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ORIGINAL PAPER

Map-based analysis of genetic loci on chromosome 2D that affect glume tenacity and threshability, components of the free-threshing habit in common wheat (*Triticum aestivum* L.)

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Abstract During the domestication of bread wheat (*Triticum aestivum* L.), evolutionary modifications that took place in seed dispersal mechanisms enhanced its suitability for agricultural production. One of these modifications involved the evolution of the free-threshing or hulless characteristic. In this study, we studied quantitative trait loci (QTL) affecting components of the free-threshing habit (threshability and glume tenacity) on chromosome 2D in a recombinant inbred line (RIL) population developed by the International Triticeae Mapping Initiative (ITMI) as well as the *tenacious glumes 1* (*Tg1*) gene in F_2 progeny (CS/CS2D F_2) of a cross between Chinese Spring and the 2D2 substitution line [Chinese Spring (*Ae. tauschii* 2D)]. In the ITMI population, two QTL affected threshability (*QFt.orst-2D.1* and *QFt.orst-2D.2*) and their location coincided with QTL affecting glume tenacity (*QGt.orst-2D.1* and *QGt.orst-2D.2*). In the CS/CS2D F_2 population, the location of QTL that affected glume tenacity (*QGt.orst-2D.1*), the size of a glume base scar after detachment (*QGba.orst-2D*), and *Tg1* (12-cM interval between *Xwmc112* and *Xbarc168*) also coincided. Map comparisons suggest that *QFt-orst-2D.1*, *QGt.orst-2D.1*, and *QGba.orst-2D* correspond to *Tg1* whereas *QFt.orst-2D.2* and *QGt.orst-2D.2* appear to represent separate loci. The observation of coincident QTL for threshability and glume tenacity suggests that threshability is a function of glume adherence. In addition, the observation of the coincident locations of *Tg1* and QTL for the force required to detach a glume and the size of a glume base scar after detachment suggests that *Tg1*'s effect on both glume tenacity and threshability resides on its ability to alter the level of physical attachment of glumes to the rachilla of a spikelet.

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Introduction

Hexaploid wheat (*Triticum aestivum* L., $2n = 42$, AABBDD) arose ~8,000 years ago from a spontaneous hybridization event between tetraploid wheat (*T. turgidum* L. $2n = 28$, AABB) and the weedy diploid goatgrass *Aegilops tauschii* Cosson ($2n = 14$, DD) (Huang et al. 2002). During the domestication of wheat, changes in spike morphology and development enhanced its suitability for agricultural practices. These changes included modifications of rachis fragility, spikelet disarticulation, awn development, pubescence, grain size, glume tenacity, and threshability. Of these modifications, one that has been investigated because of its evolutionary significance and its importance in the practical utilization of the wheat grain, is the free-threshing habit. Genotypes with non-tenacious glumes that require limited mechanical action during the de-hulling process are considered free-threshing (hulless) whereas genotypes with tenacious glumes that are not readily detached represent non-free-threshing (hulled) wheats.

Hexaploid wheat has been historically subdivided into several subspecies based on rachis fragility and the free-threshing trait (Kimber and Sears 1983). Free-threshing forms with a tough rachis include *T. aestivum* ssp. *aestivum*, ssp. *sphaerococcum*, and ssp. *compactum* whereas ssp. *spelta*, ssp. *macha*, and ssp. *vavilovii* have fragile rachises and are hulled and non-free threshing (Leighty and Boshnakian 1921; Sears 1946; Unrau 1950; Kabarity 1966; Feldman 2001). Mac Key (1966) proposed that rachis brittleness and glume tenacity are the product of the interplay between two genetic systems. One component is polygenic and the other is represented by a modifier of the polygenic system. This modifier is *Q*, an *APETALA2*-like transcription factor (Faris et al. 2003; Simons et al. 2006), on chromosome 5A (Mac Key 1954; Sears 1954; Muramatsu 1963, 1986; Kuckuck 1964; McFadden and Sears 1946) and the polygenic system involves genes on homoeologous group 3 chromosomes that primarily control rachis brittleness (Watanabe and Ikebata 2000; Watanabe et al. 2005; Nalam et al. 2006), genes on homoeologous group 2 chromosomes that affect glume adherence or tenacity (Sears 1968; Kerber and Rowland 1974; Chen et al. 1999; Simonetti et al. 1999; Taenzler et al. 2002; Jantasuriyarat et al. 2004), and QTL on other chromosomes (Simonetti et al. 1999: Jantasuriyarat et al. 2004). This model where *Q*'s effects on glume tenacity and rachis fragility is not only pleiotropic but depends on interactions with loci that control these characteristics directly is still well accepted (Luo et al. 2000).

Kerber and Dyck (1969) originally reported the existence of a factor in the D genome that affected threshability and glume tenacity in hexaploid wheat. This was later confirmed by Kerber and Rowland (1974) whose studies showed that the non-free-threshing trait of synthetic hexaploids, irrespective of whether their tetraploid parent carried *Q* or *q*, was due to the *Tg1* (*tenacious glumes 1*) gene on the short arm of chromosome 2D. Because non-free-threshing hexaploids were produced when free-threshing tetraploids were crossed with *Ae. tauschii*, the authors concluded that the dominant *Tg1* allele derived from *Ae. tauschii* interfered with or avoided the effect of *Q*.

