A Backcross Line of Thatcher Wheat with Adult Plant Leaf Rust Resistance Derived from Duster Wheat has *Lr46* and *Lr77*

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ABSTRACT

The widely grown hard red winter wheat cultivar Duster released in 2006 has remained highly resistant to leaf rust caused by *Puccinia triticina* in the southern Great Plains of the United States. In contrast, many of the winter wheat cultivars in this region are susceptible to leaf rust. The goal of this study was to identify the number and chromosome location of leaf rust resistance genes in a line of Thatcher*2/Duster wheat that was selected for adult plant leaf rust resistance. The Thatcher*2/Duster line was crossed with Thatcher (Tc) and a recombinant line inbred line (RIL) population was advanced to the F₆ generation by single-seed descent. The parents and RIL population were phenotyped for leaf rust resistance in three field plot tests and in an adult plant greenhouse test. Single-nucleotide polymorphism

(SNP) markers derived from the Illumina Infinium iSelect 90K wheat SNP array, kompetitive allele-specific polymerase chain reaction assays on chromosome 3BL, and a sequence tagged site (STS) marker on chromosome 1BL were used to construct a genetic map of the RIL population. The STS marker *csLV46G22* that is linked with resistance gene *Lr46* on chromosome 1BL, and SNP marker *IWB10344* that is linked with *Lr77* on chromosome 3BL, were significantly associated with lower leaf rust severity. Duster has at least three adult plant resistance genes for leaf rust resistance because it was previously determined to also have the adult plant resistance gene *Lr34*. Duster is a valuable source of durable leaf rust resistance for hard red winter wheat improvement in the Great Plains region.

Leaf rust of wheat caused by *Puccinia triticina* Erikss. (Bolton et al. 2008) occurs annually in the Great Plains of North America. In the hard red winter wheat region of the southern Great Plains, yield losses due to leaf rust can be significant, depending on the resistance genes present in wheat cultivars and whether or not temperature and moisture conditions favor infection and spread of *P. triticina* urediniospores. Leaf rust resistance is a priority for wheat improvement programs in this region. Cultivars with the resistance genes *Lr21*, *Lr24*, *Lr26*, *Lr37*, and *Lr39* (J. Kolmer, unpublished data) have been released since the 1980s. However, all of these genes condition race-specific resistance and are vulnerable to selection of virulent races of *P. triticina*. The leaf rust resistance of many cultivars has been eroded within a few years of release and cultivation, with the result that many of the currently grown cultivars are leaf rust susceptible.

The leaf rust resistance genes *Lr34* and *Lr46* are currently effective to all known *P. triticina* races, and are present in many currently grown wheat cultivars (Kolmer et al. 2008; Lan et al. 2014; Li et al. 2014). Both genes condition an intermediate level of leaf rust resistance that is best expressed at the adult plant stage, and have been associated with durable leaf rust resistance. Other adult plant resistance genes (*Lr67*, *Lr68*, *Lr74*, *Lr75*, and *Lr77*) that also may offer long-lasting resistance have been more recently characterized (McIntosh et al. 2017). Most of these genes do not give a high level of resistance when present singly but wheat cultivars with combinations of adult plant resistance genes

(Kolmer et al. 2018a; Messmer et al. 2000) or seedling resistance genes with adult plant genes can be highly resistant (Oelke and Kolmer 2005).

