Genetic Analysis of Resistance to Leaf Rust and Yellow Rust in Spring Wheat Cultivar Kenya Kongoni

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Abstract

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The Kenyan wheat (*Triticum aestivum* L.) 'Kenya Kongoni' exhibits high levels of adult plant resistance (APR) to leaf rust (LR) and yellow rust (YR). We determined the genomic regions associated with LR and YR resistance in a population of 148 recombinant inbred lines generated from a cross between 'Avocet-YrA' and Kenya Kongoni. Field experiments to characterize APR to LR and YR were conducted in four and two Mexican or Uruguayan environments, respectively. A linkage map was constructed with 438 diversity arrays technology and 16 simple-sequence repeat markers by JoinMap 4.1 software. Genetic analyses showed that resistance to both rusts was determined by four to five

APR genes, including *Lr46/Yr29* and *Sr2/Lr27/Yr30*. Quantitative trait loci (QTL) analysis indicated that pleiotropic APR loci QYLR.cim-1BL corresponding to *Lr46/Yr29* and QYLR.cim-7BL that is a putative novel QTL accounted for 5 to 57% and 12 to 35% of the phenotypic variation for resistance to LR and YR, respectively. These loci, in combination with another three LR QTL and two YR QTL, respectively, conferred high levels of resistance to both LR and YR in wheat under Mexican and Uruguayan environments. Among other detected QTL, QLR.cim-1DS, QLR.cim-2BL, and QYLR.cim-7BL may be new loci for APR to both rusts in common wheat.

Leaf rust (LR) and yellow rust (YR), caused by *Puccinia triticina* Erikss. and *P. striiformis* f. *tritici* Erikss., respectively, are important diseases of wheat worldwide (34). They constantly threaten wheat production in Mexico because of the pathogens' ability to overcome race-specific resistance in new varieties and also because of their ability to quickly reproduce and move over long distances (17). Similarly, in Uruguay, LR is the most widespread and important disease of wheat whereas YR is economically less important (11,12). In Mexico, wheat is grown annually on about 586,000 ha (9), mainly under irrigation in the northwest state of Sonora and in the El Bajío region, both lowland areas (<http://www.siap.sagarpa.gob.mx>). Losses of up to 63% from LR and 60% from YR have been documented in bread wheat crops in those areas (17,33,38). In Uruguay, the total wheat area is 500,000 ha and production is concentrated in the Soriano, Colonia, and Black River Departments (9). Grain yield losses of more than 50% have been reported from LR in the southwest of this country (11).

The deployment of resistant cultivars is the most efficient way to manage these diseases. The two types of resistance pertaining to LR and YR in wheat are seedling resistance and adult plant resistance (APR). Seedling resistance is usually race specific, governed by single genes often with major effects (18), and is easily overcome by new virulent races. In contrast, APR can be race nonspecific, often controlled by several genes with minor but additive effects (18,23), and usually is believed to be more durable than seedling resistance (23,41).

Thus far, more than 74 LR and 67 YR resistance genes have been cataloged (30). Among these, most are seedling resistance genes and several are not effective against prevalent races in Mexico and

Uruguay. *Lr34/Yr18/Sr57/Pm38/Ltn1* (22,39), *Yr36* (50), *Lr46/Yr29/Sr58/Pm39/Ltn2* (40,57), *Sr2/Lr27/Yr30/Pbc1* (28,43), *Lr67/Yr46/Sr55/Pm46/Ltn3* (15), *Lr68* (14), *Lr74* (U. Bansal, the University of Sydney, personal communication), and *Yr54* (3) confer APR to LR or YR in wheat. Of the preceding genes, *Lr34/Yr18/Sr57/Pm38/Ltn1*, *Lr46/Yr29/Sr58/Pm39/Ltn2*, *Sr2/Lr27/Yr30/Pbc1*, and *Lr67/Yr46/Sr55/Pm46/Ltn3* are of particular interest because they are pleiotropic to multiple diseases, including stem rust and powdery mildew (caused by *P. graminis* f. sp. *tritici* and *Blumeria graminis* f. sp. *tritici*, respectively) and are also associated with morphological traits—leaf tip necrosis (LTN) or pseudo black chaff—often used as visual markers to detect the presence of these resistances. In addition, around 80 LR (26) and 140 YR (35) quantitative trait loci (QTL) have been mapped in wheat. Many of these QTL are located in the same genetic regions for both diseases and are likely to be potential pleiotropic APR loci in wheat (26), such as the QTL on chromosomes 1BS, 2AL, 2BS, 2DL, 5AL, 5BL, 6AL, and 7BL that confer resistance to LR, YR, and powdery mildew simultaneously (26).