When the free-threshing habit was studied in a recombinant inbred line population developed from a cross between a spring wheat, Opata-85, and a synthetic hexaploid wheat, W-7984, QTL on chromosomes 2A, 2B, 2D, 5A, 6A, 6D and 7B were found to affect the free-threshing character (Jantasuriyarat et al. 2004). In the study by Jantasuriyarat et al. (2004), the QTL on the short arm of chromosomes 2D (corresponding to *Tg1*) and the long arm of chromosome 5A (corresponding to *Q*) had the largest effects on the trait. Overall, the free-threshing habit was predominantly affected by *Tg1* and to a lesser extent by *Q*. Investigations with hexaploid wheat aneuploids (Sears 1954), tetraploid wheat (Simonetti et al. 1999), and *T. monococcum* (Taenzler et al. 2002) also suggest that genes on group 2 chromosomes primarily influence the free-threshing habit by their direct effects on glume tenacity. Thus, the free-threshing phenotype of hexaploid wheat is largely the result of interactions between *tenacious glumes* loci on group 2 chromosomes and *Q* on chromosome 5A.

Q has been the subject of intense research leading to its precise localization and isolation (Faris et al. 2003; Simons et al. 2006). On the other hand, there has been a scarcity of studies involving genes that affect glume tenacity like *Tg1*. Thus, the aim of our research is to use map-based methods to study *Tg1* as an initial step towards its eventual isolation and characterization. Previously, we used quantitative trait mapping to regionally localize *Tg1* on chromosome 2D (Jantasuriyarat et al. 2004). In this study, we placed *Tg1* in a microsatellite-based linkage map of chromosome 2D, determined its chromosome bin location, assessed its relationship to a QTL described by Jantasuriyarat et al. (2004) and other genes in group 2 chromosomes, and performed a preliminary assessment of its phenotypic effect.

Materials and methods

Plant material

The localization of factors affecting threshability and glume tenacity was achieved using two mapping populations. The first mapping population consisted of recombinant inbred lines (RIL) developed by a collaborative mapping project of the International Triticeae Mapping Initiative (ITMI) (Nelson et al. 1995a, b, c; Marino et al. 1996; Van Deynze et al. 1995). Seed of the ITMI RIL population and the two parents were provided by Dr. C. Qualset (University of California, Davis). Opata-85, W-7984, and 110 ITMI RILs were previously grown in three sites (University East Farm, West Greenhouse, and Hyslop Farm Field Laboratory, Corvallis, ON) for two years (1999 and 2000) to study traits associated with the free-threshing habit (Jantasuriyarat et al. 2004). For this study, the ITMI population and its parents were again planted in un-replicated 5 m row plots at Hyslop Farm Field Laboratory in 2001.

The second mapping population (CS/CS2D) used in this study consisted of F_2 and $F_{2:3}$ progeny from a cross between Chinese Spring and the 2D2 substitution line. The 2D2 line is a substitution line where chromosome 2D from Chinese Spring was substituted by chromosome 2D from *Ae. tauschii* [Chinese Spring (*Ae. tauschii* 2D)]. Seed for the 2D2 substitution line was provided by Dr. Jan Dvorak (University of California, Davis). Chinese Spring, the 2D2 substitution line, and 93 F_2 individuals were planted at West Greenhouse, Oregon State University, in 2003. Chinese Spring, the 2D2 substitution line, and 93 $F_{2:3}$ families were planted

in un-replicated 5-m row plots at Hyslop Farm Field Laboratory in 2005.

Homoeologous group 2 cytogenetic stocks were used to assign markers to chromosomes and chromosome segments. These stocks included Chinese Spring nullisomic–tetrasomic (N2AT2B, N2BT2D, and N2DT2A), ditelosomic (Dt2DS and Dt2DL), and four deletion lines (2DS1, 2DS5, 2DL3 and 2DL9). The group 2 cytogenetic stocks were provided by Dr. B.S. Gill (Kansas State University, Manhattan). Karyotypes detailing chromosome deletion breakpoints can be found in GrainGenes' wEST database (http://wheat.pw.usda.gov/west/binmaps/wheat2_rice.html).

DNA isolation, marker analysis, and map construction

About 30–50 mg of leaf tissue from lines from the ITMI and CS/CS2D populations and the parental lines were used for DNA extraction. DNA was extracted as described by Riera-Lizarazu et al. (2000). Microsatellite markers previously placed on chromosome 2D by various research groups were used in this study (Röder et al. 1998; Pestsova et al. 2000; Somers et al. 2004). In addition, PCR-based markers for three restriction fragment length polymorphism (RFLP) probes were developed. These sequence tagged site (STS) markers were based on EST accessions AJ440662 (PSR928), BE438756 (BCD175), and BE438952 (BCD1970) (http://www.ncbi.nlm.nih.gov/). The locus *Xorw2* (primers 5′-CGTCGTTTAAACAAGACATC-3′ and 5′-CATGTGGCAGTCATCGTACA-3′) was based on AJ440662, *Xorw3* (primers 5′-TCGACCTCCAGGTCAAGGAG-3′ and 5′-GTCTCAGGTATCACCCGCGC-3′) was based on BE438756, and *Xorw4* (primers 5′-TTGCCCCATCTGTAAAAAGG-3′ and 5′-TTGGGAGGAGGAAAAGAGGT-3′) was based on BE438952.

