 16/cv. Chuanyu 12 RIL population were used to screen the parents, the 10 most resistant and 10 most susceptible lines of the cv. Chuanmai 32/cv. Chuanyu 16 population, and 25 of them showing associations with stripe rust resistance were used to genotype the entire population, and to construct a framework map for QTL analysis in this population.

3. Results

3.1 Phenotypic analysis of MDS, and their correlations and heritabilities

In the cv. Chuanyu 16/cv. Chuanyu 12 RIL population, the MDS scores were significantly correlated across the six environments, with correlation coefficients ranging from 0.49 to 0.78 ($P < 0.0001$). The frequency distributions of MDS showed continuous distributions in the different environments (Fig. 1**)**. The mean MDS of cv. Chuanyu 16 and cv. Chuanyu 12 were 48% and 99%, 10% and 77%, 20% and 91% in Chengdu 2005, 2006 and 2007, respectively, and 20% and 98%, 16% and 100%, and 14% and 89% in Yaan 2006, 2007 and 2008, respectively. The averaged MDS of the 140 RILs across all six environments was 54.0%, ranging from 0.0 to 100.0%. The heritability of MDS was 0.68 based on disease severity averaged from four environments, viz. Chengdu 2005, 2006, 2007 and Yaan 2006. The ANOVA confirmed significant variance ($P < 0.0001$) among RILs in the population (Table 1).

In cv.Chuanmai 32/cv. Chuanyu 16, MDS scores were significantly correlated across the six environments, with correlation coefficients ranging from 0.47 to 0.80 ($P < 0.0001$). The frequency distributions of stripe rust MDS showed continuous distributions over the different environments (Fig. 2). The mean MDS of cv. Chuanmai 32 and cv. Chuanyu 16 were 26% and 48%, 20% and 10%, 38% and 20% in Chengdu 2005, 2006 and 2007, respectively, and 14% and 20%, 10% and 16.0%, 15% and 14% in Yaan 2006, 2007 and 2008, respectively. The averaged MDS of the 140 RILs across six environments was 30.0%, ranging from 0.9 to 83.3%. The heritability of MDS was 0.76 based on the disease severity averaged from four environments, viz. Chengdu 2005, 2006, 2007 and Yaan 2006. ANOVA confirmed significant variance ($P < 0.0001$) among RILs in the population

(Table 1).

3.2 The overall SSR polymorphisms between Chuanyu 16 and Chuanyu 12

Among 731 SSR markers tested in Chuanyu 16 /Chuanyu 12 population, 355 SSRs showed polymorphisms between two parents; 217 SSRs displayed polymorphisms between the resistant and susceptible bulks; of them, 73 SSRs were used to genotype the 10 most resistant and 10 most susceptible lines; and finally 58 SSRs were used to genotype 140 RILs of cv. Chuanyu 16/cv. Chuanyu 12 population. The genotyping results of the SSR markers, VENTRIUP-LN2 and a CAPS marker URIC-LN2-*Dpn*Ⅱ were used to construct linkage map for QTL detection.

3.3 QTLs for APR to stripe rust in the Chuanyu 16/Chuanyu 12 RIL population

Based on the MDS data for the cv. Chuanyu 16/cv. Chuanyu 12 population, three QTLs for stripe rust resistance were detected by ICIM across six environments (Table 2; Fig. 3). According to wheat consensus maps (http://www.shigen.nig.ac.jp/wheat; http://wheat.pw.usda.gov; 42), two QTLs were located on the long arm of chromosome 1B, and one was located on the short arm of chromosome 2A. They were designated *QYr.caas-1BL.1*, *QYr.caas-1BL.2* and *QYr.caas-2AS*, and all came from the resistant parent Chuanyu 16.

