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QTL characterization of resistance to leaf rust and stripe rust in the spring wheat line Francolin#1

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Abstract Growing resistant wheat varieties is a key method of controlling two important wheat diseases, leaf rust and stripe rust. We analyzed quantitative trait loci (QTL) to investigate adult plant resistance (APR) to these rusts, using 141 F_5 RILs derived from the cross 'Avocet-*YrA*/Francolin#1'. Phenotyping of leaf rust resistance was conducted during two seasons at Ciudad Obregon, Mexico, whereas stripe rust was evaluated for two seasons in Toluca, Mexico, and one season in Chengdu, China. The genetic map was constructed with 581 markers, including diversity arrays technology and simple sequence repeat. Significant loci for reducing leaf rust severity were designated *QLr.cim-1BL*, *QLr.cim-3BS.1*, *QLr.cim-3DC,* and *QLr.cim-7DS*. The six QTL that reduced stripe rust severity were designated *QYr.cim-1BL*, *QYr.cim-2BS*, *QYr.cim-2DS*, *QYr.cim-3BS.2*, *QYr.cim-5AL,* and *QYr.cim-6AL*. All loci were conferred by Francolin#1, with the exception of *QYr.cim-2DS*, *QYr.cim-5AL,* and *QYr.cim-6AL,* which were derived from Avocet-*YrA*. Closely linked markers indicated that the 1BL locus was the pleiotropic APR gene *Lr46/Yr29*. *QYr.cim-2BS* was a seedling resistance gene designated as *YrF* that conferred intermediate seedling reactions and moderate resistance at the adult plant stage in both Mexican and Chinese environments. Significant additive interactions were detected between the six QTL for stripe rust, but not between the four QTL for leaf rust. Furthermore, we detected two new APR loci for leaf rust in common wheat: *QLr.cim-3BS.1* and *QLr.cim-7DS*.

Keywords Adult plant resistance (APR) genes · Brown rust · *Triticum aestivum* · *Puccinia triticina* · Yellow rust

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Introduction

Wheat rust diseases, leaf (brown) rust and stripe (yellow) rust, caused by *Puccinia triticina* and *P. striiformis*, respectively, are two major diseases that

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constraint wheat production worldwide. They affect up to 20 % (leaf rust) and 40 % (stripe rust) of the production area in countries such as Mexico, India, Pakistan, Bangladesh, and China (Dubin and Brennan 2009). Wheat rust epidemics are a major threat to global food security. A particularly severe leaf rust epidemic in northwestern Mexico during 1976–1977 caused an estimated 70 % loss in wheat yields (Dubin and Torres 1981), and more than 20 stripe rust epidemics have been documented worldwide (Wellings 2011). Wheat rusts can be controlled by fungicides, but this method may be limited by financial constraints, chemical availability, or inclement weather conditions affecting timely application. Breeding resistant cultivars is therefore an attractive and effective approach to control these diseases.

There are two main resistance types: seedling (or all-stage) resistance and adult plant resistance (APR). Seedling resistance is usually race specific and qualitatively inherited, so readily broken down and has a limited life span (Johnson 1981). APR is often non-race specific and therefore durable, but it is quantitatively inherited and several loci are required to obtain adequate resistance levels (Singh et al. 2004). So far, 72 and 56 loci for leaf rust and stripe rust resistance genes, respectively, have been designated (McIntosh et al. 2012). Six of these loci, *Lr34/Yr18* (Spielmeyer et al. 2005), *Yr36* (Uauy et al. 2005), *Lr46/Yr29* (Williams et al. 2006), *Lr67/Yr46* (Herrera-Foessel et al. 2011), *Lr68* (Herrera-Foessel et al. 2012), and *Yr54* (Basnet et al. 2013), confer APR to leaf rust and/or stripe rust. Of these, *Lr34/Yr18*, *Lr46/Yr29,* and *Lr67/Yr46* show pleiotropic adult plant resistance (PAPR) against multiple pathogens. Recently, *Lr34/Yr18* and *Yr36* have been cloned, and as their predicted molecular structures show unrelated molecular functions, it seems likely that there are multiple pathways for generating APR (Fu et al. 2009; Krattinger et al. 2009).

Furthermore, over 80 leaf rust and 140 stripe rust quantitative trait loci (QTL) have been described in wheat (McIntosh et al. 2012; Rosewarne et al. 2013). Many of these QTL are from the same genetic regions and are likely to be identical loci (Rosewarne et al. 2013). PAPR loci occur most commonly throughout the literature. The *Lr34/Yr18* locus has been identified in rust studies in 11 different backgrounds, *Lr46/Yr29* in nine backgrounds, and *Sr2/Yr30* in up to 11 backgrounds (Rosewarne et al. 2013). The fourth potential PAPR locus, *Lr67/Yr46*, has only been identified in a few backgrounds to date and appears underutilized. Combinations of these loci have been used as foundations for breeding durable resistance, and it is therefore useful to identify novel PAPR loci to maintain genetic diversity in breeding for rust resistance.

Francolin#1, a high-yielding spring wheat line developed by the International Maize and Wheat Improvement Center (CIMMYT), displays good agronomic characters and stable resistance to leaf rust, stripe rust, and the Ug99 stem rust races. These characters have enabled it to be released as a variety in Bangladesh, India, and Kenya (Joshi et al. 2010; Malaker and Reza 2011). It is also widely used as a parent in the CIMMYT wheat breeding program. Francolin#1 resistance to leaf rust and stripe rust is governed by a combination of two loosely linked, moderately effective seedling resistance genes (*Lr16* and *YrF*) and three to five slow rusting APR genes (Lan et al. 2014). *Lr16* (McIntosh et al. 2012) was located on chromosome 2B, although the precise position of *YrF* and locations of the APR loci to leaf rust and stripe rust in Francolin#1 were not clear (Lan et al. 2014).

This study aimed to more precisely map the seedling race-specific resistance genes *Lr16* and *YrF*; to identify APR loci to leaf rust and stripe rust in the adult plant stage; and to detect the additive interaction between significant QTL for leaf rust and stripe rust in adult plants of an Avocet-*YrA*/Francolin#1 RIL population.

Materials and methods

Plant material

A total of 141 F_5 recombinant inbred lines (RILs) were developed from a cross between spring wheat parents Avocet-*YrA* and Francolin#1. Avocet-*YrA*, hereafter termed Avocet, is a re-selection line from the Australian cultivar Avocet that lacks the resistance gene temporarily designated as *YrA*. Francolin#1 (pedigree: Waxwing*2/Vivitsi), hereafter termed Francolin for simplicity, is resistant to current Mexican pathotypes of leaf rust and stripe rust at seedling and adult stages, whereas Avocet is susceptible to these pathotypes at all growth stages. The population was generated

through single seed descent, where one random spike was harvested in each generation and advanced to the next generation by sowing as hill plots. A single seed source of the F_5 RILs and parents was used in all experiments.

Field trials

The F_5 RILs and their parents were evaluated for slow rusting APR to leaf rust at Ciudad Obregon, State of Sonora, Mexico, during the 2008–2009 and 2009–2010 crop seasons. Field plots consisted of 0.7 m paired rows with approximately 60 plants of each line. The susceptible variety 'Morocco' was used as a spreader for leaf rust and was sown around the experimental area and as hill plots in the middle of a 0.3 m pathway on one side of each experimental plot. Rust urediniospores were suspended in Soltrol 170 oil and sprayed onto Morocco with a mixture of *P. triticina* races MBJ/SP and MCJ/SP at tillering to early stem elongation stages. The avirulence/virulence formulas of MBJ/SP and MCJ/SP have been reported in previous studies (Herrera-Foessel et al. 2012; Lan et al. 2014). The main difference between the two races is partial virulence for *Lr26* in MBJ/SP, but complete virulence for this gene in MCJ/SP.

