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ORIGINAL ARTICLE

Thatcher wheat line RL6149 carries *Lr64* and a second leaf rust resistance gene on chromosome 1DS

J. A. Kolmer[1] · A. Bernardo[2] · G. Bai[3] · M. J. Hayden[4,5] · J. A. Anderson[6]

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Abstract

Key message **The leaf rust resistance gene *Lr64* in the Thatcher wheat RL6149 was mapped to chromosome 6AL with SNP and KASP markers and a second leaf rust resistance gene was mapped to chromosome 1DS.**

Abstract RL6149, a near-isogenic line of Thatcher wheat, carries leaf rust resistance gene *Lr64* on chromosome arm 6AL. The objective of this study was to develop molecular markers that can be easily used to select wheat lines with *Lr64*. RL6149 was crossed with Thatcher and F_2 plants derived from a single F_1 plant were advanced to F_6 lines by single seed descent. The 100 F_7 recombinant inbred lines (RIL) were inoculated with two races of *P.triticina* that differed widely for virulence in order to identify resistant and susceptible RIL. Thirty RIL that differed for resistance and the parental lines were genotyped with the 90 K Infinium iSelect single nucleotide polymorphism (SNP) array to find closely linked markers with *Lr64*. Seven linked SNPs on chromosome arm 6AL were converted into Kompetitive Allele Specific PCR (KASP) markers that were genotyped on the 100 RIL. A genetic linkage map for the seven KASP markers spanned 19.1 cM on chromosome arm 6AL. KASP marker *K-IWB59855* was tightly linked to *Lr64*. A second unexpected gene for leaf rust resistance also segregated in the F_7 lines. Four KASP markers that spanned 18.6 cM located the gene on chromosome 1DS. The KASP marker *K-IWB38437* was tightly linked to the second leaf rust resistance gene.

Keyword Race-specific resistance · Brown rust · Seedling resistance gene

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✉ J. A. Kolmer
jim.kolmer@ars.usda.gov

[1] United States Department of Agriculture - Agricultural Research Service, Cereal Disease Laboratory, St. Paul, MN 55108, USA

[2] Department of Plant Pathology, Kansas State University, Manhattan, KS 66506, USA

[3] United States Department of Agriculture - Agricultural Research Service, Hard Winter Wheat Genetics Research Unit, Manhattan, KS 66506, USA

[4] Agriculture Victoria Research, AgriBio, Bundoora, VIC 3083, Australia

[5] School of Applied Biology, La Trobe University, Bundoora, VIC 3083, Australia

[6] Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul, MN 55108, USA

Introduction

Leaf rust, caused by *Pucciniatriticina* Eriks., is a widespread and regularly occurring disease of wheat in many regions of the world. To date 79 wheat leaf rust resistance genes have been given permanent designations (McIntosh et al. 2017) based on chromosome location and allelism. However, the *P.triticina* population can change very rapidly in response to cultivation of resistant wheat cultivars, since the most effective resistance genes select virulent races that can either occur at very low frequencies in existing populations or arise by mutation as new races. As a result, many of the resistance genes in wheat cultivars do not provide effective resistance, since virulent races are at high frequency (Kolmer and Hughes 2018). Wild relatives of wheat have been used as important sources of leaf rust resistance (Dyck and Kerber 1985), since many of the resistance genes found in common wheat no longer provide resistance. Wild emmer wheat, *Triticum turgidum* L. Thell. ssp.*dicoccoides* (hereafter referred to as *T.dicoccoides*), a close relative of wheat

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has been identified as a donor of disease resistance genes for wheat. Generally, collections of *T.dicoccoides* are susceptible to *P.triticina*, with relatively few accessions that produce low infection type (IT) in seedling plants (Anikster et al. 2005). In native stands in Israel (Dinoor et al. 1991), *T.dicoccoides* is susceptible to the same races of *P.triticina* that are found on common wheat.