The most consistent locus with the largest effect found in all environments was *QYr.caas-2AS*, located on the short arm of chromosome 2A. It was flanked by *Xcfd36* and *Xwmc598*, and the peak LOD score was close to *Xgwm497* and URIC-LN2-*Dpn*Ⅱ. This QTL explained 18.1%, 37.3%, 27.8%, 43.0%, 14.9% and 24.7% of the phenotypic variance in Chengdu 2005, 2006, 2007 and Yaan 2006, 2007, 2008, with additive effects of 10.8, 15.4, 15.4, 22.4, 14.3 and 15.8, respectively (Table 2 and Fig. 3B). The phenotypic variance was as high as 32.2% for QTL computed by averaged MDS across all environments. The second QTL, *QYr.caas-1BL.1,* located on chromosome 1BL, and flanked by the SSR loci *Xbarc61* and *Xwmc134*, explained 6.0% and 12.8% of the phenotypic variance in Chengdu 2006 and Yaan 2007, with additive effects of 6.2 and 13.3, respectively, and the phenotypic variance explained for the averaged MDS across all environments was 11.2% (Table 2 and Fig. 3A). The third QTL, *QYr.caas-1BL.2*, also on chromosome 1BL, was detected in the marker interval *Xgwm818* – *Xgwm259*. This QTL explained 5.5%, 4.5% and 5.1% of the phenotypic variance in Chengdu 2005, Chengdu 2007 and Yaan 2007, with additive effects of 6.0, 6.3 and 8.5, respectively, and the phenotypic variance explained by the QTL for the averaged MDS across all environments was 5.8% (Table 2 and Fig. 3A).

3.4 Validation of QTLs in the Chuanmai 32/Chuanyu 16 RIL population

Based on the MDS and molecular marker data, *QYr.caas-2AS* was also detected in the cv. Chuanmai 32/cv. Chuanyu 16 RIL population with significant effects across all environments (Table 2). The QTL was flanked by *Xwmc407* and VENTRIUP-LN2, and explained 35.5%, 57.2%, 49.8%, 45.9%, 29.0%, 27.9% and 56.9% of the phenotypic variance in Chengdu 2005, 2006, 2007, Yaan 2006, 2007, 2008 and in the averaged MDS, with additive effects of 14.1, 16.2, 18.8, 19.3, 11.2, 11.1 and 15.1, respectively. QTLs *QYr.caas-1BL.1* and *QYr.caas-1BL.2* were not found in this population, possibly because there was no allelic variation between the parents at these loci (Fig. 3C).

3.5 Epistatic effects between QTLs

Among the three QTLs in cv. Chuanyu 16, an epistatic interaction between *QYr.caas-1BL.2* and *QYr.caas-2AS* was detected in all environments and averaged MDS of all environments, explaining from 4.3 to 10.4% of the phenotypic variance (Table 3).

4. Discussion

Cv. Chuanyu 16 is susceptible to *Pst* race CYR 32 at the seedling stage and resistant or moderately resistant at the adult stage, with a typical of APR to stripe rust (Caldwell 1968; Ohm and Shaner 1976; Parlevliet 1975). *QYr.caas-1BL.1*, *QYr.caas-1BL.2* and *QYr.caas-2AS* were detected in the cv. Chuanyu 16/cv. Chuanyu 12 RIL population, and *QYr.caas-2AS* was validated in the cv. Chuanmai 32/cv. Chuanyu 16 population. The present QTL analysis determined the locations and effects of APR genes for stripe rust resistance in cv. Chuanyu 16.

Christiansen et al. (2006) located *QTL.2AS* for stripe rust resistance on the short arm of chromosome 2A. This gene, located 2 cM from the SSR locus *Xwmc 407* in progenies of Kris/Wasmo and Kris/Deben, was assumed to be *Yr17*. Chhuneja et al. (2008) detected *QYrtm.pau-2A* in *T. monococcum* acc. pau14087 in a 3.6-cM interval of *Xwmc407* and *Xwmc170* on chromosome 2A. Dedryvere et al. (2009) assumed *QYr.inra-2AS.2* to be the same as *Yr17* in a Renan/Revital population. *Yr17* is in a *Lr37-Yr17-Sr38* cluster, located within a segment of the short arm of chromosome 2N of *Triticum ventricosum*. This segment was translocated to the short arm of bread wheat chromosome 2A, and introgressed into the winter bread wheat 'VPM1' (Maia 1967; Bariana and McIntosh 1993;