In 2007, a severe wheat leaf rust epidemic occurred in the Great Plains region of North America (Kolmer et al. 2009). Yield losses due to leaf rust in Kansas were 14%. Many of the commonly grown cultivars such as Jagger with *Lr37*, Overlay with *Lr39*, and Jagalene with *Lr24* were highly susceptible to leaf rust. However, the hard red winter wheat cultivar Duster (Edwards et al. 2012), released in 2006, was very resistant in the 2007 epidemic. A genetic study showed that Duster had *Lr3a*, *Lr11* (Kolmer 2017), and *Lr34* (Cao et al. 2010). Virulence to *Lr3a* and *Lr11* is very common in the *P. triticina* population in the United States; therefore, it was unlikely that these seedling resistance genes contributed to the resistance in Duster. Duster also had less rust severity than the cultivar 2174 that also has *Lr34* (Kolmer et al. 2008). Therefore, Duster must have additional leaf rust resistance genes that, combined with *Lr34*, are responsible for its high level of resistance. The Thatcher*2/Duster F₄ 36-1 line that lacked *Lr3a*, *Lr11*, or *Lr34* (Kolmer 2017) had a low infection type (IT) of flecks with small- to moderate-size uredinia surrounded by chlorosis in the adult plant stage in a greenhouse test but seedlings had high IT of large uredinia without necrosis or chlorosis. In rust nursery field plots, the Thatcher*2/Duster line 36-1 F₄ line had an intermediate level of resistance that was easily distinguished from the susceptible cultivar Thatcher (Tc) when challenged with a mixture of current *P. triticina* races. The objective of this study was to characterize and determine the chromosome locations of the additional adult plant leaf rust resistance genes derived from Duster.

MATERIALS AND METHODS

The Tc*2/Duster 36-1 F₄ line was crossed with Tc. All adult plants were grown in a greenhouse at a temperature of 18 to 25°C, with 16 h of supplemental metal halide lighting. Plants were

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*The e-Xtra logo stands for “electronic extra” and indicates that two supplementary tables are published online.

fertilized with a 14-14-14 Osmocote (Scotts Co., Marysville, OH) slow-release fertilizer. The F₁ plant was selfed and a recombinant inbred line (RIL) population was derived by single-seed descent in a greenhouse and advanced to the F₆ generation (Tc/Tc*2/Duster F₆). The additional cross to Tc was made so that the RIL population could be evaluated for leaf rust resistance without lines segregating for winter habit or large differences in heading date, which would complicate leaf rust severity ratings. Seed of the RIL population was increased for one generation in the greenhouse.

The population of 102 RIL, the Tc*2/Duster parent Tc, and other near-isogenic lines of Tc wheat with single genes for leaf rust resistance were evaluated for leaf rust response in field plots at St. Paul, MN in 2014, 2015, and 2016. In all, 50 to 60 seed of the parents, RIL, and Tc lines were planted in 2-m-long rows that were spaced 30 cm apart. Spreader rows of the leaf-rust-susceptible wheat cultivars Tc, Morocco, Max, and Little Club were planted in rows perpendicular to the RIL population. The spreader rows were inoculated with mixtures of *P. triticina* races that were representative of current races in the United States during those years (Kolmer and Hughes 2017, 2018; Kolmer et al. 2018b). The races had virulence to all seedling resistance genes present in the hard red winter and hard red spring wheat cultivars in the United States. A suspension of urediniospores and Soltrol 170 oil (Chevron-Phillips Petroleum, Bartlesville, OK) was atomized on the susceptible wheat cultivars when the spreader rows were at the jointing stage, approximately 30 days after planting. The RIL, parents, and Tc lines were evaluated for leaf rust resistance approximately 30 days after inoculation, when flag leaves of Tc had 50 to 60% leaf rust severity as measured by the modified Cobb scale (Peterson et al. 1948). The leaf rust response of the RIL, parents, and Tc lines was determined at the same time: R = necrosis surrounding small uredinia, MR = necrosis surrounding moderate size uredinia, MS = distinct chlorosis surrounding moderate to large uredinia, and S = large uredinia lacking necrosis or chlorosis. Up to five flag leaves from the middle and both ends of the row were evaluated for leaf rust severity and response. In 2014 and 2015, the rust epidemic in the field plots developed normally because there were sufficient rainfalls and dew periods to allow multiple cycles of rust infection and the plants were not stressed from lack of moisture. However, in 2016, the field plots were highly drought stressed due to hot and dry weather that set in after the plots were inoculated in the first week of June. This also reduced the number of infection cycles that year. As a result, the leaf rust severity ratings were lower overall compared with the two preceding years.