'Kenya Kongoni' is an International Maize and Wheat Improvement Center (CIMMYT) germplasm-derived spring wheat cultivar released in Kenya by the Kenya Agricultural Research Institute in 1981. It confers high levels of resistance to LR and YR in Mexico and to LR in Uruguay and manifests strong LTN at the adult plant stage. It does not carry the APR gene *Lr34/Yr18/Sr57/Pm38/Ltn1*, based on the molecular marker test with *csLV34* (21) and the gene-specific marker (24), nor does it carry *Lr67/Yr46/Sr55/Pm46/Ltn3*, based on the gene-specific marker (E. S. Lagudah, personal communication).

The objective of our study was to investigate the genetic basis of resistance to LR and YR in Kenya Kongoni by using a recombinant inbred line (RIL) population from its cross with susceptible parent 'Avocet-YrA' and to identify the genomic regions associated with resistance to the two rust diseases.

Materials and Methods

Plant materials. A population of 148 F₅ RILs was developed from the cross of the susceptible parent Avocet-YrA with resistant parent

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Kenya Kongoni. Avocet-YrA is a reselection line from the Australian 'Avocet' that lacks the temporarily designated resistance gene YrA. Kenya Kongoni (pedigree: CI8154/2*FR/3*ROM/4/WIS245/II50.17//CI8154/2*FR/3/TOB66) is susceptible to current Mexican races of LR and YR at seedling stage but resistant at adult plant stage, whereas Avocet-YrA is susceptible to these races 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. The same-single seed source of the F₄-derived F₅ RIL and parents were used in all experiments.

Field evaluation. The 148 RILs and parents were evaluated for LR resistance at El Batán, Mexico, during 2011 (hereafter referred to as the LR2011 experiment), at Ciudad Obregón, Mexico, during 2011–12 and 2012–13 (hereafter referred to as the LR2012 and LR2013 experiments), and at La Estanzuela, Uruguay, during 2012 (hereafter referred to as the LR2012U experiment). Phenotyping for YR was conducted at Toluca, Mexico, during 2011 and 2012 (hereafter referred to as the YR2011 and YR2012 experiments). The mapping population was evaluated using an augmented design in the LR2012, LR2013, and YR2012 experiments, in which 28 RILs and two parents were replicated twice and randomly distributed among the whole population. The LR2011, LR2012U, and YR2011 field experiments were conducted without replication.

Field plots consisted of 0.7-m paired rows with approximately 60 plants of each line. 'Morocco' and a mixture of six susceptible wheat lines derived from an 'Avocet/Attila' cross were used as LR and YR spreaders, respectively, in LR2011, LR2012, YR2011, and YR2012 field trials, whereas the YR differential line 'Avocet+Yr24/Yr26', susceptible to LR but resistant to YR, was used as an LR spreader in the LR2013 experiment. A mixture of Morocco, 'Thatcher', and 'Little Club' was used as the LR spreader in Uruguay under natural epidemics. 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. In Mexico, the LR epidemic was initiated by spraying the spreaders with an equal urediniospore mixture of *P. tritici* races MBJ/SP and MCJ/SP suspended in Sotrol oil (chempoint.com). The avirulence/virulence formula of MBJ/SP and MCJ/SP were reported in a previous study (14). The only difference between the two races is that MCJ/SP is completely virulent against *Lr26*, whereas MBJ/SP is partially virulent against this gene. Similarly, a mixture of *P. striiformis* isolates Mex96.11 and Mex08.13 was used to initiate the YR epidemics. Mex96.11 is virulent to Yr27 and avirulent to Yr31, whereas Mex08.13 is the opposite. In the present study, the resistant parent

Kenya Kongoni was susceptible to all of these LR and YR races in the seedling stage but resistant in the adult plant stage. Disease severities (DS) on parents and RILs were recorded three times in 2011, 2012, and 2013 using the Modified Cobb's scale (32). The first note was recorded when the susceptible parent Avocet-YrA displayed approximately 80% severity, and thereafter continued at weekly intervals until severity reached 90 to 100%. For multiple disease readings, area under disease progress curve (AUDPC) values were calculated using the method suggested by Björk and Line (4).