Stripe rust resistance was evaluated in Toluca, State of Mexico, Mexico, during 2009 and 2010, and in Chengdu, Sichuan Province, China during the 2012–2013 season. The field layout was as described for the leaf rust trial with the spreader rows being a mixture of six susceptible wheat lines derived from an Avocet/Attila cross for the Mexican stripe rust trials, and Chuanyu 12 for the stripe rust trials in China. *P. striiformis* isolates Mex96.11 and Mex08.13 were used to infect the spreader rows in Toluca. The main difference between these two isolates is virulence for *Yr27* and avirulence for *Yr31* in Mex96.11, and the opposite in Mex08.13. A mixture of stripe rust races CYR32, CYR33, and a new race V26 were used to inoculate Chuanyu 12. The avirulence/virulence formulas of CYR32 and CYR33 have been previously described in a Chinese differential set (Chen et al. 2009). For V26, the avirulence/virulence formula is *Yr1, 3, 4, H46, 5, 6, 15, 17, 18, 32, Sp, Sd/Yr2, 8, 9, 10, 12, 24* (=*26*)*, 31, Su* (Liu et al. 2010), with the notable acquisition of virulence to *Yr24* being of greatest concern. The Mexican trials were inoculated with stripe rust approximately at the end of seedling stage and the initiation of tillering stage, whereas the Chinese trial was inoculated at the begin of tillering stage.

Rust severity on the parents and lines was scored according to the modified Cobb Scale of Peterson et al. (1948). This was done once in 2009, twice in 2010, and thrice in 2013 when leaf rust severity on the susceptible parent Avocet reached 90–100 % in Obregon, and stripe rust severity on Avocet was 80–90 % in Toluca and 60–80 % in Sichuan at milk stage onward for Avocet and middle dough stage for Francolin. The host response to infection in adult plant was determined according to Roelfs et al. (1992), where 'MS' = moderately susceptible, or moderate-sized uredinia without necrotic or chlorotic tissues; 'S' = susceptible, or large uredinia without necrotic or chlorotic tissues; and 'RMR' = resistant, necrotic/chlorotic stripes with small sporulation.

Molecular analysis

DNA was extracted from the parents and RILs of approximately 20 plants per line using the CTAB method described by CIMMYT (2005). Mapping was conducted on parents and 141 RILs by genotyping with several marker systems. The diversity arrays technology (DArT) marker system was used to investigate potential polymorphisms of 1450 available markers. These were screened against the parents and the entire population. Polymorphic loci were defined as present (1) or absent (0) and designated as 'wPt,' 'rPt,' and 'tPt,' followed by numbers corresponding to a particular clone in the genomic representation. The two parents were also screened using 520 simple sequence repeat (SSR) primers, 138 of which were polymorphic and evaluated on the entire population. Relevant information for SSR primers, including those with prefixed GWM, WMC, BARC, CFA, and CFD, was obtained from GrainGenes (http://wheat.pw.usda.gov). Two sequence tagged sites (STS) markers, *csLV46* and *csGS*, were used to show the association with *Lr46* (E. Lagudah Pers. comm.) and *Lr68* (Herrera-Foessel et al. 2012), respectively. In addition, 2 seedling resistance genes were also included. Standard PCR-based methods were used (CIMMYT 2005), with annealing temperatures according to available information for each marker. Each sample was loaded on 10 % polyacrylamide gels (29:1), and silver staining was used to visualize the amplification products (CIMMYT 2005).

Linkage map construction, QTL and statistical analyses

Genetic linkage groups were established with IciMapping 3.3 (https://www.integratedbreeding.net/supplementary-toolbox/genetic-mapping-and-qtl/icimapping) using the 'BIN' tool to reduce the redundant markers. 'COUNT' and 'Two Opt' were used for linkage criteria and algorithm, respectively, with the logarithm of odds (LOD) set at five for grouping. Inclusive composite interval mapping (ICIM) was carried out to detect the positions of QTL for final disease severity (FDS) in each environment (year), area under the disease progress curve (AUDPC), and mean of final disease severity (MFDS) across 2 and 3 years for leaf rust and stripe rust, respectively. LOD scores were calculated from 1,000 permutations for each trait to declare significant QTL at the $P = 0.05$ level. The percentages of phenotypic variance explained (PVE) by individual QTL and the additive effect at the LOD peaks were obtained though stepwise regression with IciMapping 3.3. To further elucidate the effect of smaller QTL on leaf rust, analyses were performed on a sub-population that omitted RILs with the largest-effect QTL for leaf rust. Marker orders and the chromosomal assignments of the linkage groups were based on a consensus genetic map of wheat and physical map location of DArT markers (Somers et al. 2004; Francki et al. 2009; Huang et al. 2012; http://www.cerealsdb.uk.net/CerealsDB/Documents/DOCCerealsDB.php). QTL names were designated following the recommended rules (http://wheat.pw.usda.gov/ggpages/wgc/98/Intro.htm). The significance of additive interaction for pairwise comparisons of leaf rust and stripe rust resistance QTL was conducted using the PROC GLM and *t* test in SAS software (SAS Institute, Cary, NC). Linkage maps were graphically visualized with MapChart (Voorrips 2002).

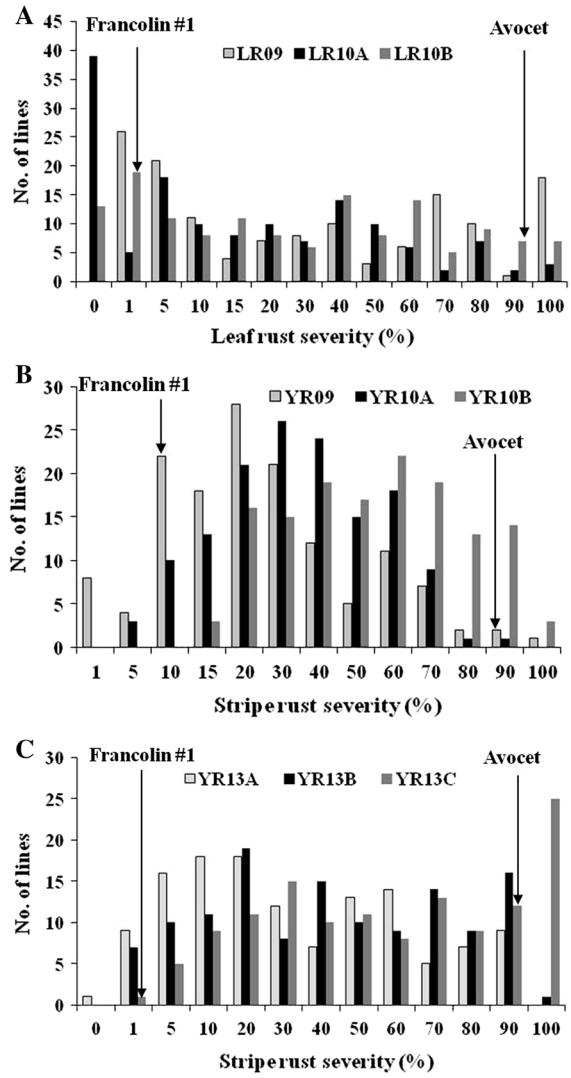


Fig. 1 Frequency distributions of 141 Avocet/Francolin#1 F_5 recombinant inbred lines (RILs) for leaf rust (**A**) severity in field trials at Ciudad Obregon during 2008–2009 (one reading: LR09) and 2009–2010 (two readings: LR10A and LR10B); stripe rust (**B**) severity at Toluca during 2009 (one reading: YR09) and 2010 (two readings: YR10A and YR10B); and stripe rust (**C**) severity at Sichuan during 2013 (three readings: YR13A, YR13B, and YR13C). Mean values for the parents, Avocet and Francolin#1, are indicated by *arrows*