The RIL population and parents were also tested for adult plant leaf rust response in a greenhouse test in manner identical to that in a previous study (Kolmer et al. 2018b). Infection types of flag leaves of the RIL and parents were evaluated 14 days after inoculation with the 0-to-4 scale used for seedling plants (Long and Kolmer 1989). The qualitative IT scores were converted to a 0-to-100 scale for quantitative trait analysis, as described previously (Supplementary Table S1) (Kolmer et al. 2018b). There was little difference in leaf rust severity among the RIL; therefore, only the converted IT scores were used for further analysis. Pearson's correlation coefficient for leaf rust severity of the RIL population between the field plot tests in 2014 to 2016 and the converted IT scores in the adult plant

greenhouse test was determined with Statistical Analysis Software (SAS Institute 2012).

Restriction quality DNA of the Tc*2/Duster parent, Tc, and the RIL population was extracted using the method described by Akbari et al. (2006). The parents and RIL population were assayed for DNA polymorphism with the 90K single-nucleotide polymorphism (SNP) wheat bead chip, as described by Wang et al. (2014). Because the parental Tc*2/Duster 36-1 line was selected for adult plant leaf rust resistance compared with Tc, SNP markers in regions associated with the resistance should be segregating in the RIL population, even though the parents were highly related, hence reducing the total number of segregating markers.

Genome Studio, v. 2011.1 (Illumina 2011), was used for SNP genotype calling of the RIL and two parents. The genotyping and quantitative trait loci (QTL) analyses were done in a manner identical to that in a previous study (Kolmer et al. 2018b), using ICM Mapping (Meng et al. 2015) to remove markers showing complete linkage. Mapmaker v2.0 for Macintosh (Lander et al. 1987) and R/qtl (Broman et al. 2003) were used for mapping the linkage groups associated with adult plant leaf rust resistance. The physical location of the SNP markers was confirmed using the Chinese Spring NRGene-IWGSC v1.0 genome assembly (<http://www.wheatgenome.org/News/Latest-news/RefSeq-v1.0-URGI>). The program QGENE (Nelson 1997) was used for composite interval mapping (CIM), with the marker nearest to the logarithm of odds (LOD) peak selected as a cofactor. The dataset was permuted 1,000 times and LOD scores for each marker interval were determined at a significance level of $\alpha = 0.05$. The segregating markers and disease severity of the RIL population in the four tests were tested for analysis of variance using PROC GLM in SAS (SAS Institute 2012).

In order to facilitate marker-assisted selection of the adult plant leaf rust resistance derived from Duster, five kompetitive allele-specific polymerase chain reaction (KASP) markers that were linked to a previously reported QTL on chromosome 3BL were added to the final genetic map (Supplementary Table S2). The KASP markers were assayed on the RIL population and parents in a manner identical to that previously described (Kolmer et al. 2018b). In addition, *csLV46G22*, a sequence-tagged site (STS) marker linked to *Lr46* (E. Lagudah, personal communication), was also added to the genetic map.

RESULTS

The Tc*2/Duster 36-1 parent had leaf rust severity of 10 to 20% and response of MR-MS in both 2014 and 2015, and had severity and response of 10% MR-MS in 2016. Tc had severity of 50 to 70% with a susceptible response in all 3 years of field plot tests. The Tc*2/Duster 36-1 line had an IT of ;22- (fleck with small uredinia surrounded by chlorosis) and Tc had IT of 3+4 in the adult plant greenhouse test. The 2014 and 2015 field plot tests were highly correlated with a Pearson coefficient of 0.87, and correlations with the 2016 field test and adult plant greenhouse test varied from 0.47 to 0.28 (Table 1).

In total, 396 SNP markers were used to construct a genetic map of Tc/Tc*2/Duster 36-1, after removal of completely linked SNP and SNP with over 10% missing data. Thirty-six linkage groups that covered 1,484 centimorgans (cM) were assembled in the genetic map using the Kosambi map function with an LOD of 10 and recombination rate of 0.3 for separation. Regions on chromosomes 3BL and 1BL were initially identified to be associated with leaf rust resistance by single-marker regression analysis. Using CIM, the STS marker *csLV46G22*, which is tightly linked to the adult plant resistance gene *Lr46*, mapped at the LOD peak on chromosome 1BL at 140.3 cM (Fig. 1A). The SNP marker *IWB14436* was 6.4 cM proximal to the LOD peak, and *IWB5678* was 4.9 cM distal to the peak. In the 2014 field test and in the greenhouse test, the LOD scores for *csLV46G22* were over 5.0 ($P < 0.01$). In the 2015 field

TABLE 1. Pearson's correlation coefficient of leaf rust severity ratings between different years of greenhouse and field plot tests of the Thatcher//Thatcher*2/Duster 36-1 recombinant inbred line population^z

Tests	Greenhouse	Field 2014	Field 2015	Field 2016
Greenhouse	...	0.40*	0.37*	0.28**
Field 2014	...	...	0.87*	0.47*
Field 2015	...	...	...	0.41*
Field 2016	...	...	...	...