Genetic and statistical analysis. The number of APR genes against LR and YR in the Avocet/Kenya Kongoni population was estimated using Mendelian segregation analysis (20,44), where RILs were classified into three phenotypic categories: homozygous parental type resistant (HPTR), homozygous parental type susceptible (HPTS), and lines with responses different from those of the two parents (OTHER) based on disease severities and infection responses. The observed frequencies for each category (HPTR, HPTS, and OTHER) were tested against the expected frequencies for different numbers of additive genes using χ^2 analysis. Moreover, the minimum number of APR genes was also estimated for the three experiments grown under an augmented design by using the quantitative approach described by Wright (59) and Mulitze and Baker (31) as $n = (GR)^2/4.57(\sigma^2_g)$, where genotypic range (GR) = phenotypic range $\times$ broad-sense heritability (h^2), and σ^2_g = genetic variance of the RILs. Analysis of variance (ANOVA) was used to calculate h^2 and σ^2_g in the augmented design experiment. In order to get a single value for each entry to be used in QTL mapping and phenotypic correlation analyses, the partially replicated designs were analyzed through the mixed-models framework using the Mixed Procedure in SAS (SAS, Institute, Cary, NC) to calculate the best linear unbiased estimators or adjusted means whereas, for the RILs without replication, the final disease severities (FDS) in each environment were used directly.

Molecular analysis and genetic linkage map construction. The CTAB method was used for the DNA extractions of parents and RILs, with approximately 20 plants per line. The two parents and RILs were analyzed using 1,450 diversity arrays technology (DART) markers and 16 simple-sequence repeat (SSR) primers for the polymorphism survey. In addition, two cleaved amplified polymorphic sequence (CAPS) markers, *csLV46G22* and *csSr2*, associated with *Lr46* (E. S. Lagudah, personal communications) and *Sr2* (47), respectively, were used for genotyping the RIL population. In total, 455 polymorphic markers were used to construct the linkage maps with Joinmap 4.1 (51). Linkage maps were graphically visualized

Table 1. Final disease severities of parents and an Avocet-YrA/Kenya Kongoni recombinant inbred line (RIL) population evaluated for leaf rust and yellow rust resistance five and two environments, respectively, and estimated number of resistance genes based on the Wright (59) quantitative method

Parent, parameter	Leaf rust severity, % (Mexico)			Leaf rust severity, % (Uruguay)	Yellow rust severity, % (Mexico)	
	2011 ^a	2012 ^b	2013 ^c	2012 ^d	2011 ^e	2012 ^f
Avocet	90	90	70	90	90	80
Kenya Kongoni	10	5	5	5	5	5
Population mean	52	41	42	51	47	37
Population range: low	10	5	1	0	5	5
Population range: high	100	100	90	99	100	90
Entry variance (σ^2_e)	...	578.5	272.4	...	...	331.5
Residual variance (σ^2_e)	...	34.8	26	...	...	31.9
Heritability (h^2)	...	0.94	0.91	...	...	0.91
Estimated number of genes ^g	...	3	5	...	...	3.9

^a Final percent leaf rust severity at El Batán, 2011 season.

^b Final percent leaf rust severity at Ciudad Obregón, 2011–12 season.

^c Final percent leaf rust severity at Ciudad Obregón, 2012–2013 season.

^d Final percent leaf rust severity at La Estanzuela, 2012 season.

^e Final percent yellow rust severity at Toluca, 2011 season.

^f Final percent yellow rust severity at Toluca, 2012 season.

^g Number of segregating genes estimated through the quantitative method.

with MapChart (53). FDS and AUDPC from each experiment for LR and YR were used for QTL mapping by composite interval mapping (CIM) with Windows QTL Cartographer v2.5 software (54). To declare a significant QTL, 1,000 permutation tests were carried out and a logarithm of odds (LOD) threshold was set at $P = 0.05$ for each trait. The percentage of phenotypic variance explained (R^2) by individual QTL and additive effects at the LOD peaks were detected by CIM with backward and forward regression method with QTL Cartographer. A wheat consensus genetic map and physical bin location of DArT markers (10,16,46,56) were used to assign marker orders and the chromosomal position of linkage groups. QTL names were designated following the recommended practice (<http://wheat.pw.usda.gov/ggpages/wgc/98/Intro.htm>).

Results

Phenotypic evaluation. The FDS of Kenya Kongoni was 5% for LR at the adult plant stage whereas, for Avocet-YrA it ranged between 70 and 90%, depending on the site (Table 1). The mean LR FDS ranged between 41 and 51% for RILs in the three environments (Table 1). The frequency distributions of RILs for LR severities were continuous in both Mexican and Uruguayan environments (Fig. 1A), indicating polygenic inheritance of APR. Approximately three to five LR APR genes were estimated based on both Wright's method (modified by Mulitze and Baker [31]) (Table 1) and the Mendelian segregation analysis (Table 2).

