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Genetic analysis of resistance to *soil-borne wheat mosaic virus* derived from *Aegilops tauschii*

M. D. Hall · G. Brown-Guedira · A. Klatt · A. K. Fritz

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Abstract Genetic Analysis of Resistance to *Soil-Borne Wheat Mosaic Virus* Derived from *Aegilops tauschii*. Euphytica. *Soil-Borne Wheat Mosaic Virus* (SBWMV), vectored by the soil inhabiting organism *Polymyxa graminis*, causes damage to wheat (*Triticum aestivum*) yields in most of the wheat growing regions of the world. In localized fields, the entire crop may be lost to the virus. Although many winter wheat cultivars contain resistance to SBWMV, the inheritance of resistance is poorly understood. A linkage analysis of a segregating recombinant inbred line population from the cross KS96WGRC40 × Wichita identified a gene of major effect conferring resistance to SBWMV in the germplasm KS96WGRC40. The SBWMV resistance gene within KS96WGRC40 was derived from accession TA2397 of *Aegilops taushcii* and is located on the long arm of chromosome 5D, flanked by microsatellite markers *Xcfd10* and *Xbarc144*. The relationship of this locus with a previously identified QTL for SBWMV resistance and the *Sbm1* gene conferring resistance to *soil-borne cereal mosaic virus* is not known, but suggests that a gene on 5DL conferring resistance to both viruses may be present in *T. aestivum,* as well as the D-genome donor *Ae. tauschii.*

Keywords *Aegilops taushii* · Disease resistance · Markers · *Soil-borne wheat mosiac virus* · Wheat

Abbreviations

SBWMV	*Soil-borne wheat mosiac virus*
SBCMV	*Soil-borne cereal mosiac virus*
WGRC	Wheat genetics resource center

Introduction

Soil-Borne Wheat Mosaic Virus (SBWMV) is a destructive pathogen of wheat that belongs to the viral group *Furovirus*. The disease was first described in Illinois by McKinney (1923) and can now be found in most winter wheat-growing regions throughout the world, including recent detection in the United Kingdom (Clover et al. 2001). Shirako and Wilson (1993) determined the complete nucleotide sequences

M. D. Hall
Department of Crop and Soil Environmental Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

G. Brown-Guedira (✉)
USDA-ARS Plant Science Research, North Carolina State University, Raleigh, NC 27606, USA
e-mail: gina_brown-guedira@ncsu.edu; gina.brown-guedira@ars.usda

A. Klatt
Department of Plant and Soil Sciences, Oklahoma State University, Stillwater, OK 74078, USA

A. K. Fritz
Department of Agronomy, Kansas State University, Manhattan, KS 66506, USA

of RNAs one and two of a SBWMV isolate collected from Nebraska. Based on this sequence and other biological characteristics, Shirako et al. (2000) concluded that four strains of the virus exist—the American, Chinese, European, and Japanese.

SBWMV is vectored by the soil inhabiting organism *Polymyxa graminis* (Rao and Brakke 1969). Symptoms of SBWMV on wheat seedlings include mostly yellow to light green leaves with darker green mottling and stunting. Depending on environmental conditions, infected seedlings may be able to recover a dark green appearance. Yield losses to SBWMV have been estimated as high as 45% in Kansas (Nykaza 1978).

During the late 1970s, SBWMV was the most devastating disease of winter wheat in Kansas (Bockus et al. 2001). Following several epidemic years, breeding for resistance to SBWMV was considered a priority by hard winter wheat breeders. With the use of specific breeding nurseries in severely infested SBWMV fields, several SBWMV resistant cultivars were developed and released, thus drastically reducing the losses due to the virus (Bockus et al. 2001). Although many winter wheat cultivars contain resistance to SBWMV, no single major resistance genes have been genetically mapped to date.