^z Asterisks * and ** indicate significant at $P < 0.001$ and 0.05, respectively.

test, the LOD score was 3.17 ($0.01 < P < 0.05$), and was not significant ($P > 0.5$) in the 2016 field test.

The second region associated with lower leaf rust severity on chromosome 3BL was in the same region as *Lr77* (Kolmer et al. 2018b). The SNP marker *IWB10344* mapped at the LOD peak at 123.4 cM on chromosome 3BL (Fig. 1B). The resistance on chromosome 3BL is likely conditioned by the adult plant resistance gene *Lr77* because *IWB10344* previously mapped at the LOD peak for *Lr77* in another RIL population (Kolmer et al. 2018b). KASP

markers for *IWB32805*, *IWB12660*, *IWB73555*, *IWB23680*, and *IWB9095* that were linked to *Lr77* (Kolmer et al. 2018b) were added to the map. Marker *IWB12660* was 3.4 cM proximal to the LOD peak, and marker *IWB23680* was 5.4 cM distal to the peak. LOD scores for *IWB10344* were greater than 4.0 in all tests ($P < 0.01$), with values > 17.0 in the field tests in 2014 and 2015 (Table 2). The corresponding R^2 values were all > 0.18 , with values > 0.50 in 2014 and 2015.

The RIL genotypes were placed into four groups based on the presence of resistance alleles at *csLV46G22* for *Lr46* and *IWB10344*

Fig. 1. Composite interval mapping (IM) of leaf rust resistance in the Thatcher//Thatcher*2/Duster 36-1 recombinant inbred line population. LOD= logarithm of odds, LS = leaf rust severity, and cM = centimorgans. **A**, Chromosome 1BL and **B**, chromosome 3BL.

for *Lr77*. In the 2014 and 2015 field tests, RIL that lacked *Lr46* or *Lr77* had up to 80% severity, RIL with only *Lr46* had 20 to 70% severity, RIL with only *Lr77* had 10 to 50% severity, and RIL with both genes had 10 to 50% severity (Fig. 2). In 2014 and 2015, RIL

with both *Lr46* and *Lr77* were not significantly different for severity compared with RIL with only *Lr77* (Table 3). In 2014 and 2015 field tests, RIL with only *Lr46* had significantly lower severity than RIL that lacked both resistance genes. In the 2016 field test, the dry conditions reduced the overall leaf rust severity in the plots. RIL with all combinations of both *Lr46* and *Lr77* had leaf rust severities of 20 to 50% (Fig. 2). In the 2016 field test, RIL with both *Lr46* and *Lr77* had significantly lower leaf rust severity than RIL with *Lr46* only (Table 3). RIL with only *Lr46* did not have significantly lower severity than RIL that lacked both genes. In the greenhouse test, the converted IT scores of RIL with both genes were significantly lower than RIL with only one of the genes (Fig. 2; Table 3), and RIL with only *Lr46* had significantly lower IT than RIL with only *Lr77*.

TABLE 2. Composite interval mapping of adult plant leaf rust resistance in the Thatcher//Thatcher*2/Duster 36-1 population

Gene	Chromosome	Marker (cM) ^y	Test	R ² value	Logarithm of odds ^z
<i>Lr77</i>	3BL	<i>IWB10344</i> (123.4)	Greenhouse	0.18	4.31*
			Field 2014	0.79	34.39*
			Field 2015	0.54	17.21*
			Field 2016	0.22	5.62*
<i>Lr46</i>	1BL	<i>csLV46G22</i> (140.3)	Greenhouse	0.48	14.57*
			Field 2014	0.21	5.23*
			Field 2015	0.14	3.17**
			Field 2016	0.06	1.76 ns

^y cM = centimorgans.
^z Asterisks * and ** indicate significant at *P* < 0.01 and 0.05, respectively; ns = nonsignificant effect at *P* < 0.05.

