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Characterization of Leaf Rust and Stripe Rust Resistance in Spring Wheat 'Chilero'

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Abstract

Since 1984, the 'Chilero' spring wheat line developed by CIMMYT has proven to be highly resistant to leaf rust and stripe rust. Amid efforts to understand the basis of resistance of this line, a recombinant inbred line (RIL) population derived from a cross between Avocet and Chilero was studied. The parents and RILs were characterized in field trials for leaf rust and stripe rust in three locations in Mexico between 2012 and 2015 and genotyped with DArT-array, DArT-GBS, and SSR markers. A total of 6,168 polymorphic markers were used to construct genetic linkage maps. Inclusive composite interval mapping detected four colocated resistance loci to both rust diseases and two stripe rust resistant loci in the Avocet × Chilero population. Among these, the quantitative trait locus (QTL) on chromosome 1BL was identified as a pleotropic adult plant resistance gene *Lr46/Yr29*, whereas *QLr.cim-5DS/QYr.cim-5DS* was a newly discovered colocated resistance locus to both rust diseases in Chilero. Additionally, one new stripe rust resistance locus on chromosome 7BL was mapped in the current population. Avocet also contributed two minor colocated resistance QTLs situated on chromosomes 1DL and 4BS. The flanking SNP markers can be converted to breeder friendly Kompetitive Allele Specific PCR (KASP) markers for wheat breeding programs.

Leaf rust (LR) caused by *Puccinia triticina* Erikss. and yellow or stripe rust (YR) caused by *P. striiformis* f. sp. *tritici* Westend. are two major diseases causing significant yield losses of wheat, especially when susceptible cultivars are widely grown. LR generally causes yield losses of less than 10%, but in severe epidemics reported losses can be as high as 30%. On the other hand, YR can cause yield losses of up to 50% and in extreme situations can completely wipe out a crop (Roelfs et al. 1992). In Mexico, yield losses of 63% caused by LR and 60% caused by YR have been reported in major wheat production areas in the state of Sonora and the El Bajio region (https://www.gob.mx/siap/). The use of resistant cultivars is considered the most cost-effective and eco-friendly approach to manage both diseases.

Rust resistance is often classified as either race-specific or race-nonspecific. Race-specific resistance is usually controlled by major genes and is effective against certain races of the pathogen with corresponding avirulence (Flor 1942). In contrast, race-nonspecific resistance is characterized by broad-spectrum effectiveness against a number of pathogen races. Race-nonspecific resistance, considered more durable, is generally expressed at the adult plant stage and governed by a number of minor-effect resistance genes. Reduced pathogen establishment and growth characterize race-nonspecific resistance. As a result, it is commonly known as "slow rusting" or "partial" or "adult plant resistance" (APR) (Caldwell 1968). A single APR gene only has a minor impact on the ability of the plant to resist disease, but "near immunity" can be achieved in a cultivar by combining three to five APR genes (Singh et al. 2000).

So far, more than 75 LR and a similar number of YR resistance genes have been characterized and mapped on specific chromosomes. Among these, three APR genes with pleotropic effects have been identified, characterized and mapped in wheat, namely *Lr34/Yr18/Sr57/Pm38* on chromosome 7DS (Dyck 1987; Lillemo et al. 2008; Singh et al. 2012b), *Lr46/Yr29/Sr58/Pm39* on chromosome 1BL (William et al. 2003), and *Lr67/Yr46/Sr55/Pm46* on 4DL (Herrera-Foessel et al. 2011). These APR genes provide durable resistance to multiple diseases. In addition, several studies have revealed dozens of quantitative trait loci (QTLs) distributed across 20 chromosomes for LR resistance (Li et al. 2014) and across all 21 chromosomes for YR resistance (Rosewarne et al. 2013). Therefore, the identification of new pleotropic/colocated resistance sources to leaf rust and stripe rust is significant for breeding durable, rust-resistant wheat cultivars in combination with high and stable yield potential and other important traits (Basnet et al. 2014). Several molecular marker platforms have been used to map rust resistance loci, including simple sequence repeats (SSRs) (Litt and Lutty 1989) and single nucleotide polymorphisms (SNPs) (Lander 1996), diversity array technology (DArT) (Jaccoud et al. 2001), and genotyping-by-sequencing (GBS) (Elshire et al. 2011). SSR markers show codominance, accuracy, high repeatability, high levels of polymorphism, chromosome specificity, and ease of manipulation (Röder et al. 1998). However, the number of available markers are limited compared with high throughput genotyping platforms. The DArT-GBS system, including DArT-silico and DArT-SNP, contains presence/absence (dominant) markers, which cannot be used to genotype early generations due to the presence of heterozygotes. However, it provides additional benefits over other genotyping platforms. The lower cost DArT-GBS has high-throughput capabilities allowing detection through the whole-genome genotyping system, scoring hundreds of polymorphic loci without the need for prior sequence information and codominance with a large number of available markers (Schouten et al. 2012).

