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ORIGINAL PAPER

QTL mapping of adult-plant resistance to stripe rust in a population derived from common wheat cultivars Naxos and Shanghai 3/Catbird

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Abstract Stripe rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Erikss., is a severe foliar disease of common wheat (*Triticum aestivum* L.) worldwide. Use of adult-plant resistance (APR) is an efficient approach to provide long-term protection of crops from the disease. The German spring wheat cultivar Naxos showed a high level of APR to stripe rust in the field. To identify the APR genes in this cultivar, a mapping population of 166 recombinant inbred lines (RILs) was developed from a cross between Naxos and Shanghai 3/Catbird (SHA3/CBRD), a moderately susceptible line developed by CIMMYT. The RILs were evaluated for maximum disease severity (MDS) in Sichuan and Gansu in the 2009–2010 and 2010–2011 cropping seasons. Composite interval mapping (CIM) identified four QTL, *QYr.caas-1BL.1RS*, *QYr.caas-1DS*, *QYr.caas-5BL.3* and *QYr.caas-7BL.1*, conferring stable resistance to stripe rust across all environments, each explaining 1.9–27.6, 2.1–5.8, 2.5–7.8 and 3.7–9.1 % of the phenotypic variance, respectively. *QYr.caas-1DS* flanked by molecular markers *XUgwm353–Xgdm33b* was likely a new QTL for APR to stripe rust. Because the interval between flanking markers for each QTL was less than 6.5 cM, these QTL and their closely linked markers are potentially useful for improving resistance to stripe rust in wheat breeding.

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Introduction

Stripe rust or yellow rust (YR), caused by *Puccinia striiformis* Westend. f. sp. *tritici* Erikss. (*Pst*), is a worldwide devastating disease of common wheat (*Triticum aestivum* L.), and is particularly prevalent in temperate and maritime wheat growing regions (Stubbs 1985; Boyd 2005; Chen 2005). In China, the disease is most destructive in the northwestern and southwestern regions, such as Gansu, Sichuan, Chongqing, Shaanxi and Yunnan, due to the cool and moist spring conditions (He et al. 2011). Since the 1950s wheat YR epidemics have occurred in China for more than 15 times, most notably the four large scales of pandemics in 1950, 1964, 1990 and 2002 (Wan et al. 2004). In recent years, many wheat cultivars have lost their resistance to YR due to the occurrence and spread of Chinese *Pst* races CYR32 and CYR33 with broad virulence patterns. From 2003 to 2011, YR occurred in about

4.1 million hectares each year posing serious risks to wheat production in China (Tang 2004; Zhao 2004; Zhang et al. 2005, 2006, 2007, 2008, 2009; National Agro-technical Extension and Service Center (NAESC) 2010, 2011).

Although YR can be controlled through the application of fungicides, resistance breeding is a more economic, effective, and environmentally friendly approach to control the disease (Line 2002; Chen 2005). Resistance to YR can be categorized as race specific resistance or race non-specific resistance (Johnson 1988), but the distinction is not always clear. Race specific resistance is normally highly effective both in seedlings and adult plant stages. However, it is readily overcome by new races that are then selected on the previously resistant cultivars (Chen and Line 1995; Carter et al. 2009). For example, due to the wide cultivation of cultivars with *Yr9* (1B.1R translocation) *Pst* races CYR29 and CYR32 became prevalent. In addition, cultivars with resistance from Fan 6 succumbed to race CYR32 in 2002 (Chen et al. 2009). In contrast, race non-specific resistance, often associated with APR, partial resistance or slow-rusting is expressed at later stages of plant development, generally qualitatively inherited and often durable (Johnson 1984; Chen 2005). Examples include the slow-rusting resistance genes *Yr18* and *Yr29*, which have provided effective resistance to YR since the early 20th century (Krattinger et al. 2009). These two genes also show partial and race non-specific resistance to leaf rust (LR), powdery mildew (PM) and stem rust (Suenaga et al. 2003; Rosewarne et al. 2006; Lillemo et al. 2008; Bhavani et al. 2011).

To date, 52 genes (*Yr1–Yr49*) for YR resistance have been catalogued, and these are assigned to 49 loci (McIntosh et al. 2011). Most of them are race-specific resistance genes that are no longer effective or likely to have short duration of effectiveness if widely deployed in cultivars (McDonald and Linde 2002; Lu et al. 2009). As a consequence, APR is being increasingly emphasized in breeding for resistance (Line 2002; Lu et al. 2009). During the last decade, many APR quantitative trait loci (locus) (QTL) for reducing YR severity have been identified with the help of molecular markers (Singh et al. 2000b; Bariana et al. 2001; Boukhatem et al. 2002; Suenaga et al. 2003; Imtiaz et al. 2004; Ramburan et al. 2004; Mallard et al. 2005; Uauy et al. 2005; Christiansen et al. 2006; Rosewarne et al. 2006; William et al. 2006; Lin and Chen 2007, 2009; Chhuneja et al. 2008; Guo et al. 2008; Melichar et al. 2008; Rosewarne et al. 2008; Santra et al. 2008; Carter et al. 2009; Dedryver et al. 2009; Lu et al. 2009; Lan et al. 2010; Hao et al. 2011; Herrera-Foessel et al. 2011; Jagger et al. 2011; Lowe et al. 2011; Chen et al. 2012) They cover almost all chromosomes except for 1A, 1D, 3A and 7A, and the QTL on 1BL, 2BS, 2BL, 3BS, 4BL, 5DL, 6BS and 7DS were frequently coincided with PM resistance QTL (He et al. 2011). Since APR is generally quantitatively inherited, it is more complicated for selection in wheat breeding than race-specific resistance (Yu et al. 2001; Lillemo et al. 2008). Nevertheless, molecular markers that are closely linked to these QTL will greatly facilitate selection for APR in breeding programs.