DISCUSSION

The RIL population with leaf rust resistance derived from Duster segregated for two adult plant genes on chromosomes 1BL and 3BL. These are most likely *Lr46* and *Lr77*. The hard red winter wheat Santa Fe that was resistant in the 2007 leaf rust epidemic was determined to have *Lr77* (Kolmer et al. 2018b). The KASP markers for *Lr77* that were initially developed in the Tc //Tc*/Santa Fe

Fig. 2. Frequency distributions of Thatcher//Thatcher*2/Duster 36-1 recombinant inbred line (RIL) population for leaf rust severity based on segregation of alleles at *csLV4622* for *Lr46* and *IWB10344* for *Lr77*. A, 2014 Field plot test; B, 2015 field plot test; C, 2016 field plot test; and D, greenhouse adult plant test.

population also worked well in mapping *Lr77* in the Duster-derived RIL. The marker order of the KASP was slightly different between the two populations. In the Santa Fe-derived population, *IWB12260* was distal to *IWB10344* but, in the Duster-derived population, was proximal to *IWB10344*. In the Duster-derived population, *IWB73555* was completely linked with *IWB10344*, but was 0.9 cm distal to *IWB10344* in the Santa Fe-derived population. The marker order was the same for the other KASP markers. Because both populations were relatively small ($n < 150$), discrepancies in the two maps of the 3BL region of *Lr77* were not unexpected. A larger population to fine map *Lr77* would be needed to resolve the genetic map of this region. Expression of *Lr77* was consistent in the two populations. In the Tc//Tc*2/Santa Fe population, *IWB13044* had very high LOD scores in the field tests in 2014 and 2015, and a lower LOD score in 2016 and in the adult plant greenhouse test. A KASP marker for *IWB10344* was tested; however, the expected polymerase chain reaction products were not amplified.

The adult-plant resistance gene *Lr46* has been characterized in a number of wheat cultivars derived from CIMMYT germplasm (Li et al. 2014). This gene was also found in two wheat cultivars from South America (Kolmer 2015; Kolmer et al. 2018a) and in a soft red winter wheat breeding line from the United States (Kolmer et al. 2012). In the Tc//Tc*2/Duster RIL population, the expression of *Lr46* varied among the three field tests and the adult plant greenhouse test. Three other RIL populations that segregated for leaf rust resistance in the *Lr46* region of chromosome 1BL were also evaluated in past years in field tests in St. Paul. In a RIL population of Tc//Tc*2/Americano 25e (Kolmer 2015), the marker associated with *Lr46* had LOD scores of 5.7 to 9.8 and, in a RIL population of Tc//Tc*2/C113227 (Kolmer et al. 2012), the LOD scores were 8.5 to 15.2. In the Tc//Tc*2/C113227 population, the *Lr46* region was the only QTL for lowered leaf severity and, in the Tc//Tc*2/Americano 25e population, a second QTL with smaller LOD scores compared with *csLV46* was also present. In a RIL population of Tc//Tc*2/Toropi (Kolmer et al. 2018a), the LOD scores for the *Lr46* marker ranged from 0.0 to 2.51. In this population, there were two other QTL for lower leaf rust severity that, overall, had larger effects than *Lr46*. The presence of other QTL for lower leaf rust severity in a segregating population may reduce the effectiveness of *Lr46*. This was also evident in the Tc//Tc*2/Duster RIL population because, in the field plot tests, the RIL with both *Lr46* and *Lr77* did not have significantly lower severity than RIL with only *Lr77*.

