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ORIGINAL PAPER

The major threshability genes soft glume (*sog*) and tenacious glume (*Tg*), of diploid and polyploid wheat, trace their origin to independent mutations at non-orthologous loci

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Abstract Threshability is an important crop domestication trait. The wild wheat progenitors have tough glumes enveloping the floret that make spikes difficult to thresh, whereas cultivated wheats have soft glumes and are free-threshing. In hexaploid wheat, the glume tenacity gene *Tg* along with the major domestication locus *Q* control threshability. The *Q* gene was isolated recently and found to be a member of the AP2 class of transcription factors. However, only a few studies have reported on the tough glume trait. Here, we report comparative mapping of the soft glume (*sog*) gene of diploid *Triticum monococcum* L. and tenacious glume (*Tg*) gene of hexaploid *T. aestivum* L. using chromosome-specific SSR and RFLP markers. The *sog* gene was flanked by *Xgwm71* and *Xbcd120* in a 6.8 cM interval on chromosome $2A^mS$ of *T. monococcum* whereas *Tg* was targeted to a 8.1 cM interval flanked by *Xwmc503* and *Xfba88* on chromosome 2DS of *T. aestivum*. Deletion bin mapping of the flanking markers assigned *sog* close to the centromere on 2AS, whereas *Tg* was mapped to the most distal region on 2DS. Both 2AS and 2DS maps were colinear ruling out the role of chromosome rearrangements for their non-syntenic positions. Therefore, *sog* and *Tg* are not true orthologues suggesting the possibility of a diverse origin.

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Introduction

The crop domestication process started ca 5,000–15,000 years ago with the conversion of wild forms (characterized by inflorescences that shatter at maturity into tough fruiting bodies which help protect seeds during natural dispersal) into cultivated forms. These cultivated plants produced non-shattering inflorescences and soft fruiting bodies, which made them suitable for human planting and harvesting. In grasses, mutations at genes controlling several spike-related traits such as rachis fragility (brittle or non-brittle rachis) and glume tenacity (hulled or free-threshing) were selected during domestication and subsequently became fixed in the cultivated populations due to positive selection pressure (Tanksley and McCouch 1997; Feuillet et al. 2008).

The ploidy levels of domesticated wheat species range from diploid (*Triticum monococcum*, $2n = 14$, AA), tetraploid (*T. turgidum*, $2n = 28$, AABB) to hexaploid (*T. aestivum*, $2n = 42$, AABBDD). Diploid and tetraploid wheat were independently domesticated from wild relatives ca 13,000 and ca 9,000 years ago, respectively (Nesbit and Samuel 1995). Hexaploid wheat originated under cultivation from hybridization of domesticated tetraploid wheat

and *Aegilops tauschii* coss. ($2n = 14$, DD) ca 8,000 years ago (Nesbit and Samuel 1995). Thus, *T. aestivum* was the last domesticated wheat species and presumably shares the same mutations that led to the domestication of tetraploid wheat in its A and B genomes. Additionally, the founding population of hexaploid wheat inherited the tenacious glume and brittle rachis genes from *Ae. tauschii* and mutations at these loci presumably occurred and were selected during the cultivation of hexaploid wheat (Salamini et al. 2002).

In the polyploid wheats, a polygenic system along with modifier genes is known to govern rachis fragility and glume tenacity (MacKey 1966). Rachis fragility is primarily controlled by genes present on the homoeologous group-3 chromosomes (Watanabe and Ikebata 2000; Nalam et al. 2006; Li and Gill 2006). All wild wheats have a brittle rachis leading to shattering of either the whole spike or individual spikelets (Li and Gill 2006). The first cultivated wheats had a non-brittle rachis (mutant *br* allele) with tough glumes and thus were non-free-threshing. The *Tg* gene controlling glume toughness in wheat is present on short arm of the group-2 chromosomes (Sears 1954; Kerber and Rowland 1974; Chen et al. 1999; Simonetti et al. 1999; Taenzler et al. 2002; Jantasuriyarat et al. 2004; Nalam et al. 2007). A major modifier gene for domestication related traits (*q* gene) is located on the long arm of chromosome 5A (MacKey 1966; Muramatsu 1986; Faris et al. 2002; Faris et al. 2005). Subsequent mutations at these loci during domestication led to the modern free-threshing wheats (genotype *brbrtgtgQQ*). Among these three genes, only *Q* has been cloned and is a member of the APETALA2 family of transcription factors (Simons et al. 2006).

Tg (tenacious glume) was first described by Kerber and Dyck (1969) as an incompletely dominant gene in synthetic allohexaploid X cultivated wheat crosses. Initial mapping efforts placed *Tg* on the short arm of chromosome 2D of wheat (Kerber and Rowland 1974; Rowland and Kerber 1974). Molecular mapping of loci influencing the free-threshing trait in the International Triticeae Mapping Initiative (ITMI) recombinant inbred line (RIL) population identified two major quantitative trait loci (QTL) on chromosome 2DS and 5AL (Jantasuriyarat et al. 2004). The QTL mapped in a region on 2DS corresponding to *Tg*, and the QTL on 5AL corresponded to the *Q* gene. This study further suggested that *Tg* has a more pronounced effect on threshability than *Q* (Kerber and Rowland 1974). Using the ITMI RIL population, Nalam et al. (2007) further reported the presence of two coincident QTL affecting free-threshing habit (threshability and glume tenacity) on short arm of chromosome 2D of wheat and suggested the likely presence of a paralog of *Tg*.