The German spring wheat cultivar Naxos exhibits a high level of resistance to YR and PM in the field although it is susceptible to Chinese *Pst* races CYR29, CYR32 and CYR33 and *Blumeria graminis* f. sp. *tritici* isolate E20 at the seedling stage, indicating typical APR to both diseases. Recently, QTL mapping for APR to PM in Naxos was performed by Lu et al. (2012); however, the inheritance of APR to YR in this cultivar has not been reported. The objectives of this study were to identify and locate APR QTL to YR in a RIL population from cross SHA3/CBRD × Naxos with molecular markers, and to assess the stability of detected QTL across environments.

Materials and methods

Plant materials

One hundred and sixty-six F_6 RILs were developed by single-seed descent from the cross Shanghai 3/Catbird (SHA3/CBRD) × Naxos, which was provided by Dr. Morten Lillemo, Norwegian University of Life Sciences. Naxos (pedigree: Tordo/St.Mir808-Bastion//Minaret), an adapted spring wheat cultivar from Germany, is highly susceptible to currently prevalent *Pst* races CYR32 and CYR33 at the seedling stage (IT = 4), but shows a high level of resistance to YR in the field. SHA3/CBRD (pedigree: Shanghai 3//Chuanmai 18/Bagula), developed by the International Maize and Wheat Improvement Center (CIMMYT), is highly susceptible to *Pst* race CYR32 at the seedling stage (IT = 4) and is moderately susceptible to YR at the adult plant stage. SHA3/CBRD has the 1B.1R translocation based on AF1/AF4, SECA2/SECA3, SCM9, IB-267, iag95 and Bmac0213 markers (Francis et al. 1995; Froidmont 1998; Saal and Wricke 1999; Mago et al. 2002; Nagy et al. 2003) and genomic in situ hybridization (GISH) analysis (Supplementary-Figs. 1 and 2). Both parents are adapted to growing conditions in China.

Genotyping

Nine hundred and fifty-two simple sequence repeat (SSR) markers were screened on SHA3/CBRD and Naxos, including BARC (Song et al. 2002), CFA, CFD and GPW (Sourdille et al. 2004), CNL and KSUM (Yu et al. 2004), GDM (Pestsova et al. 2000), GWM (Röder et al. 1998), MAG (Xue et al. 2008), SWM (Bossolini et al. 2006; Krattinger et al. 2009), UGWM (Parida et al. 2006) and

WMC (Gupta et al. 2002) markers. Polymorphic SSR markers were then used to genotype all 166 RILs from the cross SHA3/CBRD × Naxos by polyacrylamide gel electrophoresis. The population was also screened with diversity array technology (DArT) markers. In addition, six rye (*Secale cereale* L.) 1RS specific markers (Tang et al. 2009; Yu et al. 2011) were also included for detection of 1B.1R translocation.

Genetic linkage map construction

The genotypic data for markers were used to construct genetic linkage maps with the software MapManager QTX20 (Manly et al. 2001). Genetic distances between markers were calculated based on the Kosambi mapping function (Kosambi 1944). The assignment of linkage groups on chromosomes was checked against previously published wheat consensus maps (Somers et al. 2004; http://www.wheat.pw.usda.gov).

Field trials

The F_6 RILs and their parents were evaluated in Sichuan and Gansu provinces in the 2009–2010 and 2010–2011 cropping seasons. The trial in Sichuan was conducted in Pi county (103°E, 30°N, 555 m a.s.l.), close to Chengdu, and the trial in Gansu was conducted in Qingshui county (106°E, 34°N, 1,572 m a.s.l.), close to Tianshui. Both locations are hotspots for YR in China with ideal conditions for rust infection and spread. Field trials were conducted in randomized complete blocks with three replicates at each location. Each plot consisted of a single row 1.5 m in length with 25 cm between rows. Approximately 50 seeds were sown in each row. Every tenth row was planted with the highly susceptible Mingxian169 to aid the spread of the pathogen within the trial. To ensure ample field inoculum, infection rows of Mingxian169 were also planted perpendicularly and adjacent to the test rows. Inoculations at both sites were performed at the three-leaf stage with a mixture of prevalent Chinese *Pst* races. Maximum disease severities (MDS) were scored, when YR severities on Mingxian169 reached a maximum level around the 15th of April in Sichuan and 10th of June in Gansu, respectively. Field data from Gansu 2010–2011 was excluded from the statistical analysis and QTL detection due to the low YR development caused by the dry weather condition in the spring.