Dyck (1994) however, found an accession of *T.dicoccoides* designated as 8404, that had a very low infection type in seedling plants. He backcrossed the resistance into the hexaploid common wheat Thatcher. The Thatcher near isogenic line RL6149 (Thatcher*7/8404) was highly resistant to leaf rust. In segregating F_2 plants and derived F_3 families, the resistance in RL6149 segregated as a single gene and was mapped to chromosome arm 6AL (Kolmer and Anderson, unpublished data). The simple sequence repeat (SSR) marker *Xbarc104* was located 13.9 cM proximal to the gene, and *Xgwm427* was 21.0 cM proximal. The resistance gene in RL6149 was designated as *Lr64* (McIntosh et al. 2009). Since neither of the SSR markers was tightly linked to *Lr64*, they are not suitable for marker-assisted selection in wheat improvement programs. The objective of this study was to develop molecular markers with tight linkage to *Lr64* that can easily be used to select wheat germplasm with improved leaf rust resistance. During the course of this study, we also detected a second seedling resistance gene in RL6149, and it was mapped to chromosome 1DS.

Materials and methods

Thatcher was crossed with RL6149 and the F_2 seeds were advanced to F_6 generation by single seed descent in a greenhouse. The F_7 seedlings were tested for leaf rust response with two races of *P.triticina*. Race BBBDB is highly avirulent to most seedling leaf rust resistance genes, with virulence only to lines with *Lr14a, Lr14b*, and *Lr20* among the Thatcher differentials used to identify races at the USDA-ARS Cereal Disease Laboratory. Race TBBGS is currently found on wheat in the U.S. (Kolmer and Hughes 2018) and has virulence to lines with genes *Lr1, Lr2a, Lr2c, Lr3, Lr10, Lr14b, Lr21, Lr28*, and *Lr39*. The F_7 recombinant inbred lines (RIL) were inoculated with both races at two separate times for a total of four tests. The RIL and parents were grown in segmented trays with 4–6 seeds per RIL in each segment in a greenhouse at 20–23 °C and fertilized with 20–20–20 NPK solution 7 d after planting. When the primary leaves were fully expanded at 7–8 days after planting, the seedlings were inoculated with a single race of *P.triticina* using a suspension of urediniospores in Soltrol 170 (Phillips Petroleum, Bartlesville, OK) mineral oil. After inoculation the plants were dried for 1 h, and then placed in a dew chamber overnight at 18 °C. The plants were then returned to a greenhouse bench at 20–23 °C with supplemental lighting. Infection types were scored on a 0–4 scale 10–12 days after inoculation: IT of 0 (immune response) ; (hypersensitive fleck), 1 (small necrotic uredinia), and 2 (small size uredinia with prominent chlorosis) were considered as avirulent; and IT of 3 (moderate size uredinia lacking necrosis or chlorosis) to 4 (large uredinia) were considered as virulent. RIL with mixed IT were described with the most common IT first. Symbols "−" and "+" denote smaller or larger uredinia, respectively. RIL with resistant IT were coded as 2 and RIL with susceptible IT were coded as 0 for QTL analysis. A total of 104 RIL were tested for leaf rust response, and four RIL that were determined to be heterogeneous based on the presence of resistant and susceptible seedlings were not included in the mapping or QTL analysis.

Thirty of the RIL were initially selected for genotyping: 10 with resistant IT of ; (fleck) to ;1, and 10 with IT of ;2 to 2^+ were selected in two groups. Another 10 RIL with susceptible IT of 3 to 4 were selected as a third group. High quality DNA from all RIL and parents was isolated using the method recommended by Diversity Arrays Technology (DArT) (Triticarte Pty Ltd, Canberra, Australia) (Akbari et al. 2006) and were genotyped using the wheat 90 K Infinium iSelect single nucleotide polymorphism (SNP) array (Wang et al. 2014). Single nucleotide polymorphic (SNP) markers associated with resistance were evaluated for suitability for development of Kompetitive Allele Specific PCR (KASP) markers. The KASP markers were assayed on the parents and 100 of the RIL in a 5-µl volume reaction including 2.5 µl 2X KASP master mix, 0.07 µl KASP primer mix and 2.5 µl DNA (~20 ng/µl) following the manufacturer's instructions (LGC Genomics, www.lgcgenomics.com) using an ABI 7900HT fast real-time PCR system (Applied Biosystems. The KASP marker data were mapped with Mapmaker v2.0 for MacIntosh (Lander et al. 1987) using the Kosambi map function and logarithm of odds (LOD) of 10 and r of 0.3. Map order was confirmed using R/qtl (Broman et al. 2003). Composite interval mapping (CIM) was performed using QGENE (Nelson 1997). The markers closest to the LOD peaks were selected by QGENE as a cofactor. The coefficient of determination (R^2) and LOD score for the marker interval were determined with 1000 permutations of the dataset and a significance level of $\alpha = 0.05$.