Seven microsatellite primer sets (gwm455, gwm296, gwm261, gdm107, gwm484, gwm102, and gwm515) that had been previously used to map loci on chromosome 2DS were used to genotype the parents and the 110 ITMI RILs. This was necessary since only a subpopulation of 60–70 individuals had been genotyped previously with the markers of interest (Röder et al. 1998; Pestsova et al. 2000). Publicly available marker data for at least 100 ITMI RILs on chromosome 2D was obtained from GrainGenes 2.0 (http://wheat.pw.usda.gov/cgi-bin/graingenes/browse.cgi). Twenty-three molecular markers were used to construct a linkage map of chromosome 2D using the CS/CS2D F_2 population. Polymerase chain reaction (PCR) amplification of microsatellite and STS loci and agarose gel-based separation of PCR products was performed as described by Nalam et al. (2006). For molecular markers that did not have easily discernible polymorphisms on agarose gels, fluorescent detection of PCR amplification products was achieved using one primer labeled with either 5-carboxyfluroscein (5-FAM) or 4,7,2′,4′,5′,7′-hexafloro-6-carboxyrhodamin (HEX). Amplification products were electrophoresed and detected in an ABI Prism™ 3100 DNA sequencer at the Core Labs, Center for Genome Research and Biocomputing, Oregon State University.

Linkage maps for chromosome 2D were constructed using Mapmaker/Exp 3.0 (Lander et al. 1987) and JoinMap 3.0 (Van Ooijen and Voorrips 2001). Recombination fractions were converted into map distances (cM) using the Kosambi mapping function. Chromosome maps were drawn with MapChart 2.1 (Voorrips 2002).

Phenotypic assessment

The ITMI population and their parental lines (W-7984 and Opata) were evaluated for the free-threshing habit by measuring percent threshability and glume tenacity. Percent threshability was measured by processing eight randomly chosen mature spikes of each line through a gasoline-powered thresher and collecting both threshed and unthreshed seeds. Threshability was then calculated as the percentage of completely threshed seeds out of all seeds harvested. To measure glume tenacity (or adherence), a LKG-1 Hunter force gauge (AMETEK, Inc., Hatfield, PA, USA) was used to measure the force (N, Newton) required to detach a glume at its base. Glume tenacity was measured in four randomly selected spikelets of four spikes per line. Chinese Spring and the 2D2 substitution line were similarly evaluated for percent threshability and glume tenacity. The CS/CS2D F_2 population and their $F_{2:3}$ families were only evaluated from glume tenacity. In the case of $F_{2:3}$ families, four randomly selected spikelets of ten different spikes per family were evaluated. The ITMI RILs and the CS/CS2D F_2 individuals were also evaluated qualitatively for glaucousness (waxiness/glossiness) of stems and leaves. These evaluations were used to map *Iw2*, a dominant inhibitor of glaucousness, segregating in both populations.

The glume bases of Chinese Spring, the 2D2 substitution line, and CS/CS2D F_2 population were also studied (Fig. 1). Namely, we measured the size (area in mm^2) of the scar at the base of a glume after physical detachment. We evaluated two pairs of detached glumes from one to three centrally-located spikelets per line. All detached glumes were placed in florist foam and visualized using a Leica MZ6 stereo dissecting microscope (Leica Microsystems GmbH, Wetzlar, Germany) equipped with a Photometrics CoolSNAP digital camera (Roper Scientific, Inc., Trenton, NJ, USA). Digital images of glume bases were captured using RSImage 1.09 (Roper Scientific, Inc.) and ImageJ (Abramoff et al. 2004) was used to measure the size (area in mm^2) of detachment scars. Analysis of variance, mean

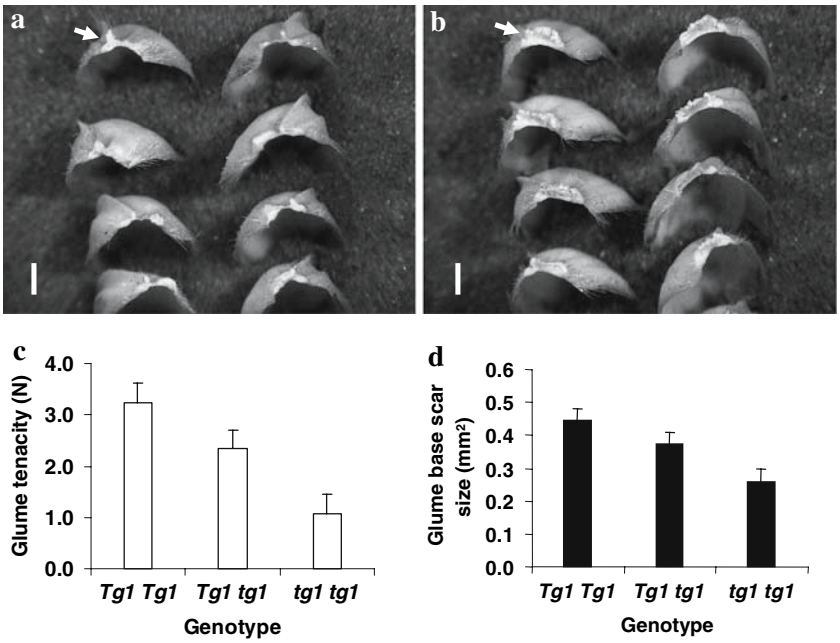

Fig. 1 Glume base detachment scars (*arrows*) from Chinese Spring (**a**), the 2D2 substitution line (**b**) and the association of *Tg1* genotype with glume tenacity (**c**) and detachment scar size (**d**) in the CS/CS2D F_2 population. In **a** and **b**, four pairs of representative glumes are shown. CS had an average detachment scar of 0.221 mm^2 whereas 2D2 had an average scar of 0.582 mm^2. Bar scale in **a** and **b** represents 1 mm. **c** Column graph showing the association of *Tg1* genotype with the average force (N) required to detach a glume (glume tenacity) in the CS/CS2D F_2 population. Glumes from *Tg1Tg1* individuals required an average of 4.241 N of force for detachment whereas individuals with the *Tg1tg1* and *tg1tg1* genotypes required 2.333 and 1.076 N, respectively. *Vertical bars* in **c** represent Fisher's least significant difference (LSD) of 0.368 N ($P < 0.0001$). **d** Column graph showing the association of *Tg1* genotype with the average detachment scar size/area (mm^2) in the CS/CS2D F_2 population. After glume detachment, *Tg1Tg1* individuals had an average glume base scar size of 0.445 mm^2 whereas individuals with the *Tg1tg1* and *tg1tg1* genotypes had average scar sizes of 0.372 and 0.259 mm^2, respectively. *Vertical bars* in **d** represent a LSD of 0.037 mm^2 ($P < 0.0001$)

comparisons, and linear regression were performed using SAS 9.1 (SAS Institute 2003).