In the tetraploid wheat, Simonetti et al. (1999) characterized the genetic loci influencing glume tenacity/threshability. They studied the free-threshing habit in the RIL population derived from a *T. turgidum* subsp. *durum* X *T. turgidum* subsp. *dicoccoides* cross and found four QTL influencing the threshability trait. These QTL were associated with chromosomes 2BS, 5AL, 5AS, and 6AS. The 2BS and 5AL QTL corresponded to the homoeologous genes *Tg* and *Q* of hexaploid wheats, respectively, where *Tg2* the putative ortholog of *Tg*, was located on chromosome 2BS. Furthermore, this study suggested the complexity of free-threshing trait in tetraploid wheat where major genes, *Tg2* and *Q* along with several minor genes are required for the complete expression of the free-threshing trait.

The glume tenacity genes located in the A-genome have been studied in *T. monococcum*. Einkorn wheat (*T. monococcum* subsp. *monococcum*) is the only cultivated diploid wheat. It has a tough rachis but is non-free-threshing due to the presence of tough glumes. Although a spontaneous free-threshing mutant of *T. monococcum* subsp. *monococcum* referred to as *T. sinskajae* has been reported to possess soft glumes (Filatenko and Kurkiev 1975 cited by Goncharov et al. 2002), the free-threshing einkorn wheat could not be used for large scale cultivation due to the association of the soft glume trait with reduced ear length (Salamini et al. 2002). A single, recessive gene *sog* controlling *s*oft glume trait in *T. sinskajae* was mapped on the short arm of chromosome $2A^m$ (Taenzler et al. 2002).

The major genetic factors responsible for glume tenacity and threshability have been located on short arm of homoeologous group-2 chromosomes in wheats of different ploidy levels (Taenzler et al. 2002; Jantasuriyarat et al. 2004) but their orthologous relationships are not known. In the present study, we characterized *sog* and *Tg*, two of the homoeologous chromosome group-2 loci influencing threshability in diploid and hexaploid wheat populations, respectively, and investigated the orthologous relationship between these genes.

Materials and methods

Plant material

A free-threshing mutant, Tm-9, derived from ethyl methanesulfonate (EMS) induced mutagenesis of TA4342-95 (Dhaliwal et al. 1987) was obtained from Dr. H.S. Dhaliwal of Indian Institute of Technology, Roorkee, India. Tm-9 was crossed as female parent with *T. monococcum* subsp. *aegilopoides* accession TA4342-96 (non-free-threshing) and an F_2 population of 118 individuals was developed. This population was used for mapping the soft glume (*sog*) gene. Progeny testing was done by evaluating 12 F_3 plants in each F_2 family to identify the heterozygous individuals.

An allelism experiment was conducted to find out if Tm-9 and the *T. sinskajae* (*sog*) reported by Taenzler et al. (2002) have the same recessive free-threshing allele.

Although the *Tg* gene in hexaploid wheat was contributed by *Ae. tauschii*, related loci in A and B genomes in hexaploid background also can influence the free-threshing phenotype. Therefore, a population segregating only for the D-genome in hexaploid wheat was developed for mapping *Tg*. The extracted tetraploid of Canthatch (AABB, $2n = 28$) was developed by E. R. Kerber (1964) and is maintained at the Wheat Genetic and Genomic Resources Center (WGGRC), Manhattan, KS. An allohexaploid (TA3419) was synthesized by crossing the extracted tetraploid Canthatch (TA3358) as a female with *Ae. tauschii* form *meyeri* (TA1599). We crossed the resulting non-free-threshing synthetic (TA3419) to the cultivar Canthatch (TA2987) and developed an F_2 population of 103 individuals. This population segregated for several morphological traits including threshability, foliage waxiness, coleoptile color, and glume color and was used for mapping the *Tg* gene. Progeny testing was done using 12–16 F_3 plants in each F_2 family.

A set of 11 group-2 deletion lines of Chinese Spring wheat (Endo and Gill 1996) were used to physically localize the threshability genes in a specific deletion bin. Deletion lines used in this study included 2AS-5, 2AL-1, 2BS-1, 2BS-4, 2BS-3, 2BL-2, 2DS-1, 2DS-5, and 2DL-3 and two new deletion lines 2BL-6/2AS, 6BL-5/2BS (Qi et al. 2003). Individual plants were grown in the greenhouse filled with Scotts Metro Mix 200 (Hummert International, Earth City, MO) using supplemental lighting for a 16 h day and 8 h dark period.

Phenotypic analysis

Threshability data of individual spikes was recorded after harvest. In the diploid wheat population, spikes of the F_2 plants and their F_3 progenies were scored for glume shape and threshability. Each spike was hand threshed and scored as either non-free- or free-threshing. The method described by Kerber and Dyck (1969) was used for testing threshability. Each spike was placed in a plastic tray with a corrugated rubber bottom lining and rubbed with a wooden block covered with the same rubber material. The threshability of each F_2 plant in the hexaploid population and the F_3 progenies also was determined by hand rubbing the individual spikes. The *Tg* gene is incompletely dominant (Kerber and Rowland 1974) and, therefore, all the heterozygotes show intermediate threshability. The F_2 genotype was verified by assaying the phenotypes of 12–16 F_3 plants from each F_2 plant.

