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Molecular genetic mapping of *Gby*, a new greenbug resistance gene in bread wheat

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Abstract The greenbug, *Schizaphis graminum* (Rhodani), is one of the major insect pests of wheat worldwide and it is important to develop a basic understanding of the chromosomal locations of known and new greenbug resistance genes. *Gby* is a new greenbug resistance gene in the wheat line 'Sando's selection 4040'. A mapping population used in this study was derived from a cross of Sando's 4040 and PI220127, a greenbug susceptible wheat land race from Afghanistan. A progeny test indicated that *Gby* is inherited as a single semi-dominant gene. A genetic linkage map consisting of *Gby*, *Xgwm322* (a wheat microsatellite marker), *XksuD2* (an STS marker) and 18 restriction fragment length polymorphism (RFLP) loci was constructed. We used DNA from Chinese Spring 7A deletion lines to show that the gwm332 and ksuD2 amplified fragments mapped in this study are located on a long arm of chromosome 7A. This suggests that *Gby* is located on wheat chromosome 7A. *Gby* was mapped to the area in the middle of the 'island' of putative defense response genes that are represented by RFLP markers (*Xpsr119*, *XZnfp*, *Xbcd98* and *Pr1b*) previously mapped to the distal part of the short arm of wheat chromosome group 7. This region of chromosome 7A is characterized by a high recombination rate and a high physical density of markers which makes *Gby* a very good candidate for map-based cloning. The selection accuracy when the RFLP markers *Xbcd98*, *Xpsr119* or *XZnfp* and *Pr1b* flanking *Gby* are used together to tag *Gby* is 99.78%, suggesting that they can be successfully used in marker assisted selection.

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Introduction

Wheat, *Triticum aestivum* L., is a major food crop around the world and an important component of the economy of the midwestern United States. Numerous arthropod pests challenge wheat production in Kansas and neighboring US Great Plains states. Yield losses caused by the greenbug, *Schizaphis graminum* Rondani, are chronic and at times severe. Greenbug outbreaks have occurred on wheat, barley, oat and sorghum crops in the United States since 1949. Annual yield losses related to greenbug damage during the 1960s and 1970s exceeded $1 billion (Anonymous 1996; Eddleman et al. 1999; LeClerg et al. 1965). The value of incorporating genes for greenbug resistance into locally adapted wheat cultivars has been estimated to be more than $20 million annually in the midwestern states of Kansas, Oklahoma, and Texas (Webster and Kenkel 1999).

Seven genes have been identified with resistance to various greenbug biotypes. These include one recessive gene, *gb1*, from *T. durum* (Table 1) Desf. (Curtis et al. 1960), the dominant genes *Gb2* and *Gb6*, from rye (*Secale cereale* L.), *Gb3* and *Gb4* from *Aegilops tauschii* Coss., and *Gb5* from *Ae. speltoides* Tausch. (Porter et al. 1982, 1991, 1994; Sebesta and Wood 1978; Tyler et al. 1985, 1987). The first greenbug resistant wheat, TAM110, was released by the Texas Agricultural Experiment Station in 1997 (Lazar et al. 1997). *Gby*, a new uncharacterized resistance gene to greenbug biotype E, was recently identified in wheat line 'Sando's selection 4040' that originated from multiple crosses including a cross between *T. aestivum* cv. Chinese Spring (CS) and *Lophopyrum ponticum* (Podp.) A. Love (see Materials and methods).

Screening for aphid resistance using greenhouse phenotype bioassays is a laborious and time-consuming process that can greatly extend the time necessary for the development of new aphid resistant cultivars. Molecular marker-assisted selection is an effective tool to accelerate production of cultivars with desirable traits in general, and with insect resistance in particular (see review by Yencho et al. 2000). DNA markers are beginning to be

Table 1 Gramineae genes conferring resistance to the greenbug, *Schizaphis graminum*. [a]*Gb*-greenbug. [b]Hexaploid wheats composed of A, B, and D genomes of seven chromosomes each; 7DS chromosome 7, D genome, short arm

