

QTL mapping of adult-plant resistance to stripe rust in a ‘Lumai 21 × Jingshuang 16’ wheat population

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Abstract

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is a devastating fungal disease in common wheat (*Triticum aestivum* L.) worldwide. Chinese wheat cultivars ‘Lumai 21’ and ‘Jingshuang 16’ show moderate levels of adult-plant resistance (APR) to stripe rust in the field, and they showed a mean maximum disease severity (MDS) ranging from 24 to 56.7% and 26 to 59%, respectively, across different environments. The aim of this study was to identify quantitative trait loci (QTL) for resistance to stripe rust in an F₃ population of 199 lines derived from ‘Lumai 21’ × ‘Jingshuang 16’. The F₃ lines were evaluated for MDS in Qingshui, Gansu province, and Chengdu, Sichuan province, in the 2009–2010 and 2010–2011 cropping seasons. Five QTL for APR were detected on chromosomes 2B (2 QTL), 2DS, 4DL and 5DS based on mean MDS in each environment and averaged values from all three environments. These QTL were designated *QYr.caas-2BS.2*, *QYr.caas-2BL.2*, *QYr.caas-2DS.2*, *QYr.caas-4DL.2* and *QYr.caas-5DS*, respectively. *QYr.caas-2DS.2* and *QYr.caas-5DS* were detected in all three environments, explaining 2.3–18.2% and 5.1–18.0% of the phenotypic variance, respectively. In addition, *QYr.caas-2BS.2* and *QYr.caas-2BL.2* collocated with QTL for powdery mildew resistance reported in a previous study. These APR genes and their linked molecular markers are potentially useful for improving stripe rust and powdery mildew resistances in wheat breeding.

Key words: common wheat — *Triticum aestivum* — *Puccinia striiformis* f. sp. *tritici* — non-specific resistance — bulked segregant analysis — molecular markers — pleiotropic effects — quantitative trait locus

Stripe (yellow) rust (YR), caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is a worldwide disease of common wheat (*Triticum aestivum* L.) (Stubbs 1985, Boyd 2005, Chen 2005). Since the 1950s, about 23 large-scale stripe rust epidemics have occurred in major wheat-production areas of the world, including China, USA, the United Kingdom, Australia and India (Wellings 2011). In China, the disease is very destructive in the north-western and south-western regions due to the cool and moist spring conditions (Wan et al. 2004). The most destructive epidemics of stripe rust in China occurred in 1950, 1964, 1990 and 2002, resulting in yield loss estimates of up to 6.0, 3.2, 1.8 and 1.3 million tonnes, respectively (Wan et al. 2004). Over the last 10 years, the importance of stripe rust in China may have fallen due to the application of fungicides and climate change. However, local stripe rust epidemics are still serious in Sichuan, Chongqing, Yunnan, Shanxi and Gansu, as well as the Shiyang and Xiangfan prefectures of Hubei, and Xinyang and Nanyang prefectures of Henan (He et al. 2011).

Although fungicides can provide adequate control of rusts, growing resistant wheat cultivars are a more economic and effective approach to control the disease, having no additional costs to farmers and no environmental pollution (Line and Chen 1995, Line 2002, Chen 2005). Of the 67 permanently designated *Yr* loci (*Yr1* – *Yr67*) and numerous temporarily designated resistance genes identified in wheat (Basnet et al. 2013, McIntosh et al. 2013), most are race-specific in effect (Chen 2005, McIntosh et al. 2013). This kind of resistance gene has been extensively used in wheat breeding because of the high levels of resistance conferred at all stages of growth and ease of selection in the field, but unfortunately, it is readily overcome by new pathogen races (Chen and Line 1995a,b, Carter et al. 2009). Historically, the acquisition of virulence for *Yr2* in the 1970s, *YrA* in the mid-1980s, *Yr9* in the 1990s, *Yr27* in 1998 in Mexico, *Yr24/Yr26* in 2008 in China and *Yr31* in 2008 in Mexico led to regional and continental epidemics and crop losses (Wellings et al. 2009, Liu et al. 2010, Wellings 2011). In contrast, adult-plant resistance or race non-specific resistance is generally quantitatively inherited and involves reduced frequencies of infection, longer latent periods, lower urediniospore production and smaller uredinial size compared to susceptible genotypes (Chen and Line 1995a, Liang et al. 2006, Lu et al. 2009). Such resistance has a higher probability of being stable and durable (Niks and Rubiales 2002). It now seems likely that genes conferring resistance to multiple diseases maintain effectiveness for long time periods (Li et al. 2014). As a consequence, there is increased interest in the development of wheat cultivars with race non-specific or adult-plant resistance (APR).