Statistical analysis

Analysis of variance was performed with the PROC GLM in the statistical analysis system (SAS) software package (SAS institute, V8). The information in the ANOVA table was used to calculate the broad sense heritability (h_b^2) for YR reaction based on the formula $h_b^2 = \sigma_g^2/(\sigma_g^2 + \sigma_{ge}^2/e + \sigma_\varepsilon^2/re)$, where $\sigma_g^2 = (MS_f–MS_{fe})/re$, $\sigma_{ge}^2 = (MS_{fe}–MS_e)/r$ and $\sigma_\varepsilon^2 = MS_e$ (Allard 1960); in this formula, σ_g^2 = genetic variance, σ_{ge}^2 = genotype × environment interaction variance, σ_ε^2 = error variance, MS_f = mean square of genotype, MS_{fe} = mean square of genotype × environment interaction, MS_e = mean square of error, r = number of replicates and e = number of environments.

QTL analysis

Stripe rust resistance QTL were detected in the population based on the mean MDS of three replicates in each environment and also on the averaged data from three environments. Composite interval mapping (CIM) analysis was performed using the software QTL Cartographer 2.5 (Wang et al. 2005). After performing a 1,000 permutation test, a LOD threshold of 2.5 was set to declare QTL as significant. A walk speed of 2.0 cM was chosen for all QTL detections. QTL effects were estimated as the proportion of phenotypic variance (R^2) explained by the QTL. The data were also analyzed with the software QTL IciMapping V3.1 (Li et al. 2007, 2008; Wang 2009) by inclusive composite interval mapping (ICIM) for detecting interactions between two QTL.

Results

Phenotypic evaluation

Stripe rust developed well in Sichuan in 2010 and 2011 and in Gansu in 2010. The MDS of the susceptible Mingxian169 control ranged from 90 to 95 %, from 95 to 100 %, from 60 to 100 % in Sichuan 2010, Sichuan 2011 and Gansu 2010, respectively. Naxos had a mean MDS of 4.7–11.7 % across the three environments, whereas SHA3/CBRD was rated with a mean MDS of 31.7–66.7 %. The frequency distributions of MDS for the 166 RILs ranging over 1–80, 4–95, 3–80 and 3–78 % in Sichuan 2010, Sichuan 2011, Gansu 2010 and the averaged MDS for all three environments, respectively, showed continuous distributions (Supplementary Fig. 3), indicative of polygenic inheritance. The broad-sense heritability of MDS was 0.65. The ANOVA showed significant differences ($P = 0.01$) in MDS among RILs, environments, replicates within environments and line × environment interactions (Table 1).

Construction of linkage maps

A total of 952 SSR markers were tested for polymorphism between SHA3/CBRD and Naxos; 279 markers (29.3 %)

Table 1 Analysis of variance of MDS scores for RILs generated from the cross SHA3/CBRD × Naxos

Source of variance	*df*	Mean square	*F* value
Line	165	2,317	2.8[a]
Environment	2	266,735	326.9[a]
Replicate	2	6,026	49.4[a]
Line × environment	330	816	6.7[a]
Error	992	122	

[a] $P = 0.01$

were polymorphic. The latter were used to genotype individual RILs from the population for construction of genetic linkage maps. Additionally, 283 polymorphic DArT markers covering all chromosomes and six molecular markers specific for 1B.1R translocation were used for mapping the population. Among the 568 polymorphic marker loci, 373 loci were assigned into 26 linkage groups.

QTL for APR to YR

Using CIM analysis, 10 QTL for APR to YR were identified on chromosomes 1AL, 1BL.1RS, 1DS, 2BL, 2DL, 5AL, 5BL, 6BS and 7BL (two QTL) based on the mean MDS in each environment and the averaged values from all three environments (Fig. 1; Table 2). The resistance alleles of the QTL on 1AL, 1DS, 2BL, 2DL and 6BS were contributed by Naxos, whereas those on 1BL.1RS, 5AL, 5BL, and 7BL (two QTL) were from SHA3/CBRD.

Using the six rye specific molecular markers, a major QTL for YR resistance was located on chromosome 1BL.1RS, designated *QYr.caas-1BL.1RS*, most closely associated with *Xiag95*. This QTL explained 27.6, 1.9, 5.3 and 7.9 % of the phenotypic variance in Sichuan 2010, Sichuan 2011, Gansu 2010 and averaged MDS, respectively.

The second consistently detected QTL with larger effect, *QYr.caas-5BL.3*, was located on chromosome 5BL between *XwPt-2707* and *Xbarc275*, and explained 2.5 to 7.8 % of the phenotypic variance in three environments and averaged MDS. The third QTL, *QYr.caas-7BL.1*, was flanked by *XwPt-8106* and *Xbarc176*, and explained 8.2, 3.7, 6.3 and 9.1 % of the phenotypic variance in Sichuan 2010, Sichuan 2011, Gansu 2010, and averaged MDS, respectively. The fourth QTL, *QYr.caas-1DS*, was identified in the marker interval *XUgwm353–Xgdm33b* on chromosome 1DS. This QTL was detected in three environments as well as the overall mean, explaining the phenotypic variance of 2.1 to 5.8 %.