Results

When tested with races TBBGS and BBBDB, the Thatcher/RL649 F_7 lines segregated 72 to 28 for resistant (IT; to 2^+) and susceptible RIL (IT 3 to 4), respectively, in both tests. This fit a 3:1 ratio ($\chi^2 = 0.014$, $p = 0.91$) which indicated two resistance genes were segregating. Analysis of the iSelect

bead chip array data from the 30 RIL selected for 90 K genotyping identified four SNP markers on chromosome arm 1DS, 16 on chromosome 5A, and 84 on chromosome arm 6AL that were associated with the resistant RIL. Based on the fixation rate of the markers in the selected RIL and the correct phasing of the RIL with the parents, chromosome 6AL was determined to most likely carry one of the resistance genes. KASP markers were developed for SNP markers *IWB57726, IWB72197, IWB73609*, *IWB114, IWB59855, IWB38521*, and *IWA4699* (Table 1) for chromosome arm 6AL which spanned 6.17 Mb based on the physical map of Chinese Spring wheat (NRGene-IWGSC v1.0 genome assembly https://www.wheatgenome.org/News/Latest-news/RefSeq-v1.0-URGI). (Supplemental Table 1). The SNP on 1DS were associated with the segregation of resistance and susceptibility in the 30 selectively genotyped RIL, although the parents were monomorphic for three of the four markers, and RL6149 was heterogeneous for the fourth marker. KASP markers were developed for *IWB38437, IWB577, IWA713*, and *IWB14612* on chromosome arm 1DS (Table 1, Supplemental Table 1).

The 11 KASP markers were assayed on the total RIL set and parents. Seven KASP markers covered a 19.1 cM region on chromosome arm 6AL (Fig. 1a). KASP marker *K-IWB59855* was 0.7 cM distal to the LOD peak of 18.7, that had an R^2 of 0.56 for both races TBBGS and BBBDB. The 54 RIL that had the RL6149 allele (C) for *K-IWB59855* had an IT of; to ;12^-, whereas 18 RIL with the Thatcher allele (A) had an IT of ; to 2^+, and 28 RIL with the Thatcher allele had a high IT of 3^+. This indicated the RIL population was segregating for a gene on chromosome arm 6AL that conditioned a very low IT, and a second gene that conditioned a low to intermediate IT.

The second region that was associated with segregation of resistance to both races was on chromosome 1DS (Fig. 1b). The four KASP markers spanned 18.6 cM. KASP marker *K-IWB38437* was 0.6 cM distal to the LOD peak of 11.10 that had an R^2 of 0.39. The four KASP markers developed for chromosome 5A showed no association with leaf rust response.

Based on IT and the alleles for *K-IWB59855* and *K-IWB38437,* the RIL were genotyped for the presence of *Lr64* on chromosome 6AL and the second gene on 1DS. Both genes were then mapped with the KASP markers from the QTL analysis. When mapped as single genes, *Lr64* mapped closest to *K-IWB59855* and the gene on 1DS mapped closest to *K-IWB38437* (Fig. 2).