Gene[a]	Origin of resistance allele	Cultivar	Wheat chromosome[b]	Reference
Gb1	*T. durum*	Dickinson	?	–
Gb2	*S. cereale*	Amigo	1A/1R	Hollenhorst and Joppa (1983)
Gb3	*A. tauschii*	Largo	7DS/L	Weng and Lazar (2002)
Gb4	*Ae. tauschii*	CI17959	7DS/L	Fritz et al. (unpublished)
Gb5	*Ae. speltoides*	CI17882	7AL	Dubcovsky et al. (1998)
Gb6	*S. cereale*	GRS 1201	1AS	Porter et al. (1994)
Gbz	*Ae. tauschii*	TA1675	7D	Zhu et al. (2004)
Gby	Unknown	Sando's 4040	7A	Boyko et al. (present study)

used to identify plant genes for insect resistance or to classify existing resistance genes in major crops (Smith 1999). Marker-assisted selection of plants based on genotype, before the phenotypic trait for resistance can be determined during plant growth, holds promise for greatly accelerating the rate of development of arthropod resistant wheat. However, information about the chromosome locations of molecular markers linked to greenbug resistance genes in wheat is very limited. Weng and Lazar (2002) reported two AFLP markers tightly linked and two wheat microsatellite markers loosely linked to *Gb3* on chromosome 7D. Preliminary results indicated that *Gby* was tentatively located on wheat chromosome 7A (K.S. Gill, personal communication).

The first objective of this research was to determine the chromosome location of *Gby* in the wheat genome. The second objective was to characterize the recombination rate and physical density of markers in the chromosome region where *Gby* is located. We were also interested in identifying molecular markers flanking *Gby* and in evaluating the potential selection accuracy (SA) for the use of these markers in a breeding program for greenbug resistance.

Materials and methods

Plant materials

A new uncharacterized *T. aestivum* source of resistance to greenbug, *S. graminum* biotype E, 'Sando's selection 4040', with the pedigree ('Chinese Spring' *L. ponticum*) × ('Arlando' × 'Leapland') × 'Comet 125' was crossed with PI220127, a greenbug susceptible *T. aestivum* land race from Afghanistan (Harvey and Martin 1990). Eighty-nine $F_{2:3}$ families from this cross were used for phenotypic screening with greenbugs and for genotyping. We also used the CS and CS 7A long arm deletion line TA4547 L4 (FL 0.18) and a 7A short arm deletion line TA4546 L6 (FL 0.21) to identify the chromosome location of PCR markers mapped in this study. All plant materials were obtained from the Kansas State University (KSU) Wheat Genetic Resource Center (WGRC). These seed stocks are currently maintained by the Plant Resistance Laboratory, Department of Entomology, KSU, Manhattan, KS, USA.

Phenotypic analyses

Eighty-nine $F_{2:3}$ families (10–16 seeds per family) were grown in a greenhouse at 27°C, 14:10 photophase. At the two-leaf stage, plants were individually infested with 3–5 adult biotype I greenbugs from a colony maintained in the KSU Department of Entomology. Plants were rated visually at the five-leaf stage, approximately 30 days after infestation. Greenbug damage was rated using a 1–6 rating scale where 1=0% damage, 2=1–24% of the leaf area damaged (chlorotic), 3=25–49% of the leaf area damaged, 4=50–74% of the leaf area damaged, 5=75–99% of the leaf area damaged, 6=100% of the leaf area damaged, plants dead or dying (Porter et al. 1982). Plants rated 1 and 2 were assumed to be the resistant (R) genotypes. Plants rated 3 and 4 were intermediate (H) genotypes, and those rated 5 and 6 were considered to be susceptible (S) genotypes. A progeny test was performed when each F_3 family was evaluated, to represent the response of each F_2 plant genotype. The F_2 plant genotypes were classified as: an F_3 family consisting of R plants only (the F_2 plant was resistant); an F_3 family consisting of R, H and S plants (the F_2 plant was heterozygous); and an F_3 family consisting of S plants only (the F_2 plant was susceptible).

DNA isolation

DNA was isolated from leaf tissue using the modified CTAB phenol extraction-ethanol precipitation methods described by Gill et al. (1991).