In the greenhouse adult plant test, *Lr46* and *Lr77* did interact to condition lower IT than either gene singly. The RIL with both genes had IT from 22⁻ to 2⁺3, and RIL with only *Lr46* or *Lr77* had IT from 22⁻ to 3⁺. Most RIL with both *Lr46* and *Lr77* had IT of 22⁻ to 22⁺. The inconsistent IT expression of *Lr46* and *Lr77* when present singly is not uncommon with regard to adult plant resistance genes. The best-characterized adult plant resistance gene, *Lr34*, also has variable expression in both greenhouse and field tests (Drijepont and Pretorius 1989; Singh and Gupta 1992). It was notable that *Lr46* expressed very strongly in the adult plant greenhouse test, more so than *Lr77*. In the Tc//Tc*2/Americano 25e RIL population, *Lr46* also expressed strongly in an adult plant greenhouse test (Kolmer 2015). The resistance conditioned by *Lr46* may be more discernable

when there is only a single cycle of rust infection, as opposed to the field tests that have multiple infection cycles.

The cultivar Duster was previously determined to have *Lr34* (Cao et al. 2010, Kolmer 2017) and the race-specific seedling resistance genes *Lr3a* and *Lr11* (Kolmer 2017). In this study, a single Tc backcross line with adult plant resistance derived from Duster was selected for further study. Other resistance genes may be present in Duster, because the selected backcross line may not have had all of the additional adult plant resistance genes in Duster. In the Tc*2/Duster F₂ families (Kolmer 2017), there was a two-gene segregation for resistance in field plots. One of the genes was *Lr34*, because half of the total families had the marker associated with *Lr34*. The remaining resistance must have been due to adult plant resistance genes because *Lr3a* and *Lr11* were not effective in the field plots. The resistant families without *Lr34* had severities of 10 to 50% MR-MS, which was consistent with the expression of resistance in the segregating RIL in the current study. The presence of *Lr77* likely masked whatever resistance effect *Lr46* had in the Tc*2/Duster F₂ families.

Duster was released in 2006 and continues to be widely grown in Oklahoma. In 2017, Duster was the second most common wheat cultivar in Oklahoma (USDA-NASS 2018). Duster has remained highly resistant to leaf rust since release and has shown an intermediate level of stripe rust resistance (Edwards et al. 2012). In research plots in Texas in the 2007 epidemic, Duster was rated as highly resistant, with only a trace level of rust infection. In contrast, the cultivar 2174, with only *Lr34* for effective resistance, had an intermediate resistance rating in the same plots. The presence of *Lr46* and *Lr77* must account for the additional resistance in Duster. Genes *Lr34* (Kolmer et al. 2011; McIntosh 1992; McIntosh et al. 2017) and *Lr46* (Kolmer et al. 2015) also condition adult plant resistance to stem rust caused by *P. graminis* f. sp. *tritici* and stripe rust caused by *P. striiformis* f. sp. *tritici*. *Lr77* has characteristics of *Lr46* and *Lr34* and may also condition nonrace-specific resistance to other wheat rusts. Duster is a valuable source of durable resistance to the three wheat rusts for the Great Plains region.