Selected RIL that varied for IT and for alleles at *K-IWB59855* on chromosome 6AL and *K-IWB38437* on 1DS were phenotyped for IT using three additional *P.triticina* races, SBDGG, TNRJJ, and MCTNB (Table 2). RIL 13, 28, 30, and 33 had the RL6149 allele for *K-IWB59855* and the

Table 1 Sequences of KASP markers for *Lr64* on chromosome 6AL and a second leaf rust resistance gene on chromosome 1DS

Chromosome	KASP	Thatcher allele	RL6149 allele	Allele-1 forward primer*	Allele-2 forward primer*	Common reverse primer
6AL	*K-IWB57726*	C	T	GCATTGCTTGTGGAG GATATATAAC	GCATTGCTTGTGGAG GATATATAAT	GAGCTTACTGCCTGCCTT GT
	K-IWB72197	G	T	CTCCTCCACTTTCTAAAT ACACTG	CTCCTCCACTTTCTAAAT ACACTT	CTCATCACCAGTGGCAAT AAG
	K-IWB73609	G	A	GAGAGGCACGATCAG GCC	GAGAGGCACGATCAG GCT	CCTTTTCGGTCCGGGTCC
	K-IWB114	C	T	CATGTGGAGGAGACG GGC	CATGTGGAGGAGACG GGT	CAGCTCTTCCTCGGCTCA
	K-IWB59855	A	C	TGAGGAATCGTCGCT GAAAGT	TGAGGAATCGTCGCT GAAAGG	GCCGCTGCCAAAAAT CCTAC
	K-IWB38521	T	C	GCCACTGATTTCATCTGT TATGT	GCCACTGATTTCATC TGTTATGC	TGCTTCTCCACCTTCACA ATT
1DS	*K-IWA4699*	G	A	TCAAAATCATCATCT TGAGGTGAAG	TCAAAATCATCATCT TGAGGTGAAA	TTCATCAAATCCTCGATT CTTGAC
	K-IWB38437	T	TC	GCTACAATGGCTAGT GTGATCT	GCTACAATGGCTAGT GTGATCC	ACAAATAGGGCATGGTAC CTTT
	K-IWB577	T	T	CAAACTGAACGAGCA GGTGAT	CAAACTGAACGAGCA GGTGAC	TCTCAATCCTAAGCATCC GGTTTA
	K-IWA713	G	GA	CAACAGGAACTCGGG AGGG	CAACAGGAACTCGGG AGGA	TGCTGTGAGATAACC GCCA
	K-IWB14612	T	TC	CCACAGTCCACACAA AGCATAT	CCACAGTCCACACAA AGCATAC	TGAGGTCTCGTGTTAATA ACTGC

*Each allele-specific forward primer was tailed with a FAM (GAAGGTGACCAAGTTCATGCT) or HEX (GAAGGTCGGAGTCAACGGATT) oligo sequence

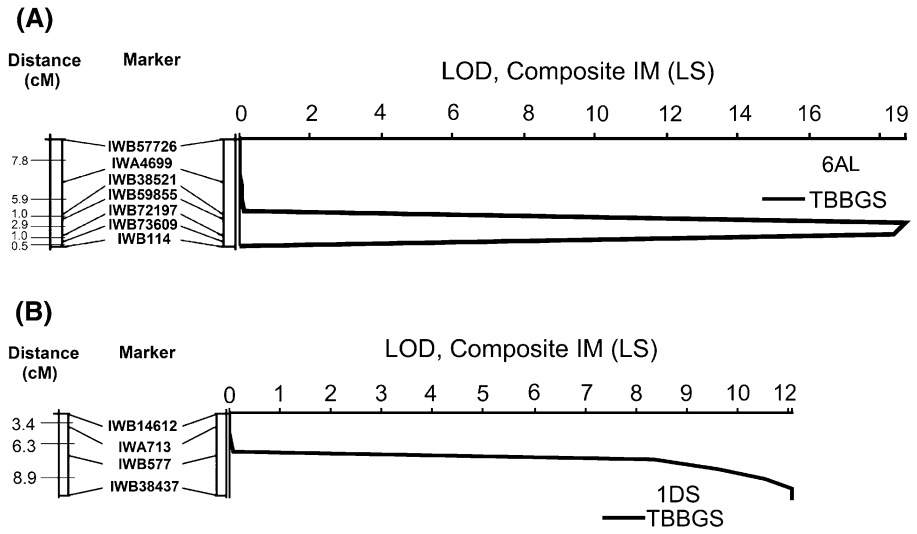

Fig. 1 Composite interval mapping of KASP markers on **a** chromosome 6AL and **b** 1DS segregating for resistance to leaf rust race TBBGS in the Thatcher/RL6149 F_7 RIL. *LS* leaf rust severity, *cM* centimorgans, *LOD* logarithm of odds