'Chilero,' a bread wheat variety developed by the International Maize and Wheat Improvement Center (CIMMYT)'s Global Wheat Program, was distributed worldwide in 1984. Since then, Chilero has remained highly resistant to LR and YR in the Mexican environment, although the genetic basis of its resistance remains unknown. Therefore, this study was conducted to 1) determine the number of genes in Chilero that control LR and YR resistance, 2) identify genomic locations of APR genes to LR and YR, and 3) find the pleotropic/colocated resistance loci to both rusts.

Materials and Methods

Genetic material. An F_4-derived F_5 population of 96 recombinant inbred lines (RILs) developed from the cross of Avocet-*YrA* and Chilero (pedigree: '4777*2//FKN/Gabo 54/3/Veery#5/4/Buckbuck/Pavon F76'

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[GID CM66684]) was used for this research. Avocet-*YrA* (hereafter referred to Avocet), also known as Avocet S, is a YR and LR susceptible selection from the Australian wheat cultivar Avocet, which does not include *YrA*. Chilero displays APR to the predominant races of both YR and LR rust fungi in Mexico, despite exhibiting susceptibility in the seedling stage to one or more races of each pathogen used in field studies. The single-head descent approach was used to develop this RIL population as described by Basnet et al. (2014). The seed of F_5 RILs along with their parents were used in each phenotypic evaluation and genotypic analysis.

Field experiments. The field evaluations were conducted at CIMMYT-Mexico experimental stations: in El Batan, near the city of Texcoco, State of Mexico; Toluca, State of Mexico; and in the Yaqui valley in Ciudad Obregon, State of Sonora (Obregon/CENEB). For the study, LR was evaluated in Obregon during the autumn-winter cycle of 2012–13 (henceforth abbreviated as LR13Y), 2013–14 (LR14Y), and 2014–15 (LR15Y) as well as in El Batan during the 2014 (LR14B) summer-fall cycle. Similarly, YR was evaluated during the summer-fall cycle of 2013 (YR13M), 2014 (YR14M), and 2015 (YR15M) in Toluca and El Batan (YR15B).

The RIL population and the parents were planted in double rows 0.7 m in length, spaced 0.3 m apart, with around 100 seeds of each RIL. A mixture of Avocet+*Yr24* and Avocet+*Yr26* lines were used as LR spreaders, whereas a mixture of six susceptible wheat lines derived from an Avocet × Attila cross, Morocco, and an Avocet near-isogeneic line carrying gene *Yr31* and *Yr17*, were used as a YR spreader in field trials. Spreaders were planted around the experimental area and as hill plots in the middle of a 0.3-m pathway on one side of each experimental plot. A mixture of Mexican *P. triticina* races MBJ/SP and MCJ/SP (in 1:1 ratio) suspended in Soltrol 170 oil was used to inoculate the LR spreader, whereas a mixture of Mexican *P. striiformis* races (Mex96.11, Mex08.13, and Mex14.191) also suspended in Soltrol 170 was sprayed onto YR spreaders within and around the experimental areas. The avirulence/virulence formulas of LR isolates MBJ/SP and MCJ/SP were described in Herrera-Foessel et al. (2012), and for the YR isolates Mex96.11 and Mex08.13 in Lan et al. (2015). Isolate Mex14.191 has the following avirulence/virulence formula: *Yr1*, *Poll/Yr2*, *6*, *7*, *8*, *9*, *17*, *27*, *31*, *32*, *A* based on the seedling reactions of the testers (Huerta-Espino et al. 2015).

Data collection. The modified Cobb scale (Peterson et al. 1948) was used to determine the percentage of the leaf area affected by rust in both RILs and parents from the milk stage onwards. In the case of repeated disease severity data, the first notes were recorded when the susceptible parent Avocet displayed approximately 70 to 80% severity and again about a week later when it displayed 90 to 100% severity. Host response to infection was determined according to Roelfs et al. (1992), where MS = moderately susceptible, or moderate-sized uredinia/sporulation without necrotic or chlorotic tissues; and S = susceptible, or large uredinia/sporulation without necrotic or chlorotic tissues.

Data analysis. Mendelian segregation analysis was used to estimate the number of resistance genes based on disease severity and reaction (Knott and Padidam 1988; Singh and Rajaram 1992), where the observed frequencies for homozygous parental type resistant (HPTR), homozygous parental type susceptible (HPTS) lines whose responses were different from those of the two parents (OTHER), were tested against the expected frequencies for different numbers of additive genes using a χ^2 test. Correlation between the two rusts across different environments was performed using the statistical software SAS version 9.4 (SAS Institute, Cary, NC), with the PROC CORR program. Calculations for phenotypic effects of single resistance QTL, according to flanking markers and tests of statistical significance for pairwise comparisons of the means when resistance locus was absent or present, were conducted using the PROC GLM and *t* test in SAS software.