Inheritance studies suggest that there are major genes conferring resistance to SBWMV in wheat. The resistances contained within the winter wheat cultivars Shawnee, Centurk, and KS73256, were reported as simply inherited single dominant resistance genes (Brunetta 1980). Merkle and Smith (1983) also reported that resistance to SBWMV was inherited as a single dominant gene. The Brazilian cultivar Embrapa 16 is reported to contain two SBWMV resistance genes (Barbosa et al. 2001). The hard red winter wheat cultivar Karl 92 contains a QTL of major effect on SBWMV on the long arm of chromosome 5D (Narasimhamoorthy et al. 2006). Barbosa et al. (2001) estimated broad sense heritability of resistance to SBWMV in the cultivar Embrapa 16 as relatively high being over 0.40.

KS96WGRC40 is a hard red winter wheat germplasm developed and released by the USDA-ARS Plant Science and Entomology Research Unit, the Kansas Agricultural Experiment Station, and the Wheat Genetics Resource Center (WGRC) at Kansas State University. KS96WGRC40 contains resistance to SBWMV, leaf rust, wheat curl mite, Stagonospora leaf blotch, and Septoria leaf blotch. KS96WGRC40 was a reselection for wheat curl mite resistance out of the germplasm KS95WGRC33. The pedigree of KS96WGRC40 is TAM107*3/TA2460//TA2397/3/TAM107*3/TA2460 (Cox et al. 1999). Many hard red winter wheat germplasms have been released by the WGRC at Kansas State University that have resistance to SBWMV derived from the progenitor species of wheat (Cox et al. 1994; Gill et al. 1991). However, the inheritance and chromosomal locations of this resistance has not been characterized. The objective of this research was to characterize and map the gene(s) conferring SBWMV resistance contained in KS96WGRC40.

Materials and methods

A segregating population was created from the cross KS96WGRC40 × Wichita. KS96WGRC40 is resistant to SBWMV while Wichita is susceptible. The population was advanced by single seed descent to the F_5 generation in the greenhouse. After the F_5 generation, lines were harvested in bulk. Seventy-seven recombinant inbred lines (RILs) were used in this study.

SBWMV Evaluation

The 77 $F_{5:7}$ RILs from the KS96WGRC40 × Wichita population were evaluated for SBWMV resistance in the field at the Kansas State University Ashland Bottoms Research Farm at Manhattan, KS during the 2004–2005 and 2005–2006 growing seasons and at the Oklahoma State Research Farm at Stillwater, OK during the 2006–2007 growing season. For each location and year, the experimental design was a randomized complete block design. Two and three replicates of each RIL were planted in one-meter rows at Manhattan, KS and Stillwater, OK, respectively. The parents of the population (KS96WGRC40 and Wichita) were included in the experiments. Lines were scored on a 0–3 scale (0 = resistant, 3 = susceptible) based on the level of stunting and mosaic observed at Feekes growth stage three (Feekes 1941). Data were averaged across locations to generate the qualitative phenotypic data used in mapping the SBWMV resistance. Lines with a mean SBWMV severity equal to 0 were classified as having the SBWMV gene.

Susceptible SBWMV checks (TAM107 and Wichita) were planted alongside each entry throughout the length of the field at Manhattan, KS to visualize SBWMV distribution. Symptomatic leaves of TAM107 and Wichita were collected and submitted to the Kansas State University Department of Plant Pathology Plant Disease Diagnostics Lab to verify SBWMV presence by ELISA.

Visual evaluations of SBWMV symptoms used in conjunction with SBWMV ELISA were recommended by Hunger and Sherwood (1985) as the best indicator of resistance. A 2.5 cm leaf sample from five random plants for each RIL and parent was collected from the first replication in the 2005–2006 field screening. Leaf samples were collected at Feekes growth stage three, stored on ice in the field, and returned to the lab where they were stored at −80°C. The leaf samples were tested for the presence of SBWMV by compound direct labeled ELISA using the protocol and supplies in an Agdia SBWMV test kit (Agdia, Elkhart, IN). Absorbencies were measured at 405 nm using a Bio-tek ELx800 microplate reader (Bio-tek, Winooski, VT). SBWMV positive and negative controls were included with the Agdia test kit. The ELISA was repeated using the same leaf extracts, and absorbance values from the two replicate SBWMV ELISA screenings were averaged.