Adult-plant resistance is more complicated for handling in wheat breeding compared with race-specific resistance because of its polygenic nature with minor effect. Nevertheless, molecular markers can be used to identify and locate genes for APR and to estimate the effect of each resistance gene, greatly facilitating selection for APR in breeding programmes. Many APR genes in wheat are associated with molecular markers, such as *Yr16* on chromosome 2DL (Devos et al. 1993), *Yr18/Lr34* on 7DS (Lagudah et al. 2006), *Yr29/Lr46* on 1BL (Rosewarne et al. 2006), *Yr30* on 3BS (Singh et al. 2000a), *Yr36* on 6BS (Uauy et al. 2005, Fu et al. 2009), *Yr39* on 7BL (Lin and Chen 2007), *Yr46/Lr67* on 4DL (Herrera-Foessel et al. 2011), *Yr48* on 5AL (Lowe et al. 2011), *Yr49* on 3DS (McIntosh et al. 2011), *Yr52* on 7BL (Ren et al. 2012a) and *Yr54* on 2DL (Basnet et al. 2013). Among them, the loci *Yr18/Lr34*, *Yr29/Lr46* and *Yr46/Lr67*, initially identified to confer resistance to stripe rust and leaf rust, also pro-

vide partial resistances to powdery mildew and stem rust, with additional designations as *Pm38/Sr57*, *Pm39/Sr58* and *Pm46/Sr55*, respectively (Lillemo *et al.* 2008, Herrera-Foessel *et al.* 2014, Li *et al.* 2014). These genes confer low to moderate levels of resistance to rusts when present alone, but in combinations with other slow-rusting genes, high levels of resistance can be achieved (Singh *et al.* 2000a, Herrera-Foessel *et al.* 2011). However, the levels of resistance can be variable across environments and genetic backgrounds. For example, *Yr29/Lr46* conferred lower levels of resistance to leaf rust and powdery mildew than *Yr18/Lr34* (Lagudah 2011), but displayed larger effects in Avocet/Pastor and Avocet/Francolin#1 genetic backgrounds (Rosewarne *et al.* 2012, Lan *et al.* 2014). *Yr18/Lr34* was cloned and shown to encode a putative ATP-binding cassette (ABC) transporter. The cloned sequence enabled development of diagnostic molecular markers that are suitable for marker-assisted selection (Fu *et al.* 2009, Krattinger *et al.* 2009, Lagudah *et al.* 2009, Yuan *et al.* 2012). In addition to these named genes, over 140 QTL for reduced stripe rust severity have been identified during the last 10 years (Rosewarne *et al.* 2013). Although APR is more durable than major gene resistance, some sources can be overcome by pathogenicity changes in the pathogen (McDonald and Linde 2002). This has led to increased emphasis in breeding programmes being placed on pleiotropic APR QTL with unique gene sequences and reputed durability. The Chinese common wheat cultivar 'Lumai 21' was a leading cultivar with outstanding yield potential and broad adaptation, covering an area of 300 000 ha in the Yellow and Huai Valleys Winter Wheat Region from 1994 to 2007 (Lan *et al.* 2010a). It exhibits a moderate level of APR to Chinese *Pst* races in the field, but is susceptible to some pathotypes at the seedling stage. It also has APR to leaf rust and powdery mildew. QTL mapping of APR to powdery mildew in the 'Lumai 21' × 'Jingshuang 16' F₃ population was reported by Lan *et al.* (2010a). However, the inheritance of APR to stripe rust in this population has not been reported. The objectives of this study were to detect QTL for stripe rust APR to in the 'Lumai 21' × 'Jingshuang 16' population using molecular markers and to assess the stability of the detected QTL across environments.

