RESEARCH

Expression of a Thatcher Wheat Adult Plant Stem Rust Resistance QTL on Chromosome Arm 2BL is Enhanced by *Lr34*

J. A. Kolmer,* D. F. Garvin, and Y. Jin

ABSTRACT

An F_6 recombinant inbred line (RIL) spring wheat (*Triticum aestivum* L.) population derived from RL6071, a stem rust susceptible line, and RL6058, a backcross line of Thatcher wheat with *Lr34* that is highly resistant to stem rust, was evaluated for adult plant stem rust resistance in North Dakota in 1999, and in Kenya in 2007 and 2008. In all three tests, most RILs that exhibited low stem rust severity had *Lr34* and most lines that had high disease severity lacked *Lr34.* Molecular mapping with DArT and simple sequence repeat (SSR) markers detected a quantitative trait locus (QTL) for adult plant stem rust resistance on chromosome arm 2BL. The RILs with both *Lr34* and DArT marker wPt*5044* on 2BL had significantly lower stem rust severities compared with lines that only had *Lr34* in North Dakota 1999 and Kenya 2008. Marker wPt*5044* alone did not significantly increase stem rust resistance. The QTL region on 2BL was not associated with any previously mapped Thatcher seedling stem rust resistance genes. The stem rust resistance in Thatcher enhanced by the presence of *Lr34* is effective to different races in North America and Kenya and mapped to the same QTL.

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Abbreviations: QTL, quantitative trait locus; RIL, recombinant inbred line; SSR, simple sequence repeat.

Thatcher is a historically important wheat cultivar in North America. Developed and released by the Minnesota Agricultural Experiment Station in 1935 (Hayes et al., 1936), Thatcher combined good agronomic characters and high quality for bread making with resistance to stem rust, caused by *Puccinia graminis* f. sp. *tritici* Eriks. & E. Henn. Thatcher was selected from the cross of Marquis/Iumillo durum//Marquis/Kanred. The cultivar Marquis had good agronomics and bread making characters, but was highly susceptible to stem rust. Thatcher has stem rust resistance derived from Kanred and Iumillo durum wheat. Thatcher was widely grown in the United States and also in Canada from the mid-1930s to the mid-1960s. Due to high bread-making quality, Thatcher was used as a recurrent parent in Canada in a backcrossing program that introduced additional genes for stem rust resistance (Green and Campbell, 1979) and resistance to wheat leaf rust, caused by *Puccinia triticina* Eriks. (Dyck, 1993a). Thatcher was also used as a parent in development of the cultivar Chris from Minnesota, which had additional stem rust resistance, plus adult plant leaf rust resistance derived from the cultivar Frontana (Samborski, 1985).

The inheritance of stem rust resistance in Thatcher has proven to be complex. Genes *Sr5, Sr9g, Sr12,* and *Sr16* have been identified in Thatcher (Green and Dyck, 1975). However, Knott (2000) determined

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that additional unidentified genes conditioned resistance to different stem rust races. Knott (2001) also showed that resistance that segregated in seedlings was related to resistance that segregated in adult plants, although the seedling resistance did not fully explain the adult plant resistance. Similarly, Gavin Vanegas et al. (2008) determined that segregation of seedling stem rust resistance in Thatcher was associated with field resistance, but that additional unidentified genes conditioned adult plant resistance. Thatcher has seedling resistance genes that do not condition resistance to historically important stem rust races such as race 15B, yet it does have additional adult plant resistance that has been difficult to characterize and transfer in breeding programs (Knott, 2001).

Dyck (1987) transferred the adult plant leaf rust resistance gene *Lr34* from several different sources into Thatcher. These Thatcher backcross lines all had better stem rust resistance that was expressed in seedling and adult plants compared with Thatcher itself. *Lr34* is present in North America spring wheat germplasm (Kolmer et al., 2008) and is an important component of stem rust resistance in Canadian cultivars that have significant amounts of Thatcher in their pedigrees (Dyck, 1993b; Liu and Kolmer, 1998). Gavin Vanegas et al. (2008) identified one microsatellite marker on chromosome arm 2BL in a Thatcher line with *Lr34* that was associated with adult plant stem rust resistance.