Marker analysis

Plant material used for the marker analysis included a RIL population, parents (KS96WGRC40 and Wichita), TAM 107 and *Aegilops tauschii* accessions TA2460 and TA2397, which are in the pedigree of KS96WGRC40.

Leaf tissue was collected from seven-day old germinated seedlings and placed in 1.5 ml microcentrifuge tubes. The tissue was stored at −80°C and then ground to a fine powder in liquid nitrogen using a mortar and pestle. Ground tissue samples were stored at −80°C. Small scale DNA extractions were performed using the modified DNA isolation protocol as described in Malik et al. (2003). DNA concentrations were adjusted to 10 ng/µl with the use of a Nano Drop NC-1000 spectrophotometer (Nano Drop Technologies, Wilmington, DE).

A bulk segregant analysis was used to identify polymorphic markers potentially linked to SBWMV resistance (Michelmore et al. 1991). Bulk DNA samples were prepared by pooling equal amounts of DNA from ten susceptible RILs and ten resistant RILs. The DNA samples of KS96WGRC40, Wichita, the resistant bulk, and the susceptible bulk were screened for polymorphisms with 249 D-genome specific microsatellite primer pairs. Only D-genome specific primer pairs were screened for polymorphism because the SBWMV resistance within KS96WGRC40 is derived from an accession of the D-genome diploid progenitor, *Ae. tauschii.* The common wheat cultivar in the pedigree of KS96WGRC40 (TAM 107) is susceptible to SBWMV.

Wheat microsatellite primers were synthesized according to the sequences published in the GrainGenes data base (http://www.wheat.pw.usda.gov), with all forward primers modified to include an 18 bp M13 sequence at the 5′ end for labeling purposes. All PCR reactions were performed in 12 µl volumes and included 2.0 µl of genomic DNA, 1.2 µl of 10× PCR buffer with magnesium chloride, 0.96 µl of 10 mM dNTP's, 0.18 µl of *Taq* DNA polymerase (5 U/µl), 5.26 µl of sterile molecular grade water, 0.96 µl of 1 µM forward primer, 0.72 µl of 10 µM reverse primer, and 0.72 µl of one of either FAM, PET, NED, or VIC 10 µM fluorescent dye labeled universal M13 primers. The 18 bp M13 tail that was added to the 5′ end of the forward primer sequence is labeled with the fluorescent dye labeled M13 universal primer under annealing conditions in the PCR following the methods of Schuelke (2000). Reactions were carried out in either a PTC-200 Thermal Cycler (MJ Research, Watertown, MA,) or a Master Cycler EP384 System (Eppendorf, Westbury, NY). Pools of four differently labeled PCR products were created for the same genomic DNA sample with the use of a Hydra II 96 channel microdispenser (Matrix, Hudson, NH). PCR fragments were resolved with an ABI Prism 3130XL Genetic Analyzer (Applied Biosystems, Foster City, CA) with GeneScan-500 LIZ as an internal size standard (Applied Biosystems, Foster City, CA). Fragment analysis was performed with GeneMarker v1.4 software (SoftGenetics, State College, PA).

Microsatellite primer pairs identified as polymorphic based on the bulk segregant analysis were screened on the entire mapping population. Linkage analysis was conducted with Mapmaker software (version 2.0 for Macintosh). Map distances were converted to centimorgans using the Kosambi function (Kosambi 1944). Linkage maps were generated

using a maximum Kosambi distance of 50 and a minimum LOD of 3.0.

The linkage analysis identified microsatellite primer pairs linked to the SBWMV resistance gene within KS96WGRC40. The chromosomal locations of these microsatellite primer pairs were previously determined in other mapping populations (Somers et al. 2004). This information was used to select more microsatellite primer pairs in the identified chromosomal region of interest. These additional microsatellite primer pairs were also screened on the population in similar fashion.