Two QTL, *QYr.caas-2DL* and *QYr.caas-5AL.2*, were detected in two environments and averaged MDS, respectively, and explained 2.9–10.2 and 3.2–3.7 % of the phenotypic variance. *QYr.caas-2DL*, flanked by *XwPt-6752* and *Xcfd47*, was located on chromosome 2DL whereas *QYr.caas-5AL.2* was located in marker interval *XwPt-1903-5AL* and *Xwmc727-5AL*. One QTL, *QYr.caas-6BS.2*, in the interval *Xwmc104–XwPt-0259* on chromosome 6BS, explained 2.9–5.7 % of the phenotypic variance across two environments.

The remaining three QTL were detected in single environment. *QYr.caas-1AL* and *QYr.caas-2BL* were in marker intervals *XwPt-2406–Xwmc59* and *XwPt-8460–XwPt-3755*, and explained 8.2 and 12.2 %, respectively, of the phenotypic variance in Gansu 2010. *QYr.caas-7BL.2* was located between *Xgwm577* and *XwPt-4300* on chromosome 7BL, explaining 14.7 % of the phenotypic variance in Sichuan 2011.

The total phenotypic variance explained by detected QTL ranged from 36.9 to 55.9 % in a simultaneous fit across the three environments, suggesting a significant effect of these QTL in reducing YR severity.

Interactions among different QTL could not be stably identified across the three environments using IciMapping V3.1. All these ten QTL associated with YR resistance showed additive effects (Table 2). To obtain the combined effects of these QTL, the flanking markers for these QTL regions were used to select RILs possessing the corresponding QTL, for example, RILs possessing the 1AL resistance allele were selected to present the effect of the 1AL QTL using the closely linked marker *XwPt-2406*. The results shown in Fig. 2 indicated that the more resistance genes a subset of RILs possess, the lower the disease severity. In addition, when four to five genes were combined in a RIL, the disease severity was less than 35 % on average (Fig. 2; Supplementary Table 1). This is consistent with a report by Singh et al. (2000a), who demonstrated that four to five APR genes, each with small to intermediate effects, may provide a high level of resistance to YR when combined in a cultivar.

Discussion

Although the German cultivar Naxos was susceptible to currently prevalent *Pst* races CYR32 and CYR33 at the seedling stage, it showed a high level of resistance when inoculated with these races in the field. Five QTL for YR resistance were detected in Naxos. Although SHA3/CBRD was moderately susceptible to YR, it actually carried five QTL for APR.

Comparison with previous reports

QYr.caas-1AL

QYr.caas-1AL, with a resistance allele contributed by Naxos, was not stable across environments, but could be related to known resistance QTL against YR. Ramburan