The FDS of Kenya Kongoni was also 5% for YR in the two field experiments whereas, for Avocet-YrA it ranged between 80 and 90% (Table 1). The mean YR FDS ranged from 37 to 47% for the RILs (Table 1). The frequency distribution of RILs for YR severity was continuous in the two field experiments (Fig. 1B). Genetic analysis showed that four to five APR genes confer YR resistance in the Avocet-YrA/Kenya Kongoni RIL population, based on the two genetic methods used (Tables 1 and 2).

The Pearson's correlation coefficient for LR FDS between each environment ranged from 0.62 to 0.80 ($P < 0.0001$) and the correlation for YR was 0.82 ($P < 0.0001$). Significant correlations were also detected between LR and YR FDS among different environments ($r = 0.35$ to 0.64 , $P < 0.0001$) (Table 3). The h^2 of FDS was 0.94, 0.91, and 0.91 in LR2012, LR2013, and YR2012, respectively, whereas the variation among RILs was 578.5, 272.4, and 331.5, respectively, based on ANOVA (Table 1).

QTL mapping for pleiotropic APR to LR and YR. Two pleiotropic APR loci against LR and YR were detected in the Avocet-YrA/Kenya Kongoni RIL population. The first QTL, *QYr.cim-1BL*, was mapped in the same region as *Lr46/Yr29* based on the near-diagnostic marker *csLV46G22*. It explained 12 to 57% and 25 to 35% of variation for LR and YR severities, respectively, and was flanked by markers *wPt-1770* and *csLV46G22* (Table 4; Fig. 2A). Another locus, *QYr.cim-7BL*, detected on the long arm of chromosome 7B in the interval of molecular markers *wPt-9925* and *wPt-8938*, explained 5 to 13% of LR and 12% of YR variance (Table 4; Fig. 2B). These two pleiotropic APR QTLs were derived from the resistant parent Kenya Kongoni.

QTL mapping for APR to LR. Four additional QTL for LR resistance were detected in the Avocet-YrA/Kenya Kongoni population. The first QTL, *QLr.cim-1DS*, was located on the short arm of chromosome 1D and was flanked by DArT markers *wPt-3738* and *rPt-4471*. It explained 6 to 21% of LR variance (Table 4; Fig. 2C). The second QTL, *QLr.cim-2BL*, detected in LR2011 and LR2013, explained 6 to 21% of the variance for LR severity. It was located between DArT markers *wPt-6174* and *wPt-8548* (Table 4; Fig. 2D). The third QTL, *QLr.cim-3BS*, was flanked by molecular markers *wPt-5209* and *csSr2* and explained 5 to 10% of the LR variance in adult plants (Table 4; Fig. 2E). The fourth QTL, *QLr.cim-5AC*, was located near the centromere of chromosome 5A and flanked by DArT markers *wPt-3187* and *wPt-7769*. It was significant only in LR2011. Except for *QLr.cim-5AC*, which came from the susceptible parent Avocet-YrA, the other QTL were derived from the resistant parent Kenya Kongoni.

QTL mapping for APR to YR. Three minor QTL for YR resistance were mapped in the Avocet-YrA/Kenya Kongoni population. The first QTL, *QYr.cim-2AS*, was detected only in YR2011. It was flanked by *Xbarc124* and *wPt-1722* and explained 5 to 6% of the YR variance for YR severity (Table 4; Fig. 2F). The second QTL, *QYr.cim-2BS*, was detected in both YR environments and mapped on the short arm of chromosome 2B at the interval of *wPt-1813* and *wPt-8072*. It explained 7 to 12% of the variation (Table 4; Fig. 2G). *QYr.cim-5BL* was only detected in YR2011 and flanked by molecular markers *Xbarc59* and *wPt-3922*. It explained 6 to 8% of YR variance (Table 4; Fig. 2H). All three QTL were derived from the resistant parent Kenya Kongoni.

Fig. 1. Frequency distributions for final disease severity in Avocet-YrA/Kenya Kongoni recombinant inbred lines (RILs) for **A**, leaf rust severity in field trials in Mexico (El Batán, 2011 and Ciudad Obregón, 2012–13) and Uruguay (La Estanzuela, 2012) and for **B**, yellow rust severity in Mexico (Toluca, 2011 and 2012).