McIntosh et al., 1995). Two markers, URIC-LN2-*Dpn*Ⅱ and VENTRIUP-LN2, were developed to characterize the 2NS/2AS chromosome segment (Helguera et al., 2003). In the present study, the 2NS-specific PCR products of VENTRIUP-LN2 (259 bp) and URIC-LN2 (285 bp) were amplified in cv. Chuanyu 16, and both markers were closely linked in coupling with *QYr.caas-2AS* in the cv. Chuanyu 16/cv. Chuanyu 12 and cv. Chuanmai 32/cv. Chuanyu 16 populations. This indicated that *QYr.caas-2AS* was located in a 2NS segment, and that it was likely to be *Yr17*. However, this deduction is difficult to reconcile in relation to the response of a *Yr17*/6*Avocet S near-isogenic line (NIL) used as a reference for *Yr17*. According to field tests in Chengdu and Yaan from 2001 to 2010, the *Yr17*/6*Avocet S NIL was resistant in all years except 2002 and 2007. cv. Chuanyu 16 and *Yr17*/6*Avocet S NIL were scored susceptible to CYR 32 at seedling tests, but the responses of lines with *Yr17* are known to be environmentally sensitive even in greenhouse tests (Wellings personal communication). At the adult-plant stage in the field, the infection type of *Yr17*/6*Avocet S NIL was 0; and the stripe rust severities were lower than 5%, whereas the corresponding scores for cv. Chuanyu 16 were infection type 4 (0 - 4 scale) and disease severities was nearly 30% in 2009 and 2010. It is now known that *Yr17*/6*Avocet S NIL along with some other Avocet S NILs carry *Yr18* in addition to the designated genes. Thus it is possible that the lower response of *Yr17*/6*Avocet S NIL compared with cv. Chuanyu 16 was due to the presence of *Yr18* in combination with *Yr17*. cv. Chuanyu 16 was derived from the cross 30020/Miannong 4//Jinmai 30; cv. Miannong 4 and cv. Jinmai 30 are cultivars susceptible to *Pst* races CYR 31, CYR 32 and CYR 33. The other parent, 30020, a breeding line at the Chengdu Institute of Biology, was probably the source of the resistance to stripe rust in cv. Chuanyu 16. This line has a complicated background, being derived from Kavkaz, Fan 6, Fan 7, NPFP, Aurora and a hexaploid triticale, but VPM1 or a derivative is not known to be involved. An alternative hypothesis that a 2N segment in cv. Chuanyu 16 carries a gene different from *Yr17* or carries a wheat gene completely linked in coupling with a 2N segment appears highly unlikely.

Although both *QYr.caas-1BL.1* and *QYr.caas-1BL.2* were mapped on 1BL, they were located to different marker intervals of *Xbarc61* - *Xwmc134* and *Xgwm818* - *Xgwm259*, respectively. According to the wheat composite map 2004-1B (http://wheat.pw.usda.gov), the distance between *Xbarc61* and *Xgwm259* is 31 cM, and that between *Xwmc134* and *Xgwm259* is 47 cM. In addition, the two QTLs were not overlapping, thus *QYr.caas-1BL.1* and *QYr.caas-1BL.2* were considered to be different. To date, 11 race-specific stripe rust resistance genes, viz. *Yr3* (first described in Lupton and Macer 1962), *Yr9* (Macer 1975), *Yr10* (Macer 1975), *Yr15* (Gerechter-Amitai et al., 1989), *Yr21* (Chen et al., 1995), *Yr24* (McIntosh et al., 1998), *Yr26* (Ma et al., 2001), *YrCH42* (Li et al., 2006), *YrH52* (Peng et al., 2000), *Yrchk* (Fanghui Liu et al., 2007) and *Yrexp1* (Lin and Chen 2008) were located on chromosome 1B. The two QTLs found in the present study are not likely to be the same as any of these genes. Four of five previously reported QTLs for stripe rust APR on 1B, *QYr.cimmyt-1BL* (William et al., 2006), *QYr.csiro-1BL* (Rosewarne et al., 2008), *QPst.jic-1B* (Melichar et al., 2008) and *QYr.saas-1BL* (Zhu et al., 2010), could be *Yr29* (summarized in Table 4). This gene, closely linked to SSR locus *Xgwm259*, has a relatively large effect on stripe rust response (William et al., 2003; Singh et al., 1998) and co-segregates with *csLV46* (personal communication with Dr. Evans Lagudah). *QYrex.wgp-1BL,* flanked by *Xwmc631* and *Xgwm268* in Express, was located at a different position from *Yr29* on 1BL, and accounted for 12.4 – 15.9% of the phenotypic variance (Lin and Chen 2009). *QYr.caas-1BL.1* in the present study was flanked by markers *Xbarc61* and *Xwmc134*. The distance between *Xwmc134* and *Xgwm259* is about 47 cM, and that between *Xwmc134* and *Xwmc631* is about 10 cM (http://wheat.pw.usda.gov; Somers et al. 2004). This indicates that *QYr.caas-1BL.1* is not only different from *Yr29*, but is also different from *QYrex.wgp-1BL*. It could be a new QTL for APR to stripe rust. *QYr.caas-1BL.2* found in the present study was flanked by *Xgwm818* and *Xgwm259*, in a similar location to *Yr29* and the four QTLs previously reported. However, the *Yr29*-specific band from *csLV46* was not amplified in cv. Chuanyu 16. In addition, *QYr.caas-1BL.2* confers a much lower level of resistance compared to that reported for *Yr29.*