Molecular marker analysis and genetic mapping

About 40–60 mg of fresh leaf tissue from the F_2 populations and parents was used for DNA extractions (Kuraparthy et al. 2007). Extracted DNA was dissolved in TE buffer and quantified using NanoDrop ND-1000 UV–VIS spectrophotometer (Agilent Technologies, Palo Alto, CA, USA). Because the chromosome location of *sog* and *Tg* is known (Rowland and Kerber 1974; Jantasuriyarat et al. 2004; Taenzler et al. 2002), we used chromosome 2A- and 2D-specific microsatellite markers for initial mapping based on previously reported maps (Röder et al. 1998; Gupta et al. 2002; Guyomarc'h et al. 2002a, b; Pestsova et al. 2000; Somers et al. 2004; Sourdille et al. 2004). Polymerase chain reaction (PCR) amplifications were performed in 20 µl reactions containing 2.5 µl of 10× PCR buffer, 1.75 µl magnesium chloride (25 mM), 2.0 µl dNTPs (2.5 mM of each dNTP), 1.0 µl each of forward and reverse primer (10 pM/µl), 0.15 µl of *Taq* DNA polymerase (Promega, Madison, WI, USA) and 75 ng of DNA in a PTC-200 thermal cycler (MJ research, Waltham, MA, USA). PCR amplification consisted of 5 min at 95°C, followed by 35 cycles of 95°C for 1 min, 50, 52, 55 or 60°C depending on the individual primer for 1 min and 72°C for 2 min and final extension at 72°C for 10 min. Amplified PCR products were resolved in 2.5% high-resolution agarose (GenePure HiRes agarose, ISC BioExpress, Kaysville UT, USA) gels with 1× Tris–borate EDTA (TBE) buffer and visualized by ethidium bromide staining. Some of the PCR products were resolved in 6.5% KB^{Plus} Gel Matrix (LI-COR) in a LI-COR 4200 DNA sequencer (LI-COR Biosciences, Lincoln, NE, USA) as per the manufacturer's instructions. PCR reactions analyzed in the LI-COR DNA Analyzer were done in a reaction volume of 10 µl. All the forward primers were added with a M13 tail sequence (Schuelke 2000). Fluorescence-labeled M13 primers 5′ IRDye® 700 and 5′ IRDye® 800 were used for detection of PCR products in the LI-COR sequencer.

RFLP clones previously mapped to the short arm of the group-2 chromosomes (Devos et al. 1993; Dubcovsky et al. 1996; Nelson et al. 1995, http://wheat.pw.usda.gov/ggpages/linemaps/Wheat/SxO_2.html) were used for physical and genetic mapping of *sog* and *Tg*. All techniques of restriction enzyme digestion, gel electrophoresis, Southern transfer, probe labeling, and filter hybridizations were performed as described by Kuraparthy et al. (2007). Additionally, ESTs (expressed sequence tags) physically mapped in the interstitial deletion bin 2DS1-0.33–0.47 (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi) in the National Science Foundation (NSF) wheat EST mapping project were selected for physical mapping of *sog*.

Linkage maps were constructed with MAPMAKER version 2.0 (Lander et al. 1987) for the Macintosh OS. Genetic distances were calculated using the Kosambi mapping function (Kosambi 1944). The 'TRY' and 'RIPPLE' commands were used to add markers to the framework map and check the final marker order. Markers were ordered at a minimum LOD score of 3.0 with the exception of some co-segregating

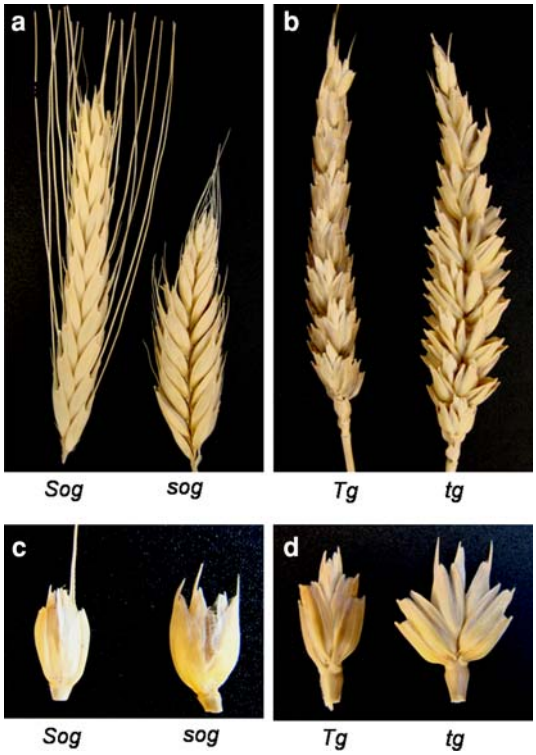

Fig. 1 Phenotypes of contrasting alleles of threshability genes *sog* and *Tg* in diploid and hexaploid wheat, respectively. Comparison of spike shape between **a** non-free-threshing *T. monococcum* (*Sog*) and free-threshing mutant Tm-9 (*sog*) and **b** non-free-threshing synthetic wheat (*Tg*) and the free-threshing cultivar Canthatch (*tg*). Spikelets showing the glume morphology differences in **c** *T. monococcum* (*Sog*) and Tm-9 (*sog*) and **d** synthetic wheat (*Tg*) and cultivar Canthatch (*tg*)

or very closely linked markers. The heterogeneity between common marker pairs on the genetic maps of chromosome $2A^m$ and 2DS was tested using the *G*-test statistic (Liu 1998).

Results

Genetic mapping of *sog*

In the free-threshing mutant Tm-9 (*sog*), the glumes were softer, longer, and broader compared to the wild type *T. monococcum* (*Sog*). In the *sog* mutant plant, the kernels were loosely covered and easy to thresh and the spikes were more compact (Fig. 1). The F_1 plants of Tm-9/*T. monococcum* subsp. *aegilopoides* were non-free-threshing suggesting that the mutant soft glume allele (*sog*) is recessive. The F_2 population segregated into 92 non-free-threshing and 26 free-threshing plants indicating monogenic inheritance (Table 1). In the F_3 generation, 27 families were homozygous for tough glumes, 60 families segregated and 24 families were homozygous for the free-threshing trait, fitting a 1:2:1 ratio (χ^2, $P = 0.64$). The F_1 obtained from the cross between Tm-9 (female parent) and *T. sinskajae* was free-threshing (data not shown) suggesting Tm-9 presumably harbors the same free-threshing allele (*sog*).