Discussion

Using conventional methods to estimate genes, resistance in Kenya Kongoni to LR and YR was found to be governed by four to five APR genes, which agrees with the QTL detected through molecular mapping. QTL on chromosomes 1BL and 3BS are most likely the known pleiotropic resistance loci *Lr46/Yr29/Sr58/Pm39* and *Sr2/Lr27/Yr30*, based on the closely linked molecular markers. Interestingly, the 3BS QTL caused a significant reduction in LR severity but had no significant effect on YR.

The 1BL QTL corresponding to pleiotropic APR gene *Lr46/Yr29/Sr58/Pm39* had the most significant effect in reducing LR and YR severities. This gene provided relatively high levels of protection for LR and YR in all environments and explained the expression of LTN in the population. This locus has also been reported in other populations (3,25,36,37,42,57,58).

Another pleiotropic QTL associated with resistance to LR and YR was found on chromosome 7BL between markers *wPt-9925* and *wPt-8938*, temporarily designated as *QYLr.cim-7BL*. Crossa et al. (7) reported that the marker *wPt-9925* may be associated with the YR APR gene *Yr39*. Lin and Chen (27) identified *Yr39* closely linked with molecular marker *Xgwm131* in spring wheat 'Alpowa'. This marker was analyzed in the parental lines Avocet-YrA and Kenya Kongoni but was found to be monomorphic. Herrera-Foessel et al. (14) mapped the slow-rusting APR gene *Lr68* in 'Parula' on chromosome arm 7BL at a distance of 7.5 centimorgans (cM) from the marker *Xgwm146*, which was tightly linked to the race-specific resistance gene *Lr14b*. Both Avocet-YrA and Kenya Kongoni possessed the negative allele of the *cs7BLNLR* marker, known to be tightly linked with *Lr68/Lr14b*. In their study with 'Attila' wheat, Rosewarne et al. (37) found a QTL with significant effect on chromosome 7BL between markers *Xwmc273-Xgwm146* and *XP32/M59-Xgwm344* for LR and YR resistance, respectively. The SSR markers *Xgwm344* and *Xgwm146*, also known to be associated with *Lr68/Lr14b*, were used to genotype the parents and RILs and were found to be located at a distance of 27.3 and 32.0 cM, respectively, from the *QYLr.cim-7BL*. Due to the long distances of the *Lr68/Lr14b* linked markers from *QYLr.cim-7BL* in the Avocet-YrA/Kenya Kongoni RIL population, it is likely that this QTL is an uncharacterized pleiotropic slow-rusting APR gene that confers resistance to LR and YR. Moreover, *Lr68/Lr14b* is not known to confer APR to YR to date.

The LR QTL *QYLr.cim-1DS* on chromosome 1DS between markers *wPt-3738* and *wPt-4471* was more significant in Uruguay, with an LOD of 10 and PVE of 10%. In Mexico in 2011, the same markers were associated with a QTL for LR resistance but with a lower LOD and PVE of 3 to 5 and 5.6%, respectively. The DaRT marker *wPt-3738* was associated with grain yield (7) and the LR

race-specific resistance gene *Lr42*. The gene was flanked by markers *Xwmc432* and *Xcdf15* and mapped on chromosome 1DS (49). Basnet et al. (3) also found *Lr42* in 'Quaiu 3' wheat using the same SSR marker, *Xwmc432*. This marker was used in the parents of our study and turned out to be monomorphic. Avocet-YrA and Kenya Kongoni were susceptible to the races used in the present study at the seedling stage and, therefore, are not expected to carry *Lr42*.

The LR QTL *QYLr.cim-2BL* was located in the interval of *wPt-6174* and *wPt-8548*. Previous studies also have shown LR QTL on 2BL, indicating that this region is important for slow-rusting resistance to LR. Chromosome 2BL is of interest in this study because it showed an LOD and PVE of 3 to 13 and 6 to 20%, respectively. Rosewarne et al. (37) found a significant QTL on chromosome 2BL for YR derived from Avocet-YrA flanked by the SSR markers *Xgwm1027* and *Xgwm61*. The QTL on 2BS in the present study was derived from Kenya Kongoni. It is difficult to clarify the relationship between these two QTL because the common molecular marker was not available; however, this chromosomal region requires further investigation.