5. Conclusion

APR to stripe rust in cv. Chuanyu 16 were conferred by three QTLs designated *QYr.caas-1BL.1*, *QYr.caas-1BL.2* and *QYr.caas-2AS. QYr.caas-2AS* with a major effect on APR was located in a similar position to *Yr17*, and since it was associated with markers specific for a 2NS chromosome introgression, we suggest it is *Yr17* despite inconsistencies in pedigree and stripe rust response data. *QYr.caas-1BL.1* and *QYr.caas-1BL.2* showed minor effects on stripe rust response. *QYr.caas-1BL.1* was likely to be a new gene; *QYr.caas-1BL.2* could be different from *Yr29* although it mapped to a similar position.

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Table 1. Analysis of variance of maximum disease severities (MDS) for stripe rust on RILs derived from crosses cv. Chuanyu 16/ cv. Chuanyu 12 and cv. Chuanmai 32/cv. Chuanyu 16

Population	Source of variation	*df*	Sum of squares	Mean square	*F* value
cv. Chuanyu 16/ cv. Chuanyu 12	Block	6	72640.5	12106.8	71.5**
	Environments	3	152285.8	50761.9	299.7**
	Lines	139	863262.8	6210.5	36.7**
	Line×environment	417	238465.0	571.9	3.4**
	Error	833	141114.1	169.4	
	Corrected total	1398	1473479.0		
cv. Chuanmai 32/ cv. Chuanyu 16	Block	6	60291.5	10048.6	64.7**
	Environments	3	98569.8	32856.6	211.6**
	Lines	139	683689.1	4918.6	31.7**
	Line×environment	417	150683.0	361.4	2.3**
	Error	834	129479.7	155.3	
	Corrected total	1399	1120971.0		

** Significance at $P < 0.0001$

Table 2. QTLs for APR To stripe rust detected in two RIL populations derived from crosses cv. Chuanyu 16/ cv. Chuanyu 12 and cv. Chuanmai 32/ cv. Chuanyu 16