Marker resources

Twenty-three wheat microsatellite markers (WMS) representing the group 7 chromosomes of hexaploid wheat were chosen for mapping. The WMS designation, primer sequences, fragment size, and chromosome location of the amplified loci in wheat have been described previously (Plaschke et al. 1996; Röder et al. 1995, 1998). The sequences of the two STS primers for the *KSUD2* marker used in this study were L: CGAATGTTTC-TACTGCGCTGT and R: CTCCCTGTTTGTGGA-AAGCT (Talbert et al. 1994).

Four defense-related gene clones were received from collections maintained by the KSU WGRC and the KSU Department of Plant Pathology. Twelve EST clones and a CH4 clone were received from the USDA Western Regional Research Center, Albany, Calif., USA and from E. Lagudah, CSIRO, Canberra, Australia, respectively. Thirty-six anonymous clones that map to proximal, interstitial and distal physical regions of the short arm of wheat group 7 chromosomes were obtained from a collection maintained by the WGRC, and also from K. Devos, M. Sorrells and the USDA Western Regional Research Center. All clones were used for RFLP analysis.

Southern hybridization and PCR assays

DNA of each parent, resistant bulk and susceptible bulk (DNA from 10 lines in each category combined in equal amounts) was evaluated to identify polymorphic molecular markers. Identified markers were used to evaluate genetic segregation in the mapping population using DNA of the 89 F_3 families (at least 10 plants per family) representing the F_2 plants.

For Southern blotting and hybridization, DNA was digested with the restriction enzymes (*EcoRI*, *EcoRV*, *DraI*, *HindIII*, *BamHi* and *XbaI*). DNA fragments were separated in an 0.8% agarose gel, transferred to Hybond-N^+ nylon membranes and hybridized with ^{32}P-labeled DNA probes according to standard Southern blotting and hybridization protocols (Sambrook et al. 1998) and a company manual (Amersham Pharmacia Biotech).

Reaction mixtures, annealing temperatures and thermocycler settings for WMS and STS PCR amplification and fragment detection have been described previously (Plaschke et al. 1996; Röder et al. 1995, 1998; Talbert et al. 1994). In order to detect polymorphism between parents, a PCR amplified ksuD2-product was digested with the restriction enzyme *DraI*.

Linkage and statistical analysis

Linkage analysis was performed as previously described by Boyko et al. (1999) using Mapmaker 2.0 (Lander et al. 1987). Briefly, markers were grouped at an LOD threshold of 3.0. The frame (basic) map was constructed at LOD≥2.0. Markers that mapped at LOD<2.0 were placed on the frame map in their most probable positions. Genetic linkage distances (cM) were estimated using the Kosambi mapping function (Kosambi 1944). In order to identify the chromosome region where *Gby* is located, the *T. aestivum* genetic map constructed in this study was compared to the wheat group 7 chromosome consensus physical map of Hohmann et al. (1994, 1995) using markers common to both maps.

To characterize the recombination rate and the physical density of markers in regions of wheat chromosome 7A, comparisons were made between the genetic and physical size of wheat chromosome 7A using procedures described by Boyko et al. (2002). For this type of analysis, the genetic linkage map constructed using random markers is required to obtain unbiased results. The chromosome 7A genetic map constructed in this study contains markers that were non-randomly chosen for mapping. Once the approximate chromosome arm region where *Gby* was located was identified, we used markers from that region to find those closely linked to *Gby*, thus saturating this specific chromosome region with molecular markers. For this reason, we did not use the linkage map constructed in the present study to evaluate the relationship between the genetic and physical size of the wheat chromosome 7A. Instead, the Wheat-Synthetic/Opata map of chromosome 7A obtained from Graingenes (http://wheat.pw.usda.gov/ggpages/maps.shtml) and the wheat chromosome 7A physical map (Hohmann et al. 1994), both constructed using randomly chosen markers, were used to calculate the recombination rate and physical density of markers in different chromosome 7A segments.

We defined the recombination rate of a whole chromosome or its segment as the number of cM/μm. We first calculated the observed recombination rate (R_o) for each interval as R_o=cM_i/S_i; where cM_i is the observed cM length of the ith interval, and S_i is the physical length of the same interval/segment in micrometers. We then calculated an expected recombination rate R_e=cM/L; where cM is the observed genetic length of chromosome 7A and L is the observed physical length of chromosome 7A in micrometers, previously measured by Friebe et al. (1992). A goodness-of-fit (GOF) test of observed versus expected recombination rate was performed (McClave and Dietrich 1982).