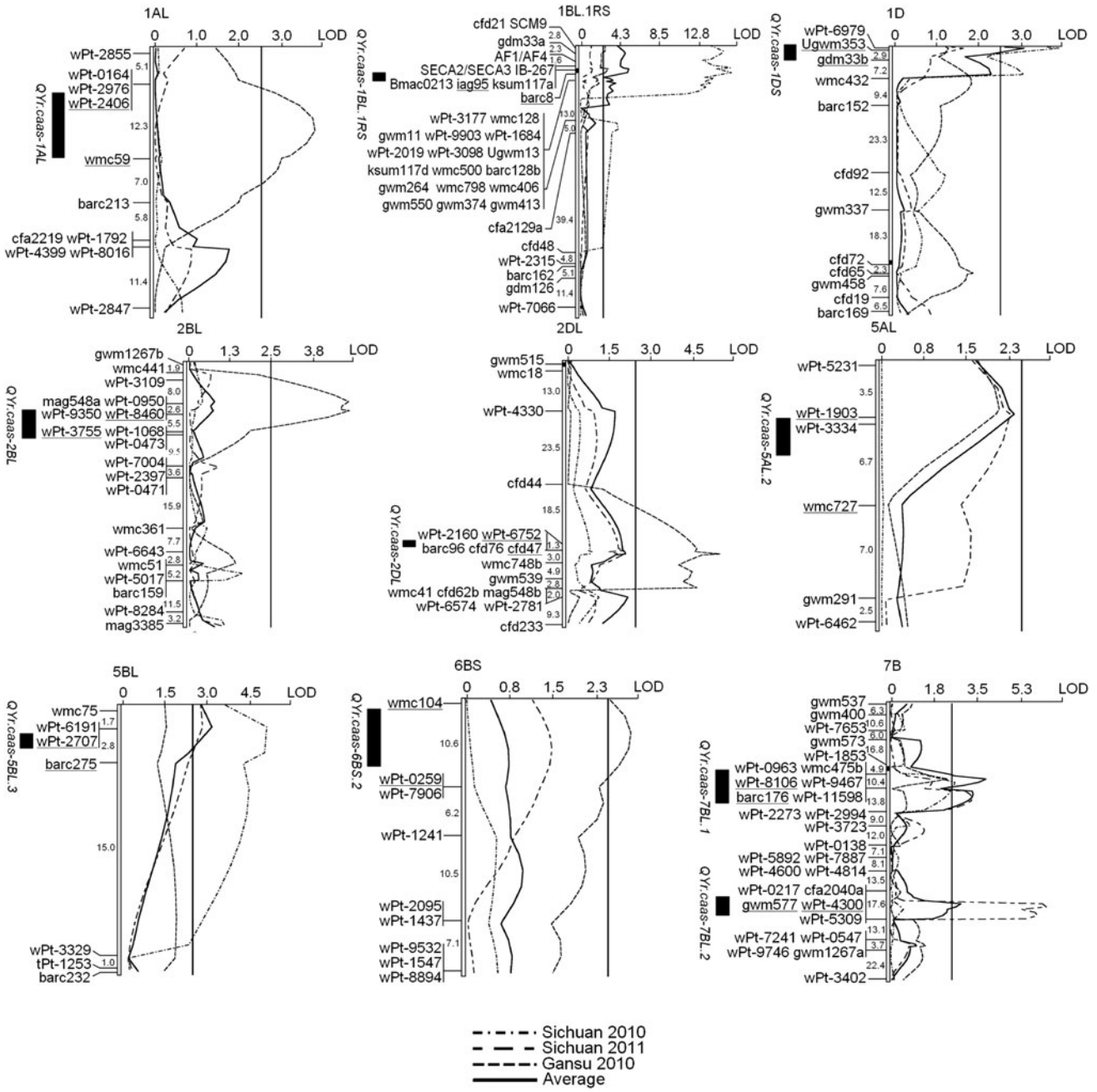

Fig. 1 LOD contours for QTL on chromosomes 1AL, 1BL.1RS, 1DS, 2BL, 2DL, 5AL, 5BL, 6BS, 7BL (two QTL) that reduce stripe rust severity in the RIL population from SHA3/CBRD × Naxos. The short arms are toward the *top* and the approximate positions of centromeres are indicated by *solid squares* in the *vertical axis*. Genetic distances are shown in centiMorgans (cM) to the *left* of the *vertical axis*. Markers closely linked to each QTL are *underlined*. The approximate positions of QTL are indicated by *oblong black squares* to the *left* of markers and their heights represent the interval distances of flanking markers. LOD thresholds of 2.5 are indicated by *dashed vertical lines* in the graphs

et al. (2004) identified an APR QTL on chromosome 1A, designated *QYr.sgi-1A*, which was also inconsistently detected across environments. Furthermore, Dedryver et al. (2009) identified a QTL on 1A in cultivar Renan, only at one scoring. Because of different kinds of flanking markers used in these studies, the relationships among these QTL are uncertain.

QYr.caas-1DS

This is the first report of QTL for YR resistance on chromosome 1D. Considering that Naxos was highly susceptible to currently prevalent *Pst* races CYR32 and CYR33 at seedling stages, *QYr.caas-1DS* contributed by Naxos is likely a new QTL for APR to YR.

Table 2 Quantitative trait loci for stripe rust resistance detected by CIM in the SHA3/CBRD × Naxos RIL population across three environments and averaged MDS over three environments

QTL[a]	Sichuan 2010			Sichuan 2011			Gansu 2010			Average			Source of resistance
	LOD[b]	Add[c]	R^2 (%)[d]	LOD	Add	R^2 (%)	LOD	Add	R^2 (%)	LOD	Add	R^2 (%)	
QYr.caas-1AL							3.8	−5.1	8.2				Naxos
QYr.caas-1BL.1RS	16.3	9.5	27.6	1.3	4.1	1.9	3.0	4.2	5.3	5.3	4.8	7.9	SHA3/CBRD
QYr.caas-1DS	3.9	−4.1	5.8	1.6	−4.3	2.4	1.3	−2.6	2.1	3.1	−3.5	4.5	Naxos
QYr.caas-2BL							4.9	−6.0	12.2				Naxos
QYr.caas-2DL				2.1	−5.0	3.1	5.6	−5.7	10.2	2.1	−2.9	2.9	Naxos
QYr.caas-5AL.2				2.3	5.4	3.7	2.1	3.3	3.4	2.4	3.0	3.2	SHA3/CBRD
QYr.caas-5BL.3	5.2	4.8	7.8	2.9	6.2	4.5	1.6	2.8	2.5	3.2	3.5	4.7	SHA3/CBRD
QYr.caas-6BS.2				1.5	−4.8	2.9	2.9	−4.2	5.7				Naxos
QYr.caas-7BL.1	2.6	5.7	8.2	1.7	5.7	3.7	2.3	4.8	6.3	3.9	5.2	9.1	SHA3/CBRD
QYr.caas-7BL.2				6.4	11.9	14.7				2.9	4.5	6.3	SHA3/CBRD

[a] QTL were detected with a minimum LOD score of 2.5 in at least one environment