The initial chromosome location of the *sog* gene was determined using chromosome 2A-specific microsatellite markers. A total of 60 microsatellite markers were surveyed for polymorphism between Tm-9 and *T. monococcum* subsp. *aegilopoides* accession 4342-95 and 51 primers amplified at least one fragment suggesting approximately 85% transfer rate of hexaploid wheat microsatellites to *T. monococcum* (Table S1, S2). Among the 19 microsatellites that showed polymorphisms between the parents, 16 produced co-dominant and 3 gave dominant polymorphism. Eight of the polymorphic microsatellite markers showed linkage with the *sog* gene and were mapped on chromosome $2A^mS$. The microsatellite marker *Xgwm71* was located 3.3 cM from *sog* towards the distal end of the short arm of chromosome $2A^m$. However, we could not place any marker proximal to *sog*. Furthermore, *Xgwm71* amplifies two alleles each in *T. aestivum* and *T. monococcum*; one has been mapped close to the centromere and the other has been mapped distally on the short arm of chromosome 2A in published genetic maps of hexaploid wheat (Röder et al. 1998; Somers et al. 2004). In our *T. monococcum* population, only one of the alleles of *Xgwm71* was segregating and, thus, the precise genetic location of *sog* on the short arm of chromosome $2A^m$ was difficult to determine based on microsatellite markers alone.

Table 1 Segregation of threshability alleles in the diploid and hexaploid wheat populations

	Generation	Total no. of plants	Observed ratio[a]	Expected ratio	χ^2	*P* value[b]
Tm-9 X TA4342-95 (Diploid wheat)	F_2	118	92:26	3:1	0.553	0.46
	F_3	111[c]	27:60:24	1:2:1	0.89	0.64
TA2987 X TA3419 (Hexaploid wheat)	F_2	103	82:21	3:1	1.17	0.28
	F_3	102[d]	26:57:19	1:2:1	2.36	0.307

[a] Plants were categorized as non-free-threshing (NFT): free-threshing (FT) in F_2 and as NFT: segregating: FT in F_3 generation

[b] χ^2 values were tested at a 0.05 level of significance

[c,d] Seven families from the diploid wheat F_2 population and one family from hexaploid F_2 population could not be phenotyped in F_3 due to lack of sufficient seeds

In order to find flanking marker for the *sog* locus, 62 RFLP markers that were previously mapped on group-2 homoeologous chromosomes were analyzed (http://wheat.pw.usda.gov/ggpages/linemaps/Wheat/SxO_2.html). Parental genomic DNA was digested with six restriction enzymes (*Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII, *Sca*I, *Xba*I) and surveyed for polymorphism. Thirty-five probes detected polymorphism with at least one enzyme (Table S1, S4). Among the 35 polymorphic probes, 12 RFLP markers were mapped in the *T. monococcum* F_2 population. One RFLP marker *Xbcd120* was mapped 3.5 cM proximal to *sog*. In an effort to physically assign *sog* to a specific chromosome region on short arms of group-2 chromosomes, 14 EST markers physically mapped in the 2DS1-0.33–0.47 deletion bin were utilized (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi, Table S5). ESTs mapped in the interstitial bin were chosen due to lack of prior information on the physical location of *sog*. Nine ESTs showed polymorphism among Tm-9 and *T. monococcum* subsp. *aegilopoides* (Table S1, S5) and three of these were found linked to *sog*. The closest EST marker, *XBE443771*, was mapped 4.3 cM distal to *sog*. As a result, *sog* was placed in a 6.8 cM interval flanked by microsatellite marker *Xgwm71* on distal end and *Xbcd120* on the proximal end (Fig. 2). The markers flanking *sog* have been placed in the proximal deletion bin C-2AS5-0.78 (Erayman et al. 2004; Sourdille et al. 2004) on chromosome 2A of wheat, thus assigning *sog* to the proximal 78% of the short arm. In the consensus physical map of group-2 chromosomes (Conley et al. 2004), the closest EST marker to *sog* (*XBE443771*) has been placed in the deletion interval delineated by FL0.33 and FL0.47 (FL, fraction length of distance from centromere), hence *sog* was placed in the proximal 50% of the short arm of group-2 homoeologous chromosomes of wheat (Fig. 2).

Genetic mapping of *Tg*

The Canthatch (TA2987) parent is free-threshing with softer and open glumes, whereas the synthetic parent (TA3419) is non-free-threshing with tough glumes that adhere tightly to the kernel (Fig. 1). The F_1 plants of this cross had somewhat tough glumes and were intermediate in threshability suggesting that *Tg* is a partially dominant gene. Phenotypic analysis of the F_2 population of 103 individuals gave a good fit for single gene segregation (χ^2, $P = 0.28$, Table 1). Segregation in the F_3 generation also fit the expected 1:2:1 ratio (χ^2, $P = 0.31$). These results confirmed that the free-threshing character of Canthatch is recessive in nature and that a single gene controls glume tenacity and threshability in this population.