The objective of this study was to further genetically dissect the adult plant stem rust resistance in Thatcher that is enhanced by the presence of *Lr34*. The F_6 RIL population of RL6071 × RL6058 characterized by Gavin Vanegas et al. (2008) was mapped with a large number of molecular markers that allowed a chromosomal region associated with stem rust resistance to be identified. A further objective was to determine if the Thatcher-*Lr34* stem rust resistance was also effective to the stem rust races that are currently found in East Africa (Jin et al., 2008; Jin et al., 2009). We wished to determine if *Lr34* had the same enhancement effect and if the same chromosomal regions in Thatcher were associated with adult plant stem rust resistance to races found in North America and in East Africa.

MATERIALS AND METHODS

Plant Materials

An F_6–derived recombinant inbred line (RIL) population derived by single seed descent from RL6071 × RL6058 was previously described (Gavin Vanegas et al., 2008). RL6071 (Prelude/8*Marquis) is a stem rust and leaf rust susceptible spring wheat line. RL6058 (Thatcher*6/PI58548) is a Thatcher backcross line with *Lr34* and is highly stem rust resistant. The mapping population consisted of 92 RILs that were tested for stem rust response as adult plants in Fargo, North Dakota in 1999 and in Njoro, Kenya in 2007 and 2008.

Stem Rust Severity Evaluation

The RILs, parental lines, and Thatcher were evaluated for stem rust resistance in Fargo North Dakota in 1999 as previously reported (Gavin Vanegas et al., 2008). The lines were planted in late April and evaluated in late July. Spreader rows of stem rust susceptible Wolfe barley (*Hordeum vulgare* L.) and wheat cultivars Little Club and Baart were needle inoculated with a mixture of stem rust races TMLK, TPMK, RTQQ, QFCQ, and QTHJ, as described in the North American stem rust race nomenclature (Roelfs and Martens, 1988). The lines were evaluated for severity of stem rust infection using the modified Cobb scale (Peterson et al., 1948).

The RILs, parental lines, and Thatcher were evaluated for stem rust response in Njoro, Kenya in 2007 and 2008. Test entries were planted in double 1-m row plots in mid June. To facilitate inoculum increase and uniform dissemination within the nursery, a continuous row of stem rust spreader (a mixture of susceptible cultivars Duma with *Sr31* and K-Mwanba with *Sr24*) was planted perpendicular to all entries 2 wk before test entries were planted. The spreader rows were inoculated by dusting with a mixture of urediniospores and talc powder in 2007, and by dusting and needle inoculation in 2008. The inoculum was a bulk collection of urediniospores collected from plots of Duma of stem rust races TTKSK and TTKST (Jin et al., 2008; Jin et al., 2009). The RL6071 × RL6058 mapping population exhibited a strong photosensitive response, and most entries were relatively late, at flowering to late milk stages when stem rust severity evaluations were taken. The ratio of resistant to susceptible lines was used to determine the number of segregating genes at each location. A χ^2 test (Steel and Torrie) was used to determine if the observed ratio significantly deviated from the expected ratio.

Molecular Mapping and QTL Analysis

Parents and the RILs were evaluated by the Diversity Arrays Technology (DArT) methodology by Triticarte Pty Ltd (Akbari et al., 2006) to identify a large number of segregating molecular makers. In addition, 18 simple sequence repeat (SSR) wheat markers that were polymorphic between the two parents (*Xbarc55, Xbarc45, Xbarc10, Xbarc183, Xbarc159, Xbarc139, Xbarc73, Xbarc91, Xbarc18, Xbarc167, Xbarc101*, *Xbarc128, Xgwm501, Xgwm148*, *Xwmc592*, *Xwmc154, Xwmc175,* and *Xwmc360*) and the perfect marker for *Lr34* (Lagudah et al., 2009) were scored in the RIL population. Mapmaker v2.0 for MacIntosh with the Kosambi mapping function was used to construct the linkage map. A logarithm of odds (LOD) of 4.0 was used for two point mapping with a Θ of 0.2.