Materials and Methods

Plant materials: One hundred and ninety-nine F₂-derived bulk lines (hereafter described as F₃ lines) were produced from 'Lumai 21' × 'Jingshuang 16'. 'Lumai 21', developed by the Yantai Academy of Agricultural Sciences, Shandong province, in 1991, is susceptible to Chinese *Pst* races CYR29 and CYR32 at the seedling stage, but is moderately resistant in the field. 'Jingshuang 16' (pedigree: Lovrin 10 × Youmanghong 7), released in Beijing in 1985, is highly susceptible to *Pst* races CYR29 and CYR32 at the seedling stage, but shows a moderate level of APR to stripe rust (Wang *et al.* 2006). *Pst* races CYR29 and CYR32 were provided by Dr. Gangming Zhan, College of Plant Protection, Northwest Agricultural and Forestry University, Yangling, Shaanxi.

Field trials: The F₃ lines and parents were evaluated for stripe rust response during the 2009–2010 and 2010–2011 cropping seasons in Gansu and Sichuan provinces. Both locations are hotspots for stripe rust with ideal conditions for infection and spread. Field trials were conducted in randomized complete blocks with three replicates at each location. Plots consisted of single 1.5-m rows with 25-cm spacing. Approximately 50 seeds were sown in each row. Every tenth row was planted with the highly susceptible cultivar Mingxian 169 to aid spread of the pathogen within the trial. To ensure ample inoculum infection, rows of Mingxian 169 were also planted perpendicularly and adjacent to the test rows. Inoculations were carried out using mixtures of predominantly *Pst* races CYR29 and CYR32

at the beginning of January in Sichuan. In Gansu, mixed *Pst* races CYR29 and CYR32 were inoculated around April 20. The parameter for analysis was maximum disease severity (MDS), scored as the percentage of leaf area covered by stripe rust when the disease severities on Mingxian 169 reached maximum levels around April 15 in Sichuan and June 10 in Gansu. The field data from Gansu 2010–2011 were excluded from the statistical analysis and QTL detection due to low stripe rust development.

Statistical analysis: Mean MDS was used in analysis of variance performed with PROC GLM in the statistical analysis system (SAS) software package (SAS institute, V8; Cary, North Carolina, USA.). The information in the ANOVA table was used to calculate broad-sense heritability (h_b^2) of stripe rust resistance based on the formula

$$h_b^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{ge}^2/r + \sigma_e^2/re)$$

(Allard 1960), where $\sigma_g^2 = (MS_f - MS_e)/r$, $\sigma_{ge}^2 = (MS_{fe} - MS_e)/r$ and $\sigma_e^2 = MS_e$; in this formula, σ_g^2 = genetic variance, σ_{ge}^2 = genotype × environment interaction variance, σ_e^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 replications and e = number of environments.

Genotyping: A total of 1375 simple sequence repeat (SSR) markers were screened on 'Lumai 21' and 'Jingshuang 16'. Then, pooled DNA representing contrasting bulks for stripe rust response were screened for polymorphism with 422 SSR markers polymorphic between the parents; these included BARC (Song *et al.* 2002), CFA and CFD (Sourdille *et al.* 2004), CFE (Zhang *et al.* 2005), CWEM (Peng and Lapitan 2005), GDM (Pestsova *et al.* 2000), GWM (Röder *et al.* 1998) and WMC (Gupta *et al.* 2002) markers. SSR markers that showed similar patterns of polymorphism between the bulks and between parents were used to genotype all 199 F₃ lines from the 'Lumai 21' × 'Jingshuang 16' cross.

Map construction and QTL analysis: Genetic linkage maps were constructed using Map Manager QTX20 (Manly *et al.* 2001). Markers were assigned to linkage groups with a minimum logarithm of the odds (LOD) threshold of 3.0, and genetic distances between markers were estimated for recombination values based on the Kosambi mapping function (Kosambi 1944). The ordering of markers and assignment of linkage groups to chromosomes were checked against a public wheat consensus map (Somers *et al.* 2004).