Twenty-five of the 49 tested microsatellite markers specific for chromosome 2D were polymorphic between the parents, TA2987 and TA3419 (Table S1, S3). Among the polymorphic microsatellite primers, 17 were co-dominant. Ten SSR markers were linked to the *Tg* gene and mapped on the short arm of chromosome 2D. *Xwmc503*, the closest linked microsatellite marker to *Tg*, was located 2.2 cM towards the distal end of chromosome 2D. As was the case with *sog* mapping, we were unable to find a closely linked SSR marker for *Tg* on the proximal side. In an attempt to identify flanking marker for the *Tg* locus, 58 previously mapped homoeologous group-2 RFLP markers were chosen (Table S4). Parental DNA was digested with the same six enzymes used for mapping *sog*. Nineteen probes were polymorphic between parents with at least one enzyme combination (Table S1, S4). Nine RFLP markers showed linkage with *Tg*. Two RFLP markers *Xfba88* and *Xfba400* which co-segregated with each other were mapped 5.9 cM proximal to *Tg* on 2DS. Fourteen ESTs physically mapped in the 2DS1-0.33–0.47 deletion bin that were initially used for physical mapping of *sog* were also used to screen the parents of the hexaploid population for polymorphism (Table S5). Seven ESTs were polymorphic between Canthatch and the synthetic (Table S1 and S5) and one EST marker, *XBE443771* showed linkage with *Tg*. However, *XBE443771*, mapped proximal to *Tg* on chromosome 2DS (Fig. 2). *Tg* was localized in a 8.1 cM interval between markers *Xwmc503* and *Xfba88* (Fig. 2). By using *Xfba88* as a probe on a set of group-2 deletion lines, *Tg* was mapped in the chromosome deletion bin 2BS-3 (FL 0.84–1.00) on 2B and 2DS-5 (FL 0.47–1.00) on 2D (Fig. 3). Thus, in the consensus physical map of group-2 chromosomes of wheat (Conley et al. 2004), *Tg* was placed in the distal 16% of the short arm (Fig 2).

Comparative mapping

We compared the genetic linkage maps of the *sog* and *Tg* regions constructed using diploid and hexaploid wheat populations, respectively (Fig. 2). Twenty-one microsatellite, RFLP and EST markers spanning 75.3 cM were mapped on chromosome $2A^mS$ in the diploid map, whereas 20 DNA markers mapped on short arm of chromosome 2D spanned 104.5 cM in the hexaploid map. Both maps shared seven common loci namely *Xbarc124*, *Xfba88*, *Xfba400*, *Xfba272*, *Xpsr130*, *Xcdo405*, and *XBE443771*. Although the order of RFLP markers along the $2A^m$ and 2D maps was in complete agreement with each other and with the previously published homoeologous group-2 RFLP maps (http://wheat.pw.usda.gov/ggpages/linemaps/Wheat/SxO_2.html), the genetic distance between individual markers varied considerably. In order to facilitate the comparison of recombination frequency, we used markers common between the $2A^mS$ and 2DS linkage maps and divided the genetic maps into four major marker intervals. The chromo-