Single factor regression was first completed with Statistical Analysis Software (SAS v9.1, Cary NC) to identify DArT and SSR markers associated with adult plant stem rust resistance. Statistical Analysis Software was also used to determine χ^2 values for differences in frequency distribution of stem rust severity in RILs with and without *Lr34* and for paired *t* tests of RILs that varied for markers associated with stem rust resistance. Composite interval mapping with *Lr34* serving as a cofactor was conducted with QGENE (Nelson, 1997), to determine the coefficient of determination (R^2) and LOD scores for each marker interval, at a significance level of $\alpha = 0.05$ and with 1000 permutations of the dataset.

RESULTS

Stem Rust Phenotypes

The stem rust susceptible parent RL6071 had high severity levels exceeding 50% stem rust infection in all

field evaluations (Table 1). The stem rust resistant parent RL6058 had very low severity levels of 0 to 5% in North Dakota 1999 and in Kenya 2007, and a range of 5 to 20% in Kenya 2008. The cultivar Thatcher had 20 to 30% severity in North Dakota 1999, 10% in Kenya 2007, and 40 to 60% in Kenya 2008. The RILs of RL6071 × RL6058 varied from 0% to 60% in North Dakota 1999 and from 0% to 80% in Kenya 2007. In Kenya 2008, stem rust severity was higher with a range of 20 to 80% on the F_6 lines. The stem rust severity ratings of the RILs for all three locations had significant ($P < 0.001$) correlation coefficients: 0.57 for North Dakota 1999 with Kenya 2007, 0.52 for North Dakota 1999 with Kenya 2008, and 0.54 for Kenya 2007 with Kenya 2008.

Effect of *Lr34* on Stem Rust Severity in RILs

For all three tests, most of the RILs that had the lowest stem rust severity had *Lr34* (Fig. 1) and most RILs that had the highest stem rust severity lacked *Lr34*. From single factor regression the R^2 for *Lr34* on stem rust severity in the segregating RILs was 0.45 in North Dakota 1999, 0.20 in Kenya in 2007, and 0.19 in Kenya in 2008. All R^2 values were significant at $P < 0.001$. The distribution of stem rust severities in the RILs with *Lr34* was significantly different ($P < 0.001$) based on χ^2 values from that observed in the RILs that lacked *Lr34* in all three locations. *Lr34* itself did not condition stem rust resistance, as susceptible F_6 lines with it had severities of >60%, and lines without *Lr34* with low severity were also found. However, some lines varied for severities at different locations. Line #88 that lacked *Lr34* had 10% stem rust severity in North Dakota 1999, and had severities of 30% and 50%, respectively in Kenya 2007 and Kenya 2008. Six lines that lacked *Lr34* had 60 to 70% stem rust severities in Kenya 2008 and varied between 20 and 60% severities in North Dakota 1999, and 10 to 40% severities in Kenya 2007. Some lines had similar severities at all three locations. Line #66 that had *Lr34* had 60% severity in North Dakota 1999 and 50% severity in both Kenya 2007 and Kenya 2008. Line #41 that lacked *Lr34* had 25% severity in North Dakota 1999, and 20% severity in both Kenya 2007 and Kenya 2008.