Twenty-three WGRC germplasm releases, six hard red winter wheat cultivars, and two *Ae. tauschii* accessions were genotyped using the closest marker identified from the molecular genetic linkage mapping of SBWMV resistance.

Results

The classification of each RIL as resistant or susceptible based on the phenotypic evaluation was consistent between the 3 years of field screening (Table 1). The distribution of SBWMV at Manhattan, KS in the 2004–2005 field screening was sporadic. In instances where the susceptible checks did not show SBWMV symptoms, phenotypic data were not recorded on the adjacent RIL. Reliable data were obtained on at least one replication for each of the RILs in 2004–2005. The SBWMV in the 2005–2006 field screening was evenly distributed in the first replication as all plants of TAM107 and Wichita were uniformly infected in the first block of the experiment. The second block of the experiment did not show any symptomatic expression of SBWMV on the susceptible checks TAM107 and Wichita. Therefore, phenotypic data were not taken on the second replication in 2005–2006. Heavy levels of SBWMV were observed in all three replications of the experiment at Stillwater, OK during 2006–2007. The phenotypic data were averaged across years and locations for each RIL and despite heterogeneity of virus infection at the Manhattan, KS location each year, few changes in classification of lines were observed among the three locations. In the few instances where changes were observed, only lines with a mean SBWMV severity equal to 0 were classified as resistant.

The observed segregation of lines indicated resistance to SBWMV in KS96WGRC40 is conferred by a single gene. Thirty-eight RILs were classified as resistant; 39 RILs were classified as susceptible. This segregation ratio is not significantly different from 1:1 ($\chi^2 = 0.013$, $P > 0.95$) expected if KS96WGRC40 contains a single SBWMV resistance gene.

Average absorbance values of the ELISA for the RILs ranged from 0.1525 for the resistant parent KS96WGRC40 to 3.2520 observed for the susceptible parent Wichita (Table 1). SBWMV resistant and

Table 1 Phenotypic expression of *soil-borne wheat mosaic virus* (SBWMV) symptoms at three locations, SBWMV ELISA absorbance values, and *Xcfd10* genotype of eight recombinant inbred lines (RIL) from a KS96WGRC40/Wichita population

Sample	Phenotypic expression of SBWMV symptoms[a]			SMBWV ELISA Absorbance values (405 nm)[b]	Xcfd10 Genotype (bp)
	Manhattan, KS 2004–2005	Manhattan, KS 2005–2006	Stillwater, OK 2006–2007		
RIL #57	0	0	0	3.13	290
RIL #76	0	0	0	2.39	290
RIL #103	0	0	0	3.06	290
RIL #13	2	3	1.7	3.16	290
RIL #42	2	3	2.3	2.85	290
RIL #4	0	0	0	0.17	280
RIL #21	0	0	0	0.17	280
KS96WGRC40	0	0	0	0.18	280
Wichita	3	3	3	3.25	290

[a] Rated on a 0–3 scale where 0 = dark green plants with no mosaic and 3 = stunted plants showing heavy yellowing and mosaic

[b] Mean absorbance values from two replicate tests, each consisting of combined leaf extracts from five random plants in a naturally infected SBWMV field in Manhattan, KS, 2006

susceptible RILs were easily separated based on average absorbance values. Lines with an average absorbance value <1 were resistant. Lines with an average absorbance value >2 were susceptible. No line had an average absorbance value >1 and <2. Lines could also be easily separated visually by inspecting the microplate sample well color with a yellow sample well indicating the presence of SBWMV and a clear sample well the absence of SBWMV. In all instances where a RIL was classified as susceptible based on the phenotypic expression of symptoms, the ELISA test result was positive for the presence of SBWMV. However, three lines were classified as resistant in all 3 years of the experiment based on visual evaluation of SBWMV symptoms, but were positive for the presence of SBWMV based on ELISA (Table 1).