Population	Location and year	QTL[a]	Marker interval	AE[b]	LOD[c]	PVE (%)[d]	Total PVE[e] (%)
cv. Chuanyu 16/ cv. Chuanyu 12	Chengdu 2005	*QYr.caas-1BL.2*	*Xgwm818-Xgwm259*	6	2.1	5.5	23.6
		QYr.caas-2AS	*Xcfd036- Xwmc598*	10.8	6.1	18.1	
	Chengdu 2006	*QYr.caas-1BL.1*	*Xbarc61-Xwmc134*	6.2	2.3	6.0	43.3
		QYr.caas-2AS	*Xcfd036- Xwmc598*	15.4	13.8	37.3	
	Yaan 2006	*QYr.caas-2AS*	*Xcfd036- Xwmc598*	22.4	16.1	43.0	43.0
	Chengdu 2007	*QYr.caas-1BL.2*	*Xgwm818-Xgwm259*	6.3	2.2	4.5	32.3
		QYr.caas-2AS	*Xcfd036- Xwmc598*	15.4	10.8	27.8	
	Yaan 2007	*QYr.caas-1BL.1*	*Xbarc61-Xwmc134*	13.3	3.3	12.8	32.8
		QYr.caas-1BL.2	*Xgwm818-Xgwm259*	8.5	2.1	5.1	
		QYr.caas-2AS	*Xcfd036- Xwmc598*	14.3	5.4	14.9	
	Yaan 2008	*QYr.caas-2AS*	*Xcfd036- Xwmc598*	15.8	8.6	24.7	24.7
	Average	*QYr.caas-1BL.1*	*Xbarc61-Xwmc134*	8.6	4.0	11.2	49.2
		QYr.caas-1BL.2	*Xgwm818-Xgwm259*	6.3	3.1	5.8	
		QYr.caas-2AS	*Xcfd036- Xwmc598*	14.6	14.4	32.2	
cv. Chuanmai 32/ cv. Chuanyu 16	Chengdu 2005	*QYr.caas-2AS*	*Xwmc382*-VENTRIUP-LN2	-14.1	13.0	35.5	35.5
	Chengdu 2006	*QYr.caas-2AS*	*Xwmc382*-VENTRIUP-LN2	-16.2	25.5	57.2	57.2
	Yaan 2006	*QYr.caas-2AS*	*Xwmc382*-VENTRIUP-LN2	-19.3	18.1	45.9	45.9
	Chengdu 2007	*QYr.caas-2AS*	*Xwmc382* VENTRIUP-LN2	-18.8	20.0	49.8	49.8
	Yaan 2007	*QYr.caas-2AS*	*Xwmc382*-VENTRIUP-LN2	-11.2	10.0	29.0	29.0
	Yaan 2008	*QYr.caas-2AS*	*Xwmc382*-VENTRIUP-LN2	-11.1	10.0	27.9	27.9
	Average	*QYr.caas-2AS*	*Xwmc382*-VENTRIUP-LN2	-15.1	24.9	56.9	56.9

[a] QTL that extend across single one-log support confidence intervals were assigned the same symbol.

[b] AE indicated additive effect of resistance allele; positive value in the first cross and negative values in the second indicate that the QTL came from Chuanyu 16.

[c] LOD indicated Logarithm of odds score.

[d] PVE indicated the phenotypic variance explained by individual QTL.

[e] Total PVE indicated the phenotypic variance explained by all QTLs in one environment.

Table 3. Summary of digenic epistatic QTLs in a RIL population derived from Chuanyu 16/Chuanyu 12 across environments

Location and year	$QTL_1 \times QTL_2$	LOD[a]	PVE (%)[b]
Chengdu 2005	*QYr.caas-1BL.2×QYr.caas-2AS*	4.3	10.4
Chengdu 2006	*QYr.caas-1BL.2×QYr.caas-2AS*	3.0	5.6
Yaan 2006	*QYr.caas-1BL.2×QYr.caas-2AS*	2.3	4.3
Chengdu 2007	*QYr.caas-1BL.2×QYr.caas-2AS*	5.9	10.0
Yaan 2007	*QYr.caas-1BL.2×QYr.caas-2AS*	2.3	5.7
Yaan 2008	*QYr.caas-1BL.2×QYr.caas-2AS*	1.9	4.4
Average	*QYr.caas-1BL.2×QYr.caas-2AS*	4.1	6.7

[a] LOD indicated Logarithm of odds score.

[b] PVE indicated the phenotypic variance explained by digenic epistatic QTL.

Table 4. Four QTLs for stripe rust response on chromosome 1BL that could be *Yr29*

QTL	Carrier	Interval	PVE (%)[a]	Reference
QYr.cimmyt-1BL	Pavon 76	*Xgwm140 - Xgwm259*	33- 40	William et al. 2006
QYr.csiro-1BL	Attila	*LTN - XP55/*M55		Rosewarne et al. 2008
QPst.jic-1B	Guardian	*Xgwm818 - Xgwm259*	22-45	Melichar et al. 2008
QYr.saas-1BL	Chuanmai 107	*Xcwem32 - Xgwm818*	27.4	Zhu et al. 2010

[a] PVE indicated the phenotypic variance explained by individual QTL.