Stripe rust resistance QTL were detected by inclusive composite interval mapping (ICIM) using the software QTL IciMapping V3.1 (Li *et al.* 2007, 2008, Wang 2009), based on the MDS for each environment and those averaged from all environments combined. After performing a 1000 permutation test, a LOD threshold of 2.5 was set to declare QTL as significant. A walk speed of 1.0 cM was chosen for all QTL detections. QTL effects were estimated as the phenotypic variance explained (PVE) and additive effects explained by the QTL. In this study, the genotype of 'Lumai 21' was defined as 2, and the genotype of 'Jingshuang 16' was defined as 0. Thus, the allele from 'Lumai 21' reduces stripe rust MDS when the additive effect is negative.

Results

Phenotypic evaluations

Stripe rust developed well across environments, except for Gansu in 2010–2011. The frequency distributions of stripe rust MDS for the 199 F₃ lines in three environments and averaged MDS for three environments revealed continuous distributions (Fig. 1), indicating polygenic inheritance. The averaged MDS of the F₃ lines across three environments was 36.5%, ranging from 8.1 to 80.6%. The MDS of the susceptible control Mingxian 169 ranged from 60 to 100%, from 90 to 100% and from 50 to 90% in Sichuan 2009–2010, Sichuan 2010–2011 and Gansu 2009–2010 seasons, respectively. 'Lumai 21' was rated with a mean

MDS of 45.0%, 56.7% and 24.0% in the Sichuan 2009–2010, Sichuan 2010–2011 and Gansu 2009–2010 seasons, respectively, whereas ‘Jingshuang 16’ had a mean MDS of 26–59% across all three environments.

The MDS data were significantly correlated across the three environments, ranging from 0.655 to 0.710 ($P < 0.01$) (Table 1), and the broad-sense heritability of MDS was 0.86. ANOVA revealed significant differences ($P = 0.01$) in MDS among F_3 lines, environments, replicates within environments and line $\times$ environment interactions (Table 2).

Detection of QTL for stripe rust resistance

Five QTL for APR to stripe rust were identified on chromosomes 2B (two loci), 2DS, 4DL and 5DS based on ICIM using the MDS in each environment and the averaged value from all three environments (Fig. 2, Table 3). They were designated *QYr.caas-2BS.2*, *QYr.caas-2BL.2*, *QYr.caas-2DS.2*, *QYr.caas-4DL.2* and *QYr.caas-5DS*, respectively.

A QTL for stripe rust response was located on chromosome 2DS, flanked by *Xbarc168* and *Xwmc18*, explaining 6.5%, 18.2%, 2.3% and 13.8% of the phenotypic variance in Sichuan 2009–2010, Sichuan 2010–2011, Gansu 2009–2010 seasons and the averaged MDS, respectively. The QTL with large effect, which is consistently detected secondly, *QYr.caas-5DS*, were located on 5DS between *Xgwm190* and *Xgwm180* and explained 5.1–18.0% of the phenotypic variance in the three environments as well as the overall mean. The remaining three QTL were detected in single environments. *QYr.caas-2BL.2* and *QYr.caas-4DL.2* were in marker intervals *Xcfd73-Xgwm47* and *Xbarc98-Xbarc1148* and explained 6.2% and 7.6%, respectively, of the phenotypic variance in the Gansu 2009–2010 season. *QYr.caas-2BS.2* was located between *Xbarc156* and *Xbarc1147* on chromosome 2BS, explaining of 7.4% the phenotypic variance in the averaged MDS. Table 3 indicates that the additive effects of *QYr.caas-2BS.2*, *QYr.caas-2BL.2*, *QYr.caas-2DS.2* and *QYr.caas-4DL.2* were negative, indicating the resistance alleles at these four QTL were from ‘Lumai 21’. The allele on 5DS,

Table 1: The correlation analysis table of the mean maximum disease severity (MDS) across three environments