Results

Phenotypic evaluation in the adult plant stage

The FDS (%) and reaction to leaf rust were '90 S' for Avocet and '0' for Francolin at anthesis stage, whereas they were '100 S' and '1 MS' at around the mid milk stage during the two crop seasons. MFDS for leaf rust of RILs was ranged from 34.7 to 38.1 % in the two experiments. The frequency distribution of RILs for leaf rust severity was continuous with a pronounced skew toward resistance (Fig. 1A, indicating that a large effect locus for leaf rust was present in the Avocet/Francolin population. The FDS and reaction types against stripe rust at the adult plant stage for

Table 1 Phenotypic Pearson's correlations for leaf rust (LR09 and LR10) and stripe (yellow) rust (Toluca, YR09 and YR10; Sichuan, YR13) in the 141 Avocet/Francolin#1 F_5 RILs population using the final disease score (FDS) for each season

	LR09	LR10	YR09	YR10	YR13
LR10	0.83*	–			
YR09	0.55*	0.52*	–		
YR10	0.76*	0.73*	0.69*	–	
YR13	0.42*	0.39*	0.50*	0.57*	–

* Significant at $P < 0.0001$

Avocet and Francolin were '80 S' and '1 R' at early milk and dough stages for Avocet and Francolin, respectively, and they were '90 S' and '10 RMR' at mid milk and soft dough stages for Avocet and Francolin, respectively. MFDS for stripe rust of the RILs ranged from 28.6 to 57.5 % in the 3 years. The RILs showed approximately normal distributions for FDS in Toluca (Fig. 1B), and the frequency of stripe rust severity in Sichuan (Fig. 1C) was highly skewed to right side for the third reading, with both sites indicating polygenic inheritance of APR to stripe rust.

Correlation analysis

Correlation coefficient (r) of leaf rust severity for the Avocet/Francolin RILs was 0.83 between the 2 years (Table 1), whereas it was ranged from 0.50 to 0.69 ($P < 0.0001$) for stripe rust severity between the 3 years (Table 1). There were significant correlations in disease severity ($r = 0.39$–0.76, $P < 0.0001$) between leaf rust and stripe rust in all environments (Table 1).

Genetic linkage mapping

A total of 581 markers were used to construct the genetic linkage map and spanned 886, 1402, and 794 in the A, B, and D genomes, respectively. In all, 23 linkage groups were defined, with representatives from each chromosome with the exceptions of chromosomes 3D and 5D. Only the genetic maps of relevance are reported herein (those relating to the location of seedling genes and QTL).

Two seedling leaf rust and stripe rust resistance genes, *Lr16* and *YrF*, respectively, mapped 63.5 cM apart on the short arm of chromosome 2B. The markers flanking *Lr16* were *Xwmc764* (9.4 cM) and *Xwmc661* (1.4 cM), and those flanking *YrF* were *Xgwm374* (2.0 cM) and *Xwmc474* (1.8 cM; Fig. 2). These SSR markers may be useful for marker-assisted selection in wheat breeding, especially in the case of *YrF*.

QTL mapping for slow rusting APR to leaf rust and stripe rust

The *Lr46/Yr29* locus for resistance to leaf rust and stripe rust was identified in this population through close proximity of the QTL to the near-diagnostic marker *csLV46*. This locus was derived from Francolin, and for consistency, within this study we have given the designations *QLr.cim-1BL* and *QYr.cim-1BL*. These were the most consistent QTL for both rusts in field tests. This locus showed high LOD scores (18.8–25.4 for leaf rust and 6.4–24.6 for stripe rust) and PVE (32.5–44.5 % for leaf rust and 11.7–43.6 % for stripe rust) across all environments in both Mexico and China (Table 2; Fig. 3A).

QTL mapping for slow rusting APR to leaf rust

Three QTL that had an exclusive effect on leaf rust infection were detected in the Avocet/Francolin population. The large effect QTL *QLr.cim-3BS.1*, flanked by DArT markers *wPt-664393* and *wPt-5390*, was only detected in the 2009 trial with a PVE of 30.4 % (Table 2; Fig. 3B). The second minor QTL for slow rusting APR to leaf rust, *QLr.cim-7DS*, flanked by molecular markers *wPt-744857* and *Xgwm295*, had a PVE value of 3.3 % in the 2009 trial and 4.2 % in the analysis of MFDS for leaf rust (Table 2; Fig. 3D). The third QTL, *QLr.cim-3DC*, while not statistically significant in the full population, was detected in a sub-population of RILs that did not carry the *Lr46* locus. In this analysis, it showed significance in the 2010 FDS; in the 2010 AUDPC scores; and in the MFDS for leaf rust (Table 2; Fig. 3C). It was located in the interval of DArT markers *wPt-732670* and *wPt-742537* and accounted for 17.8–25.4 % PVE in the subpopulation of 71 F_5 RILs. All of these QTL were derived from the resistant parent Francolin.

QTL mapping for APR to stripe rust

ICIM analysis detected five QTL for APR to stripe rust in 141 F_5 RILs. A major QTL for stripe rust resistance,

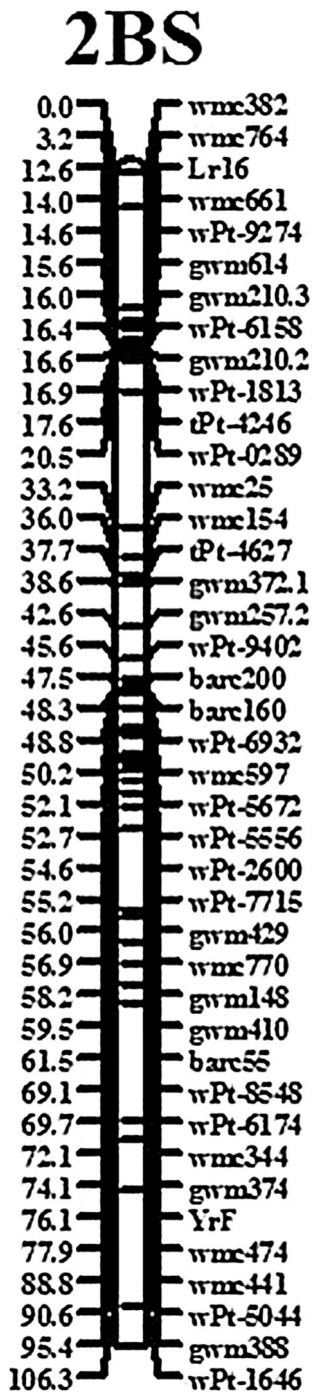


Fig. 2 Linkage map of the seedling resistance genes *Lr16* and *YrF*, and closely linked molecular markers on chromosome 2BS in the 141 Avocet/Francolin#1 F_5 RIL population. Locus names and corresponding locations on the genetic map are indicated on the right side. Map distances in cM are shown on the left side