[b] Logarithm of odds (LOD) score

[c] Additive effect of resistance allele

[d] Percentages of phenotypic variance explained by individual QTL

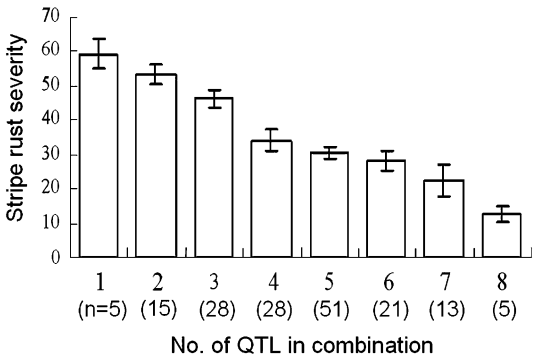

Fig. 2 The effect of different QTL combinations on stripe rust severity in different classes. The *number* in *abscissa* indicates the number of QTL combined in each subset of RILs, for example, one means the class of RILs possessing one QTL. The *numbers* in *parentheses* indicate the number of RILs in each class. The *error bars* indicate the standard error of sample means. A detailed list of the RILs in each class is shown in Supplementary Table 1

QYr.caas-1BL.1RS

The short arm of rye chromosome 1 (1RS) carries a variety of disease resistance genes, viz., *Yr9*, *Pm8*, *Lr26* and *Sr31* from 'Petkus' and *SrR* from 'Imperial' rye (Mago et al. 2002). Based on GISH analysis, SHA3/CBRD carries a translocated chromosome in which the entire 1RS has replaced the entire 1BS (Supplementary Fig. 2). Theoretically, there should not be recombination between 1BS and 1RS. However, we still found a cluster of markers with low recombination frequency on 1RS (Fig. 1). This is most likely due to inaccurate genotypic data as most of these markers are dominant markers. Although *Xcfd21* and *Xgdm33a* were mapped on the short arm of wheat homoeologous group 1 in several consensus maps (Somers et al. 2004; http://www.wheat.pw.usda.gov), both of them gave specific amplification in SHA3/CBRD while no corresponding PCR products were detected in Naxos. The two SSR markers are therefore specific to 1B.1R translocation in the present population. *QYr.caas-1BL.1RS* was close to centromere on chromosome 1BL.1RS, most closely associated with *Xiag95-1RS*. This QTL was possibly located on chromosome 1RS in a 1BL.1RS translocation line SHA3/CBRD. The stripe rust resistance gene *Yr9* was also located on 1RS, which in turn was located 26.1 ± 4.3 cM from the centromere (Singh et al. 1990). However, this gene has succumbed to the *Pst* races used in the present study both at seedling and adult-plant stages (Yang and Ren 2001; Ren et al. 2009). Therefore, *QYr.caas-1BL.1RS* is likely different from *Yr9*. Recently, Luo et al. (2008) reported two genes (*YrCN17* and *YrR212* in cultivars CN17 and R212) for stripe rust resistance located on 1RS. Both genes are resistant to *Pst* races CYR31 and CYR32. Ren et al. (2009) also identified the gene (*YrCn17*) in the line R14, and concluded that this gene is likely to be an allele of *Yr9* based on allelism tests. But, these are major resistance genes rather than a QTL.

QYr.caas-2BL

Several QTL for YR resistance were reported on wheat chromosome 2BL, including *QYR1*, *QYr.inra-2BL*, *QTL 2BL*, *QYraq.cau-2BL* and *QYr.csiro-2BL* (Boukhatem et al. 2002; Mallard et al. 2005; Christiansen et al. 2006; Guo et al. 2008; Rosewarne et al. 2008). *QTL 2BL* was located between *Xwmc149* and *Xwmc317a* with a map distance of

about 15 cM from *QYr.caas-2BL* based on the consensus map (Somers et al. 2004), indicating that this QTL was unlikely to be the same locus as *QYr.caas-2BL*. *QYr.csiro-2BL* flanked by *Xgwm1027–Xgwm619* is also different from *QYr.caas-2BL* because it is more than 20 cM from *QYr.caas-2BL* (Somers et al. 2004). In contrast, *QYR1*, *QYr.inra-2BL* and *QYraq.cau-2BL* were located in the marker interval *Xgwm47–Xgwm501*, *Xbarc101–Xgwm120* and *Xwmc175–Xwmc332*, respectively, which are very closely linked to *QYr.caas-2BL* (Somers et al. 2004). *QYR1* and *QYr.inra-2BL* were derived from cultivar Camp Remy. They accounted for 46.0 and 61 % of the phenotypic variance, respectively. Another one, *QYraq.cau-2BL*, was contributed by cultivar Aquileja and explained up to 61.5 % of the phenotypic variance. However, *QYr.caas-2BL* detected in the present study explained 12.2 % of the phenotypic variance and the resistance gene came from Naxos. Pedigree analysis did not show any common ancestors between Naxos and the two cultivars. It is possible that *QYr.caas-2BL* is different from these QTL. However, this needs to be confirmed by allelism test in the future.