	Sichuan 2010	Sichuan 2011	Gansu 2010
Sichuan 2010	1		
Sichuan 2011	0.710**	1	
Gansu 2010	0.655**	0.663**	1

**Significant at $P = 0.01$.

Table 2: Analysis of variance of maximum disease severity (MDS) scores for F_3 lines generated from ‘Lumai 21’ $\times$ ‘Jingshuang 16’

Source of variation	df	Mean square	F value	P value
Lines	198	2158.3	13.7**	<0.0001
Environments	2	154726.9	984.2**	<0.0001
Replicates (Environment)	6	7689.7	48.9**	<0.0001
Lines $\times$ environments	396	299.7	1.9**	<0.0001
Error	1188	157.2		

**Significant at $P = 0.01$.

derived from ‘Jingshuang 16’, also significantly reduced stripe rust severity. The total phenotypic variance explained by all five QTL ranged from 23.3 to 30.4% in a simultaneous fit across the three environments, suggesting an obvious effect of these QTL in reducing YR severity. Interactions among different QTL were not identified across the three environments.

Discussion

The Chinese cultivar ‘Lumai 21’ not only shows good and stable slow-mildewing resistance, but also is moderately resistant to stripe rust at the adult-plant stage. Four APR QTL for stripe rust were detected in ‘Lumai 21’. Based on the pedigree of ‘Lumai 21’ (Lumai 13/Yumai 2), the four APR QTL are likely derived from Yumai 2, a leading cultivar and a core-breeding parent in Henan. The other parent ‘Jingshuang 16’ showed a moderately

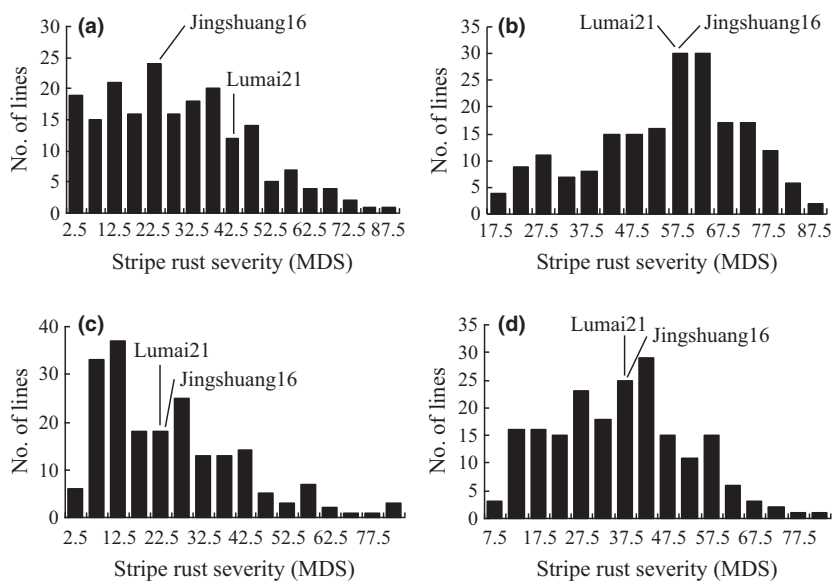


Fig. 1: a–d, Frequency distribution of stripe rust maximum disease severity (MDS) for F_3 lines from the wheat cross ‘Lumai 21’ $\times$ ‘Jingshuang’ 16 in three environments and averaged MDS. a, MDS, Sichuan 2010; b, MDS, Sichuan 2011; c, MDS, Gansu 2010; and d, averaged MDS across all three environments. Mean disease severity for the parents, ‘Lumai 21’ and ‘Jingshuang 16’, is indicated by lines