We also calculated the physical density of markers (number of markers per micrometer) in different chromosome intervals/segments. The observed physical density of markers was calculated as P_o=M_i/S_i; were M_i is the number of markers in the ith interval, and the S_i is the physical size of the same segment in micrometers. The expected physical density of markers was calculated as P_e=M/L; were M is the number of markers on the genetic map of chromosome 7A, and L is the physical length of chromosome 7A in micrometers. The observed and expected physical density of markers was also calculated based on physical map data only. A GOF test was performed for the observed versus expected physical density of markers and the physical density of markers in distal versus interstitial and proximal regions.

We also calculated values of recombination per marker in the *XksuA1–XksuD25* and *Xbcd93–XPr1b* segments of the genetic map constructed in this study as follows: R_{si}=cM_{si}/N_{si} where cM_{si} is the observed cM length of ith segment, and N_i is a number of markers in the ith segment. A chi-square test (McClave and Dietrich 1982) to compare R_{si} values was then performed.

A GOF test was also performed on the observed versus expected segregation of greenbug resistance in the 89 $F_{2:3}$ families from the cross ‘Sando’s selection 4040’ (*Gby*, R) × PI220127 (S).

The SA of marker assisted selection using two markers flanking *Gby* was calculated as SA=1−(A×B), where A and B are frequencies of recombination between the gene of interest and each individual marker, and (A×B) is the probability of simultaneous recombination between *Gby* and both flanking markers. For the formula for calculation of the intersection of two independent events see McClave and Dietrich (1982).

Results

Among the 89 $F_{2:3}$ families representing F_2 plants from the cross Sando's selection 4040 (*Gby*, R) × PI220127 (S), 25 families were homozygous resistant, representing F_2 genotype RR; 49 were segregating for resistance and susceptibility, representing F_2 genotype RS; and 27 were homozygous susceptible, representing F_2 genotype SS. The theoretically expected 1:2:1 segregation ratio for a single gene among 89 F_2 progenies would be 22.25 (RR):44.5 (RS):22.25 (SS) which was not significantly different from the observed segregation ratio obtained in our study (χ^2=0.003, α=0.001).

Thirty-four RFLP and two WMS markers showed polymorphisms between the parents and between the resistant and susceptible bulks (as an example see Fig. 1a). Polymorphic bands were scored in the mapping population to determine the genetic linkage between those markers and *Gby*. Grouping these loci at an LOD threshold of 3.0 yielded one linkage group of 23 loci. The remaining 13 marker loci were unlinked.

A wheat chromosome genetic linkage map (Fig. 2) was constructed, consisting of *Gby*, *Xgwm322* (a wheat microsatellite marker), *XksuD2* (an STS marker) and 18 RFLP loci. The latter included *XZnfp* (a putative zinc finger protein), *Xpsr119* (similar to the ferredoxin-NADP$^+$ reductase gene), *Xbcd98* (similar to an mRNA with unknown function) and *XPr1b* (a pathogenesis-related protein) flanking the *Gby* locus (Fig. 1b). The remaining four RFLP markers from the linkage group did not map at a LOD that would allow their placement on the map. DNA from CS and the CS lines TA4547 L4 and TA4546 L6 carrying long arm and short arm deletions, respectively, was PCR amplified using the gwm332 and ksuD2 primers. The results show that the DNA fragments amplified by these primers and mapped in this study are located on the long arm of chromosome 7A in CS (Fig. 1c).

The recombination rate in various regions of wheat 7A chromosome was calculated. The distal region of chromosome 7A had an observed recombination rate (R_o) of 74.5 cM/µm and an observed physical marker density (PD_o) of 18.8 markers per µm which was significantly higher than expected (R_e=20.9 and PD_e=3.5, respectively; α=0.005). The interstitial and proximal 7A short arm regions had R_o=14.5 cM/µm and PD_o =2.0 markers/µm which did not differ from the expected values.