Molecular marker analysis

From the 249 D-genome specific microsatellite primer pairs screened in the bulk segregant analysis, 48 were polymorphic between the parents. A preliminary linkage analysis identified one of these markers, CFD10, to be associated with SBWMV resistance. Marker locus *Xcfd10* is located on chromosome 5DL according to the consensus map of hexaploid wheat (Somers et al. 2004). Additional microsatellite primer pairs located on chromosome 5DL near *Xcfd10* were selected to further genotype the RIL population. Six polymorphic microsatellite markers were used to construct a genetic linkage map in the region of the SBWMV resistance (Fig. 1). The *Xcfd10* marker was the most closely linked to virus resistance and was located 9.5 cM proximal to the resistance gene (Fig. 1). Marker *Xcfd10* amplified a 280 bp fragment in KS96WGRC40 and a 290 bp fragment in Wichita (Table 2). Marker *Xbarc144* was located 11.1 cM distal to the resistance gene and amplified 221 and 237 bp fragments in KS96WGRC40 and Wichita, respectively.

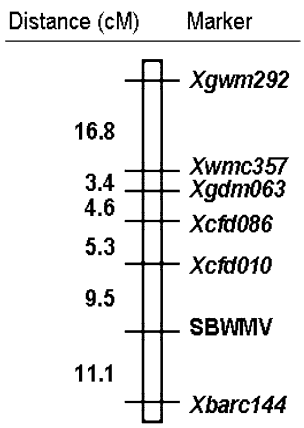

Fig. 1 Partial genetic linkage map of wheat chromosome 5DL constructed from 77 $F_{5:7}$ recombinant inbred lines from a KS96WGRC40/Wichita population

To determine the source of SBWMV resistance in germplasms KS96WGRC40, and KS95WGRC33, marker analysis was done on the wheat parent TAM 107 and *Ae. tauschii* accessions TA2397 and TA2460. The 280 bp *Xcfd10* fragment associated with resistance was amplified from TA2397,

Table 2 Allele sizes (bp) amplified by microsatellite marker *Xcfd10* in 23 WGRC wheat germplasms, six hard red winter wheat cultivars, and two *Aegliops tauschii* accessions

Germplasm	*Xcfd10*
WGRC01	290
WGRC15	290
WGRC02	290
WGRC16	320
WGRC03	290
WGRC21	290
WGRC04	290
WGRC22	290
WGRC23	290
WGRC10	290
WGRC26	290
WGRC11	290
WGRC32	290
WGRC12	290
WGRC33	280
WGRC34	290
WGRC35	290
WGRC36	290
WGRC37	290
WGRC38	290
WGRC39	290
WGRC40	280
Overley	290
Jagger	285
Heyne	290
TAM107	290
Karl92	290
Wichita	290
TA2397	280
TA2460	290

KS96WGRC40, and KS95WGRC33 (Table 2). This suggests that KS96WGRC40 and KS95WGRC33 contain the same SBWMV resistance gene that was derived from TA2397. Genomic DNA of several other WGRC germplasm releases and hard red winter wheat varieties was amplified with the CFD10 primer pair. None of the lines tested had the same allele as KS96WGRC40 and KS95WGRC33 (Table 2).

Discussion

We determined that the SBWMV resistance in KS96WGRC40 is conferred by a major SBWMV resistance gene located on chromosome 5DL. The microsatellite marker *Xcfd10* linked to SBWMV resistance can be used for marker-assisted breeding of resistant cultivars. Getting reliable data on reaction to SBWMV is dependent on adequate distribution of the virus within a field and appropriate environmental conditions for infection. The non-uniform distribution of infection we observed throughout the field at Manhattan, KS in 2 years of our experiment is evidence of the complicating factors that wheat breeders face in selecting for SBWMV resistance. Replicating genotypes and using widespread planting of susceptible checks throughout the field helped us to visualize virus distribution for evaluation of the mapping population. While this is a useful approach, it requires a large amount of space in an infected field. Wheat breeders often do selection for SBWMV resistance among large numbers of lines in early generations without replication. This can result in carrying along susceptible genotypes that escaped infection.