QTL analysis

Phenotypic data and linkage maps were used for quantitative trait locus (QTL) analysis using QTL Cartographer 2.5 (Basten et al. 1999). For analyses involving the ITMI population, a whole genome map with ~500 loci described by Jantasuriyarat et al. (2004) was used in conjunction with the map of chromosome 2D that was constructed for this study. Least square trait means from each environment (except for un-replicated experiments) and means across environments were analyzed. QTL were mapped using composite interval mapping (CIM) (Zeng 1993, 1994) with a maximum of five co-factors selected using the forward-selection backward-elimination stepwise regression procedure. For QTL analyses involving the CS/CS2D population, glume tenacity and detached glume base scar size (area) measurements and a map of chromosome 2D were used. In all cases, a 5-cM scan window was used for all analyses and the likelihood ratio (LR) statistic was computed every 1 cM. Based on previous work (Jantasuriyarat et al. 2004), a LOD score (Z) of 3.0 or likelihood ratio (LR) of 14 (Basten et al. 1994, 1999) was deemed an adequate threshold for QTL identification.

Results

Phenotypic data

The mean trait values for percent threshability and glume tenacity for the ITMI population are presented in Table 1. W-7984 is a synthetic wheat with highly tenacious glumes that required a minimum of ~11 N of force to either detach or break a glume from a spikelet. Consequently, W-7984 was not easily threshed (33.6% threshability). Opata-85, on the other hand, required only 2.4 N of force to achieve glume detachment and was found to be very threshable (97.9% threshability). Glume tenacity measured as the force (N) necessary to separate glumes from their spike rachises ranged from 0.75 to 7.53 N in the ITMI population. Percent threshability for the ITMI RILs ranged from 11.76 to 98.76%.

Chinese Spring was easily threshed (94.5%) whereas the 2D2 substitution line showed less threshability (66.8%) (Table 1). This was consistent with the observation that the

Table 1 Mean, range (minimum and maximum), and SD of free-threshing habit-associated trait values for W-7984, Opata-85 and 110 ITMI RILs as well as Chinese Spring, the 2D2 substitution line, and 93 F_2 progeny (CS/CS2D F_2s)

Environment	Lines	Threshability[a] (%)	Glume tenacity[b] (N)	Glume scar size[c] (mm^2)
Hyslop Farm, 2001	W-7984	33.6b	10.8a[d]	ND[e]
	Opata-85	97.9a	2.36b	ND
	ITMI RILs			
	Mean	65.7	3.39	ND
	Range	11.8–98.8	0.75–7.53	ND
	SD	18.7	1.51	ND
West greenhouse, 2003	2D2	66.8b	5.93a	0.58a
	Chinese Spring	94.5a	1.49b	0.22b
	CS/CS2D F_2s			
	Mean	ND[e]	2.05	0.35
	Range	ND	0.50– 4.50	0.16 – 0.55
	SD	ND	0.96	0.09

Mean trait values for W-7984 and Opata 85 or Chinese Spring and the 2D2 substitution line [Chinese Spring (*Ae. tauschii* 2D)] followed by the same letter are not significantly different ($P < 0.001$)

[a] Threshability is expressed as the percentage of threshed seeds (number of threshed seeds/total number of seeds × 100)

[b] Glume tenacity is expressed as the force (N, Newton) necessary to detach a glume at its base in a spikelet

[c] Detached glume base scar size is expressed as an area in mm^2

[d] W-7984 has extremely tenacious glumes. Thus, the value presented represents an average minimum force (N) required to either detach or break a glume

[e] *ND* Not determined

2D2 substitution line had more tenacious glumes (5.9 N) than Chinese Spring (1.5 N). Glume tenacity values for the CS/CS2D F_2 population ranged from 0.50 to 4.50 N. With respect to Chinese Spring and the 2D2 line, we did not observe obvious differences in the overall shape or texture of their glumes. On the other hand, there were marked differences on the level of adherence of a given glume to the base of a spikelet when we studied the size of detached glume scars (Fig. 1a, b). The 2D2 substitution line had significantly ($P < 0.001$) larger glume base scars (0.582 mm^2) than Chinese Spring (0.221 mm^2). Glume base scar size for the CS/CS2D F_2 population ranged from 0.162 to 0.546 mm^2 (Table 1). Glume tenacity and glume scar size were positively correlated ($R^2 = 0.52$, $P < 0.0001$) in the CS/CS2D F_2 population.

QTL analysis

Two QTL that affected percent threshability were identified on chromosome 2D (Table 2). The QTL were designated *QFt.orst-2D.1* and *QFt.orst-2D.2* (Table 2). *QFt.orst-2D.1* explained from 22 to 61% of the phenotypic variance. In the analysis over three environments, *QFt.orst-2D.1* explained 42% of the phenotypic variance. *QFt.orst-2D.2* explained 19–51% of the phenotypic variance. A combined analysis across environments showed that *QFt.orst-2D.2* explained 38% of the phenotypic variance. The locus most closely associated with *QFt.orst-2D.1* was *Xgwm261* and with *QFt.orst-2D.2* was *Xgwm455*.