The number of genes that segregated for stem rust resistance was estimated at the three locations in two separate groups, with and without *Lr34* (Table 2). In North Dakota 1999, the segregation of lines with *Lr34* fit a 15:1 ratio, which indicated up to four genes conditioned resistance. In lines without *Lr34,* the segregation fit both two and three gene ratios, depending on the threshold (50% or 60%) used to group susceptible lines. In Kenya 2007 and Kenya 2008, lines with *Lr34* segregated in two and three gene ratios, again depending on the threshold used to group susceptible lines. In Kenya 2007, lines without *Lr34* segregated in a single gene ratio, regardless of the susceptible grouping. In Kenya 2008, lines without *Lr34* segregated in a two gene ratio. Since the presence of *Lr34* had a major effect on the segregation of stem rust severity in the F_6 lines, *Lr34* was treated as a cofactor (Steel and Torrie, 1980) in the subsequent QTL analysis of stem rust severity in the F_6 lines.

Table 1. Stem rust severities of parental wheat lines RL6071, RL6058, Thatcher, and RL6071 × RL6058 F_6 lines in field plot evaluations in North Dakota and Kenya.

Line	Location		
	North Dakota 1999	Kenya 2007	Kenya 2008
RL6071	50–60%	60–70%	70%
RL6058	1–5%	0%	5–20%
Thatcher	20–30%	10%	40–60%
F_6 Lines	0–60%	0–80%	20–80%

Identification of a Stem Rust Resistance QTL Enhanced by *Lr34*

A total of 280 DArT markers were generated, of which 256 were polymorphic. The linkage map spanned 1091 cM with an average of one marker per 3.97 cM. A subset of 152 DArT and SSR markers spaced 1 to 35cM apart was used for detection of QTL. Twenty-nine linkage groups were assembled for QTL analysis. Composite interval mapping analysis of the stem rust severity scores of the RILs at the three locations identified a QTL region that was associated with stem rust severity. SSR markers *Xbarc101, Xwmc175, Xgwm501*, and *Xwmc360* mapped in this region along with several DArT markers located on chromosome 2B. *Xbarc101, Xwmc175,* and *Xgwm501* are located on the chromosome 2BL consensus map (Somers et al., 2004), and *Xgwm360* was mapped to chromosome 2B. In North Dakota 1999, the marker interval wPt*4199*–wPt*5680* explained 19% of the stem rust severity variation, with a reduction of 5.9% in severity for the allele from RL6058 (Table 3, Fig. 2). In Kenya 2007 and Kenya 2008, the marker interval wPt*4199*–*Xmc175* accounted for 13% and 8% of the stem rust severity variation, respectively, with mean reductions in severity of 6.4% and 3.9%. Based on 1000 permutations of the dataset, the LOD value for the interval in North Dakota 1999 was 4.2, and in Kenya 2007 was 2.7, and both were significant at $P < 0.01$ and $P < 0.05$, respectively. The LOD score for Kenya 2008 of 1.7 in this interval was not significant.

At all three locations the DArT marker wPt*5044* had the highest R^2 value associated with stem rust severity. The effect of wPt*5044* on stem rust severity in combinations of F_6 lines that varied for *Lr34* is seen in Table 4. In North Dakota 1999 and Kenya 2007, RILs with the wPt*5044* allele from RL6058 that also had *Lr34* exhibited significantly lower severity compared with lines that had the allele from RL6071. At both of these locations the wPt*5044* allele did not significantly reduce stem rust severity in RILs that lacked *Lr34*. In Kenya 2008 the reverse was observed, as the wPt*5044* allele from RL6058 had no significant effect in