Molecular analysis. DNA of parents and RILs was extracted from approximately 20 plants per line using the CTAB method (Dreisigacker et al. 2016). The diluted DNA of each RIL and parents was sent to Triticarte PtY. Ltd., Canberra, Australia (www.triticarte.com.au), for DArT-GBS analysis. In addition, 150 SSR markers genotyped the whole population.

A total of 6,168 polymorphic molecular markers were used to construct linkage maps with Joinmap 4.1 software (Van Ooijen 2006). Inclusive composite interval mapping (ICIM) was used to detect and map QTLs providing resistance to both rusts by IciMapping 4.1 software (Meng et al. 2015) based on final disease severity and the mean of final disease severity (LRM and YRM) across four experiments for each LR and YR. MapChart was used to draw the graphically visualized linkage maps (Voorrips 2002).

Results

Phenotyping of parents and RILs for resistance to LR and YR. The parents, Avocet and Chilero, displayed final LR severity (host response) of 80 to 90% (S) and 10 to 15% (MS), respectively, across all seasons. Mean LR severity among RILs ranged from 48.7 to 68.3% during four years of evaluation (Supplementary Table S1). The frequency distribution of RILs for LR severities was continuous across the tested environments (Fig. 1A), which indicates the absence of major genes and quantitative inheritance of APR to LR in this population. Mendelian segregation analysis indicated the presence of three to five APR genes that confer resistance to LR in the Avocet × Chilero population.

The final YR severity and host response of Avocet and Chilero was 100% S and 1 to 30% MS, respectively. The mean of YR severity among RILs ranged from 57.9 to 71.7% across all environments. The frequency distribution of RILs for YR was continuous with a pronounced skewedness toward susceptibility across the tested environments (Fig. 1B). Based on the Mendelian segregation analysis method, three to six APR genes were estimated to provide resistance to YR.

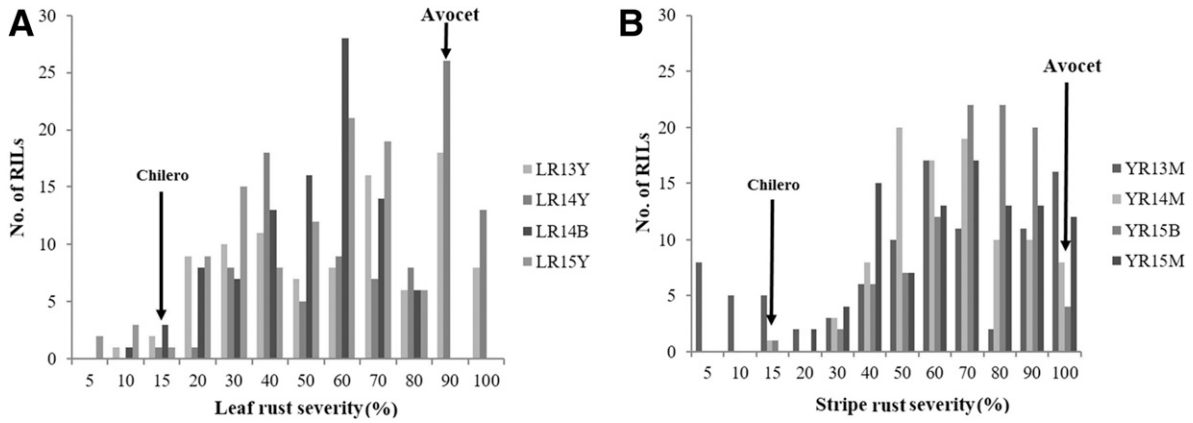

Fig. 1. Frequency distribution of recombinant inbred lines (RILs) of the cross Avocet × Chilero, for final leaf rust severity (**A**) trials in Obregon cycles 2012–13 (LR13Y), 2013–14 (LR14Y), and 2014–15 (LR15Y), and El Batan cycle 2014 (LR14B); for final stripe rust severity (**B**) in Toluca cycles 2013 (YR13M), 2014 (YR14M), and 2015 (YR15M), and in Batan cycle 2015 (YR15B). The parent mean values are indicated by arrows.

Pearson correlation coefficients (r) for LR severity of RILs ranged from 0.78 to 0.91, while they were 0.46 to 0.84 for YR severity among RIL over four years (Table 1). In addition, highly significant correlations were also observed between LR and YR severity (r = 0.50 to 0.78, $P < 0.0001$) in all tested environments.

Linkage map construction. A total of 23,536 DArT and 150 simple sequence repeat (SSR) markers were genotyped for both parents and 96 RILs. Finally, 6,168 polymorphic molecular markers (6,151 DArT and 17 SSR) were used to construct the genetic linkage map, spanning 2,544, 3,093, and 792 cM in the A, B, and D genomes, respectively. A total of 68 linkage groups were defined on the 21 chromosomes (Supplementary Table S2) and only the linkage groups related to the location of QTL are reported.