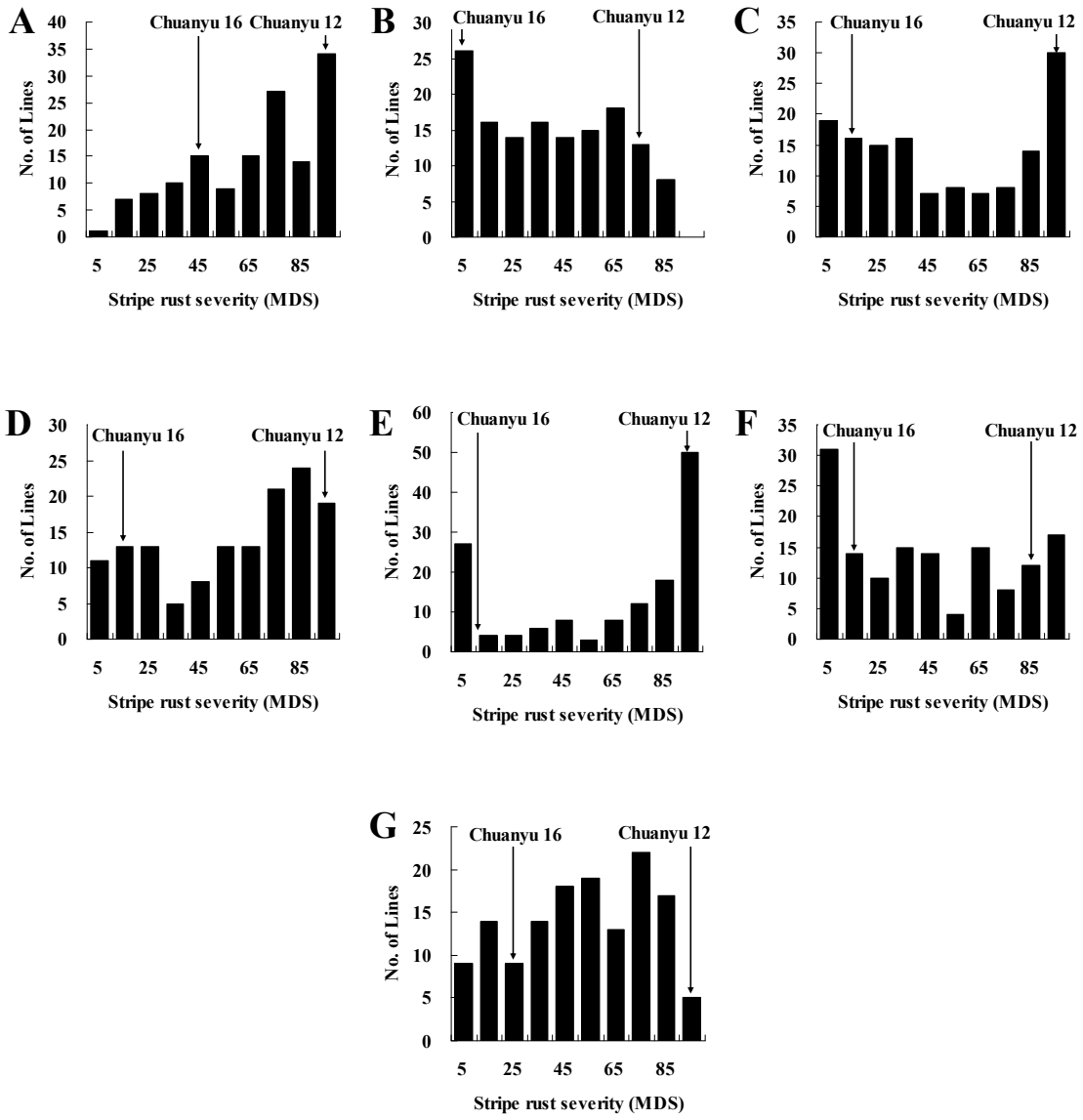
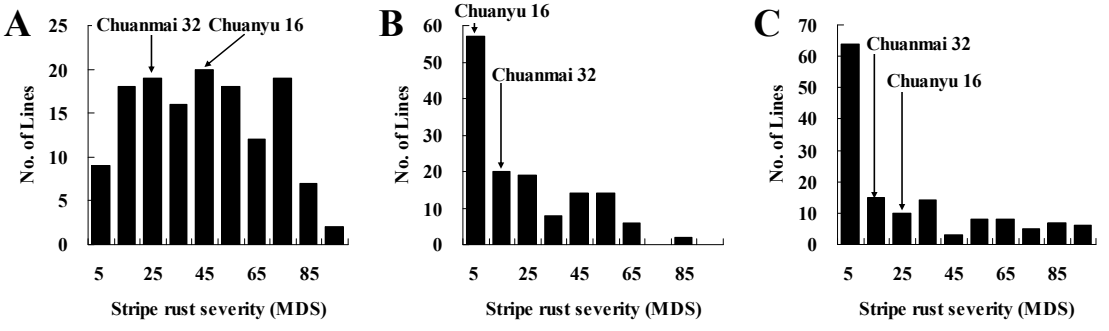