QYr.caas-2DL

The APR gene *Yr16* was located on the centromeric region of chromosome 2D (Worland and Law 1986; Mallard et al. 2005), with a map distance of about 23 cM from *QYr.caas-2DL* (Hart et al. 1993; Somers et al. 2004). This gene is therefore different from *QYr.caas-2DL*. Recently, Jagger et al. (2011) identified a QTL flanked by SSR markers *Xgwm320* and *Xgwm301* on 2DL in the German cultivar Alcedo. It was approximately 18 cM from *QYr.caas-2DL* (Somers et al. 2004), suggesting that this locus is also likely different from *QYr.caas-2DL*. Suenaga et al. (2003) reported a QTL on 2DL in the cultivar Fukuho-Komugi, closely linked to the marker *Xgwm349*, which corresponds to the interval for *QYr.caas-2DL* (Somers et al. 2004). It explained 10.1–11.4 % of the phenotypic variance in YR severity across environments, which is similar to *QYr.caas-2DL* in the present study. Melichar et al. (2008) also identified a QTL at the same chromosomal region in the UK wheat cultivar Guardian, which explained 8.0–11.0 % of the phenotypic variance. Thus, these two QTL and *QYr.caas-2DL* might be same or closely linked.

QYr.caas-5AL.2

Boukhatem et al. (2002) mapped a QTL, flanked by RFLP markers *Xfbb209* and *Xabg391*, and linked to the SSR marker *Xgwm126*. This QTL should be different from *QYr.caas-5AL.2* based on a map distance of about 25 cM between them (Somers et al. 2004). Chhuneja et al. (2008) identified a QTL on 5AL between *Xbarc151* and *Xcfd12*, with a map distance of 58 cM from *QYr.caas-5AL.2* (Somers et al. 2004). In addition, it was derived from the diploid A genome wheat species *T. boeoticum* (acc. Pau5088), indicating that this QTL was also different from *QYr.caas-5AL.2*. Lan et al. (2010) located a QTL on 5AL in the Chinese landrace wheat Pingyuan 50, flanked by *Xwmc410* and *Xbarc261*, in the same region as *QYr.caas-5AL.2*. Because pedigree analyses showed no relationship between SHA3/CBRD and Pingyuan 50, this QTL is also likely different from *QYr.caas-5AL.2*. Recently, a QTL (*Yr48*) with large effect, flanked by *Xwmc727* and *Xgwm291* on 5AL, was validated in PI610750 (Lowe et al. 2011), at a similar position to *QYr.caas-5AL.2* (Somers et al. 2004). However, PI610750 (pedigree: Croc1/*Aegilops tauschii* (synthetic 205)//Kauz) is a synthetic wheat derivative from CIMMYT's Wide Cross Program, and it has no common ancestor with SHA3/CBRD, suggesting that *Yr48* may be different from *QYr.caas-5AL.2*. Therefore, *QYr.caas-5AL.2* is possibly a new QTL for APR to YR.

QYr.caas-5BL.3

Mallard et al. (2005) reported a QTL for YR resistance, flanked by *Xgwm234* and *XDuPw115a* on 5BL, in the same region as *QYr.caas-5BL.3*. It might be in a translocated region from chromosome 5BS of cultivar Cappelle Desprez (Mallard et al. 2005; Lu et al. 2009). Lu et al. (2009) reported two APR QTL to YR on 5BL in cultivar Libellula. One of two QTL, *QYr.caas-5BL.2*, flanked by *Xbarc142* and *Xgwm604*, was located to a similar position as *QYr.caas-5BL.3* (Somers et al. 2004). It explained 2.6 % of the phenotypic variance in one environment, which showed lower effect and stability than *QYr.caas-5BL.3*.

QYr.caas-6BS.2

A number of genes for YR resistance have been reported on chromosome 6BS. Among them, *QYr.jirc-6B* (Suenaga et al. 2003), *Yr36* (Uauy et al. 2005), *QYrst.wgp-6BS.1* (Santra et al. 2008) and *QYr.caas-6BS* (Lan et al. 2010) were close to the centromere on 6BS, more than 20 cM away from *QYr.caas-6BS.2*. These QTL were therefore different from *QYr.caas-6BS.2*. All-stage resistance gene *Yr35* (Dadkhodaie et al. 2010) on chromosome 6BS is linked to SSR marker *Xgwm508*, with a map distance of about 18 cM from *QYr.caas-6BS.2* (Somers et al. 2004). Dedryver et al. (2009) reported *QYr.inra-6B* flanked by SSR markers *Xgwm518* and *Xgwm608* with a map distance of about 13 cM from *QYr.caas-6BS.2* (Somers et al. 2004). Santra et al. (2008) detected a QTL on bin 6BS-satellite in cultivar Stephens, flanked by SSR markers *Xgwm132* and *Xgdm113* that coincided with *QYr.caas-6BS.2* (Somers

et al. 2004). This QTL explained a large proportion of the phenotypic variance (R^2 = 25–43 %) across environments, whereas *QYr.caas-6BS.2* only explained 2.9–5.7 % across environments.

QYr.caas-7BL.1 and QYr.caas-7BL.2

Lin and Chen (2007) identified *Yr39* from cultivar Alpowa on chromosome 7BL, flanked by *Xgwm43* and *Xgwm131*. In the present study, the QTL *QYr.caas-7BL.1* was located between *XwPt-8106* and *Xbarc176*. The map distance between that QTL and *QYr.caas-7BL.1* is approximately 6 cM (Somers et al. 2004). Thus, these two genes might be either at the same position or closely linked with each other. According to significant differences in map distance between *QYr.caas-7BL.1* and the other QTL on 7BL (Imtiaz et al. 2004; Somers et al. 2004; Rosewarne et al. 2008), *QYr.caas-7BL.1* described here might be different.