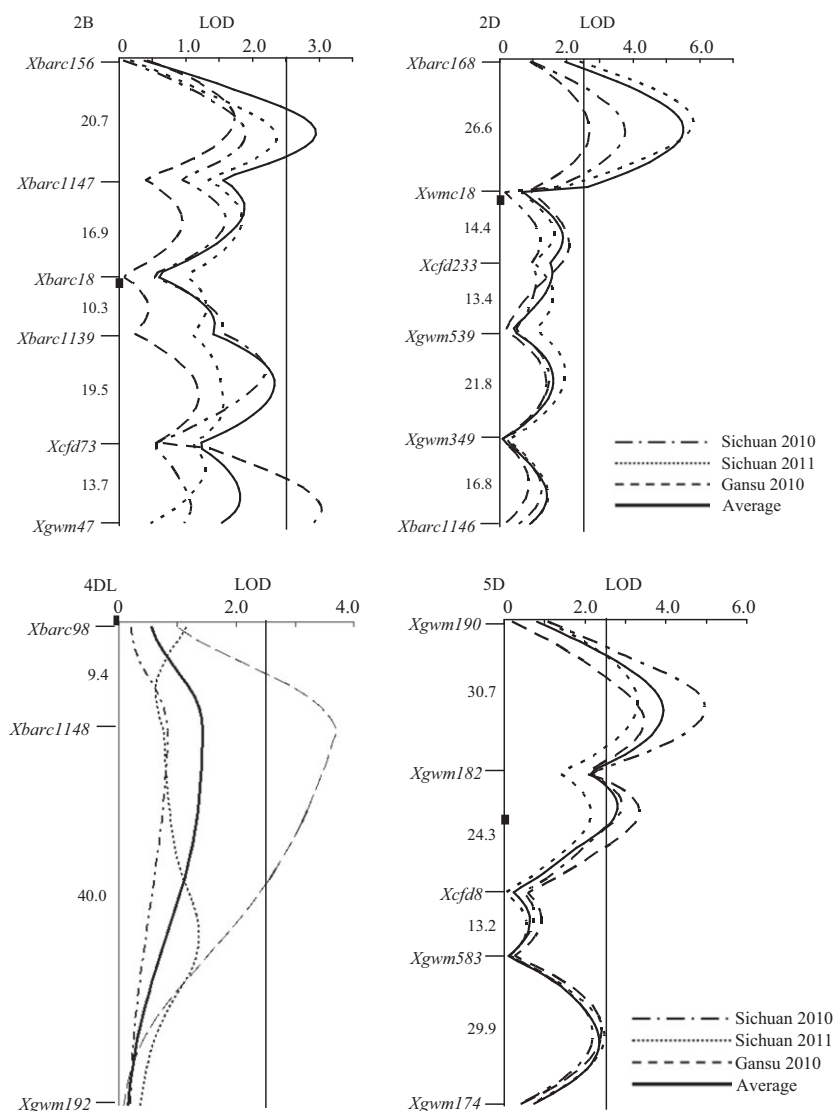


Fig. 2: Logarithm of the odds (LOD) contours for QTL on chromosomes 2B (2 QTL), 2DS, 4DL and 5DS that reduce stripe rust severity in the F_3 population from 'Lumai 21' $\times$ 'Jingshuang 16'. The short arms are towards the top, and approximate positions of centromeres are indicated by solid squares in the vertical axis. Genetic distances are shown in centiMorgans (cM) to the left of the vertical axes. LOD thresholds of 2.5 are indicated by dashed vertical lines

resistant reaction with MDS from 26 to 59% in field tests and contributed one APR QTL (*QYr.caas-5DS*) to the cross.

Nineteen stripe rust resistance QTL have been mapped on chromosome 2B by molecular markers (Boukhatem *et al.* 2002, Ramburan *et al.* 2004, Mallard *et al.* 2005, Christiansen *et al.* 2006, Guo *et al.* 2008, Rosewarne *et al.* 2008, Carter *et al.* 2009, Dedryver *et al.* 2009, Lan *et al.* 2010b, Lowe *et al.* 2011, Chen *et al.* 2012, Ren *et al.* 2012b, Vazquez *et al.* 2012, Xu *et al.* 2013), and these QTL are concentrated in four chromosomal regions (Rosewarne *et al.* 2013). In this study, the cultivar 'Lumai 21' contained two QTL, viz. *QYr.caas-2BS.2* and *QYr.caas-2BL.2*, more than 30 cM apart, on chromosome 2B. *QYr.caas-2BS.2* was flanked by *Xbarc156* and *Xbarc1147* and was in the *QRYr2B.2* region, whereas *QYr.caas-2BL.2*, flanked by *Xcfd73* and *Xgwm47*, coincides with the *QRYr2B.3* region (Somers *et al.* 2004, Rosewarne *et al.* 2013). However, these two QTL were detected only in a single environment, and they showed lower effects and stability than the other reported QTL. This indicated that the expression of the two QTL in 'Lumai 21' might be influenced by environmental factors.