Figure 1. A to G, Frequency distributions of stripe rust maximum disease severities (MDS) in a RIL population derived from cv. Chuanyu 16/cv. Chuanyu 12. A, Chengdu 2005; B, Chengdu 2006; C, Yaan 2006; D, Chengdu 2007; E, Yaan 2007; F, Yaan 2008; G, Averaged MDS across six environments. Mean disease severities for the parents, cv. Chuanyu 16 and cv. Chuanyu 12, are indicated by arrows



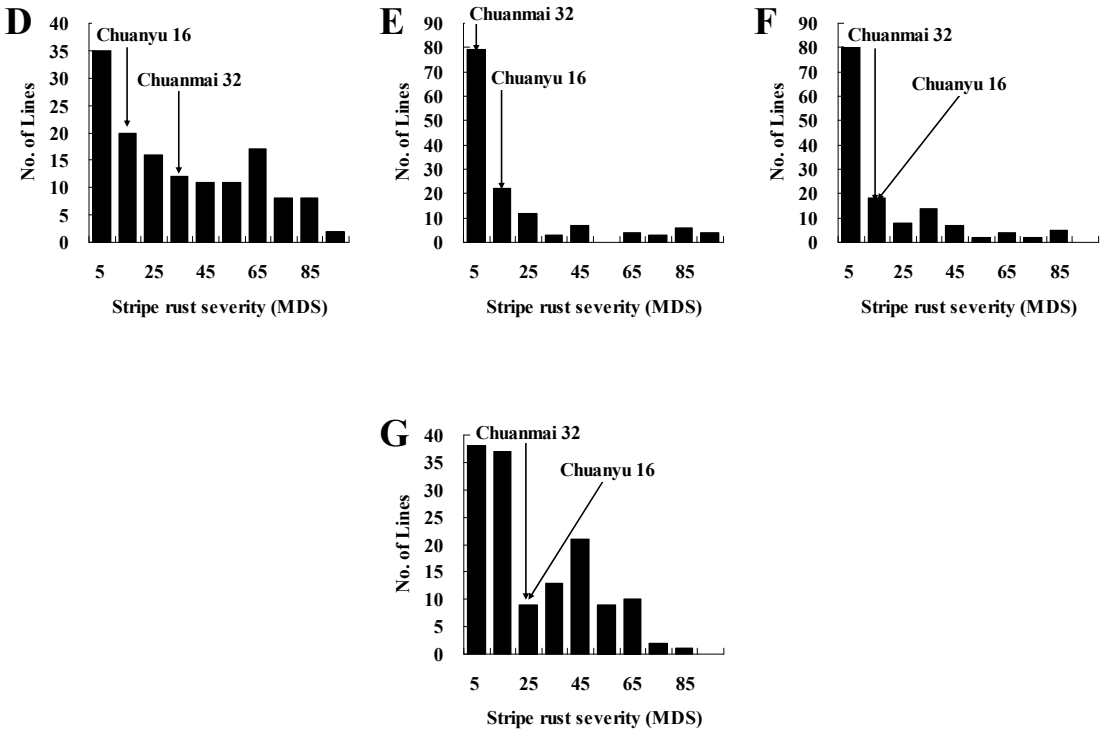
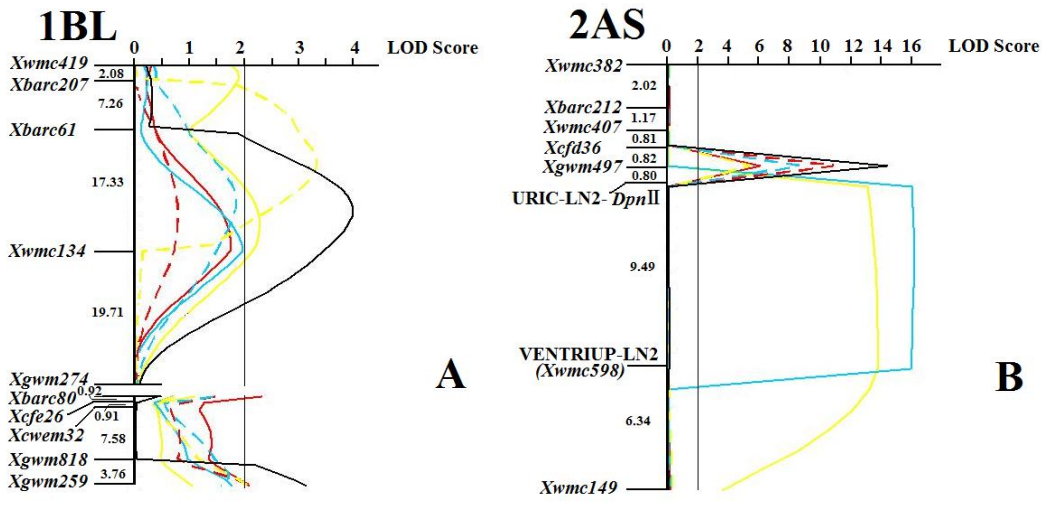