Two QTL that affected glume tenacity, designated *QGt.orst-2D.1* and *QGt.orst-2D.2*, were also detected on chromosome 2D (Table 2). *QGt.orst-2D.1* explained 18–25% of the phenotypic variance in the environments tested. In the analysis across environments, *QGt.orst-2D.1* explained 46% of the phenotypic variance. *QGt.orst-2D.2* explained 13–31% of the phenotypic variance. This QTL explained 31% of the phenotypic variance across environments. The loci most closely associated with *QGt.orst-2D.1* and *QGt.orst-2D.2* were *Xgwm261* and *Xgwm455*, respectively. The peaks of the two QTL were separated by a distance of ~12 cM. W-7984 contributed the higher value allele for QTL that affected glume tenacity while percent threshability increased with the Opata-85 alleles at these QTL.

QTL analysis, with glume tenacity data from the CS/CS2D F_2 population, was also carried out (Table 3). A single major QTL that explained 67% of the phenotypic variance was placed in an interval flanked by *Xgwm261* and *Xbarc168*. Because the location of this QTL coincided with *QGt.orst-2D.1* and *QFt.orst-2D.1* (Fig. 2a, b), we have also named this QTL *QGt.orst-2D.1*. A QTL that affected the size of glume base scars after detachment (*QGba.orst-2D*) was also detected on chromosome 2D. *QGba.orst-2D*, flanked by *Xgwm261 and Xbarc168*, explained 55% of the

Table 2 Free-threshing habit-associated quantitative trait loci (QTL) for the ITMI population

Trait	QTL symbol	Environment	QTL peak position, cM (nearest locus)	2-LOD support limit, cM range	LR [a] statistic	R^2 [b]	Additive effect [c]
Percent threshability	*QFt.orst-2D.1*	Hyslop Farm 1999	43.2 (*Xgwm261*)	40.1– 47.2 (*Xgwm296–Xgdm107*)	86.3	0.48	−13.7
		East Farm 2000	43.2 (*Xgwm261*)	40.1–45.2 (*Xgwm296–Xgdm107*)	112.9	0.61	−14.7
		Hyslop Farm 2001	43.2 (*Xwmc25*)	34.1–49.2 (*Xgwm455–X gdm107*)	32.8	0.22	−9.14
		Combined	41.2 (*Xgwm261*)	38.1–45.2 (*Xgwm261–X gdm107*)	87.6	0.42	−11.2
Percent threshability	*QFt.orst-2D.2*	Hyslop Farm 1999	31.7 (*Xgwm455*)	27.7–34.1 (*Xbcd102–Xgwm455*)	51.3	0.33	−11.3
		East Farm 2000	31.7 (*Xgwm455*)	27.7–34.1 (*Xbcd102–Xgwm455*)	71.1	0.51	−13.5
		Hyslop Farm 2001	29.7 (*Xbcd102*)	25.7–34.1 (*Xbcd102–Xgwm455*)	27.7	0.19	−8.28
		Combined	31.7 (*Xgwm455*)	27.7–34.1 (*Xbcd102–Xgwm455*)	64.8	0.38	−10.56
Glume tenacity	*QGt.orst-2D.1*	East Farm 2000	41.2 (*Xgwm261*)	38.1– 47.2 (*Xgwm261–Xgdm107*)	30.7	0.18	0.44
		Greenhouse 2000	41.2 (*Xgwm296*)	38.1–45.2 (*Xgwm261–Xgdm107*)	42.0	0.25	0.37
		Hyslop Farm 2001	41.2 (*Xgwm261*)	40.2–47.2 (*Xgwm296–Xgdm107*)	43.3	0.18	0.78
		Combined	43.2 (*Xgwm261*)	41.2–47.2 (*Xgwm261–Xgdm107*)	81.7	0.46	0.64
Glume tenacity	*QGt.orst-2D.2*	East Farm 2000	27.7 (*Xbcd102*)	25.7–34.1 (*Xbcd102–Xgwm455*)	17.6	0.13	0.36
		Greenhouse 2000	29.7 (*X bcd102*)	25.7–34.1 (*Xbcd102 –Xgwm455*)	24.9	0.18	0.31
		Hyslop Farm 2001	33.7 (*Xgwm455*)	27.7–33.7 (*X bcd102–X gwm455*)	52.1	0.31	0.85
		Combined	31.7 (*Xgwm455*)	27.7–34.1 (*Xbcd102–X gwm261*)	47.2	0.31	0.51

Location, significance, effect, and proportion of phenotypic variation explained based on composite interval mapping (CIM) analysis

[a] LR is the likelihood ratio test statistic 2 ln (L_0/L_1), where (L_0/L_1) is the ratio of likelihoods between the hypothesis that there is no QTL in the tested interval (L_0) and the hypothesis that there is a QTL in the tested interval (L_1) (Basten et al. 1994, 1999). The relationship between LR and LOD score (Z) is LR = 4.6 × Z

[b] R^2 is the proportion of the phenotypic variance explained by the QTL after accounting for co-factors

[c] Additive effects indicates an additive main effect of the parent contributing the higher value allele: in the ITMI population, positive values indicate that higher value alleles are from W-7984 and the negative values indicate that higher value alleles are from Opata-85

Table 3 Free-threshing habit-associated quantitative trait loci (QTL) for the Chinese Spring × 2D2 F_2 population grown in the greenhouse (2003)