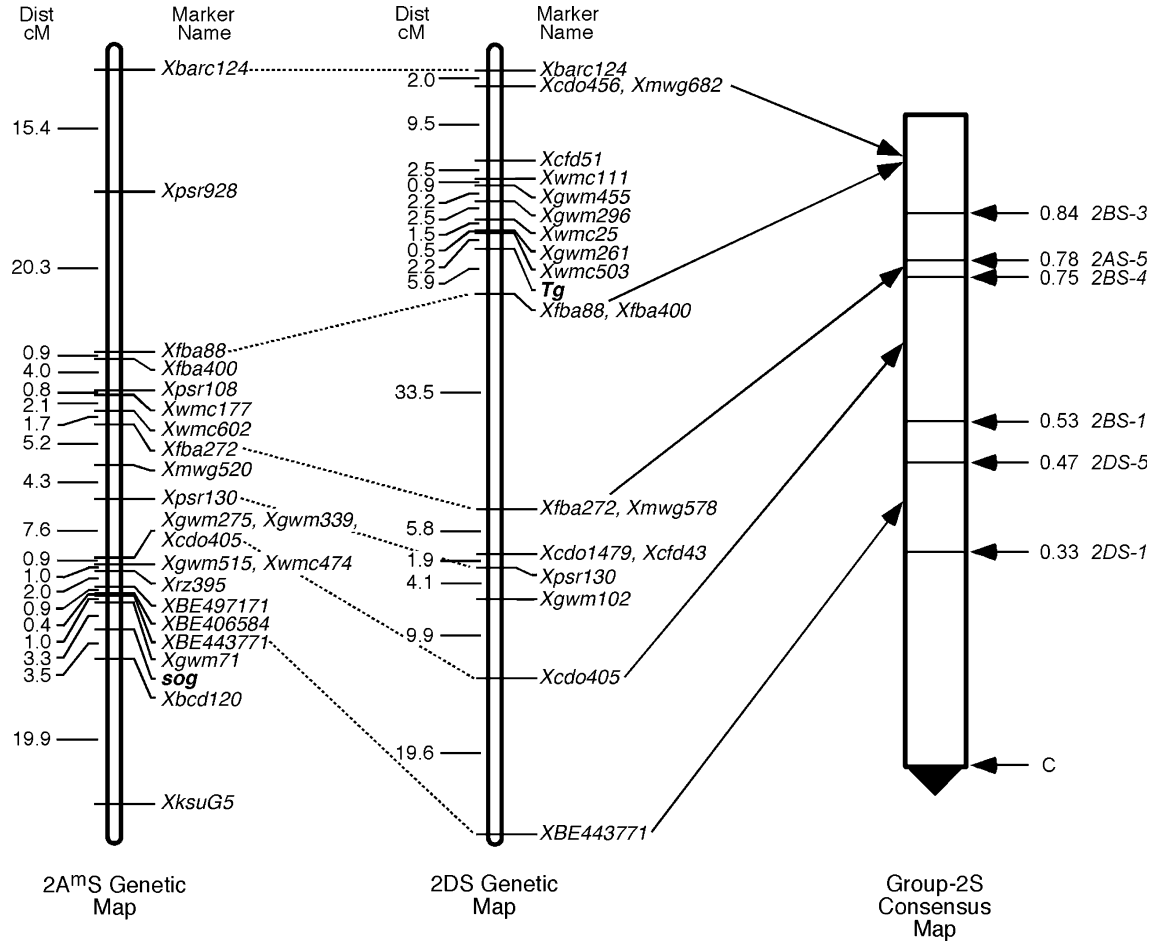

Fig. 2 Genetic and physical mapping of threshability genes *sog* and *Tg*. Each map is oriented *top* to *bottom* from telomere towards centromere. Common marker loci between the two genetic maps are connected by *dotted lines*. The threshability loci *sog* and *Tg* are represented in *bold*. Map distances are given in cM. The centromere on chromosome $2A^m$ map is located between marker loci *Xbcd120* and *XksuG5*. The co-segregating markers have been placed next to each other on the genetic maps. The group-2S consensus physical map has been redrawn based on Conley et al. 2004. Each section of consensus physical map represents a bin delimited by deletion breakpoints expressed as fraction of the arm length from the centromere. The breakpoints of various deletions, along with their FL values, are marked by *arrows* on the right of the consensus map. *Black solid lines* indicate the deletion bin location of RFLP and EST markers in the consensus physical map that are common between $2A^m$ and 2DS genetic maps

some region between markers *Xbarc124* and *Xfba88* in the genetic map was designated as interval I, the region between *Xfba400* and *Xfba272* as interval II and the region between *Xfba272* and *Xcdo405* as region III (Table 2). We tested the linkage heterogeneity using the *G*-test statistic (Liu 1998) with the hypothesis that true linkage between the marker pairs should be the same for chromosome $2A^mS$ and 2DS genetic maps. The *G*-statistic indicated that recombination data among given marker pairs is consistent with homogeneity of linkage except for marker pair *Xfba88* and *Xfba272* ($G = 14.253$, $P = 0.0026$, Table 2), which was not unusual because this marker pair spanned 33.5 cM in the 2DS genetic map compared to 9.5 cM in the 2AS map.

Comparative mapping analyses of the *sog* and *Tg* regions revealed that these genes occupy non-syntenic regions on homoeologous group-2 chromosomes. This is evident by comparing the map position of threshability genes, *sog* and *Tg* with respect to a common marker such as *Xfba88,* which flanked *Tg* at 5.9 cM on proximal side but was placed 36.1 cM distal to *sog* (Fig. 2). Furthermore, physical mapping using a set of CS deletion lines for group-2 chromosomes placed *sog* in the proximal 50% of the short arm relative to *Tg*, which was targeted to the distal most 16% of short arm in the consensus physical map of the group-2 chromosomes (Fig. 2).

Discussion

Threshability is an important domestication trait because free-threshing forms of wheat are essential for cultivation. Various genetic loci are known to influence threshability in

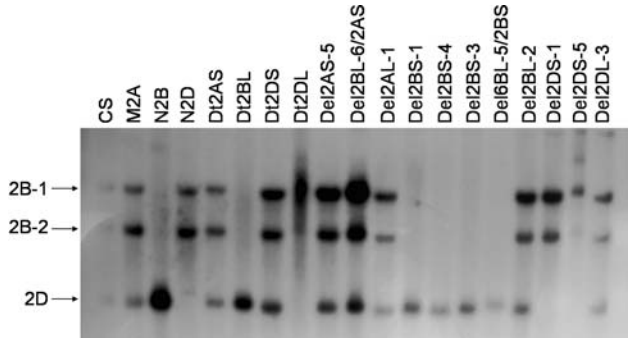

Fig. 3 Deletion bin based physical mapping of *Tg* by mapping flanking RFLP marker *Xfba88* in Chinese Spring (*CS*) group-2 aneuploid stocks and deletion lines. Autoradiograph image showing the hybridization pattern of RFLP probe FBA88 on monosomic (*M*), nullisomic (*N*), ditelosomic (*Dt*) and deletion lines (*Del*) of group-2 chromosomes

wheat. In the present study, two major threshability genes in wheat, soft glume, and tenacious glume were characterized and their orthologous relationship was investigated.

The soft glume gene of diploid wheat *T. monococcum* was mapped to the short arm of chromosome 2 using wheat microsatellite and RFLP markers. Genetic mapping placed *sog* it in a 6.8 cM interval flanked by marker loci *Xgwm71* and *Xbcd120*, both of which have been mapped near the centromere on group-2 chromosomes of wheat (Röder et al. 1998; Somers et al. 2004; Nelson et al. 1995). Taenzler et al. (2002) assigned the *sog* gene to chromosome $2A^m$ using AFLP (amplified fragment length polymorphism) markers. However, because of the nature of markers used, they could not target *sog* to a specific region of the chromosome. We used chromosome-specific RFLP and EST markers to assign *sog* to a specific deletion-bin based on the physical map of chromosome 2A of wheat. Therefore, this is the first report to precisely locate *sog*, the threshability gene in diploid wheat, to a specific chromosome region in wheat.