We detected a second QTL, *QYr.caas-7BL.2*, which was in the marker interval *Xgwm577–XwPt-4300*, at the end of chromosome 7BL. As shown in Fig. 1, this QTL was approximately 63.5 cM from *QYr.caas-7BL.1*. Rosewarne et al. (2008) also identified a QTL in the telomere region of chromosome 7BL, flanked by *XP32/M59* and *Xgwm344*, but it was approximately 20 cM away from *QYr.caas-7BL.2* (Somers et al. 2004). Nevertheless, Imtiaz et al. (2004) identified *QYr.nsw-7B* closely linked to *Xgwm611*, with a map distance of only 1 cM from *QYr.caas-7BL.2* (Somers et al. 2004). It was contributed by the susceptible variety "Tiritea" and accounted for 42.0 and 37.0 % of variation in adult plant resistance under greenhouse and field conditions. Consequently, *QYr.caas-7BL.2* may be the same as *QYr.nsw-7B*, or they are closely linked genes.

Pleiotropic effects of detected genes

Previous studies indicated that APR genes involved in resistance to rusts are clustered on wheat chromosomes or showed pleiotropic effects, such as, *Yr18/Lr34* (Suenaga et al. 2003; Spielmeyer et al. 2007), *Yr29/Lr46* (Rosewarne et al. 2006), *Yr30/Sr2* (Singh et al. 2000b), and *Yr46/Lr67* (Herrera-Foessel et al. 2011). Many studies confirmed that the same principle also applies to rusts and PM. For example, Lillemo et al. (2008) conducted QTL mapping for resistance to PM, LR and YR in a population from the cross between Saar and Avocet S, and found that QTL for PM resistance coincided with *Yr18/Lr34* and *Yr29/Lr46*, and designated as *Pm38* and *Pm39*, respectively. He et al. (2011) integrated all APR QTL for YR and PM resistance into a linkage map based on DNA marker information, and found eight gene clusters (≥5 QTL) conferring resistance to both YR and PM simultaneously. In addition, the durable stem rust resistance gene *Sr2* was also associated with LR (*Lr27*) and PM resistance (Lagudah 2011; Mago et al. 2011).

The APR QTL to PM in the same population of SHA3/CBRD × Naxos was characterized by Lu et al. (2012). Compared with the study, *QYr.caas-1BL.1RS* contributed by SHA3/CBRD was in the same region as a PM resistance QTL from the same parent, and *QYr.caas-2BL* corresponded well with a PM resistance QTL which was from Naxos, indicating pleiotropic effects of the resistance loci. Besides, there are coincident QTL for YR and PM resistance close to the centromere on 2DL, but the resistance is contributed by opposite parents. *QYr.caas-1BL.1RS* and *QYr.caas-2BL* may play an important role for resistance breeding to both YR and PM.

The same population was also used for QTL mapping of *Fusarium* head blight (FHB) resistance (Lu et al., manuscript to be submitted). Comparison with this study shows that both *QYr.caas-1DS* and *QYr.caas-2BL* are co-located with FHB resistance QTL with the alleles for resistance contributed by Naxos. *QYr.caas-1DS* is therefore a valuable resistance resource for breeding to both YR and FHB while *QYr.caas-2BL* could be used to simultaneously improve resistance levels to YR, PM and FHB. Based on the same study, *QYr.caas-5AL* with YR resistance contributed by SHA3/CBRD coincided with a FHB resistance QTL from the same parent, while *QYr.caas-2DL* and *QYr.caas-5BL.3* located to similar positions as FHB resistance QTL, but with resistance contributed by the opposite parents. Further studies are necessary to elucidate these effects, which can more likely be explained by close linkage of resistance genes than pleiotropy as both these FHB resistance QTL were associated with anther extrusion, which does not play any role as a resistance mechanism against YR.

Breeding and application

In this study, we detected four QTL conferring stable resistance to YR across environments, including *QYr.caas-1BL.1RS*, *QYr.caas-1DS*, *QYr.caas-5BL.3* and *QYr.caas-7BL.1*, and they were closely linked to the SSR markers *Xbarc8*, *XUgwm353*, *Xbarc275* and *Xbarc176*, respectively. As the interval of flanking markers for each QTL was less than 6.5 cM, these closely linked SSR markers could be used for improving resistance to YR resistance in wheat breeding.

As the research on race non-specific genes becomes more and more extensively, especially following the cloning of APR genes *Yr18* and *Yr36* (Krattinger et al. 2009; Fu et al. 2009), the mechanisms of APR are becoming better understood. The durability of any gene or gene combination continues to elude prediction and remains a matter of "time will tell" (Lowe et al. 2011).

Nevertheless, the QTL reported in the present study, particularly *QYr.caas-1DS* was a new QTL for APR to YR, which should enable diversification of the genetic basis of partial and durable resistance to YR. Their closely linked molecular markers can be used in marker-assisted selection and pyramiding of APR genes to YR in wheat breeding.

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