Table 1. Pearson's correlation coefficient between final disease severities of RILs in four environments for leaf rust (LR13Y, LR14Y, LR15Y, and LR15B) and stripe rust (YR13M, YR14M, YR15M, and YR15B)[z]

	LR13Y	LR14Y	LR14B	LR15Y	YR13M	YR14M	YR15M
LR14Y	0.91**						
LR14B	0.78**	0.80**					
LR15Y	0.86**	0.88**	0.84**				
YR13M	0.54**	0.52**	0.51**	0.50**			
YR14M	0.72**	0.76**	0.77**	0.77**	0.62**		
YR15M	0.73**	0.76**	0.78**	0.75**	0.58**	0.84**	
YR15B	0.50**	0.52**	0.56**	0.56**	0.46**	0.70**	0.73**

[z] **: $P < 0.0001$.

QTLs for APR to both rusts in Chilero. Two colocated resistance loci in Chilero imparted resistance to both LR and YR. *QLr.cim-1BL/QYr.cim-1BL* was found to be the most consistent locus with the largest effect and flanked by DArT markers 1164928 and 2289154 on the long arm of chromosome 1B (Table 2). This resistance locus was detected in all LR experiments, while for YR it was detected over three years as well as YRM, explaining 42.6 to 74.5% and 20.0 to 55.2% of LR and YR variations, respectively (Fig. 2A; Table 2). The second colocated QTL, *QLr.cim-5DS/QYr.cim-5DS*, was located on the short arm of the chromosome 5D (Table 2). The DArT markers 100002510 and 3948152 flanked this QTL, explaining 5.2 to 34.0% and 4.7% of LR and YR variations, respectively (Fig. 2B; Table 2).

In addition, two YR resistance QTLs were located on wheat chromosomes 6BS and 7BL, designated as *QYr.cim-6BS* and *QYr.cim-7BL*, respectively. *QYr.cim-6BS,* flanked by markers 4396419 and 1209575, was detected in YR14M, YR15M, and YR15B. It explained 12.9 to 13.9% of YR variation (Fig. 2C; Table 2). The second QTL, *QYr.cim-7BL*, was flanked by markers 100006719 and 1112830. It was consistently identified in all the environments and YRM and explained 12.3 to 48.4% of YR variation (Fig. 2D; Table 2).

QTLs for APR to both rusts in Avocet. Two colocated minor resistance QTLs for LR and YR, *QLr.cim-1DL/QYr.cim-1DL* and *QLr.cim-4BS/QYr.cim-4BS*, were mapped on chromosomes 1DL and 4BS, respectively. *QLr.cim-1DL/QYr.cim-1DL* was detected in LR2012Y, LR2013Y, LR2014Y, YR2014M, and YR2015M environments. It was flanked by markers wPt-741613 and snp999473 (Table 2), and explained 12.4 to 28.7% and 11.6 to 13.2% of LR and YR variation, respectively. The second QTL, *QLr.cim-4BS/QYr.cim-4BS*, was

Table 2. Position and effects of quantitative trait loci (QTLs) for adult plant resistance (APR) to leaf rust (LR) and stripe rust (YR) based on final disease severity over all tested environments using inclusive composite interval mapping (ICIM) by IciMapping 4.1 software in the Avocet × Chilero recombinant inbred line (RIL) population

QTL[v]	Env	Position[w]	LeftMarker	RightMarker	LOD[x]	PVE (%)[y]	Add[z]
LR/YR							
QLr.cim-1BL	LR13Y	74	snp1137809	snp1697802	37.2	64.6	18.2
	LR14Y	74	snp1137809	snp1697802	39.3	69.0	18.8
	LR15Y	74	1164928	2289154	11.3	42.6	18.3
	LR14B	74	snp1137809	snp1697802	23.9	49.4	12.6
	LRM	75	1164928	2289154	42.9	74.5	20.5
QYr.cim-1BL	YR13M	62	snp1112007	snp2263671	18.8	20.0	12.9
	YR14M	62	snp1112007	snp2263671	21.0	47.1	12.1
	YR15B	76	2289154	4005037	9.4	24.8	8.6
	YR15M	75	1164928	2289154	21.9	53.3	15.5
	YRM	75	1164928	2289154	30.5	55.2	13.1
QLr.cim-1DL	LR13Y	21	wPt-741613	snp999473	5.9	22.6	–6.7
	LR14Y	20	snp1099827	wPt-741613	4.8	12.4	–4.3
	LR15Y	16	100458285	3944329	4.3	14.4	–4.4
QYr.cim-1DL	YR14M	26	100001883	3934217	5.3	11.6	–6.6
	YR15M	32	3934217	wPt-732579	3.4	13.2	–5.7
QLr.cim-4BS	LR14Y	14	snp100456066	3946892	3.8	12.1	–4.3
	LR15Y	22	4010053	snp100495483.2	2.7	13.7	–8.7
QYr.cim-4BS	YR15M	13	1118129	snp100456066	6.2	15.8	–6.2
QLr.cim-5DS	LR13Y	20	100002510	3948152	12.2	34	8.4
	LR15Y	19	1695607	100093377	2.6	5.2	52.7
QYr.cim-5DS	YR13M	20	100002510	3948152	7	4.7	6.9
YR							
QYr.cim-6BS	YR14M	66	4396419	1209575	9.9	13.8	7.8
	YR15B	66	4396419	1209575	2.9	12.9	4.2
	YR15M	68	3384782	4440245	8.8	13.9	8.1
QYr.cim-7BL	YR13M	190	100006719	1112830	9	11.2	10.7
	YR14M	190	100006719	1112830	7.8	16	8.1
	YR15B	190	100006719	1112830	2.7	12.3	4.2
	YR15M	190	100006719	1112830	11.8	40.6	13.2
	YRM	190	100006719	1112830	21.9	48.4	16