The recombination per marker value in the *XksuA1–XksuD25* segment (R_{si}=3.8 cM per marker) was not significantly different from that in the *Xbcd93–XPr1b* segment (R_{si}=2.8 cM per marker) of the 7A genetic map constructed in this study.

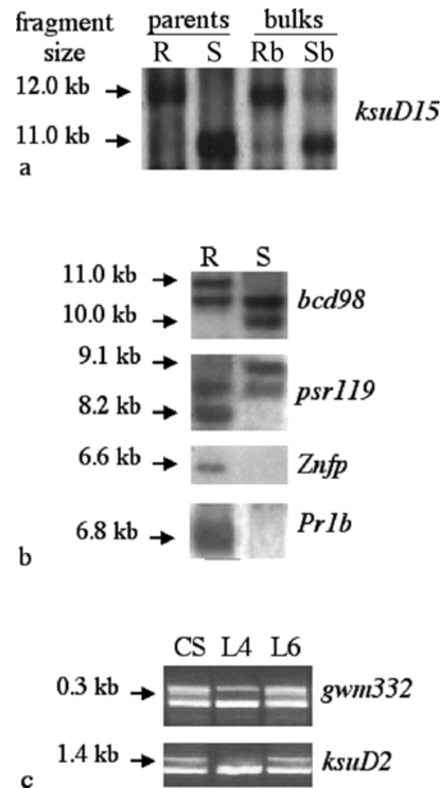

Fig. 1a–c Autoradiographs illustrating **a** bulk segregant analysis using *ksuD15*, and **b** parent polymorphism of RFLP markers flanking *Gby* (*Xbcd98*, *Xprs119*, *XZnfp*, and *XPr1b*). Arrows point to polymorphic bands. *R* - *Gby* resistant parent 'Sando's selection 4040', *S* - susceptible parent PI220127, *Rb* resistant bulk, *Sb* susceptible bulk. Information on restriction enzymes used in each case is presented on Fig. 2. **c** Photograph of PCR products amplified using gwm332 and ksuD2 primers and DNA of CS and its chromosome 7A long arm deletion line TA4547 L4 (FL 0.18) and a short arm deletion line TA4546 L6 (FL 0.21)

Gby was flanked by the following RFLP loci on wheat chromosome 7AS: *XPr1*b, proximally at 3.8 cM a recombination frequency RF=3.8% or 0.038), and *Xprs119*, *Xbcd98* and *XZnfp*, distally at 7.5 cM (RF=5.8% or 0.058) (Fig. 2). The SA of marker assisted selection using *XPr1* was calculated as SA=1 −0.038=0.962 or 96.2%. Using *Xprs119*, *Xbcd98* or *XZnfp* SA=1−0.058=0.942 or 94.2%. The combined SA using two flanking markers to tag *Gby* was SA=1 −(0.038×0.058)=1−0.0022=0.9978 or 99.78%.

Discussion

The phenotypic evaluation of segregation of *Gby* in 89 $F_{2:3}$ families indicated that this resistance is inherited as a single semi-dominant gene. This mode of inheritance allowed us to incorporate the *Gby* segregation data into a wheat microsatellite and RFLP marker data set used for the construction of the genetic linkage map (Fig. 2).