QYr.cim-2BS, was centrally located over the mapped location of the seedling resistance gene *YrF*. The PVE of this locus was 10.4–22.7 % in adult plants and was detected across all trials in Toluca and Sichuan (Table 2; Fig. 3E). The second QTL for APR to stripe rust, *QYr.cim-2DS*, was located in the interval of DArT markers *wPt-3812* and *wPt-3728* and had PVE of 5.3 % in the 2010 trial and 8.0 % in MFDS over the three years (Table 2; Fig. 3F). The third minor QTL, *QYr.cim-3BS.2,* was located in the interval of markers *wPt-8446* and *Xbarc133* and had PVEs of 4.4–9.0 % across two environments (Table 2; Fig. 3G). *QYr.cim-5AL* was the fourth minor QTL for APR to stripe rust. This locus was located in the interval of *wPt-733649* and *wPt-4262*, and the PVE was ranged from 6.2 to 7.4 % across three environments (Table 2; Fig 3H). The last locus was *QYr.cim-6AL*, which was flanked by DArT markers *wPt-733679* and *wPt-733476* and was a significant QTL in 2010 and 2013 with PVEs of 6.7–8.8 % (Table 2; Fig 3I). *QYr.cim-2BS* and *QYr.cim-3BS.2* were derived from Francolin while *QYr.cim-2DS*, *QYr.cim-5AL,* and *QYr.cim-6AL* were derived from Avocet.

Additive effects of leaf rust and stripe rust QTL

The F_5 RILs were divided into 16 and 27 genotypes based on the presence of four leaf rust and six stripe rust resistance QTL. The flanking molecular markers of each QTL were used to determine the presence of parental alleles in adult plants. Although slight reductions in leaf rust severity occurred when all four QTL were present together, the disease severities were not significantly different from the lines with *QLr.cim-1BL* alone, except in 2010 (Table 3). In contrast, a significant additive effect for stripe rust was found between RILs that possessed six QTL and those with five QTL across 3 years with a MFDS reductions of 6.8–25 % (Table 4). RILs with all six QTL displayed a near immune response to stripe rust.

Discussion

Francolin was highly resistant to leaf rust in two Mexican environments and to stripe rust in two Mexican and one Chinese environment. Resistance

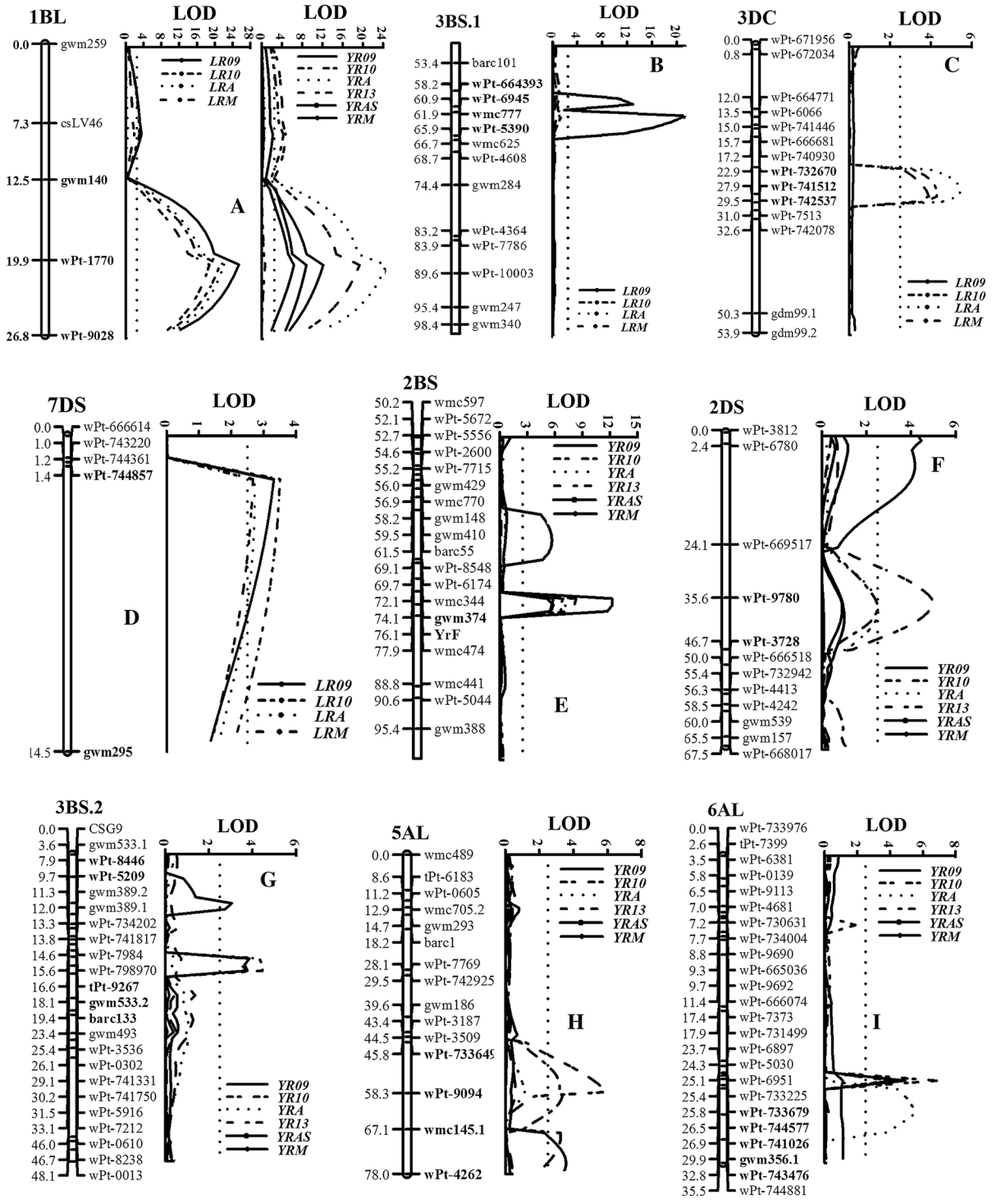
Table 2 Position and effect of quantitative trait loci (QTL) that were detected for adult plant resistance (APR) to leaf rust (LR) and stripe rust (YR) in the given year, using final disease severity (FDS), area under the disease progress curve (AUDPC), and the mean of final disease severity (MFDS) for the given pathogen in the 141 Avocet/Francolin#1 RIL population