The major determinant of threshability in hexaploid wheat, *Tg*, was localized to an 8.1 cM interval flanked by *Xwmc503* and *Xfba88* on chromosome 2DS. Previous studies (Jantasuriyarat et al. 2004; Nalam et al. 2007) aimed at QTL mapping of genetic factors responsible for glume tenacity and threshability in hexaploid wheat also identified major QTL on chromosome 2DS using recombinant inbred lines of ITMI population. Although, both studies measured glume tenacity and percent threshability as separate traits, the QTL location for glume tenacity coincided with the QTL for percent threshability in the linkage map (Jantasuriyarat et al. 2004; Nalam et al. 2007). These QTL were closely associated with the microsatellite marker *Xgwm261* on chromosome 2DS. In our 2DS linkage map, *Xwmc503*, the closest flanking marker to *Tg* was mapped 0.5 cM proximal to *Xgwm261*. Considering the fact that QTL cannot be precisely mapped with the small populations used in these studies, the glume tenacity QTL (Jantasuriyarat et al. 2004; Nalam et al. 2007) and *Tg* gene might represent the same locus. However, mapping of the glume tenacity QTL (*Tg1*) in a CS/CS2D F_2 population localized *Tg1* to a 12 cM region between markers *Xwmc112* and *Xbarc168* (Nalam et al. 2007). *Xwmc112* and *Xbarc168* were non-polymorphic and thus, were not mapped in our population but *Xwmc112* has been located 8.0 cM proximal to *Xwmc503* on chromosome 2DS in the published consensus microsatellite map for chromosome 2DS (Somers et al. 2004). In our linkage map, *Tg* was mapped 2.2 cM proximal to *Xwmc503* suggesting that *Tg* and *Tg1* may represent the same genetic locus. Alternatively, two coincident genetic factors may control threshability and glume tenacity on chromosome 2DS as has been indicated by Nalam et al. 2007. The genetic background (minor loci in D genome) also may have had an effect on the phenotype, which further affected the mapping results. Consequently, further research is needed to confirm the relationship between *Tg* and *Tg1*.

Various molecular mapping and comparative mapping studies within the *Triticeae* have established that gene synteny is well conserved among the homoeologous group-2 chromosomes in wheat (Devos et al. 1993; Nelson et al. 1995). Homoeologous chromosomes are essentially collinear except for some minor rearrangements (Conley et al. 2004; Devos et al. 1993). A threshability gene is found on the short arm of each homoeologous group-2 chromosome and therefore, all these threshability genes (*sog*, *Tg2* and

Table 2 Recombination frequency distribution between different molecular marker intervals in the genetic linkage maps of short arm of chromosome $2A^m$ and 2D in relation to location of threshability genes *sog* and *Tg*, respectively

Chromosome interval region on linkage maps	Molecular markers encompassing the interval	Genetic distance in the given marker interval (cM)		*G*	*P* value[a]
		$2A^mS$ map	2DS map		
I	*Xbarc124-Xfba88*	35.7	29.7	1.856	0.603
II	*Xfba88-Xfba272*	9.5	33.5	14.253	0.0026*
III	*Xfba272-Xcdo405*	17.1	21.8	0.244	0.9702

[a] *P* values are obtained by testing linkage heterogeneity between marker pairs using the *G*-test statistic

Significant values are indicated by asterisk

Tg) may be orthologues (Simonetti et al. 1999; Taenzler et al. 2002; Jantasuriyarat et al. 2004). However, experimental evidence in support of this hypothesis is lacking. In the present study, we compared the map positions of *sog* and *Tg* using homoeologous group-2-specific RFLP markers and found these genes to be non-orthologous. The *sog* and *Tg* genes occupy different positions on the genetic map of short arm of homoeologous group-2 chromosome as demonstrated by RFLP marker *Xfba88*, which flanks *Tg* at 5.9 cM on the proximal end of chromosome 2DS and is placed 36.1 cM distal to *sog* on chromosome $2A^mS$. The RFLP marker, *Xfba88*, also has been mapped in the deletion bin 2BS-3 (FL 0.84–1.00) on chromosome 2B of wheat, which targets *Tg* to the distal 16% of the short arm in the consensus physical map of the group-2 chromosomes. The EST marker locus, *XBE443771*, which is genetically mapped 4.3 cM distal to *sog* on $2A^mS$ and 80.7 cM proximal to *Tg* on 2DS in this study, has been physically mapped in deletion bin 2DS-1 delineated by FL0.33 and FL0.47 in the consensus physical map of group-2 chromosomes of wheat (Conley et al. 2004) and thereby placing *sog* in the proximal half of the short arm of group-2 chromosomes. This clearly suggests that *sog* and *Tg* genes are not orthologues.

Comparing the map distances between the same loci on chromosome $2A^m$ and 2D also indicated the local variability in recombination frequencies between these linkage maps. Significantly higher recombination was observed between *Xfba88* and *Xfba272* marker loci in the chromosome-2D map as compared to the chromosome-$2A^m$ genetic map. The most likely reason for a greater genetic distance in the *Xfba88* and *Xfba272* marker interval may be that the parents of both populations (both diploid and hexaploid levels) are biologically different with respect to recombination in this region. This assumption is further supported by a higher *G*-statistic value for this marker pair and also by the fact that marker interval lengths on the corresponding regions on the 2D map developed in this study are quite similar to those from other mapping studies involving cultivated x synthetic wheat crosses (Nelson et al. 1995; Korzun et al. 1998; Pestsova et al. 2000).

Uneven distribution of genes and recombination in the wheat genome has been widely documented (Gill et al. 1996; Sandhu et al. 2001; Akhunov et al. 2003). In this study, the major threshability gene in hexaploid wheat, *Tg*, has been localized in the most distal deletion bin of chromosome 2DS. In the consensus physical map of group-2 chromosomes, *Tg* is targeted to the distal 16% of the short arm between breakpoints FL0.84 and FL1.00 (Fig. 3), implying that *Tg* lies in a high-recombination region. Several studies in wheat have demonstrated that despite the large genome of wheat (1.6×10^{10} bp), genes present in regions of high-recombination are amenable to map-based cloning (Feuillet et al. 2003; Huang et al. 2003; Yan et al. 2003, 2004; Simons et al. 2006). Thus isolating *Tg* using a positional cloning approach should be feasible. Because the deletion bin location of *Tg* is already known, specific deletion-bin mapped wheat ESTs (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi) can be readily utilized to identify markers closely linked to *Tg*. Furthermore, a genome wide analysis of mapped wheat ESTs has shown large blocks of conserved collinearity between wheat and rice genomes (Gale and Devos 1998; Sorrells et al. 2003). High conservation of synteny between wheat chromosome 2 and rice chromosomes 4 and 7 has been well-established (Ahn et al. 1993; Sorrells et al. 2003; Conley et al. 2004). Therefore, rice genomic sequence information can be used as an additional source of markers to enrich *Tg* region to aid in its cloning.