[v] QTLs extending across the same confidence intervals were assigned with the same symbol.
[w] Peak position in centi-Morgans from the first linked marker of the relevant linkage group.
[x] Logarithm of odds (LOD) score to detect QTLs.
[y] PVE is the proportion of phenotypic variance explained by the QTL.
[z] Additive effect of phenotypic variance for each QTL.

detected in LR2014, LR2015, and YR2015 environments. It was flanked by markers snp100456066 and 3946892, and explained 12.1 to 13.7% and 2.2 to 15.8% of LR and YR variation, respectively (Table 2) in the adult plant stage.

Single QTL analysis of *QLr.cim-5DS/QYr.cim-5DS*. RILs were divided into two groups: RILs carrying *QLr.cim-5DS/QYr.cim-5DS* and RILs not-carrying *QLr.cim-5DS/QYr.cim-5DS*, based on the flanking markers of *QLr.cim-5DS/QYr.cim-5DS*. Mean leaf rust severity of RILs carrying this QTL ranged from 15 to 80%, whereas the severity of RILs without this locus was 20 to 90% (Fig. 3A). On the other hand, the mean for stripe rust severity for genotypes carrying this QTL was 20 to 80%, and for those not carrying this locus was 30 to 90% (Fig. 3B). QTL *QLr.cim-5DS/QYr.cim-5DS* reduced leaf rust severity by 10 to 23% while an 11 to 21% stripe rust reduction was observed (Table 3).

Discussion

Mendelian analyses showed that around three to five APR genes for LR and three to six APR genes for YR were segregated in the Avocet × Chilero population, while four colocated resistance QTLs and three YR resistance QTLs were detected using the ICIM based on 1,000 permutations. In addition, two minor resistance QTLs derived from Avocet were also mapped in the population, confirming that in order to achieve near immune response to the rust fungi, four to five genes with additive effects need to be combined (Singh et al. 2000). A significant correlation between LR and YR (r = 0.50 to 0.78) was found, an indicator that colocated/pleiotropic effect loci are conferring resistance to both rusts. William et al. (2006) reported three colocated resistance loci on chromosomes 1BL, 4BL, and 6AL to both rusts with a higher correlation (r = 0.68 to 0.85) between LR and YR severities in the Avocet × Pavon 76 F_6 RIL population.

Lan et al. (2015) observed in the Avocet × Sujata population that the estimation of gene number usually represents the minimum number of polygenic loci segregating in a population. They estimated that the numbers of genes on the χ^2 and Wright's method were similar to the number of QTLs detected, despite a slight discrepancy. These results are similar to the results found in the present study, where the estimation of gene number in the Avocet × Chilero population with the χ^2 method (three to five APR genes for LR and three to six for YR) was comparable to significant QTLs reported (four QTLs for LR and seven for YR).

The pleiotropic resistance locus on chromosome 1BL identified in Chilero corresponds to the known APR gene *Lr46/Yr29* based on the closely linked molecular markers and leaf tip necrosis (LTN) in the adult plant stage. This resistance gene was widely used in CIMMYT germplasm and conferred partial resistance to LR and YR (Singh et al. 1998). The effectiveness of this locus in providing partial resistance to wheat rusts and resistance performance depends on environmental conditions and genetic background (Lan et al. 2015). *Lr46/Yr29* explained 7 to 65% and 8 to 66% of LR and YR severity variation, respectively, in different biparental mapping populations under different experimental conditions (Basnet et al. 2013; Calvo-Salazar et al. 2015; Lan et al. 2014, 2015; Ren et al. 2017; Rosewarne et al. 2012).

The QTL *QLr.cim-5DS/QYr.cim-5DS* was located on the short arm of the chromosome 5D. So far, leaf rust resistance gene *Lr1* has been mapped on the long arm of chromosome 5D (Crossa et al. 2007; Feuillet et al. 1995). *Lr1* does not have any effect on stripe rust. Messmer et al. (2000) found a leaf rust resistance QTL flanked by markers *Xpsr906a* and *Xpsr580a* on 5DL in cultivar Oberkulmer, which explained 9.1% of leaf rust variance in the adult plant stage. Bariana et al. (2007) found a colocated resistance QTL to leaf rust and stripe rust on chromosome 5DS in Cranbrook. It was flanked by marker *psr326b* and explained 8% of LR and YR variation. It was more than 25 cM away from *QLr.cim-5DS/QYr.cim-5DS* based on the wheat consensus map (Akbari et al. 2006; Chalmers et al. 2001), suggesting that this QTL could be a new colocated resistance locus from Chilero.