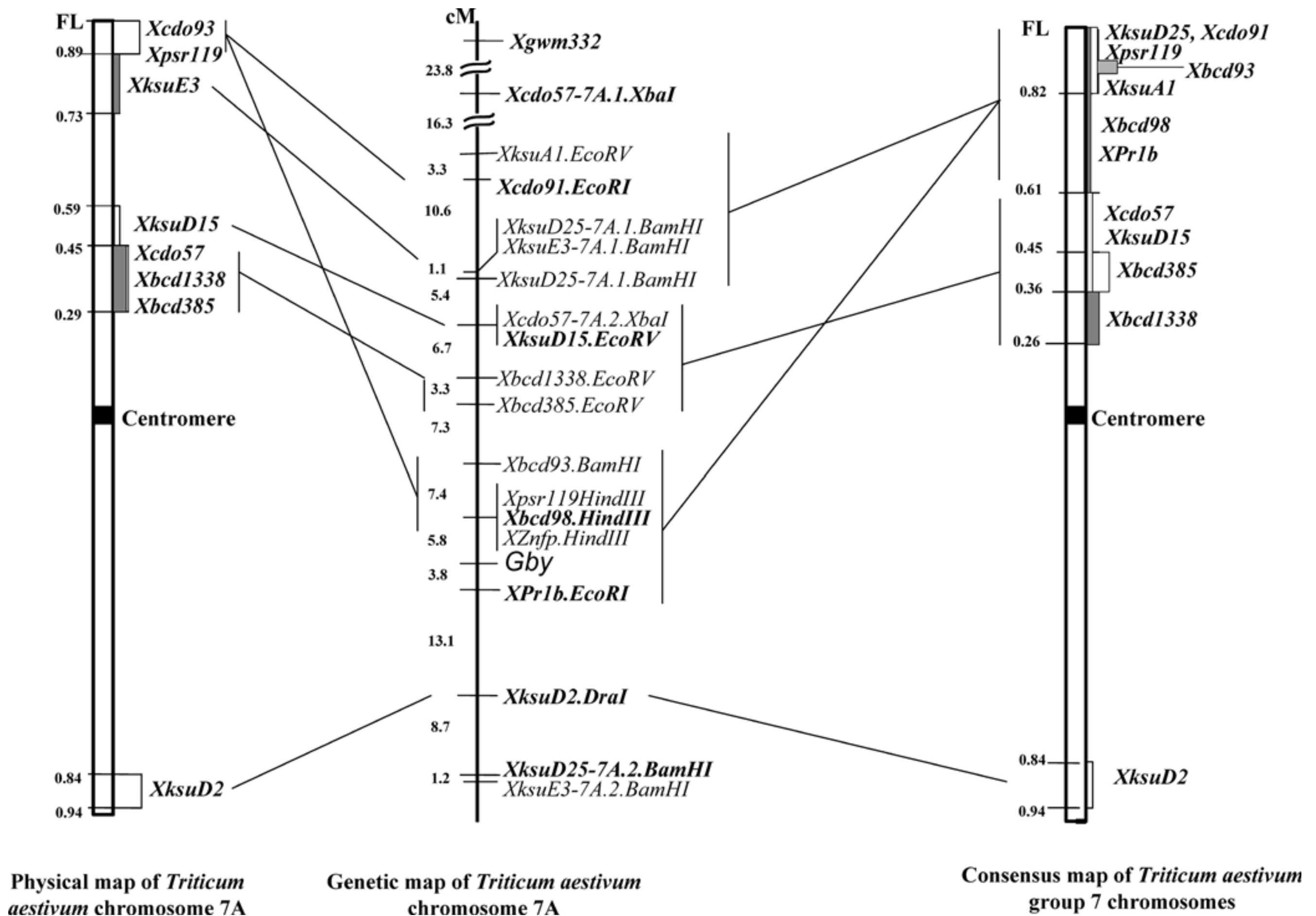

Fig. 2 Wheat chromosome 7A genetic and physical map and a consensus map of wheat homologous group 7 chromosome showing anonymous RFLP marker loci, greenbug resistance gene (*Gby*), and defense related genes and sequences. Loci of the basic map, ordered at LOD>2.0 are printed in bold. Lines drawn between the chromosome maps connect common loci. cM centimorgans, FL fraction length positions of chromosome break points. Names of STS (*XksuD2*) and RFLP loci on the genetic map are accompanied by the name of the restriction enzyme used to digest the PCR product or wheat genomic DNA for Southern blotting and hybridization

The gwm332 and ksuD2 amplified fragments that are specific to wheat chromosome 7A long arm (Fig. 1c) belong to the linkage group that included *Gby*, demonstrating that *Gby* is located on wheat chromosome 7A. This conclusion is in agreement with preliminary results obtained by K.S. Gill (personal communication). A comparison of the genetic linkage map constructed from our data to the wheat chromosome group 7 physical maps of Hohmann et al. (1994, 1995) indicated that *Gby* is located on a chromosome fragment previously mapped to the distal region of the short arm of wheat chromosome 7A (Fig. 2). However, it also suggests a rearrangement of chromosome 7A in our mapping population, where part of the distal region of a short arm was possibly translocated into an interstitial or pericentromeric region of this chromosome. Mapping *Xgwm332* to a distal region of the chromosome 7A short arm also may be an indication of additional rearrangement that has occurred in this chromosome. However, comparison of the values of recombination per marker in the *XksuA1–XksuD25* segment and *Xbcd93–Pr1b* segment (see Fig. 2) showed no significant difference between those values, suggesting that the latter segment still maintains a recombination similar to that in a distal region of the 7A short arm.