Traits	QTL	Position	Left Marker	Right Marker	LOD	PVE(%)	Add[b]
LR09 FDS	*QLr.cim-1BL*	20	*csLV46*	*wPt-9028*	25.4	36.9	21.9
	QLr.cim-3BS.1	62	*wPt-664393*	*wPt-5390*	21.4	30.4	19.9
	QLr.cim-7DS	2	*wPt-744857*	*gwm295*	3.3	3.3	6.6
LR10 FDS	*QLr.cim-1BL*	20	*wPt-1770*	*wPt-9028*	18.8	32.5	18.5
	QLr.cim-3DC[a]	28	*wPt-741512*	*wPt-742537*	3.9	17.8	12
LR10 AUDPC	*QLr.cim-1BL*	20	*wPt-1770*	*wPt-9028*	22.1	44.5	137.8
	QLr.cim-3DC[a]	27	*wPt-732670*	*wPt-741512*	5.4	25.4	98.1
LR MFDS	*QLr.cim-1BL*	20	*csLV46*	*wPt-9028*	21.2	34.1	19.5
	QLr.cim-7DS	2	*wPt-744857*	*gwm295*	3.5	4.2	6.8
	QLr.cim-3DC[a]	27	*wPt-732670*	*wPt-741512*	4.3	19.9	12.1
YR09 FDS	*QYr.cim-1BL*	20	*wPt-1770*	*wPt-9028*	8.8	14.4	8.4
	QYr.cim-2BS	76	*gwm374*	*YrF*	5.8	10.4	7.2
	QYr.cim-3BS.2	8	*wPt-8446*	*wPt-5209*	3.1	4.4	4.8
YR10 FDS	*QYr.cim-1BL*	20	*csLV46*	*wPt-9028*	19.4	25.8	11.8
	QYr.cim-2BS	75	*gwm374*	*YrF*	8.3	12.2	8.2
	QYr.cim-2DS	36	*wPt-9780*	*wPt-3728*	5	5.3	−5.4
	QYr.cim-5AL	58	*wPt-733649*	*wPt-9094*	6	6.4	−5.9
	QYr.cim-6AL	26	*wPt-733679*	*wPt-744577*	6.8	7.9	−6.6
YR10 AUDPC	*QYr.cim-1BL*	20	*wPt-1770*	*wPt-9028*	24.6	43.6	82.9
	QYr.cim-2BS	75	*gwm374*	*YrF*	7.9	12.8	45.1
	QYr.cim-6AL	30	*gwm356.1*	*wPt-743476*	5.4	6.7	−35.1
YR13 FDS	*QYr.cim-1BL*	8	*csLV46*	*gwm140*	4.3	14.3	12.5
	QYr.cim-2BS	75	*gwm374*	*YrF*	6.9	16.9	13.2
	QYr.cim-3BS.2	19	*gwm533.2*	*barc133*	4.5	9	9.6
	QYr.cim-5AL	59	*wPt-9094*	*wmc145.1*	3.4	6.2	−8
	QYr.cim-6AL	26	*wPt-733679*	*wPt-744577*	4	7.1	−8.7
YR13 AUDPC	*QYr.cim-1BL*	20	*wPt-1770*	*wPt-9028*	6.4	11.7	201.2
	QYr.cim-2BS	75	*gwm374*	*YrF*	5.8	13.4	215.9
	QYr.cim-2DS	1	*wPt-3812*	*wPt-6780*	4.5	8	−166.8
	QYr.cim-3BS.2	17	*tPt-9267*	*gwm533.2*	3.9	7.1	157.3
	QYr.cim-5AL	75	*wmc145.1*	*wPt-4262*	3.6	7.4	−160.7
	QYr.cim-6AL	26	*wPt-733679*	*wPt-744577*	4.9	8.8	−177.7
YR MFDS	*QYr.cim-1BL*	20	*csLV46*	*wPt-9028*	9.3	12.4	7.8
	QYr.cim-2BS	75	*gwm374*	*YrF*	12.8	22.7	10.5
	QYr.cim-3BS.2	19	*gwm533.2*	*barc133*	3.7	5.2	5.0
	QYr.cim-6AL	26	*wPt-733679*	*wPt-744577*	6.4	8.2	-6.4

[a] *QLr.cim-3DC* was detected in the subpopulation of RILs lacking *Lr46*

[b] Additive effect of phenotypic for each QTL

in Avocet/Francolin F_5 RILs was shown to be controlled by a combination of minor seedling resistance genes and APR QTL. Using ICIM, we detected four and six resistance loci for leaf rust and stripe rust, respectively, based on FDS, AUDPC, and MFDS. These results are consistent with genetic analysis of the Avocet/Francolin population (Lan et al. 2014), which inferred that at least three leaf rust and five


1BL
LOD
LOD
0.0 gwm259
7.3 csLV46
12.5 gwm140
19.9 wPt-1770
26.8 wPt-9028
LR09
LR10
LRA
LRM
YR09
YR10
YRA
YR13
YRAS
YRM
A
3BS.1
LOD
53.4 barc101
58.2 wPt-664393
60.9 wPt-6945
61.9 wmc777
65.9 wPt-5390
66.7 wmc625
68.7 wPt-4608
74.4 gwm284
83.2 wPt-4364
83.9 wPt-7786
89.6 wPt-10003
95.4 gwm247
98.4 gwm340
B
3DC
LOD
0.0 wPt-671956
0.8 wPt-672034
12.0 wPt-664771
13.5 wPt-6066
15.0 wPt-741446
15.7 wPt-666681
17.2 wPt-740930
22.9 wPt-732670
27.9 wPt-741512
29.5 wPt-742537
31.0 wPt-7513
32.6 wPt-742078
50.3 gdm99.1
53.9 gdm99.2
C
7DS
LOD
0.0 wPt-666614
1.0 wPt-743220
1.2 wPt-744361
1.4 wPt-744857
14.5 gwm295
D
2BS
LOD
50.2 wmc597
52.1 wPt-5672
52.7 wPt-5556
54.6 wPt-2600
55.2 wPt-7715
56.0 gwm429
56.9 wmc770
58.2 gwm148
59.5 gwm410
61.5 barc55
69.1 wPt-8548
69.7 wPt-6174
72.1 wmc344
74.1 gwm374
76.1 YrF
77.9 wmc474
88.8 wmc441
90.6 wPt-5044
95.4 gwm388
E
2DS
LOD
0.0 wPt-3812
2.4 wPt-6780
24.1 wPt-669517
35.6 wPt-9780
46.7 wPt-3728
50.0 wPt-666518
55.4 wPt-732942
56.3 wPt-4413
58.5 wPt-4242
60.0 gwm539
65.5 gwm157
67.5 wPt-668017
F
3BS.2
LOD
0.0 CSG9
3.6 gwm533.1
7.9 wPt-8446
9.7 wPt-5209
11.3 gwm389.2
12.0 gwm389.1
13.3 wPt-734202
13.8 wPt-741817
14.6 wPt-7984
15.6 wPt-798970
16.6 tPt-9267
18.1 gwm533.2
19.4 barc133
23.4 gwm493
25.4 wPt-3536
26.1 wPt-0302
29.1 wPt-741331
30.2 wPt-741750
31.5 wPt-5916
33.1 wPt-7212
46.0 wPt-0610
46.7 wPt-8238
48.1 wPt-0013
G
5AL
LOD
0.0 wmc489
8.6 tPt-6183
11.2 wPt-0605
12.9 wmc705.2
14.7 gwm293
18.2 barc1
28.1 wPt-7769
29.5 wPt-742925
39.6 gwm186
43.4 wPt-3187
44.5 wPt-3509
45.8 wPt-733649
58.3 wPt-9094
67.1 wmc145.1
78.0 wPt-4262
H
6AL
LOD
0.0 wPt-733976
2.6 tPt-7399
3.5 wPt-6381
5.8 wPt-0139
6.5 wPt-9113
7.0 wPt-4681
7.2 wPt-730631
7.7 wPt-734004
8.8 wPt-9690
9.3 wPt-665036
9.7 wPt-9692
11.4 wPt-666074
17.4 wPt-7373
17.9 wPt-731499
23.7 wPt-6897
24.3 wPt-5030
25.1 wPt-6951
25.4 wPt-733225
25.8 wPt-733679
26.5 wPt-744577
26.9 wPt-741026
29.9 gwm356.1
32.8 wPt-743476
35.5 wPt-744881
I