Trait	QTL symbol	QTL peak position, cM (nearest locus)	2-LOD support limit, cM range	LR[a] statistic	Effects			
					a[b]	d[c]	d/a[d]	R^2[e]
Glume tenacity	*QGt.orst-2D.1*	24.8 (*Xwmc112*)	21.3–28.9 (*Xgwm261–Xbarc168*)	86.62	−1.18	0.03	−0.03	0.67
Glume base scar size (area)	*QGba.orst-2D*	27.8 (*Xwmc112*)	21.3–32.8 (*Xgwm261–Xbarc168*)	63.68	−0.095	0.025	−0.26	0.55

Genetic distances presented in the table were calculated before the integration of *Tg1* into the linkage map for chromosome 2D. Location, significance, effect, and proportion of phenotypic variation explained based on interval mapping (IM) analysis

[a] LR is the Likelihood ratio test statistic 2 ln (L_0/L_1), where (L_0/L_1) is the ratio of likelihoods between the hypothesis that there is no QTL in the tested interval (L_0) and the hypothesis that there is a QTL in the tested interval (L_1) (Basten et al. 1994, 1999). The relationship between LR and LOD score (Z) is LR = 4.6 × Z

[b] Additive effects indicate an additive main effect of the parent contributing the higher value allele

[c] Dominance effect indicates a dominance main effect of the parent contributing the higher value allele

[d] d/a: degree of dominance

[e] R^2 is the proportion of the phenotypic variance explained by the QTL after accounting for co-factors

phenotypic variance. The location of *QGba.orst-2D* coincided with the location of *QGt.orst-2D.1*. QTL analysis showed that the mode of inheritance for glume tenacity and glume base scar size was additive with some dominance. The 2D2 line contributed the higher value alleles for all QTL (Table 3). Markers associated with these QTL were all placed in the deletion bin 2DS5-0.47–1.00 (Fig. 2c).

Genotyping and localization of Tg1

QTL analysis suggested that a major factor with mostly additive gene action was responsible for differences in glume tenacity and detached glume base scar size in the CS/CS2D population. In order to genetically localize this factor that represents *Tg1*, the glume tenacity of the CS/

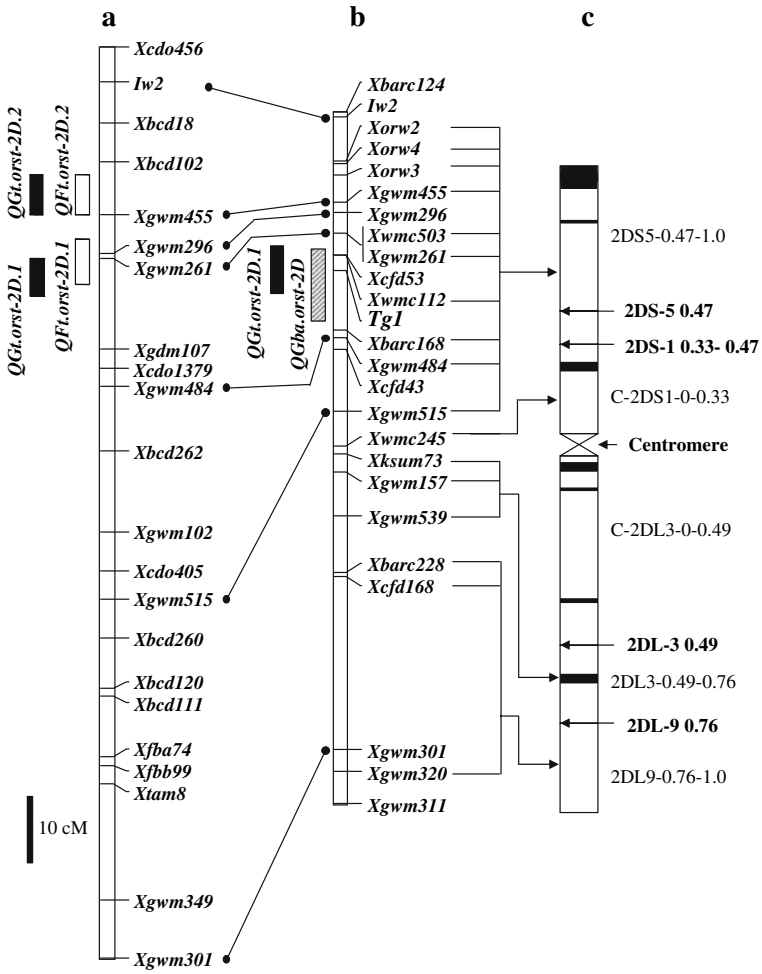

Fig. 2 Genetic linkage maps of chromosomes 2D showing the location of QTL for free-threshing habit associated traits and the *tenacious glumes 1* locus (*Tg1*) as well as their relationship to chromosome deletion bins. **a** Genetic linkage map of chromosome 2D and QTL for free-threshing habit associated traits using the ITMI RIL population. *Open bars* indicate the 2-LOD interval for the QTL that affected percent threshability (*QFt.orst-2D.1* and *QFt.orst-2D.2*). *Solid bars* indicate the 2-LOD interval for QTL that affected glume tenacity (*QGt.orst-2D.1* and *QGt.orst-2D.2*). **b** Genetic linkage map of chromosome 2D using the CS/CS2D F_2 mapping population showing the location of a QTL that affected glume tenacity and glume base scar size (area) as well as the location of the *tenacious glumes 1* (*Tg1*) gene. A *solid bar* indicates the 2-LOD interval for a QTL that affected glume tenacity (*QGt.orst-2D.1*) and a thatched bar indicates the 2-LOD interval for a QTL that affected the size (area) of detached glume base scars (*QGba.orst-2D*). STS loci *Xorw2, Xorw3*, and *Xorw4* may correspond to the RFLP loci *Xpsr928, Xbcd175*, and *Xbcd1970*, respectively. The lines between linkage maps **a** and **b** connect common markers. **c** Deletion bin map of chromosome 2D. *Arrows* indicate deletion breakpoints. *Lines* and *arrows* show the deletion bin location in c for loci in map **b**. *Dark bands* on the chromosome indicate the location of C-bands (Gill et al. 1991)