LITERATURE CITED

- Akbari, M., Wenzl, P., Caig, V., Carling, J., Yang, S., Uszynski, G., Mohler, V., Lehmensiek, A., Kuchel, H., Hayden, M. J., Howes, N., Sharp, P., Vaughn, P., Rathmell, B., Huttner, E., and Kilian, A. 2006. Diversity arrays technology (DArT) for high-throughput profiling of the hexaploid wheat genome. *Theor. Appl. Genet.* 113:1409-1420.
- Bolton, M. D., Kolmer, J. A., and Garvin, D. F. 2008. Wheat leaf rust caused by *Puccinia triticina*. *Mol. Plant Pathol.* 9:563-575.
- Broman, K. W., Wu, H., Sen, S., and Churchill, G. A. 2003. QTL mapping in experimental crosses. *Bioinformatics* 19:889-890.
- Cao, S., Carver, B. F., Zhu, X., Fang, T., Chen, Y., Hunger, R. M., and Yan, L. 2010. A single-nucleotide polymorphism that accounts for allelic variation in the *Lr34* gene and leaf rust reaction in hard red winter wheat. *Theor. Appl. Genet.* 121:385-392.
- Drijepont, S. C., and Pretorius, Z. A. 1989. Greenhouse evaluation of adult-plant resistance conferred by the gene *Lr34* to leaf rust of wheat. *Plant Dis.* 73:669-671.
- Edwards, J. T., Hunger, R. M., Smith, E. L., Horn, G. W., Chen, M. S., Yan, L., Bai, G., Bowden, R. L., Klatt, A. R., Rayas-Duarte, P., Osburn, R. D., Giles, K. L., Kolmer, J. A., Jin, Y., Porter, D. R., Seaborn, B. W., Bayles, M. B., and Carver, B. F. 2012. 'Duster' wheat: A durable, dual-purpose cultivar adapted to the southern Great Plains of the USA. *J. Plant Regist.* 6:37-48.
- Illumina. 2011. GenomeStudio genotyping module software, Release 1.0. Illumina, San Diego, CA.
- Kolmer, J. A. 2015. A QTL on chromosome 5BL in wheat enhances leaf rust resistance of *Lr46*. *Mol. Breed.* 35:74.
- Kolmer, J. A. 2017. Genetics of leaf rust resistance in the hard red winter wheat cultivars Santa Fe and Duster. *Crop Sci.* 57:2500-2505.
- Kolmer, J. A., Bernardo, A., Bai, G., Hayden, M. J., and Chao, S. 2018a. Adult plant resistance derived from Toropi wheat is conditioned by *Lr78* and three minor QTL. *Phytopathology* 108:246-253.
- Kolmer, J. A., Garvin, D. F., and Jin, Y. 2011. Expression of a Thatcher wheat stem rust resistance QTL on chromosome arm 2BL is enhanced by *Lr34*. *Crop Sci.* 51:526-533.
- Kolmer, J. A., and Hughes, M. E. 2017. Physiologic specialization of *Puccinia triticina* on wheat in the United States in 2015. *Plant Dis.* 101:1496-1506.

TABLE 3. Mean severities of Thatcher//Thatcher*2/Duster 36-1 F₆ recombinant inbred lines in three field plot tests and an adult plant greenhouse test^a

Genotype	Greenhouse	Field 2014	Field 2015	Field 2016
<i>Lr46-Lr77</i>	68.00 A	68.00 A	61.33 A	42.00 A
<i>Lr46-Lr77</i>	28.42 C	51.61 B	44.82 B	36.43 AB
<i>Lr46-Lr77</i>	45.45 B	21.36 C	26.36 C	32.72 BC
<i>Lr46-Lr77</i>	13.32 D	17.22 C	23.89 C	28.21 C

^a Infection type scores converted to a 0-to-100 scale for quantitative trait analysis. Genotypes in each column with a different letter differ significantly for leaf rust severity based on Tukey's honest significance difference in PROC GLM in SAS.