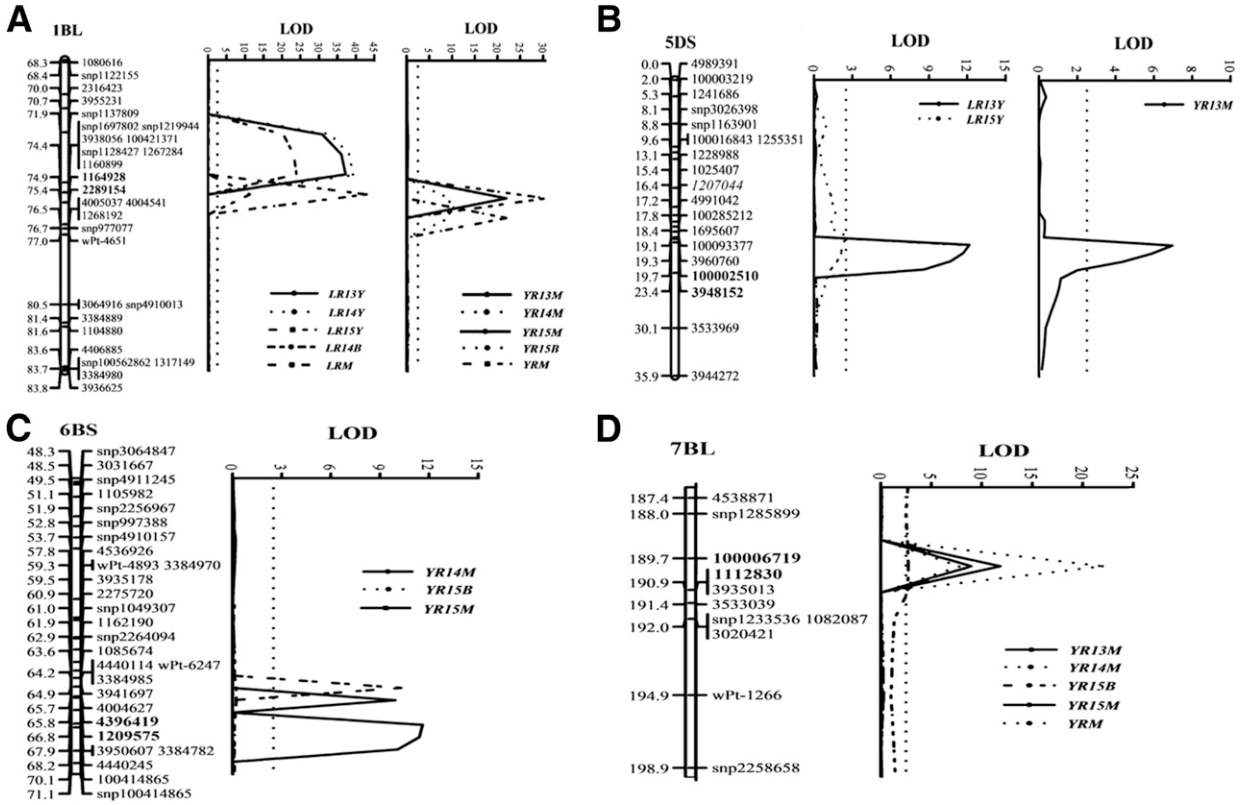

Fig. 2. Graphics of quantitative trait loci (QTLs) for adult plant resistance (APR) to leaf rust on chromosomes IB (**A**) and 5D (**B**), and for stripe rust resistance on chromosomes IB (**A**), 5D (**B**), 6B (**C**), and 7B (**D**), respectively, identified by using IciMapping 4.1 in the Avocet × Chilero recombinant inbred line (RIL) population. The LOD thresholds were detected based on 1,000 permutations. Positions (in cM) of the molecular markers along chromosomes are shown on the vertical axes. The phenotypic data for leaf rust tested in four environments (LR13Y, LR14Y, LR15Y, and LR14B); for stripe rust phenotypic data also evaluated in four environments (YR13M, YR14M, YR15M, and YR15B); and the mean of final disease severity over the tested environments (LRM and YRM).