On the contrary, *sog*, the threshability gene in diploid wheat, has been genetically mapped close to the centromere (our results, Röder et al. 1998; Nelson et al. 1995). Based on a study by Erayman et al. (2004), 29% of the wheat genome is presumed to be gene-rich region and these regions have been divided into 18 major and 30 minor gene-rich regions. RFLP markers flanking *sog*, *Xrz395* and *Xbcd120* have been placed in gene-rich region 2S0.5 (FL 0.47–0.57) on chromosome 2S, which physically places *sog* in the proximal half of the chromosome arm. This gene-rich region spans a physical length of 21 Mb and has a recombination frequency of 1.5 Mb/cM, thus emphasizing that *sog* is located in a relatively low-recombination region. Efforts to isolate *sog* using map-based cloning approach therefore might prove ineffective.

Comparative mapping analysis of QTL regions corresponding to seed size, spike disarticulation, and day length-insensitive flowering traits in sorghum, rice, and maize led to the hypothesis that domestication traits among cereals might represent repeated selection on the same underlying genes or genomic regions and suggest convergent domestication (Paterson et al. 1995). However, our results on comparative mapping of the *sog* and *Tg* gene regions in wheat and with related genes in other cereals do not support this hypothesis. Wheat, barley, rice, maize, and sorghum are the major cereals crops that are closely related evolutionarily (Kellogg 2001) and also share a high degree of gene conservation (Gale and Devos 1998). Among these cereal crops, two *Tg*-related genes that control the ease of threshability have been reported. In maize, *tga1* (*teosinte glume architecture1*), which causes the stony fruitcase appearance in progenitor teosinte (Dorweiler et al. 1993; Wang et al. 2005) and in barley the naked caryopses gene *nud* that is responsible for hulled/hullless spikes (Taketa et al. 2008) have been isolated. The wheat tough glume gene, *Tg*, maps in a region (chromosome 2S) that is syntenic to maize chromosomes 2 and 7 (Ahn et al. 1993; Gale and Devos 1998) whereas the

maize tough glume gene, *tga1*, is located on chromosome 4 of maize (Dorweiler et al. 1993). Additionally, the maize *tga1* orthologue in wheat maps to the group-7 chromosomes of wheat (Wanlong Li personal communication). Similarly, the *nud* gene is mapped on chromosome 7H of barley, which is homoeologous to wheat group-7 chromosomes. Hence, *tga1* of maize and *nud* of barley are non-orthologous to the wheat group-2 chromosome threshability genes. Similar results have been reported for shattering genes in wheat where *Br1* does not have any orthologue in syntenic regions of barley, rice, maize or sorghum (Li and Gill 2006).

With the available evidence, it is conceivable that the wheat threshability genes (genetic loci on group-2 chromosomes) do not share an ancestral relationship with related genes in other cereals and they probably originated after the separation of the wheat lineage from the last common cereal ancestor. Additionally, because *sog* and *Tg*, the threshability genes in wheat, also are non-orthologous (present study), these genes might not have been derived from a common ancestral gene but arose by independent mutations in A- and D-genome diploid progenitors after their evolution from a common parent 2.5–4.5 million years ago (Huang et al. 2002). Another possibility could be that the *sog* and *Tg* are homologous genes, but occupy non-orthologous positions on the homoeologous chromosome arms. The putative mechanism for such a phenomenon has been described for explaining non-orthologous relations among different cereal genomes where ancient gene duplication in the common ancestor is followed by the loss of one gene copy in one species and the loss of the second copy in the other species (Ware and Stein 2003). One such example of a duplication/deletion event has been provided by the comparative analysis between genomes of the *Triticeae* species and those of rice, sorghum, and maize in the *Sh2/A1* region (Li and Gill 2002).

In addition to the major tough glume genes on group-2 chromosomes of wheat, some minor genes and modifiers also are involved in determining the threshability trait. The QTL affecting percent threashability have been identified on chromosome 6A and 6D (Simonetti et al. 1999; Jantasuriyarat et al. 2004), suggesting that loci other than those on group-2 chromosomes and chromosome 5A (*Q* gene) also may be involved in control of the threshability trait in wheat. On other hand, *Secale cereale* L., *Thinopyrum elongatum* (Host) D. R. Dewey and several *Aegilops* species carry the tough glume genes on the group-2 chromosomes as has been demonstrated by their chromosome-2 addition and substitution lines in wheat (Friebe et al. 1999; Cheng and Murata 2002; Dvorak 1980). The monosomic and disomic additions of chromosome VI of *Th. elongatum* (homoeologous to group-2 chromosomes of wheat) to *T. aestivum* resulted in plants with tenacious glumes (Dvorak and Knott 1974; Dvorak 1980). Hence, the threshability trait seems to be under the control of several major and minor genes and will involve an in-depth genetic analysis to elucidate the pathways relating to various threshability genes in wheat. The precise physical and genetic mapping of threshability genes and exploring their orthologous relationship is the first step towards isolating these genes and understanding their genetic interactions.

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