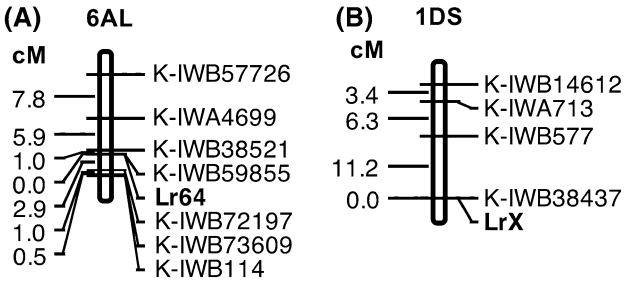

Fig. 2 Genetic maps of **a** *Lr64* on chromosome 6AL and **b** a leaf rust resistance gene on chromosome 1DS

Thatcher allele for *K-IWB38437*, which indicated that these RIL had *Lr64*, but lacked the gene on 1DS. These RIL had very low IT with the races tested. RIL 34, 75, 78 and 79 had the Thatcher allele at *K-IWB59855* and had the RL6149 allele for *K-IWB38437*. These RIL had an intermediate IT of ;12 to 23 to the five races. RIL 32 and 94 that had the RL6149 allele for *K-IWB59855* had a low IT of; to ;12 to the five races, which was very similar to the ITs for RL6149. RIL 32 was heterozygous for alleles at *K-IWB38437* and RIL 94 had the C allele. These two RIL have *Lr64* and may also have the gene on 1DS. RL6149 was heterogeneous for alleles TC for *K-IWB38437*, and Thatcher had the T allele.

Discussion

The F_7 RIL of Thatcher/RL6149 segregated for two seedling resistance genes. One of these genes was *Lr64* located on chromosome arm 6AL. A second gene mapped to

Table 2 Infection types to five *Puccinia triticina* races and KASP marker data for Thatcher/RL6149 F_7 lines

RIL- Wheat line	*Lr64–K-IWB59855-*6AL	*LrX–K-IWB38437-*1DS[a]	Races				
			BBBDB	TBBGS	SBDGG	TNRJJ	MCTNB
RIL 13	C	T	;1^-	;12^-	;	;12^-	22^-
RIL 28	C	T	;	;	;1^-	;1	;1
RIL 30	C	T	;	;1^-	;	;12^-	;1
RIL 32	C	TC	;1^-	;2	;	;12	;
RIL 33	C	T	;	;	;	;1^-	;1^-
RIL 34	A	C	;12–22+	2^+3	;12	22^+	2^+3
RIL 75	A	C	;12–22^+	23	;12^-	23	23
RIL 78	A	C	;12	23	12	22^+	2^+
RIL 79	A	C	;12	22^+	22^+	2^+3	22^+
RIL 94	C	C	;2^-	;1^-	;	;1^-	;
RL6149 (*Lr64*, *LrX*[a])	C	TC	;1^-	;$1^=$	;	;1^-	;
Thatcher	A	T	3^+4	3^+4	3^+4	3^+4	3^+4

[a]Unknown resistance gene on chromosome 1D

chromosome 1DS. *Lr42* and *Lr60* are seedling leaf rust resistance genes also located on chromosome 1DS. KASP markers linked to both genes were monomorphic between Thatcher and RL6149 (A. Bernardo, unpublished data), which indicated that the 1DS gene derived from RL6149 is unlikely to be one of these genes. Gene *Lr21* is also on 1DS, however race TBBGS is virulent (IT of $3^{+}4$) on wheat lines with this gene. Intercrosses of the Thatcher lines that have *Lr21, Lr42* and *Lr60* with a RIL that lacks *Lr64* but has the 1DS gene will be made in order to determine the allelic relationship between the genes on 1DS.