The QTL *QYLr.cim-3BS* for LR resistance on 3BS, detected in the Avocet-YrA/Kenya Kongoni population, was associated with the tightly linked genes *Sr2/Lr27/Yr30*. The *P. trititica* races used in our experiments were virulent on the complementary leaf rust resistance genes *Lr27+Lr31*; hence, the QTL effect is unlikely to be associated with *Lr27*. Previous studies identified QTL for LR on chromosome 3BS (8,19,36,43,48). Spielmeier et al. (47)

Table 3. Phenotypic correlations for final leaf rust severity in Mexico (El Batán, 2011; Ciudad Obregón, 2011–12 and 2012–13) and Uruguay (La Estanzuela, 2012) and yellow rust severity in Mexico (Toluca, 2011 and 2012) for an Avocet-YrA/Kenya Kongoni RIL population^a

Environment	LR2011 ^b	LR2012 ^c	LR2013 ^d	LR2012U ^e	YR2011 ^f
LR2012	0.75**	...	...	...	...
LR2013	0.72**	0.80**	...	...	...
LR2012U	0.66**	0.62**	0.65**	...	...
YR2011	0.53**	0.61**	0.57**	0.35**	...
YR2012 ^g	0.56**	0.64**	0.64**	0.36**	0.82**

^a Asterisks (**) indicate means significant at $P < 0.0001$.

^b Final leaf rust severity at El Batán, 2011 season.

^c Final leaf rust severity at Ciudad Obregón, 2011–12 season.

^d Final leaf rust severity at Ciudad Obregón, 2012–13 season.

^e Final leaf rust severity at La Estanzuela, 2012 season.

^f Final yellow rust severity at Toluca, 2011 season.

^g Final yellow rust severity at Toluca, 2012 season.

Table 2. Estimated number of resistance genes through Mendelian segregation analysis for adult plant resistance to leaf rust and yellow rust in 148 Avocet-YrA/Kenya Kongoni F₃ recombinant inbred lines (RILs)

Response category ^d	Number of RILs					
	Leaf rust (Mexico) ^a			Leaf rust (Uruguay) ^b	Yellow rust ^c (Mexico)	
	2011	2012	2013	2012	2011	2012
HPTS	6	8	6	8	2	2
HPTR	2	1	2	1	2	2
OTHER	139	138	135	138	143	142
Missing	1	1	5	1	1	2
Total	148	148	148	148	148	148
Number of genes	4	4	4	4	5	5
<i>P</i> value	0.32	0.09	0.35	0.09	0.92	0.92

^a Based on leaf rust severity recorded in three seasons (El Batán, 2011; Ciudad Obregón, 2011–12 and 2012–13).

^b Based on leaf rust severity recorded at La Estanzuela, 2012 season.

^c Based on yellow rust severity recorded at Toluca, 2011 and 2012 seasons.

^d HPTS = homozygous parental type susceptible, HPTR = homozygous parental type resistant, and OTHER = lines with responses different from those of the parents. *P* value is for the χ^2 test. Expected ratios of RILs grouped under HPTR, HPTS, and OTHER are 0.037:0.037:0.926 and 0.016:0.016:0.968 for segregation of four and five additive genes, respectively, in the F₄-derived F₅ generation, assuming that HPTR lines were derived from plants that were homozygous for all resistance genes, HPTS lines were derived from plants where all resistance genes were absent, and lines grouped as OTHER were derived from plants with all other possible combinations of resistance genes.

determined that a 120-bp allele of the microsatellite locus *Xgwm533* was linked to *Sr2* in several lines. Mago et al. (28) developed a CAPS marker, *csSr2*, associated with the presence or absence of the gene, which was also used in this study. The *QLr.cim-3BS* effects were significant in Mexico and Uruguay and similar in all experiments. In contrast, the effect of minor APR gene *Yr30* (48,57) was not significant in the Avocet-*YrA*/Kenya Kongoni population.

A minor YR QTL *QYr.cim-2AS* was detected in Kenya Kongoni only during YR2011. It was flanked by molecular markers *Xbarc124* and *wPt-1722* with an LOD of 3 and PVE of 5 to 6%. Hao et al. (13) detected a QTL for YR resistance in U.S. wheat line Pioneer 26R61 at a similar chromosomal position. It was flanked by SSR markers *Xbarc124* and *Xgwm359* and explained 23 to 24% of YR variation in adult plant stage. In addition, several QTL have been reported in this region in wheat lines Y16DH70 (1), Recital (8), Camp Remy

(29), Stephens (52), Kukri (2), and *T. monococcum* (5). The QTL in *T. monococcum* should be different from *QYr.cim-2AS*, based on the origin, but the relationship between *QYr.cim-2AS* and others needs further investigation.

A QTL associated with moderately effective YR resistance was located on chromosome 2BS. The *QYr.cim-2BS* is positioned between markers *wPt-1813* and *wPt-6158* and had a range of 3 to 5 LOD and 6 to 10% PVE. This region is rich in race-specific resistance genes, including *Yr31* (45) and *Yr27* (55), that show an intermediate infection type when scored in seedling tests against avirulent races and also confer moderate to high levels of resistance when present alone in adult plants with avirulent races. Based on seedling tests (results not shown), we can conclude that the genes *Yr27* and *Yr31* were absent in Kenya Kongoni, due to its high infection types in seedlings with races avirulent to these genes.