◀**Fig. 3** Likelihood plots of quantitative trait loci (QTL) to leaf rust on chromosomes 1BL (**A**), 3BS.1 (**B**), 3DC (**C**), and 7DS (**D**); and to stripe rust on chromosomes 1BL (**A**), 2BS (**E**), 2DS (**F**), 3BS.2 (**G**), 5AL (**H**), and 6AL (**I**), identified by IciMapping 3.3 in the 141 lines of the Avocet/Francolin#1 RILs population. The significant LOD threshold was based on 1,000 permutations. Positions (in cM) of the molecular markers along chromosomes are shown on the vertical axes using cumulated genetic distances. LR09 and LR10 represent final disease severity (FDS) of leaf rust phenotypic data at Ciudad Obregon during 2008–2009 and 2009–2010, respectively, YR09 and YR10 represent FDS of stripe rust phenotypic data in Toluca in 2009 and 2010, respectively, and YR13 indicates FDS of stripe rust phenotypic data in Sichuan in 2013. LRA, YRA, and YRAS represent the area under the disease progress curve (AUDPC) of leaf rust in Ciudad Obregon in 2009–2010, stripe rust in 2010 in Toluca, and stripe rust in 2013 in Sichuan, respectively; and finally, LRM and YRM represent the mean of FDS of leaf rust in 2008–2009 and 2009–2010, and over FDS of stripe rust in 2009, 2010 and 2013, respectively

stripe rust resistance genes with additive effects were present in the population. In this study, we identified the APR gene *Lr46/Yr29* and the seedling resistance gene *Lr16* using molecular markers and seedling reactions.

The 1BL QTL was identified using markers closely linked to the APR gene *Lr46/Yr29* (Rosewarne et al. 2012). This locus is considered a PAPR locus and has been widely used in CIMMYT germplasm as a partial basis for resistance against leaf rust and stripe rust (Singh et al. 1998; Williams et al. 2006; Lillemo et al. 2008; Rosewarne et al. 2012). It has provided APR to leaf rust and stripe rust for more than 40 years (Singh et al. 1998) and co-segregates with the leaf tip necrosis gene *Ltn2* (Rosewarne et al. 2006), an APR gene for powdery mildew, *Pm39* (Lillemo et al. 2008), and a recently designated APR gene for stem rust, *Sr58* (Singh et al. 2013). Previous studies have shown that *Lr46/Yr29* has consistent effects against leaf rust and stripe rust, although these generally appear smaller than that of *Lr34/Yr18* (Lagudah 2011). Rosewarne et al. (2012) showed that the line 'Pastor' contained *Lr46/Yr29,* and this locus explained 16.7–25.4 and 15.1–22.1 % of leaf rust and stripe rust variation, respectively, in a 'Pastor'-derived F_5 population. In the current study, this locus explained 32.5–44.5 and 11.7–43.6 % of leaf rust and stripe rust variation, respectively. However, *Lr46/Yr29* was less effective for leaf rust in India (Agarwal and Saini 2009), though it has performed well against both rust diseases in Mexico, China, and Brazil (Lillemo et al. 2011). It is possible that the *Lr46/Yr29* effect is too minor to be detected in India that it is temperature sensitive (Lagudah 2011), or that disease data were recorded too late in the season to differentiate the minor effect.

The leaf rust seedling race-specific resistance gene *Lr16* was present in Francolin (Lan et al. 2014) and was located on chromosome 2BS (Fig. 1). McCartney et al. (2005) reported that the microsatellite locus *Xwmc764* mapped at 1 cM to *Lr16* in RL4452/AC Domain, 9 cM in BW278/AC Foremost, and 3 cM in HY644/McKenzie populations. In our population, we mapped this marker at 9.4 cM from the resistance locus and identified *Xwmc661* within 1.4 cM. The diagnostic value of *Xwmc661* was very high as out of 350 advanced lines, and 348 had the resistance or susceptible SSR allele that corresponded with low or high seedling IT (full dataset not shown). The SSR markers *Xwmc661* and *Xwmc764* flanked the resistance locus, and together, they would be excellent tools for combining *Lr16* with other leaf rust resistance genes in wheat breeding.

In both Mexican and Chinese trials, the seedling-effective stripe rust resistance gene *YrF*, identified in Francolin (Lan et al. 2014), showed effectiveness against stripe rust in adult plants. It was located on chromosome 2BS and flanked by SSR markers *Xwmc474* and *Xgwm374*. Three officially designated seedling-effective resistance genes have been detected on chromosome 2BS including *Yr27* (Wellings 1992), *Yr31* (Singh et al. 2003), and *Yr41* (Luo et al. 2008).

Yr27 originated from Selkirk (pedigree: McMurachy/Exchange//3*Redman) and existed in a number of CIMMYT lines such as Ciano79, Nacozari 76, Tesia 79, Opata 85, and Attila (Wellings 1992). It was closely linked to the restriction fragment length polymorphism markers *Xbcd152-2B* and *Xcdo405-2B* and was genetically independent of *Lr16* (McDonald et al. 2004). *YrF* appears slightly closer to *Lr16* than *Yr27* as the Francolin population recorded a recombination frequency of 0.36 between *YrF* and *Lr16* (Lan et al. 2014). Furthermore, the *P. striiformis* isolate Mex96.11 is virulent on *Yr27* in seedling tests and Opata 85 displayed an IT of '7,' while Francolin maintained a resistant IT of '34' against this pathotype based on the 0–9 Scale (Lan et al. 2014). *Yr31* is another race-specific resistance gene with an intermediate IT at the seedling stage and moderate resistance when present alone in adult plants. It was detected in the CIMMYT wheat cultivars Pastor and Chapio and was ineffective to isolate Mex08.31 in Mexico in 2009

Table 3 Mean leaf rust severity of lines containing combinations of the indicated QTLs from the Avocet/Francolin#1 RILs population, highlighting the additive effects of the QTL

Genotypic class	RILs (No.)	Mean leaf rust severity (%)		
		LR09 FDS	LR10 FDS	LR MFDS
None	12	96.0 A	83.0 A	89.5 A
7DS	3	73.3 B	70.0 A	71.7 A
3DC	7	75.7 B	67.1 A	71.4 A
3BS.1	8	63.8 B	54.4 B	59.1 B
3BS.1 + 3DC	6	66.7 B	46.7 B	56.7 B
3BS.1 + 7DS	7	50.0 C	55.0 B	53.9 B
3DC + 7DS	4	55.0 C	31.3 C	43.1 B
3BS.1 + 3DC + 7DS	7	29.3 D	32.3 C	30.8 C
1BL + 3BS.1	5	8.4 E	14.0 C	11.2 D
1BL + 3BS.1 + 3DC	4	8.0 E	12.8 C	10.4 D
1BL	5	6.4 E	13.2 C	9.8 D
1BL + 3DC	8	7.3 E	4.3 D	5.8 D
1BL + 3BS.1 + 7DS	4	6.5 E	6.5 D	6.5 D
1BL + 3BS.1 + 3DC + 7DS	8	2.3 E	4.6 D	3.5 D
1BL + 3DC + 7DS	4	3.0 E	2.8 D	2.9 D
1BL + 7DS	7	2.3 E	3.0 D	2.7 D

Different letters following the mean indicates significant differences based on a *t* test ($P < 0.01$)

(Rosewarne et al. 2012) and in sub-sequent years, and under Chinese field conditions in 2010 (Yang et al. 2013). Compared to 80–100 % severities of the Avocet near-isogenic line for *Yr31*, the severity of an Avocet/Francolin F_5 RIL, postulated to possess only *YrF* based on the absence of flanking molecular markers for other APR QTL, displayed disease severities ranging from 10 to 50 % depending on year and scoring time (data not presented). These results clearly demonstrate that *YrF* is different from *Yr31*. *Yr41* was identified in the Chinese wheat cultivar Chuannong 19 (pedigree: Qian1104A/R935) and closely linked to the SSR marker *Xgwm410* within 0.3 cM (Luo et al. 2008). IT data and pedigree history suggest that *YrF* is different from *Yr41*, as Chuannong 19 has seedling IT of '0' against the Chinese pathotypes CYR31 and CYR32, whereas Francolin had an IT of '4' based on the 0–9 Scale (J. Feng Pers. Comm.).