The stripe rust resistance QTL *QYr.cim-6BS* was located in the short arm of chromosome 6B and explained 12.9 to 26.4% of the YR variation. The high-temperature adult-plant (HTAP) stripe rust resistance gene, *Yr36* (closely linked to the *Gpc-B1* gene), was mapped on chromosome 6BS from the durum wheat cultivar Langdon and linked to SSR marker *Xbarc10*. Gene *Yr36* is approximately 50 cM away from *QYr.cim-6BS* based on the DArT map (Crossa et al. 2007; Marone et al. 2012). Thus, *QYr.cim-6BS* should be different from *Yr36*. Santra et al. (2008) found two QTLs, *QYrst.wgp-6BS.1* and *QYrst.wgp-6BS.2*, which explained 32 to 45% and 25 to 43% of stripe rust variation, respectively, in the wheat cultivar Stephens. These QTLs were flanked by SSR markers *Xbarc101* and *Xbarc136*, and *Xgwm132* and *Xgdm113* (mapped in a 17.5 cM region), respectively. *Yr36* was different from the two QTLs reported based on allelism tests. However, according to the DArT map, the QTL *QYr.cim-6BS* from Chilero is located in the same region of QTL *QYrst.wgp-6BS.2* reported in Stephens (Santra et al. 2008).

The stripe rust resistance *QYr.cim-7BL* locus was located on the long arm of chromosome 7B and detected across all environments explaining 12.3 to 48.4% of YR variation. So far, known YR resistance genes *Yr39* (Coram et al. 2008; Crossa et al. 2007), *Yr59* (Zhou et al. 2014), and *Yr67* (McIntosh et al. 2014; Bansal, personal communication) have been reported on this chromosome. *Yr59* flanked by markers *Xwgp5175* and *Xbarc32* and explained 31.8 to 54.7% of the YR severity variation. It was identified in a line PI 178759 (collected from Iraq). This gene was also reported to be located 21 to 28 cM away from *Yr39,* which flanked by *Xwgp45* and *Xwgp43* explaining 64.2% of stripe rust variation in the wheat cultivar Alpowa. On the other hand, based on the DArT linkage map, *QYr.cim-7BL* was estimated to be located approximately 21 to 28 cM away from *Yr39* (Marone et al. 2012). *Yr67* was identified in the wheat line C591 and closely linked to SSR marker *cfa2040* with a genetic distance of 8 cM (McIntosh et al. 2014; Bansal, personal communication). In addition, Lan et al. (2015) also mapped a single stripe rust resistance gene at the same chromosome location in Sujata. However, *QYr.cim-7BL* was located in the same chromosome location as *wPt-1330* and *wPt-5816* on the distal end of 7BL based on DArT consensus map (Francki et al. 2009), which is closely linked to SSR marker *gwm344* with a genetic distance of 8 cM away from *Yr67*. Therefore, *QYr.cim-7BL* is most likely a new locus conferring APR to YR in Chilero.

Additionally, Avocet contributed two colocated resistance QTLs to LR and YR on chromosomes 1DL and 4BS. Several leaf-rust resistance genes have been mapped in wheat chromosome 1D; however, most of them are race-specific, such as *Lr21* (Kerber and Dyck 1969) and *Lr42* (Cox et al. 1994). *Lr21* was mapped in the cultivar KS86WGRC02 on chromosome 1DS and closely linked to the RFLP marker KSUD14 identified as an excellent marker for selection of lines carrying *Lr40* and *Lr21* in diverse wheat breeding and wild *Aegilops tauschii* populations (Huang and Gill 2001). *Lr42* showed recessive inheritance and was mapped in an F_2 population (KS93U50/Morocco) (Liu et al. 2013) and Avocet × Quaiu 3 (Basnet et al. 2014). *Lr42* is located on the distal end of chromosome 1DS and flanked by markers, *Xwmc432* and *Xgdm33*. Ren et al. (2012) identified a QTL to stripe rust (*QYr.caas-1DS*, flanked by markers *Xgwm353* and *Xgdm33b*) on chromosome 1DS in cultivar Naxos that explained 2.1 to 5.8% of the phenotypic variation. *Yr25* was located on chromosome 1D and identified in several cultivars based on pathogen-race differentiation (Calonnec and Johnson 1998). QTL *QLr.cim-1DL/QYr.cim-1DL* detected in this study is located in long arm of chromosome 1D and conferred resistance to both leaf rust and stripe rust.

Stripe rust resistance QTL, *QYr.cim-4BS*, was mapped on the short arm of 4B from Avocet based on the DArT consensus map (Crossa et al. 2007; Marone et al. 2012). Several resistance genes (race-specific) have been mapped on the chromosome 4B. The *Lr25* gene was transferred from *Secale cereale* L. and showed good resistance to leaf rust in Southeast Asia. It was closely linked to codominant SSR marker *Xgwm251* and placed 3.8 cM away from the *Lr25* locus on 4BL (Singh et al. 2012a). Singh et al. (1999) reported that *Lr12* is either completely linked with *Lr31* or is the same gene. In addition, *Lr31* is located on chromosome 4BS, indicating that *Lr12* must also be located on 4BS. Singh and Bowden (2011) identified and mapped *Lr12* on chromosome 4BL in wheat line TcLr12 and flanked by markers *Xgwm251* and *Xgwm149*. Suenaga et al. (2003) found a stripe rust resistance QTL in cultivar Oligoculm that was closely linked to marker *Xgwm538* on the long arm of chromosome 4B. In the present study, QTL *QYr.cim-4BS* is located on the short arm of chromosome 4B and confers resistance to both rusts. In addition, Rosewarne et al. (2012) identified four minor QTLs from Avocet on chromosomes 3A, 4B, 6A, and 7A. These loci had relatively low LOD and PEV