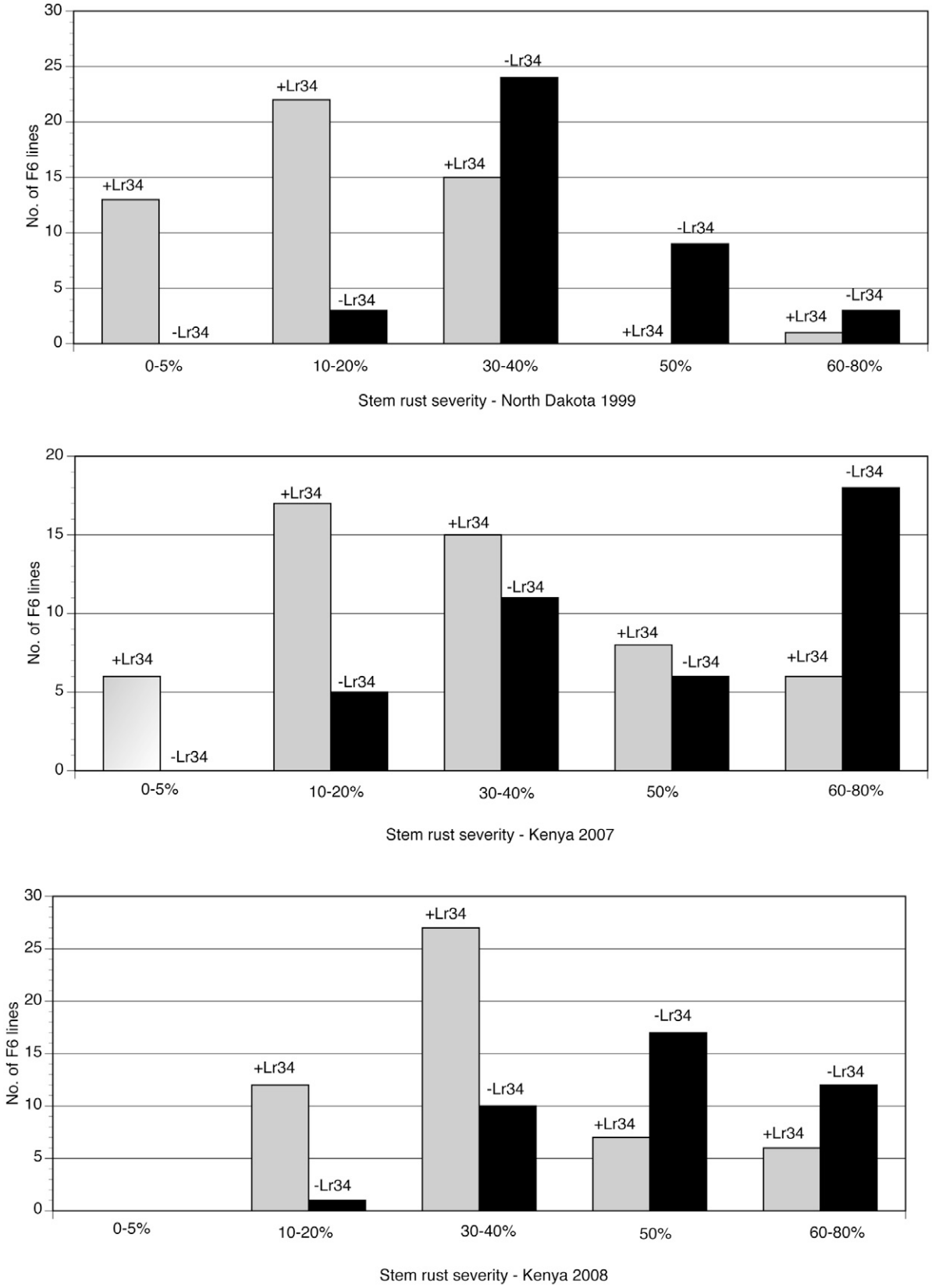

Figure 1. Distribution of stem rust severity in F_6 lines of RL6071 × RI6058 in North Dakota 1999 and Kenya 2007 and 2008.

RILs with *Lr34*, yet stem rust severity was reduced significantly in RILs that lacked *Lr34.*

RL6071, RL6058, Thatcher, and the three parents of Thatcher (Kanred, Marquis, and Iumillo durum) were haplotyped for SSR markers *Xbarc101, Xwmc175,* and *Xgwm501* on chromosome 2BL (Table 5). Thatcher and RL6058 had the same allele as Iumillo durum for marker *Xbarc101.* For *Xgwm501,* Thatcher, RL6058, and Iumillo

Table 2. Segregation of stem rust resistance in F_6 lines of RL6071 × RL6058 at three locations.