The 2BS region is rich with resistance genes, and the recombination frequencies between *Yr27*, *Yr31,* and *Lr23* have been determined (Singh et al. 2003). These were 0.148, 0.131, and 0.295, respectively, between *Yr27* and *Yr31*, *Yr27* and *Lr23*, and *Yr31* and *Lr23* (Singh et al. 2003). Luo et al. (2008) investigated the genetic distances between *Yr27*, *Yr31,* and *Yr41* and gave map distances of 17.4 cM between *Yr41* and *Yr27*, and 6.2 cM between *Yr41* and *Yr31*. Based on this information and closely linked marker chromosome information, the likely gene order of the designated resistance genes from the top of 2BS to the centromere is *Lr16-Yr31-Yr41-YrF-Yr27-Lr23*. The diagnostic value of *Xwmc474* was better than *Xgwm374* for gene prediction in 350 advanced wheat backgrounds (data not shown). Molecular markers and seedling responses confirmed that *YrF* in Francolin was derived from Vivitsi (Lan et al. 2014).

The APR QTL for stripe rust, *QYr.cim-2DS*, was flanked by DArT markers *wPt-3812* and *wPt-6780* and was derived from Avocet. It was located on the short arm of chromosome 2DS-5 region, based on the DArT physical map (http://www.cerealsdb.uk.net/CerealsDB/Documents/FORM_DArT_1A.php). Suenaga et al. (2003) detected a stripe rust resistance QTL in this region of 2DS, which was closely linked to *Xgwm261* and explained 5.7–6.9 % of the stripe rust variance in the wheat cultivar Oligoculm. A locus in the same region, derived from the Italian wheat cultivar Libellula, was detected by Lu et al. (2009); it was flanked by SSR markers *Xcfd51* and *Xgwm261* and

Table 4 Mean stripe rust severity of lines containing combinations of the indicated QTLs from the Avocet/Francolin#1 RIL population, highlighting the additive effects of the QTL

Genotypic classes	RILs (No.)	Mean stripe rust severity (%)			
		YR09 FDS	YR10 FDS	YR13 FDS	YR MFDS
None	1	90.0 A	90.0 A	90.0 A	90.0 A
6AL	3	76.7 B	83.3 A	96.7 A	85.3 A
2DS + 3BS.2 + 5AL + 6AL	5	44.0 C	88.0 A	100.0 A	77.4 A
2DS + 5AL	3	53.3 B	63.3 B	100.0 A	72.0 A
2DS + 3BS.2 + 6AL	2	35.0 C	80.0 A	95.0 A	70.0 A
2DS + 5AL + 6AL	3	45.0 C	80.0 A	85.0 A	70.0 A
2DS + 6AL	3	53.3 B	73.3 A	73.3 A	66.7 A
5AL	2	55.0 B	75.0 A	70.0 A	66.5 A
3BS.2 + 5AL + 6AL	3	46.7 C	80.0 A	80.0 A	66.0 A
3BS.2 + 6AL	3	56.7 B	83.3 A	60.0 A	65.7 A
1BL + 5AL + 6AL	3	38.3 C	60.0 B	80.0 A	59.3 B
2DS	2	37.5 C	60.0 B	70.0 A	56.0 B
1BL + 2BS + 2DC + 5AL + 6AL	3	8.7 D	53.3 B	80.0 A	47.3 B
1BL + 6AL	3	33.3 C	53.3 B	53.3 B	46.7 B
1BL + 2DS + 5AL + 6AL	2	15.0 D	46.7 B	73.3 A	44.7 B
2BS + 2DS + 3BS.2 + 5AL	2	22.5 C	55.0 B	45.0 B	41.0 B
2BS + 3BS.2 + 6AL	6	14.2 D	61.7 B	37.0 B	37.3 C
2BS + 2DS + 3BS.2	4	15.0 D	52.5 B	40.0 B	35.8 C
1BL + 5AL	2	20.0 D	40.0 B	30.0 B	32.5 C
1BL + 2DS + 3BS.2 + 5AL	2	15.0 D	30.0 C	45.0 B	30.0 C
1BL + 3BS.2	2	25.0 C	40.0 B	20.0 B	28.0 C
1BL + 3BS.2 + 5AL	2	25.0 C	35.0 B	25.0 B	28.5 C
1BL + 2BS + 2DS + 3BS.2 + 6AL	2	8.0 D	25.0 B	50.0 B	27.5 C
1BL + 2BS + 3BS.2 + 5AL	2	10.0 D	30.0 C	40.0 B	27.0 C
1BL + 2BS + 2DS + 6AL	2	8.0 D	30.0 C	30.0 B	21.5 C
1BL + 2BS + 3BS.2 + 5AL + 6AL	4	7.8 D	31.3 C	25.0 B	21.5 C
1BL + 2BS + 2DS + 3BS.2 + 5AL + 6AL	1	1.0 E	10.0 D	0 C	5.5 D

Different letters following the mean indicate significant differences based on a *t* test ($P < 0.01$)

explained 8.1–12.4 % of stripe rust variance. These loci might be the same as *QYr.cim-2DS,* based on the combined genetic maps of SSR and DArT markers (Francki et al. 2009). Several other studies have identified a different region on chromosome 2DL that affected stripe rust (Bariana et al. 2001; Suenaga et al. 2003; Mallard et al. 2005; Melichar et al. 2008; Powell 2010; Agenbag et al. 2012; Ren et al. 2012). Some of these studies appear to be linked through the use of parental material that likely derived the 2DL QTL from the resistant wheat cultivar Cappelle Desprez.

QLr.cim-3BS.1 and *QYr.cim-3BS.2* were derived from Francolin and have been mapped to the short arm of chromosome 3B for leaf rust and stripe rust resistance, in the intervals of *wPt-664393-wPt-5390* and *wPt-8446-Xgwm533.2*, respectively. The stripe rust resistance gene, *Yr30* (Singh et al. 2000), an APR gene for stem rust resistance, *Sr2* (Speilmeyer et al. 2003) a fusarium head blight resistance gene, *Fhb1* (Cuthbert et al. 2006) and a morphological marker for pseudo-black chaff (Hare and McIntosh 1979) were located in the same chromosome region as *QYr.cim-3BS.2*. Francolin displays pseudo-black chaff in the field (Singh et al. 2011), so it is likely that we identified *Yr30* in Toluca (2009), China (2013), and the MFDS for stripe rust. It is currently presumed that a pleiotropic gene is responsible for the phenotypic effects of

these loci (Rosewarne et al. 2013), but this can only be confirmed through gene cloning. The *QLr.cim-3BS.1* was only detected in the 2009 (Obregon) trial with very high LOD score and PVE values. That a high effect QTL was only detected in one of two environments indicates either race specificity or environmental factors impacting on effectiveness of resistance. Messmer et al. (2000) detected a QTL for durable leaf rust resistance on chromosome 3B in the spelt winter line Oberkulmer. It was flanked by *Xpsr919a-Xpsr1101b* with a PVE of 9.3 % in adult plants. Furthermore, Chu et al. (2009) found *QLr.fcu-3BL* for leaf rust resistance in the synthetic hexaploid wheat line TA4152-60, flanked by *Xbarc164* and *Xfcp544*. However, Francolin is neither spelt wheat nor synthetic, and it is likely that *QLr.cim-3BS.1* is a new locus for adult plant resistance to leaf rust in common wheat.