Gby was mapped to an area in the middle of a ‘gene island’ distally flanked by putative defense response gene sequences such as a zinc finger protein sequence (*XZnfp*), ferredoxin NADP^{+} oxidoreductase (*Xpsr119*), and a sequence encoding an mRNA of unknown function, and proximally by a pathogenesis-related protein sequence (*XPr1b*). This result is in agreement with previously published data showing that resistant and/or defense response genes map in clusters (Boyko et al. 2002).

An analysis of the Wheat-Synthetic/Opata map obtained from GrainGenes (http://wheat.pw.usda.gov/ggpages/maps.shtml) and the wheat 7A physical map (Hohmann et al. 1994) showed that wheat chromosome 7AS is characterized by a low recombination rate and a low physical density of markers in its pericentromeric and interstitial regions, while having a high recombination rate and a high physical density of markers in its distal/telomeric regions (see Results section). A high rate of

recombination in the distal region of wheat 7AS suggests that it will be difficult to find a molecular marker tightly or completely linked to genes of interest in this area, making it difficult to develop markers for marker-assisted selection. This problem can be overcome by using two molecular markers flanking the gene of interest. The SA estimate for the *Xprs119*, *Xbcd98* or *XZnfp* and *Pr1b* markers flanking *Gby* was 99.78%, indicating that these markers have good potential to be successfully used to select *Gby* plants in segregating populations. The high physical density of markers combined with the high recombination rate in the distal wheat 7AS region also creates an opportunity to identify markers flanking, and in very close physical proximity to, *Gby*. Such markers will be useful in screening various wheat clone libraries in order to select and eventually clone *Gby*-related sequences.

Wheat chromosome 7A is also known to harbor the *Gb5* greenbug resistance gene (Tyler et al. 1987), originally located on chromosome 7S of *Ae. speltoides* (Tausch.) which can substitute for both wheat chromosomes 7A (Friebe et al. 1991) and 7B (Maestra and Naranjo 1998). Dubcovsky et al. (1998) showed that the *Ae. speltoides* chromosome segment containing *Gb5* was transferred to the distal one-third of the long arm of wheat chromosome 7A. It is noteworthy that the distal one-third of the long arms of wheat group 7 chromosomes also contain several disease resistance genes in the A, B, and D genomes, a large cluster of NBS-LRR gene analogs in the D genome, and numerous defense response-related genes (Boyko et al. 2002). The telomeric regions of the wheat 7D short arm, syntenic to the region where *Gby* is located on wheat 7A, also contain several disease resistance genes and an NBS-LRR gene analog. Other defense-related genes encoding oxalate oxidase (A genome), carboxypeptidase (B genome), ankyrin, lipase, a GTP-binding protein, a cysteine proteinase, peroxidase (D genome), and a sequence similar to the ferredoxin-NADP$^+$ reductase gene (A and D genomes) also map in that region (see Boyko et al. 2002). Combined, all this information suggests that the telomeric 7A short arm and long arm regions both contain groups of genes related to early arthropod and disease recognition and defense response. An analysis of the wheat chromosome 7A map constructed in the present study also reveals a putative duplication that may have occurred between the telomeric regions of the wheat chromosome 7AS and 7AL arms. The loci of *KSUE3* and *KSUD25* were mapped in both regions (see Fig. 2). Therefore, it is possible that this putative duplication also contains sequences evolved into two clusters of pest defense response and resistance genes, including greenbug resistance genes, that are located in both regions. Additional research is necessary to support this hypothesis and to establish a more exact relationship between *Gby* and *Gb5*.

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