Location	Stem rust severity					*Lr34*	Resistant/ susceptible	Expected ratio	Probability
	1–5%	10–20%	30–40%	50%	60–70%				
North Dakota 1999	13	22	15	0	1	+	50:1	7:1	0.00
								15:1	0.21
	0	3	24	9	3	–	27:12	3:1	0.41
							36:3	7:1	0.36
Kenya 2007	6	17	15	8	6	+	38:14	3:1	0.75
							46:6	7:1	0.83
	0	5	11	6	18	–	22:18	1:1	0.53
							16:24	1:1	0.21
Kenya 2008	0	12	27	7	6	+	39:13	3:1	1.0
							46:6	7:1	0.83
	0	1	10	17	12	–	28:12	3:1	0.47
							11:29	1:1	0.01

Table 3. Composite interval mapping analysis of stem rust resistance on chromosome 2BL of wheat with *Lr34* as a cofactor in three field plot tests in the RL6071 × RL6058 F6 population.

Location	Marker interval	Interval position (cM)	R^2 value	Logarithm of odds (LOD)	Additive effect
North Dakota 1999	wPt*4199*–wPt*5680*	14.1–43.6	0.19	4.2 ($P < 0.01$)	5.9
Kenya 2007	wPt*4199*–*Xwmc175*	14.1–31.6	0.13	2.7 ($P < 0.05$)	6.4
Kenya 2008	wPt*4199*–*Xmc175*	14.1–31.6	0.08	1.7 NS	3.9

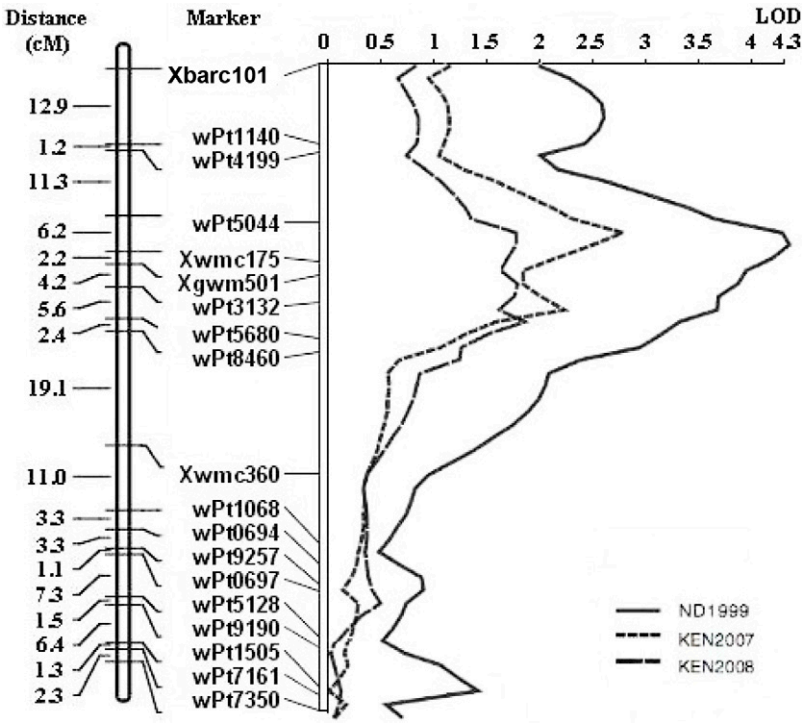

Figure 2. Composite interval regression map of QTL on chromosome 2BL associated adult plant stem rust resistance in F_6 lines of RL6071× RI6058. The LOD and R^2 values for each test are listed in Table 3.

durum had a null allele. Thatcher and Iumillo durum had a null allele for *Xwmc175*, and RL6058 had a unique banding pattern that was not present in either Thatcher, the parents of Thatcher, or RL6071.