Figure 2. A to G, Frequency distributions of stripe rust maximum disease severities (MDS) in a RIL population derived from cv. Chuanmai 32/cv. Chuanyu 16. A, Chengdu 2005; B, Chengdu 2006; C, Yaan 2006; D, Chengdu 2007; E, Yaan 2007; F, Yaan 2008; G, Averaged MDS across six environments. Mean disease severities for the parents, cv. Chuanmai 32 and cv. Chuanyu 16, are indicated by arrows



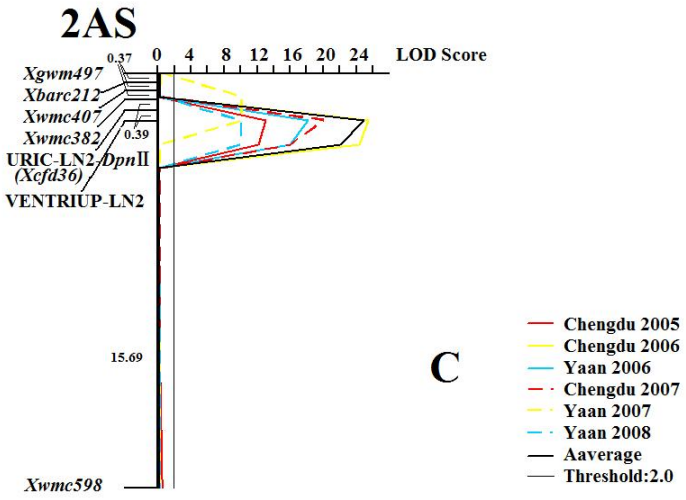


Figure 3. Likelihood plots of QTLs for APR to stripe rust on chromosomes 1BL (A), 2AS (B) identified by inclusive composite interval mapping in the population cv. Chuanyu 16/cv. Chuanyu 12; 2AS (C) identified by inclusive composite interval mapping in the population cv. Chuanmai 32/cv. Chuanyu 16. The LOD threshold for significance is 2.0. Positions (in cM) of the molecular markers along chromosomes are shown on the vertical axis; numbers between marker names are genetic distances between SSR loci. Short arms are toward the top.

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