Bariana *et al.* (2001) reported a QTL flanked by SSR markers *Xwmc111* and *Xwmc25* on chromosome 2DS in cultivar

Katepwa. This region was also identified in wheat cultivars *Oligoculm* and *Libellula* (Suenaga *et al.* 2003, Lu *et al.* 2009). That QTL was approximately 24 cM from *QYr.caas-2DS.2* based on the consensus map (Somers *et al.* 2004), suggesting that it is different. Agenbag *et al.* (2012) identified a QTL (*QYr.ufs-2D*) flanked by SSR markers *Xgwm102* and *Wpt-664520* on 2DS in the French cultivar *Cappelle-Desprez*. *QYr.caas-2DS.2* mapped to the same region, but contributed more to phenotypic variation (maximum of 18.2%). Mallard *et al.* (2005) identified a QTL (*QYr.inra-2DS*) in a similar chromosomal region in the French cultivar *Camp Remy*, explaining 24.0–69.0% of the phenotypic variance across years, indicating an obviously stronger effect across environments than both *QYr.ufs-2D* and *QYr.caas-2DS.2*. However, the ancestral relationship between these French cultivars and 'Lumai 21' is not as clear as for *Cappelle-Desprez* and *Camp Remy*. There is a large region in the proximal part of chromosome 2DL that contains QTL from four parents, viz. *Fukuho-komugi*, *Guardian*, *Alcedo* and *Naxos*. This region is more than 20 cM proximal to *QYr.caas-2DS.2* (Suenaga *et al.* 2003, Somers *et al.* 2004, Melichar *et al.* 2008, Jagger *et al.* 2011, Ren *et al.* 2012c). These QTL seem to be different from *QYr.caas-2DS.2*.

Table 3: Quantitative trait loci (QTL) for adult-plant resistance (APR) to stripe rust detected by inclusive composite interval mapping (ICIM) in the 'Lumai 21' × 'Jingshuang 16' F₃ population across three environments

Location and year	QTL	Marker interval	LOD	PVE (%)	Add
Sichuan 2010	<i>QYr.caas-2DS.2</i>	<i>Xbarc168-Xwmc18</i>	3.7	6.5	-5.2
	<i>QYr.caas-5DS</i>	<i>Xgwm190-Xgwm182</i>	5.0	18.0	14.0
	<i>QYr.caas-2DS.2</i>	<i>Xbarc168-Xwmc18</i>	5.8	18.2	-5.0
Sichuan 2011	<i>QYr.caas-5DS</i>	<i>Xgwm190-Xgwm182</i>	3.3	5.1	6.6
	<i>QYr.caas-2BL.2</i>	<i>Xcfd73-Xgwm47</i>	3.0	6.2	-2.5
	<i>QYr.caas-2DS.2</i>	<i>Xbarc168-Xwmc18</i>	2.7	2.3	-2.6
Gansu 2010	<i>QYr.caas-5DS</i>	<i>Xgwm190-Xgwm182</i>	3.4	9.5	10.0
	<i>QYr.caas-4DL.2</i>	<i>Xbarc98-Xbarc1148</i>	3.7	7.6	-7.6
	<i>QYr.caas-2BS.2</i>	<i>Xbarc156-Xbarc1147</i>	2.9	7.4	-3.0
Averaged MDS in 3 environments	<i>QYr.caas-2DS.2</i>	<i>Xbarc168-Xwmc18</i>	5.5	13.8	-5.4
	<i>QYr.caas-5DS</i>	<i>Xgwm190-Xgwm182</i>	3.9	9.2	8.6

QTL were detected with a minimum LOD score of 2.5 in at least one environment; LOD, logarithm of odds score; PVE, percentages of the phenotypic variance explained by individual QTL; Add, additive effect of resistance allele.