DISCUSSION

A QTL that conditions adult plant stem rust resistance in Thatcher wheat was found on chromosome 2BL. The expression of the stem rust resistance is enhanced by the presence of the adult plant leaf rust resistance gene *Lr34*. Thatcher has seedling resistance genes *Sr5* on chromosome 6DS, *Sr12* on 3BS, and *Sr9g* and *Sr16* on 2BL (McIntosh et al., 1995). None of these seedling resistance genes is expected to contribute to the adult plant resistance of RL6058 in this study since the *P. gramins* f. sp. *tritici* isolates used in North Dakota 1999 and in both years in Kenya have virulence to these genes. Virulence to *Sr5, Sr9g, Sr12,* and *Sr16* is present in many *P. gramins* f. sp.

Table 4. Mean stem rust severities for RILs of RL6071 × RL6058 with combinations of *Lr*34 and DArT marker wPt*5044*.

Location	*Lr34* +	*Lr34* –	wPt*5044*
North Dakota 1999	9.3 A†	37.8 A	+
	25.4 B	42.2 A	–
Kenya 2007	24.0 A	43.8 A	+
	38.6 B	54.4 A	–
Kenya 2008	34.4 A	44.8 A	+
	40.7 A	53.9 B	–

† Means with different letters in the same column within each location are significantly different based on paired *t* test ($p < 0.05$).

tritici races (McIntosh et al., 1995). However, the peak of the QTL on 2BL mapped about 4 cM from *Xwmc175,* which is within 1 cM of the *Sr9* locus (Tsilo et al. (2007). Gavin Vanegas et al. (2008) determined that seedling resistance to races TPMK and RKQQ in the F_6 lines of RL6071 × RL6058 was significantly associated with adult plant stem rust resistance. These races are virulent to seedlings of Thatcher, but have low infection types to RL6058. However, in this study the seedling resistance to TPMK, RKQQ, and TTKS did not map to any of the linkage groups generated, including the one on 2BL. A more saturated molecular map may allow the seedling resistance to be mapped. Brennan (1975) using cytological methods determined that adult plant stem rust resistance in Thatcher was located on chromosomes 6A and 2B. The QTL described in this study may be the same resistance on 2B. Nazareno and Roelfs (1981) found in F_6 lines of Baart × Thatcher that adult plant stem rust resistance was associated with lines that had *Sr12*. In this study we found no evidence for adult plant resistance in RL6058 on either chromosome 6A or 3BS. As indicated by the haplotypes of SSR markers *Xbarc101* and *Xgwm501,* the adult plant resistance on 2BL in Thatcher and RL6058 was likely derived from Iumillo durum. RL6058 had a different allele from Thatcher, the parents of Thatcher, and RL6071 for *Xwmc175*, which may have been the result of a more recent mutation at this locus. Iumillo durum also contributed *Sr9g* and *Sr12* to Thatcher (McIntosh et al., 1995). *Sr16* on 2BL was contributed by the common wheat Kanred that is susceptible to stem rust isolates with virulence to *Sr16*. It is very unlikely that *Sr16* contributes to the adult plant stem rust resistance in Thatcher.

In all three tests, *Lr34* had a major effect on the expression of adult plant stem rust resistance. *Lr34* located on chromosome 7DS by itself does not condition stem rust resistance, as the cultivar Chinese Spring is highly susceptible to stem rust and has *Lr34* (Dyck, 1991). Kerber and Aung (1999) indicated that *Lr34* likely inhibits the expression of a stem rust resistance suppressor that is located on chromosome 7D (Kerber and Green, 1980) and is common in Thatcher-type spring wheats. When the suppressor locus was mutated or eliminated in nullisomic 7D lines, elevated stem rust resistance was obtained. *Lr34* had the same effect on stem rust resistance as did mutation or elimination of the suppressor locus. *Lr34* conditions non-race-specific resistance to *P. triticina* and appears to encode a putative ATP-binding cassette (ABC) transporter (Krattinger et al., 2009). How this sequence confers nonspecific resistance to leaf rust is not yet known; however, the unique sequence of this resistance gene may relate to its ability to enhance the stem rust resistance genes in Thatcher either directly or by interfering with the suppressor of stem rust resistance on chromosome 7D. Bolton et al. (2008) showed that in adult plants, *Lr34*-mediated resistance response to leaf rust infection included up-regulation of genes associated with defense- and stress-related proteins, secondary metabolic enzymes, transcriptional regulation, and cell-signaling proteins. *Lr34* also up-regulated genes in different metabolic pathways that contributed to increased carbon flux through the tricarboxylic cycle, implying a high energy cost for *Lr34*-mediated resistance. However, it is not known at this point if the unique functional role of *Lr34* in responding to pathogen infection is related to the enhanced expression of stem rust resistance in Thatcher wheat.