Table 4. Position and effect of quantitative trait loci (QTL) detected for adult plant resistance (APR) to leaf rust and yellow rust using final disease severity (FDS) and area under the disease progress curve (AUDPC) through composite interval mapping (CIM) by QTL Cartographer in the Avocet-*YrA*/Kenya Kongoni RIL population

Environment	QTL ^a	Position ^b	Left marker	Right marker	LOD ^c	R ² (%) ^d	Add ^e
LR11 FDS	<i>QLr.cim-1BL</i>	12	<i>wPt-1770</i>	<i>csLV46G22</i>	14	24	-10
	<i>QLr.cim-1DS</i>	0	<i>wPt-3738</i>	<i>rPt-4471</i>	4	6	-5
	<i>QLr.cim-2BL</i>	0	<i>wPt-6174</i>	<i>wPt-8548</i>	12	21	-9
	<i>QLr.cim-5AC</i>	36	<i>wPt-3187</i>	<i>wPt-7769</i>	3	5	4
LR11AUDPC ^f	<i>QLr.cim-1BL</i>	12	<i>wPt-1770</i>	<i>csLV46G22</i>	16	28	-34
	<i>QLr.cim-1DS</i>	0	<i>wPt-3738</i>	<i>rPt-4471</i>	5	7	-17
	<i>QLr.cim-2BL</i>	0	<i>wPt-6174</i>	<i>wPt-8548</i>	12	20	-28
	<i>QLr.cim-2DL</i>	12	<i>wPt-668017</i>	<i>wPt-666518</i>	3	5	-14
	<i>QLr.cim-5AC</i>	37	<i>wPt-3187</i>	<i>wPt-3884</i>	4	5	15
	<i>QLr.cim-1BL</i>	22	<i>csLV46G22</i>	<i>wPt-729773</i>	20	51	-20
LR12 FDS	<i>QLr.cim-3BS</i>	5	<i>wPt-5209</i>	<i>csSr2</i>	3	5	-6
	<i>QLr.cim-7BL</i>	12	<i>wPt-9925</i>	<i>wPt-0194</i>	3	6	-7
	<i>QLr.cim-1BL</i>	23	<i>csLV46G22</i>	<i>wPt-729773</i>	25	57	-111
LR12 AUDPC ^g	<i>QLr.cim-3BS</i>	5	<i>wPt-5209</i>	<i>csSr2</i>	6	8	-41
	<i>QLr.cim-7BL</i>	12	<i>wPt-9925</i>	<i>wPt-0194</i>	4	7	-38
	<i>QLr.cim-1BL</i>	24	<i>csLV46G22</i>	<i>wPt-729773</i>	5	12	-11
LR12U ^h	<i>QLr.cim-1DS</i>	0	<i>wPt-3738</i>	<i>rPt-4471</i>	11	21	-14
	<i>QLr.cim-3BS</i>	2	<i>wPt-5209</i>	<i>csSr2</i>	5	10	-10
	<i>QLr.cim-7BL</i>	32	<i>wPt-8938</i>	<i>wPt-9013</i>	7	13	-12
	<i>QLr.cim-1BL</i>	11	<i>tPt-6091</i>	<i>wPt-1770</i>	9	24	-10
LR13 FDS	<i>QLr.cim-7BL</i>	0	<i>wPt-8981</i>	<i>wPt-2273</i>	3	5	-5
	<i>QLr.cim-1BL</i>	13	<i>wPt-1770</i>	<i>wPt-734314</i>	13	31	-63
LR13 AUDPC ⁱ	<i>QLr.cim-2BL</i>	1	<i>wPt-6174</i>	<i>wPt-8548</i>	3	6	-28
	<i>QLr.cim-2DL</i>	32	<i>wPt-2781</i>	<i>Xbarc159</i>	3	6	-27
	<i>QYr.cim-1BL</i>	12	<i>wPt-1770</i>	<i>csLV46G22</i>	17	35	-13
	<i>QYr.cim-2AS</i>	0	<i>Xbarc124</i>	<i>wPt-1722</i>	3	5	-5
YR11 FDS	<i>QYr.cim-2BS</i>	15	<i>wPt-1813</i>	<i>wPt-4613</i>	4	7	-6
	<i>QYr.cim-5BL</i>	135	<i>barc59</i>	<i>wPt-3922</i>	4	8	-6
	<i>QYr.cim-1BL</i>	13	<i>wPt-1770</i>	<i>csLV46G22</i>	15	32	-142
	<i>QYr.cim-2AS</i>	0	<i>Xbarc124</i>	<i>wPt-1722</i>	3	6	-59
YR11 AUDPC ^j	<i>QYr.cim-2BS</i>	9	<i>wPt-1813</i>	<i>wPt-4613</i>	5	8	-71
	<i>QYr.cim-5BL</i>	135	<i>Xbarc59</i>	<i>wPt-3922</i>	3	6	-64
	<i>QYr.cim-1BL</i>	11	<i>tPt-6091</i>	<i>csLV46G22</i>	10	25	-11
	<i>QYr.cim-2BS</i>	21	<i>wPt-6158</i>	<i>wPt-5188</i>	4	8	-6
YR12 FDS	<i>QYr.cim-7BL</i>	12	<i>wPt-9925</i>	<i>wPt-744632</i>	5	12	-8
	<i>QYr.cim-1BL</i>	11	<i>tPt-6091</i>	<i>csLV46G22</i>	14	34	-143
YR12 AUDPC ^k	<i>QYr.cim-2BS</i>	29	<i>wPt-3949</i>	<i>wPt-8072</i>	5	12	-86
	<i>QYr.cim-7BL</i>	11	<i>wPt-9925</i>	<i>wPt-0194</i>	6	12	-85