CS2D F_2 population and their $F_{2:3}$ derivatives were evaluated. The distribution of glume tenacity values of the F_2 population grown in the greenhouse (2003) was continuous and is consistent with earlier descriptions of *Tg1* as a semi-dominant gene (Kerber and Rowland 1974). Thus, classification of all individuals with respect to their genotype at the *Tg1* locus in this generation was not possible. Glume tenacity assessments of $F_{2:3}$ progeny planted at Hyslop farm in 2005, did allow the classification of F_2 plants from which they were derived. If the glumes of a $F_{2:3}$ family were uniformly tenacious the genotype of the F_2 progenitor was deduced to be homozygous for the dominant *Tg1* allele (*Tg1Tg1*) whereas the F_2 progenitor of a $F_{2:3}$ family with uniformly non-tenacious glumes was classified as being homozygous for the recessive *tg1* allele (*tg1tg1*). Finally, the F_2 progenitor of a $F_{2:3}$ family that segregated for glume tenacity was classified as a heterozygote (*Tg1tg1*). This progeny test allowed the localization of *Tg1* to a 12-cM interval between the markers *Xwmc112* and *Xbarc168* (Fig. 2b).

The relationships between genotype at the *Tg1* locus and both glume tenacity and glume base scar size are shown in Fig. 1c and d, respectively. All genotypic classes (*Tg1Tg1*, *Tg1tg1*, and *tg1tg1*) required significantly ($P < 0.0001$)

different levels of force to effect glume detachment. Individuals with the *Tg1Tg1* genotype required the greatest force (3.24 N) for glume detachment followed by individuals with the *Tg1tg1* (2.33 N) and *tg1tg1* (1.08 N) genotypes (Fisher's least significant difference, LSD, was 0.37 N). Similarly, the size of glume base scars was greatest ($P < 0.0001$) for individuals with the *Tg1Tg1* genotype (0.45 mm^2) followed by those from individuals with the *Tg1tg1* (0.37 mm^2) and *tg1tg1* (0.26 mm^2) genotypes (LSD 0.04 mm^2).

Discussion

In this study, we used two mapping populations and quantitative trait mapping to localize factors affecting components of the free-threshing character on chromosome 2D of common wheat (*T. aestivum*). In analyses using the ITMI RIL population, two QTL that affected both glume adherence and percent threshability were identified. This is consistent with a previous study (Jantasuriyarat et al. 2004) showing that threshability and glume tenacity were negatively correlated and suggesting that threshability was a function of glume adherence. If glume adherence is high, threshability is low and vice versa. The location of *QGt.orst-2D.1* and *QFt.orst-2D.1*, in the ITMI population map, and *Tg1*, in the CS/CS(2D) map, suggest that these QTL represent the action of *Tg1* (Fig. 2). In a previous study involving the ITMI population, *Tg1* had been regionally localized on chromosome 2D but the presence of a second set of QTL (*QGt.orst-2D.2* and *QFt.orst-2D.2*) was overlooked (Jantasuriyarat et al. 2004). It is likely that our inability to detect these coincident QTL in an earlier study was due to missing data, a more sparse coverage of the chromosomal regions in question, and the reported difficulty of separating linked QTL (Haley and Knott 1992; Whittaker et al. 1996). Nonetheless, our results are in line with a report of an additional gene/factor on chromosome 2D, besides *Tg1*, that also affects glume adherence in wheat (Ternowskaya and Zhirov 1993). Whether or not this factor corresponds to the QTL identified in our study needs further study.

The presence of factors that affect glume architecture on homoeologous group 2 chromosomes dates back to Sears' (1954) observations that plants that were nullisomic for chromosomes 2A, 2B, or 2D had papery glumes while plants that were tetrasomic for these chromosomes had glumes that were stiffer than normal disomic plants. Other genetic studies have also shown that factors on homoeologous group 2 chromosomes directly affect hulledness and the free-threshing trait by controlling glume adherence or tenacity (Sears 1968; Kerber and Rowland 1974; Simonetti et al. 1999; Chen et al. 1999; Taenzler et al. 2002; Jantasuriyarat et al. 2004). However, the relationship between these loci has not been studied. Evidence for a possible orthologue of *Tg1* was presented by Taenzler et al. (2002) who mapped a *soft glume* (*Sog*, Dorofeev and Navruzbekov 1982) locus on chromosome $2A^m$ of *T. monococcum*. However, recent genetic and chromosome bin mapping work suggest that the *Sog* gene is linked to the centromere (Sood et al. 2007) whereas *Tg1* occupies a more distal segment in the short arm of chromosome 2D. Thus, *Tg1* and *Sog* do not appear to be orthologous genes. Another difference between *Sog* and *Tg1* is that the dominant *Sog* allele increases spike compactness significantly whereas *Tg1* does not have that effect (Jantasuriyarat et al. 2004). Simonetti et al. (1999) found a QTL on chromosome 2B that predominantly affected threshability in a RIL population derived from a cross between a *T. turgidum* ssp. *durum* and *T. turgidum* ssp. *dicoccoides*. This QTL was attributed to a locus named *tenacious glumes 2* (*Tg2*) that was interpreted to be a homoeologue of *Tg1*. Due to the sparse marker coverage of the pertinent region on chromosome 2B, we could not determine whether *Tg2* was orthologous to *Tg1* or *QGt.orst-2D.2*. Thus, more precise mapping of *Tg2* is needed to clarify their relationship.