The joint presence of *Lr34* and the 2BL QTL accounted for 64% of the stem rust resistance variation in North Dakota 1999, 33% in Kenya 2007, and 27% in Kenya 2008. Thus additional chromosomal regions associated with adult plant stem rust resistance are likely present in Thatcher wheat but were not mapped in this study. Since only one half of the RILs had *Lr34,* this would have likely reduced the ability of the mapping population to detect stem rust resistance QTLs whose expression is enhanced by the presence of *Lr34*. We are currently developing a population that is segregating for the Thatcher stem rust resistance but is fixed for the presence of *Lr34*. A population of this type with a higher saturation of markers may allow the mapping of further QLTs for the adult plant stem rust resistance.

Table 5. Alleles for three SSR loci on chromosome 2BL in the three parents of Thatcher, Thatcher, and wheat lines RL6058 and RL6071.

SSR locus	Wheat line: Iumillo durum	Kanred	Marquis	Thatcher	RL6058	RL6071
Xbarc101	A†	B	C	A	A	C
Xwmc175	null	A	B	null	C	B
Xgwm501	null	A	B	null	null	B

† Cultivars with the same letter have the same SSR alleles.

Thatcher and RL6058 had higher stem rust severities in Kenya 2008 compared with the two other tests. The reduced effectiveness of the Thatcher resistance in Kenya 2008 may account for the lower R^2 values and nonsignificant LOD score for the 2BL QTL at this location. RL6058 and RL6071 are photoperiod sensitive, and in equatorial Kenya with a 12-h daylength the RILs had a slower developmental stage progression compared with the North Dakota location. This may have allowed an increased level of stem rust severity to develop on the parental lines and the RILs. Thatcher will head out in less than 50 d in environments with 14-h or longer daylengths (Klaimi and Qualset, 1973), as occurs in the U.S. Midwest and Canada. The optimal daylength for Thatcher in North Dakota 1999 allowed the RILs to develop at a faster rate compared with the lines in Kenya, potentially reducing the amount of stem rust that developed on the resistant genotypes. The Thatcher stem rust resistance can be affected by inoculum pressure. In the 1950s epidemics of race 15B in the United States and Canada, Thatcher was considered to be susceptible, yet in later years with reduced amounts of inoculum, Thatcher was considered to be moderately resistant to race 15B and its derivatives (Kolmer et al., 1991).

The adult plant stem rust resistance in Thatcher that is enhanced by *Lr34* has provided resistance to stem rust races in North America, Africa, and Australia (Spielmeyer et al., 2008). *Sr2* derived from Yaroslav emmer is the only currently characterized stem rust resistance gene that conditions resistance in adult plants to a wide range of stem rust races (McIntosh et al., 1995). Given the recent emergence of *P. graminis* f. sp. *tritici* races in East Africa that have virulence to many currently used race-specific seedling *Sr* genes (Wanyera et al., 2006), an emphasis on adult plant stem rust resistance that is effective to many races may be needed in the future. The combination of Thatcher resistance with *Lr34* is an additional source of adult plant resistance that is effective against widely different stem rust races.

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