Suenaga et al. (2003) reported a QTL for stripe rust resistance on chromosome 4DL in the Israeli wheat Oligoculm. This QTL was closely linked to *Xwmc399* and contributed only a low level of resistance (variance range 2.5–8.0%). This QTL was approximately 24 cM from *QYr.caas-4DL.2* (He et al. 2011) indicating it is different from *QYr.caas-4DL.2*. Hiebert et al. (2010) and Herrera-Foessel et al. (2011) located an APR gene (*Yr46/Lr67*) on 4DL in the Thatcher derivative RL6077 that was closely linked to markers *Xgwm165* and *Xgwm192* and fell within the marker interval carrying *QYr.caas-4DL.2* based on the consensus map (Somers et al. 2004). Ren et al. (2012b) and Rosewarne et al. (2012) also identified a minor stripe rust resistance QTL at the same chromosomal region in Chinese wheat cultivar Bainong 64 and CIMMYT line Pastor, explaining 3.9–8.0% and 2.8–4.9% of the phenotypic variances, respectively. Of the two, *QYr.caas-4DL* contributed by Bainong 64 and *Yr46* might be the same as both confer partial resistance to stripe rust, leaf rust and powdery mildew (Liu et al. 2014). However, it is clear that Pastor did not have associated QTL for stripe rust and leaf rust resistances at this locus (Rosewarne et al. 2012) and therefore appear to be different. Although the locus in 'Lumai 21' conferred resistance to both stripe rust and leaf rust, there was no significant effect in reducing the severity of powdery mildew (Lan et al. 2010a, Liu et al. 2014). We tested 'Lumai 21' and 'Jingshuang 16' using the SNP marker *csSNP856* that was co-segregating with *Lr67/Yr46* locus (Herrera-Foessel et al. 2014) and did not find any polymorphisms between two parents indicating that *QYr.caas-4DL.2* is different from *Yr46*. The effects of the potential pleiotropic APR QTL might therefore be influenced by different genetic background.

QYr.caas-5DS in cultivar 'Jingshuang 16' is close to the centromere. Singh et al. (2000b) identified a QTL for APR to stripe rust in Mexican cultivar Opatá 85 on chromosome 5DS, flanked

by *Xfbb238* and *Xfba114* and located in the same region as *QYr.caas-5DS* based on the consensus map (Somers et al. 2004). However, the QTL explained 8.0% of the phenotypic variance in only one environment which showed a lower effect and stability than *QYr.caas-5DS*.

The same 'Lumai 21' × 'Jingshuang 16' population was previously used for QTL mapping of powdery mildew (PM) resistance and three QTL for APR to PM were identified on chromosomes 2B (2 QTL) and 2D (Lan et al. 2010a). In comparison with the present study, *QYr.caas-2BS.2* and *QYr.caas-2BL.2* collocated with QTL for PM resistance with the resistance alleles contributed by 'Lumai 21'. This is consistent with a report by Liu et al. (2014), who demonstrated that *QPm.caas-2BS.2* and *QPm.caas-2BL.2* from 'Lumai 21' provided significant levels of resistance to stripe rust ($P < 0.01$). However, *QPm.caas-2DL* did not show a significant effect in reducing stripe rust severity (Liu et al. 2014). Although *QYr.caas-2DS.2* was collocated with *QPm.caas-2DL*, they are likely different genes.

In the present study, we detected two QTL conferring stable resistance to stripe rust across environments, including *QYr.caas-2DS.2* and *QYr.caas-5DS*, and corresponding linked SSR markers. These two QTL and their linked markers could be used to achieve stable stripe rust resistance in wheat breeding. *QYr.caas-2BS.2* and *QYr.caas-2BL.2* may confer resistance to multiple diseases and therefore might be useful for improving stripe rust and powdery mildew resistances by marker-assisted selection.

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