Testing for the presence of viral coat-protein by ELISA is a useful method for evaluating resistance to SBWMV. However, three RIL (#57, #76, and #103) from our population consistently showed no visual symptoms of SBWMV infection when tested in three environments yet contained high levels of SBWMV coat protein based on ELISA absorbance values. Residual heterozygosity in the RILs is not a likely cause of this observation since none of the RILs appeared to be segregating for resistance when evaluated in the field and heterozygote were not observed in the marker analyses. The marker analysis shows that these three lines contain the susceptible allele marker locus *Xcfd10*, the closest linked marker to the resistance within KS96WGRC40 (Table 1) which was considered as recombination between the gene and the marker loci. Other researchers have reported positive SBWMV ELISA absorbance values in resistant cultivars (Armitage et al. 1990; Hunger et al. 1989; Hunger and Sherwood 1985) with resistant genotypes often reaching ELISA values equaling those found in susceptible genotypes as the plants mature.

Our marker data suggest that the SBWMV resistance gene within KS96WGRC40 was derived from *Ae. tauschii* accession TA2397. The SBWMV resistances in WGRC germplasm releases KS85WGRC01, KS89WGRC04, KS91WGRC12, KS92WGRC16, KS92WGRC21, KS92WGRC22 and KS96WGRC39 were derived from diverse accessions of *Ae. tauschii* while resistance in KS96WGRC36 was derived from *T. timopheevii* ssp. *aremiacum* (G. Brown-Guedira unpublished data). All of these germplasm lines, except KS92WGRC16, amplified the 290 bp fragment observed in the recurrent wheat parents. Recombination between the marker and the SBWMV resistance gene may have occurred in the WGRC releases having resistance transferred from *Ae. tauschii*. Alternatively, these germplasms could contain additional SBWMV resistance genes located elsewhere in the D-genome.

Although *Xcfd10* is ~10 cM from the SBWMV resistance gene, the 280 bp allele associated with resistance from *Ae. tauschii* was not present in any of the common wheat germplasm accessions and cultivars that we surveyed. It is therefore likely that this marker would be polymorphic between the donor of resistance and susceptible lines of common wheat. Interestingly, the region distal to *Xcfd10* on chromosome 5DL of wheat appears to be important for SBWMV resistance in *T. aestivum* as well as in *Ae. tauschii.* Narasimhamoorthy et al. (2006) identified a QTL in the wheat cultivar Karl 92 on chromosome 5DL linked to *Xcfd10* and *Xcfd86*. The 290 bp allele for *Xcfd10* amplified in Karl 92 was in that case associated with resistance identified from *T. aestivum*.

Bass et al. (2006) mapped a gene for resistance to *Soil-borne cereal mosaic virus* (designated *Sbm1*) in the UK cultivar Cadenza. This gene was also located in the distal region of chromosome arm 5DL, 5.2 cM proximal to *Xbarc144*. *Soil-borne cereal mosaic virus* (SBCMV) is the approved species name for a European mosaic virus which causes symptoms similar to those caused by SBWMV in the US. The

relationship between SBCMV and SBWMV is debatable. Diao et al. (1999) found only 70% homology between the two viruses. It is unclear if European cultivars with resistance to SBCMV would also contain resistance to SBWMV or vice versa. Further testing is needed to determine if the gene(s) for SBWMV resistance identified in KS96WGRC40 and Karl 92 are the same or allelic to *Sbm1*.

The identification of a gene(s) for resistance to SBWMV and SBCMV on 5DL in an accession of *Ae. tauschii* collected in Afghanistan and two diverse cultivars of winter wheat (one from the US and one from the UK) indicate that this resistance locus may be widespread in wheat. However, diversity for resistance to these viruses does exist. In at least one case a germplasm has been developed having resistance to SBWMV derived from the tetraploid species *T. timopheevii* ssp. *aremiacum* that does not carry the D-genome of hexaploid wheat. Bass et al. (2006) suggest that there are at least two sources of resistance to SBCMV in European wheat cultivars. Additional genetic analysis of the resistance present in cultivars of *T. aestivum* and germplasm lines developed from crosses with related species is needed to assess the level of diversity of resistance to SBWMV and SBCMV.

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