Tg1 was localized to an interval flanked by *Xwmc112* and *Xbarc168*. This chromosomal interval is near the genetic location of two well-characterized genes that affect plant development as well as adaptation and agronomic performance. These are *Rht8*, a gene that affects plant height, and *Ppd-D1*, a gene that affects photoperiod response (Korzun et al. 1998). A barley homoeologue of *Ppd-D1* has been isolated recently (Turner et al. 2005) but the identity of *Rht8* is still unknown. Thus, the *Tg1* region is particularly interesting because it harbors major genes involved in wheat domestication, adaptation, and improvement. With current map-based methods and the availability of various genomic resources in wheat, the isolation of genes in this region is now possible. In order to gauge the feasibility of using map-based methods to this end, we mapped the pertinent markers using chromosome 2D Chinese Spring deletion stocks. Ten markers associated with the *Tg1* region were placed in deletion bin 2DS5-0.47–1.0 that spans the terminal 53% of the short arm of chromosome 2D (Fig. 2c). Erayman et al. (2004) showed that the gene-containing fraction (29%) of the wheat genome was organized in 18 major and 30 minor gene-rich regions (GRRs). The location of *Tg1* with respect to consensus GRRs could not be unambiguously determined because the RFLP loci, *Xbcd102* and *Xcdo1379*, flanking *Tg1* have been placed in GRRs 2S0.9 and 2S0.8, respectively. The GRR 2S0.9 spans a physical segment of 39 Mb with a recombination frequency of 1.3 Mb/cM whereas the GRR 2S0.8 represents a physical segment of ~7 Mb with a recombination frequency of 215 Kb/cM (Erayman et al. 2004). Regardless of which GRR harbors *Tg1*, cloning a

gene in these areas of the chromosome using map-based methods should be feasible.

Synthetic hexaploids derived from hybridizations between tetraploid durum wheat (*T. turgidum*) and *Ae. tauschii* are non-free-threshing despite being homozygous for the dominant *Q* allele (Kerber and Dyck 1969; Kerber and Rowland 1974). In this study, W-7984 (a synthetic hexaploid) exhibited extremely tenacious glumes requiring at least 11 N of force to effect glume detachment or breakage. Consequently, the threshability of this genotype was quite low (34%) compared to the common wheat varieties Opata 85 (98%) and Chinese Spring (95%). The 2D2 substitution line also exhibited greater glume tenacity (5.9 N) compared to the common wheats (Opata 85 and Chinese Spring) but its glumes were less tenacious than W-7984 (Table 1). Thus, the 2D2 substitution line had threshability values that were lower than common wheats but higher than W-7984. In the case of W-7984, the free-threshing trait results from the action and interaction of *Tg1*, *Q*, and various other genetic loci (Jantasuriyarat et al. 2004). On the other hand, our analysis suggests that differences between Chinese Spring and the 2D2 substitution line with respect to glume tenacity and threshability are due to the action of one factor, *Tg1*, on chromosome 2D because they are nearly identical for the rest of the genome.

The glumes of the 2D2 substitution line (*Tg1Tg1*) and Chinese Spring (*tg1tg1*) were indistinguishable with respect to overall shape and appearance. On the other hand, when we looked at glume bases we found that the 2D2 substitution line had significantly larger detachment scars compared to Chinese Spring (Fig. 1a, 1b; Table 1) showing that its glumes were more firmly attached than those of Chinese Spring. When we studied the CS/CS2D population, we found that QTL for the force required to detach a glume (*QGt.orst-2D.1*), glume base scar size (*QGba.orst-2D*), and *Tg1* had coincident locations (Fig. 2b; Table 3). In addition, our analysis showed an association between genotype at the *Tg1* locus and both glume tenacity and glume base scar size (Fig. 1c, d). Individuals with the *Tg1Tg1* genotyped required the greatest force to effect glume detachment (3.241 N) and had the largest glume base scars after detachment (0.445 mm^2) followed by individuals with the *Tg1tg1* (2.333 N and 0.372 mm^2, respectively) and *tg1tg1* (1.076 N and 0.259 mm^2, respectively) genotypes. These observations suggest that *QGt.orst-2D.1* and *QGba.orst-2D* represent the action of *Tg1* and that *Tg1*'s effect on glume tenacity appears to reside on its ability to alter the level of physical attachment of glume bases to the rachilla of a spikelet.

Morphological and anatomical studies in the genus *Triticum* have shown that glumes are not deciduous tissues and that abscission layers do not form at the point of their attachment to the rachilla of the spikelet (Morrison 1994). Consequently, glume tenacity or adherence appears to be principally a function of the lignification of parenchyma cells at the base of the glume. In the case of common wheat (*T. aestivum*), non-tenacious glumes at maturity are only partially lignified and there is shrinkage of tissue at the glume base (Schröder 1931 cited by Morrison 1994). Conversely, genotypes with tenacious glumes show greater parenchyma cell lignification and reduced glume base tissue contraction. Thus, we suspect that *Tg1*'s effect on glume adherence and threshability might be mediated by its ability to modulate the lignification of parenchyma cells at the base of a given glume. Further research is needed to explore this possibility.

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