QLr.cim-3DC was detected near the centromere of chromosome 3D, based on the DArT physical map, in the sub-population of RILs lacking *Lr46*. Basnet et al. (2013) detected *QLr.tam-3D/QYr.tam-3D* in the CIMMYT wheat line Quaiu#3. It was flanked by the markers *wpt-672034* and *Xbar125* in the proximal region of chromosome arm 3DS and explained 3–6 and 3.2–4.3 % of leaf rust and stripe rust variation, respectively. The flanking markers for this QTL are 17.2 cM from the *QLr.cim-3DC,* based on our linkage map, and we did not detect effects of *QLr.cim-3DC* on stripe rust in this study.

The minor QTL for APR to stripe rust, *QYr.cim-5AL*, was derived from Avocet and had significant effects on stripe rust in Toluca (2010) and China (2013) trials. Boukhatem et al. (2002) detected one locus affecting stripe rust response on chromosome 5A in Opata 85, which was flanked by molecular markers *Xfbb209* and *Xabg391* and accounted for 15 % of stripe rust PVE. A QTL for stripe rust in the Chinese landrace Pingyuan 50, *QYr.caas-5AL*, was flanked by microsatellite markers *Xwmc410* and *Xbarc261* and accounted for 5.0–19.9 % of stripe rust PVE (Lan et al. 2010). *QYr.caas-5AL.2* was derived from SHA3/CBRD and had PVEs of 3.4–3.7 % for stripe rust. It was associated with molecular markers *wPt-5231*, *wPt-1903*, *wPt-3334,* and *Xwmc727* (Ren et al. 2012). Rosewarne et al. (2012) also detected a minor QTL for stripe rust on 5AL in Pastor, which was flanked by DArT markers *wPt-0837* and *wPt-5231* and explained 3.9–6.6 % of the stripe rust PVE in adult plants. It is difficult to clarify the relationship between *QYr.cim-5AL* and QTL in Opata 85, Pingyuan 50, Sha3/CBRD, and Pastor based only on their chromosome locations. However, another APR QTL from *T. boeticum*, *QYrtb.pau-5A* (Chhuneja et al. 2008), was clearly originated from a different source to *QYr.cim-5AL*.

A QTL for APR to stripe rust in Avocet, *QYr.cim-6AL*, was located in the interval of *wPt-733679-Xgwm356*. This locus from the susceptible parent Avocet has been identified in several genetic populations (William et al. 2006; Lillemo et al. 2008; Rosewarne et al. 2012). However, two additional QTL, *QYr.uga-6AS* and *QYrex.wgp-6AS*, detected in red wheat cultivars Express (Lin and Chen 2009) and Pioneer 26R61 (Hao et al. 2011), respectively, differ from that of *QYr.cim-6AL* as they were located on the distal end of 6AS with a genetic distance around 42–94 cM from *QYr.cim-6AL,* based on wheat consensus maps (Somers et al. 2004). Furthermore, stripe rust resistance genes *Yr38* (Marais et al. 2006), *YrHua* (Cao et al. 2005), and *Yr42* (Marais et al. 2009), transferred from *Aegilops sharonensis*, *Psathyrostachys huashanica,* and *Aegilops neglecta*, respectively, have been mapped to this chromosome but were different from *QYr.cim-6AL,* based on their origin. The Avocet QTL is likely contributed by a translocation from *Agropyron elongatum*, which was also known to carry the stem rust resistance gene *Sr26* (William et al. 2006). These results further confirm that the susceptible line can also provide partial resistance for breeding durable rust-resistant wheat.

QLr.cim-7DS was located on chromosome 7DS and flanked by markers *wPt-744857* and *Xgwm295*. Numerous studies have placed the *Lr34/Yr18* locus in this region, and it always has a significant effect in all environments tested and confers relatively high LOD and PVE scores (Singh et al. 2000; Boukhatem et al. 2002; Suenaga et al. 2003; Imtiaz et al. 2004; Ramburan et al. 2004; Navabi et al. 2005; Lillemo et al. 2008; Lu et al. 2009; Bariana et al. 2010; Zwart et al. 2010; Yang et al. 2013). Although *Xgwm295* is in close proximity to the *Lr34/Yr18* locus, the phenotypic effects of the Francolin QTL are not typical of *Lr34/Yr18*. *QLr.cim-7DS* from Francolin was only effective in 2009 (Obregon) for the MFDS of leaf rust and had very minor PVEs (3.3 and 4.2 %, respectively). Furthermore, this locus had no effect on stripe rust, effectively ruling out the possibility of it being the *Lr34/Yr18* locus. *QLr.cim-7DS* appears to be another minor leaf rust resistance locus on chromosome 7DS in Francolin.

The closely linked molecular marker *csLV46* indicated that *Lr46/Yr29* was present in Francolin for both leaf rust and stripe rust resistance. This locus did not display any significant additive effects when combined with other QTL against leaf rust, though there were significant additive effects with other stripe rust resistance QTL. In the Francolin population, the *Lr46* effect is very strong and reduced MFDS of leaf rust to 9.8 %. Statistically, this does not leave much room for additive genes to have much effect. There were no lines in this population that contained the *Lr46/Yr29* locus without other stripe rust resistance QTL. However, in lines that had this locus in combination with one or two minor QTL, stripe rust severity remained around 46–59 %. Not only does this PAPR locus have less of an effect against stripe rust than leaf rust, it also shows that more minor additive genes are required for high levels of APR-based resistance in stripe rust, and that there is more likelihood of additive effects.

Conclusion

The resistance of Francolin to leaf rust and stripe rust is governed by a combination of seedling resistance genes and APR QTL. Seedling resistance genes *Lr16* and *YrF* have been mapped to chromosome 2BS and closely linked to the SSR markers *Xwmc661* and *Xwmc474*, respectively. These markers could be used in breeding for resistance to leaf rust and stripe rust. QTL analysis indicated that four loci for leaf rust resistance and six loci for stripe rust resistance were present in the F_5 RILs from the crosses between Avocet and Francolin. Among these, *QYr.cim-2BS* was the seedling resistance gene *YrF* and showed effects on stripe rust in adult plants in both Mexican and Chinese trials. *YrF* is probably a new seedling resistance gene on chromosome 2BS, derived from the Francolin parent, Vivitsi. *QLr.cim-3BS.1* was a new resistance locus to leaf rust in 2009 (Obregon). *Lr46/Yr29* had a large effect against leaf rust in isolation and did not significantly interact in an additive fashion with other QTL for leaf rust; however, it only showed an intermediate effect against stripe rust and interacted significantly with other stripe rust QTL in this population.

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