A single gene was expected to segregate in the RIL population. In the initial mapping of resistance derived from RL6149, only the resistance gene on 6AL was detected. In the previous study, F_2 plants were phenotyped, and their genotypes were confirmed in F_3 families. Scoring single F_2 plants that carry a resistance gene that has an intermediate IT can be difficult, since plants heterozygous for the gene can often have a near susceptible IT (Kolmer and Dyck 1994). In the F_2 seedling test, plants with the 1DS gene may have been scored as susceptible, and the derived F_3 families may have been scored as homozygous susceptible. The RIL population in this study, which was derived from the same single F_1 plant in the initial study, was almost uniformly homozygous for both resistance genes, allowing for easier and consistent scoring of IT.

Dyck (1994) studied the leaf rust resistance in *T.dicoccoides* line 8404, the resistant parent of RL6149. In a cross with a susceptible line of *T. durum*, the resistance from 8404 segregated for three seedling resistance genes. In crosses with Thatcher, resistance derived from 8404 segregated for two different resistance genes. One produced a very low IT with almost all races tested, and was consistent with *Lr64* on chromosome arm 6AL. A second gene detected in RL6150 was also derived from 8404. Based on IT and intercrosses with other Thatcher lines, this gene was determined to be *Lr33,* which is on chromosome 1BL. The origin of the 1DS gene derived from RL6149 is not clear. One possibility is that line 8404 was not a tetraploid wheat. RL6149 is perhaps a mixture of genotypes, as evidenced by the heterogeneity of the SNP-KASP markers on 1DS. Single plant selections of RL6149 should be homozygous for all KASP markers, Furthermore, the plants of RL6149 that were used for crossing were not those that were later genotyped. The origin of the 1DS gene may be clear if the RL6149 parental plants had been genotyped. Of the four KASP markers on 1DS, the single F_1 hybrid must have received the non-Thatcher allele. Resistant RIL that have intermediate IT and the Thatcher allele at *K-IWB59855* and the RL6149 allele at *K-IWB38437* have been crossed with Thatcher in order to develop a larger population for fine mapping the 1DS gene. Segregation of the F_2 progeny from this cross indicated that the 1DS resistance gene is recessive (J. Kolmer, unpublished data).

The resistance in RL6149 is highly effective to the current North American *P.triticina* population. In field plot tests RL6149 usually has severities of trace to 5% level of infection, with a highly resistant response of small necrotic uredinia. In greenhouse testing of *P.triticina* isolates from North America, most races produce very low IT on RL6149, although one race produced a mesothetic IT of flecks and large uredinia in the initial study (Dyck 1994) and Kolmer (2014) reported that a *P.triticina* race type virulent on durum wheat had high IT to RL6149. RIL with the two genes separated will be increased and tested in field plots and in additional seedling tests to determine the effects of the individual genes. RIL #13 (Thatcher/RL6149-RIL13) has been designated as the single gene line with *Lr64*.

In conclusion, the KASP markers for *Lr64* on chromosome 6AL and the second gene on 1DS will be useful for rapid introgression of these genes into wheat germplasm. Resistance derived from RL6149 is highly effective to the current population of *P.triticina* in North America, especially when used in combination with adult plant resistance genes such as *Lr34* (Kolmer et al. 2008) and *Lr77* (Kolmer et al. 2018) that have conditioned long lasting resistance and are present in U.S. wheat cultivars. Use of molecular markers will facilitate the selection of wheat germplasm with highly effective seedling and adult plant leaf rust resistance genes.

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Author contribution statement JAK designed the study, developed the mapping population, phenotyped the population, mapped the population, did the quantitative trait analysis, and prepared the manuscript. MJH genotyped the selected RIL, identified SNPs linked to the resistance genes, and revised the manuscript. AB and GB designed the KASP markers and conducted the KASP assays on the population and revised the manuscript. JAA participated in the initial mapping of *Lr64* and revised the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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