- Kolmer, J. A., and Hughes, M. E. 2018. Physiologic specialization of *Puccinia triticina* on wheat in the United States in 2016. *Plant Dis.* 102:1066-1071.
- Kolmer, J. A., Lagudah, E. S., Lillemo, M., Lin, M., and Bai, G. 2015. The *Lr46* gene conditions partial adult-plant resistance to stripe rust, stem rust, and powdery mildew in Thatcher wheat. *Crop Sci.* 55:2557-2565.
- Kolmer, J. A., Lin, M., and Bai, G. 2012. Genetics of leaf rust resistance in the winter wheat line CI13227. *Crop Sci.* 52:2166-2172.
- Kolmer, J. A., Long, D. L., and Hughes, M. E. 2009. Physiologic specialization of *Puccinia triticina* on wheat in the United States in 2007. *Plant Dis.* 93:538-544.
- Kolmer, J. A., Singh, R. P., Garvin, D. F., Viccars, L., William, H. M., Huerta-Espino, J. H., Obonnaya, F. C., Raman, H., Orford, S., Bariana, H. S., and Lagudah, E. S. 2008. Analysis of the *Lr34/Yr18* rust resistance region in wheat germplasm. *Crop Sci.* 48:1841-1852.
- Kolmer, J. A., Su, Z., Bernardo, A., Bai, G., and Chao, S. 2018b. Mapping and characterization of the new adult plant leaf rust resistance gene *Lr77* derived from Santa Fe winter wheat. *Theor. Appl. Genet.* 131:1553-1560.
- Lan, C., Rosewarne, G. M., Singh, R. P., Herrera-Foessel, S. A., Huerta-Espino, J., Basnet, B. J., Zhang, Y., and Yang, E. 2014. QTL characterization of resistance to leaf rust and stripe rust in the spring wheat line Francolin#1. *Mol. Breed.* 34:789-803.
- Lander, E. S., Green, P., Abrahamson, J., Barlow, A., Daly, M. J., Lincoln, S. E., and Newburg, L. 1987. MAPMAKER: An interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. *Genomics* 1:174-181.
- Li, Z., Lan, C., He, Z., Singh, R. P., Rosewarne, G. M., Chen, X., and Xia, X. 2014. Overview and application of QTL for adult plant resistance to leaf rust and powdery mildew in wheat. *Crop Sci.* 54:1907-1925.
- Long, D. L., and Kolmer, J. A. 1989. A North American system of nomenclature for *Puccinia recondita* f. sp. *tritici*. *Phytopathology* 79:525-529.
- McIntosh, R. A. 1992. Close genetic linkage of genes conferring adult-plant resistance to leaf rust and stripe rust of wheat. *Plant Pathol.* 41: 523-527.
- McIntosh, R. A., Dubcovsky, J., Rogers, J., Morris, C., and Xia, X. C. 2017. Catalogue of Gene Symbols for Wheat, 2017 Supplement. Online publication. Yokohama, Japan. <https://shigen.nig.ac.jp/wheat/komugi/genes/symbol-ClassList.jsp>
- Meng, L., Li, H., Zhang, L., and Wang, J. 2015. QTL IciMapping: Integrated software for genetic linkage map construction and quantitative trait locus mapping in biparental populations. *Crop J.* 3:269-283.
- Messmer, M. M., Seyfarth, R., Keller, M., Schachermayr, G., Winzeler, M., Zanetti, S., Feuillet, C., and Keller, B. 2000. Genetic analysis of durable leaf rust resistance in winter wheat. *Theor. Appl. Genet.* 100:419-431.
- Nelson, J. C. 1997. QGENE: Software for marker-based genomic analysis and breeding. *Mol. Breed.* 3:239-245.
- Oelke, L. M., and Kolmer, J. A. 2005. Genetics of leaf rust resistance in spring wheat cultivars Norm and Alsen. *Phytopathology* 95:773-778.
- Peterson, R. F., Campbell, A. B., and Hannah, A. E. 1948. A diagrammatic scale for estimating rust intensity on leaves and stems of cereals. *Can. J. Res.* 26c:496-500.
- SAS Institute. 2012. The SAS System for Windows, Release 9.4. SAS Institute, Cary, NC.
- Singh, R. P., and Gupta, A. K. 1992. Expression of wheat rust resistance gene *Lr34* in seedlings and adult plants. *Plant Dis.* 76:489-491.
- USDA-NASS. 2018. Oklahoma wheat variety report. Online publication. United States Department of Agriculture–National Agricultural Statistics Service (USDA-NASS). https://www.nass.usda.gov/Statistics_by_State/Oklahoma/Publications/Oklahoma_Crop_Reports/2018/ok-wheat-variety-2018.pdf
- Wang, S., Wong, D., Forrest, K., Allen, A., Chao, S., Huang, B. E., Maccaferri, M., Salvi, S., Milner, S. G., Cattivelli, L., Mastrangelo, A. M., Whan, A., Stephen, S., Barker, G., Wieseke, R., Plieske, J., International Wheat Genome Sequencing Consortium, Lillemo, M., Mather, D., Appels, R., Dolferus, R., Brown-Guidira, G., Korol, A., Akhunova, A. R., Feuillet, C., Salse, J., Morgante, M., Pozniak, C., Luo, M.-C., Dvorak, J., Morell, M., Dubcovsky, J., Ganai, M., Tuberosa, R., Lawley, C., Mikoulitch, I., Cavanagh, C., Edwards, K. J., Hayden, M., and Akhunov, E. 2014. Characterization of polyploid wheat genomic diversity using a high-density 90000 single nucleotide polymorphism array. *Plant Biotechnol.* 12: 787-796.