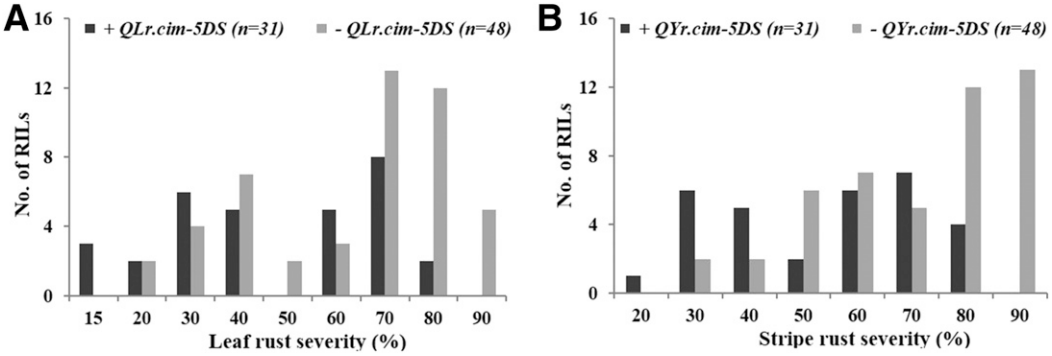

Fig. 3. Comparison of recombinant inbred lines (RILs) from Avocet × Chilero for mean leaf rust severity and mean stripe rust severity in the presence or absence of the colocated QTL, *QLr.cim-5DS/QYr.cim-5DS*. **A,** Effect of *QLr.cim- 5DS* on leaf rust, present (+*QLr.cim-5DS*) and absent (-*Qlr.cini-5DS*). **B,** Effect of *QYr.cim-5DS* on stripe rust, present (+*QYr.cim-5DS*) and absent (-*Qyr.cim-5DS*). The number of RILs in each category is shown in parentheses.

Table 3. Frequencies of Avocet × Chilero recombinant inbred lines (RILs) with resistance locus *QLr.cim-5DS* and *QYr.cim-5DS*, showing mean leaf rust and stripe rust severities (%), when resistance genes were absent or present[x]

LR resistance locus	RILs (No)	LR13Y (%)[y]	LR14Y (%)	LR14B (%)	LR15Y (%)	LRM (%)	YR resistance locus	YR13M (%)[z]	YR14M (%)	YR15M (%)	YR15B (%)	YRM (%)
–*QLr.cim-5DS*	48	71 a	75 a	56 a	53 a	64 a	–*QYr.cim-5DS*	65 a	72 a	76 a	75 a	72 a
+*QLr.cim-5DS*	31	48 b	62 b	43 b	43 b	49 b	+*QYr.cim-5DS*	44 b	56 b	57 b	64 b	56 b

[x] Different letters within each column following the mean indicate significant differences based on the *t* test ($P < 0.01$).

[y] Disease severity (%) determined for leaf rust at Ciudad Obregón during the 2012–13 (LRY13), 2013–14 (LRY14), and 2014–15 (LRY15) seasons, at El Batán 2014 (LRB14), and the mean of leaf rust over four years (LRM).

[z] Disease severity (%) determined for stripe rust at Toluca during the 2013 (YRM13), 2014 (YRM14), and 2015 (YRM15) seasons, at El Batán 2015 (YRB15), and the mean of stripe rust over four years (YRM).

values, and were often inconsistent across environments. Thus, *QYr.cim-4BS* might be the same resistance locus as detected by Rosewarne et al. (2012).

Responding to the severity of bread wheat rust epidemics, breeders have identified a source of durable, long-lasting resistance from within the plant itself, discovering the disease can be controlled by race-nonspecific APR genes. According to this finding, Chilero, a high yielding spring wheat line developed by CIMMYT, is a promising source of APR for combating rust through wheat breeding. With the availability of molecular markers for four colocated resistance loci, the resistance from Chilero can be easily transferred to other germplasm through marker assistant selection (MAS). In addition, three transgressive RILs combining three QTLs on chromosomes 1BL (*Lr46/Yr29*), 1DL, and 5DS showed leaf rust severities lower than 10% in field conditions, while the lowest stripe rust severities were observed in RILs carrying QTLs on chromosomes 1BL (*Lr46/Yr29*), 5DS, and 6BL. All of these RILs can be used as a new complex APR source to bread durable resistant wheat cultivar. Unfortunately, we did not obtain any RILs combining all detected resistance loci due to limited population size. Single gene mapping populations for RIL carrying QTL 5DS is under development for fine mapping. The closely linked molecular markers for *QLr.cim-5DS/QYr.cim-5DS* will also be converted to breeder-friendly kompetitive allele specific PCR (KASP) markers for utilization in MAS.

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