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

^b Peak position in centimorgans from the first linked marker of the relevant linkage group.

^c Logarithm of odds (LOD) score based on 1,000 permutations.

^d R² is the proportion of phenotypic variance explained by the QTL.

^e Additive effect for each QTL; a negative sign indicates a QTL effect from Kenya Kongoni.

^f AUDPC for leaf rust at El Batán, 2011.

^g AUDPC for leaf rust at Ciudad Obregón, 2011–12.

^h LR12U leaf rust at La Estanzuela, 2011–12.

ⁱ AUDPC for leaf rust at Ciudad Obregón, 2012–13.

^j AUDPC for yellow rust at Toluca, 2011.

^k AUDPC for yellow rust at Toluca, 2012.

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Fig. 2. Likelihood plots of quantitative trait loci (QTL) for adult plant resistance to leaf rust (LR) on chromosomes **A**, 1BL; **B**, 7BL; **C**, 1DS; **D**, 2BL; and **E**, 3BS and to yellow rust (YR) on chromosomes **A**, 1BL; **B**, 7BL; **F**, 2AS; **G**, 2BS; and **H**, 5BL identified by QTL Cartographer in an Avocet-YrA/Kenya Kongoni recombinant inbred line population. The significant logarithm of odds (LOD) thresholds were detected based on 1,000 permutations. Positions (in centimorgans) of the molecular markers along each chromosome are shown on the vertical axes; cumulated genetic distances of linkage group are also given. LR11, LR12, and LR13 represent LR phenotypic data in Mexico (El Batán, 2011; Ciudad Obregón, 2012–13) and Uruguay (La Estanzuela, 2012). YR11 and YR12 represent YR phenotypic data for Mexico (Toluca, 2011 and 2012). LR11A, LR12A, LR13A, LR13UA, YR11A, and YR12A represent area under the disease progress curve for LR in Mexico (El Batán, 2011 and Ciudad Obregón 2012–13) and Uruguay (La Estanzuela, 2012) and for YR in Mexico (Toluca, 2011 and 2012).

Another small effect locus conferring resistance to YR was found on chromosome 5BL (*QYr.cim-5BL*) between the markers *Xbarc59* and *wPt-3922*. Chu et al. (6) identified an APR QTL, *QLr.fcu-5BL*, on the same chromosome between SSR markers *Xgdm116-Xbarc59* with a small effect on LR resistance and which explained about 7% of the phenotypic variation. In our study, the phenotypic variation for YR resistance ranged from 5 to 9%. Interestingly, the same marker, *Xbarc59*, was linked to resistance loci in both studies.

Kenya Kongoni, released in Kenya in 1981, has remained resistant to LR and YR in Mexico, Uruguay, and Kenya. Our study shows that the resistance to LR and YR is controlled by four to five slow-rusting APR loci. Because Kenya Kongoni does not possess seedling resistance, it can be a valuable parent in breeding programs to achieve durable resistance to both rusts by crossing with other elite germplasm and pyramiding the resistance loci into a single cultivar using the closely linked molecular markers.

Fig. 2. Continued from preceding page

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