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Cytological and microsatellite mapping of the gene for brittle rachis in a *Triticum aestivum-Aegilops tauschii* introgression line

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Summary

Aegilops tauschii (Coss.) Schmal. ($2n = 2x = 14$, DD), a wild relative of wheat has been considered to be a valuable source of variation for improvement of cultivated wheats. However, undesirable genes can be incorporated into the cultivated varieties from wild relatives. The spontaneous spike shattering caused by the brittle rachis character is of adaptive value in wild grass species, but not in cultivated varieties. The rachis of R-61, which was derived from the cross of *T. aestivum* cv. Bet Hashita with an accession of *Ae. tauschii*, was brittle. Using telosomic stocks, the brittle rachis gene Br^{61} (tentatively designated) of B-61 was located on the short arm of chromosome 3D and the distance of Br^{61} to the centromere was 31.9 cM. The distance of Br^{61} from the centromeric marker *Xgdm72* was 25.3 cM on the short arm of chromosome 3D. The location of Br^{61} was similar to Br_1 whose location was determined by telosomic mapping and microsatellite mapping. Discrepancy of disarticulation type was found between R-61 and *Aegilops tauschii* suggesting that the recombination around the regions of Br_1 locus and Br^t locus created the wedge type disarticulation of R-61.

Introduction

Wild relatives of wheat represent a potential source for crop improvement. *Aegilops tauschii* (Coss.) Schmal. ($2n = 2x = 14$, DD) is the diploid genome donor of wheat (*Triticum aestivum* L. em. Thell., $2n = 6x = 42$, AABBDD) (Kihara, 1944; McFadden & Sears, 1946). Cox et al. (1990) made direct crosses between wheat and *Aegilops tauschii* to introduce genes from this species into the wheat genome. Fritz et al. (1995a,b) analyzed winter wheat × *Ae. tauschii* populations to assess introgression and quantitative traits. The D-genome introgression lines will provide better information for breeding, since the introduced segments have been genetically identified by Pestsova et al. (2001) who developed a set of *Triticum aestivum-Ae. tauschii* introgression lines by backcrossing. These introgression lines were chromosome substitution lines with different segments of individual chromosomes of *Ae. tauschii* in a common wheat "Chinese Spring" background. Undesirable phenotypes are likely to be incorporated into the cultivated varieties by use of wild relatives. One such character, brittle rachis which causes spontaneous spike shattering is of adaptive value in wild grass species, though not in cultivated varieties. Since the development of synthetic hexaploid wheat by McFadden and Sears (1946), the brittle rachis of *T. spelta* L. has been regarded as a pleiotropic effect of the spelt gene (*q*) which is responsible for hulled grain (Cao et al., 1997). There has been no study on the function of the gene for brittle rachis of *Ae. tauschii.* The gene for brittle rachis, Br_1 of *T. aestivum* is located on the short arm of chromosomes 3D (Chen et al., 1998; Watanabe et al., 2002). A D-genome introgression line, R-61 was derived from the cross, *T. aestivum* cv. Bet Hashita with an accession of *Ae. tauschii* to introduce

a disease resistance gene. The gene for brittle rachis of R-61 was tentatively designated as Br^{61}. The rachis of R-61 breaks below the node above the insertion point of the spikelet, thus creating a wedge-shaped spikelet unit attached to the rachis internode beneath, whereas the rachis of *Ae. tauschii* breaks at the node, thus creating a barrel-shaped spikelet. The gene for brittle rachis, Br^t, of *Ae. tauschii* is also located on the short arm of chromosome 3D (Watanabe et al., 2005).

The present study aimed to locate the genes which cause the wedge type of brittle rachis in a D-genome introgression line, R-61.

Materials and methods

Plant materials and assessment of brittle rachis

R-61, a *T. aestivum-Ae. tauschii* accession and its recipient hexaploid cultivar, Bet Hashita, were obtained from Dr. Uri Kushnir, Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel. R-61 has brittle rachides, whereas Bet Hashita has tough rachides. A cultivar with brittle rachis, *Triticum aestivum* cv. KU511, was used to assess allelic relationships. Hybrids of KU511/R-61 and Bet Hashita/R-61 were made. Rachis brittleness is defined when a spike having a rachis that disarticulated when the tip of the spike was bent by up to 45° relative to the peduncle. Two observers independently assessed rachis fragility and classified the accessions into two classes, brittle and tough.

Telosomic mapping of the gene for brittle rachis

To confirm the chromosome arm location of the gene for brittle rachis in R-61, we made the following crosses; euploid Chinese Spring (CS, $2n = 42$) and ditelosomic (dT) lines, CS dT 3DL ($2n = 40+2t; 20''+t''$) and CS dT 3DS ($2n = 40+2t; 20''+t''$) as female to R-61. F_2 seed was harvested from monotelodisomic ($2n = 41 + t$) F_1 plants, which showed the pairing, $20'' + t1''$, in pollen mother cells at metaphase *I* of meiosis. F_2 progenies were grown and classified for rachis brittleness. To map the gene for brittle rachis of R-61, monotelodisomic F_1 ($2n = 41 + t$) plants of CS dT 3DS/R-61, which showed the pairing, $20'' + t1''$, in pollen mother cells at metaphase *I*, were crossed as female to CS. Testcross progenies were grown and classified for chromosome number and brittle rachis. The F_1 and testcross progenies were checked for chromosome constitution. Progenies of four F_2 plants with tough rachis from the crosses CS dT 3DL/R-61 were also checked to determine the chromosome constitution of F_2 plants. Before planting, root tips of the seedlings were taken, treated with ice-cold distilled water for 24 h, and fixed in a 3:1 mixture of 99% methanol and glacial acid, stained with aceto-carmine and squashed on a glass slide under a cover glass. Chromosomes were counted using a light microscope.

Microsatellite mapping of the gene for brittle rachis

To assess the linkage relationships between microsatellite markers and the gene for brittle rachis, a cross between the parents Bet Hashita (tough rachis) and R-61 (brittle rachis) was made and the F_1 plants were backcrossed to Bet Hashita to obtain $55B_1F_1$ seeds (Bet Hashita*2/R-61). The rachis of Bet Hashita was tough, whereas that of R-61 was brittle. An F_2 population was also grown to assess segregation for brittle rachis. R-61 was also crossed with *T. aestivum* cv. KU511 to assess allelic relationships at the Br_1 locus. F_1 plants from this cross were grown in the greenhouse and were bagged just before flowering to obtain F_2 seeds. Nuclear DNA was isolated from leaves of single F_2 plants using a Qiagen Dneasy mini kit. To map the genes, we used the wheat *Xgwm* microsatellite markers located on chromosome 3D, which were developed for *T. aestivum* and *Ae. tauschii* and described by Röder et al. (1998), Pestsova et al. (2000) and Song et al. (2005). Further microsatellite markers were provided by Dr. M. S. Röder under the aegis of a material transfer agreement between Gifu University and IPK-Gatersleben, Germany. The markers are transferable from *T. aestivum* to *Ae. tauschii* and *vice versa* (Sourdille et al., 2001; Guyamr'ch et al., 2002).

Polymerase chain reactions (PCR) were performed with minor modification as described by Plaschke et al. (1995). After electrophoresis of PCR products in 10% acrylamide gel, amplified fragments were detected by silver staining. Multipoint linkage values in centiMorgans (cM) were calculated using Map Manager QTX (http://mapmgr.roswellpark.org/).

Results and discussion

Rachis of D genome introgression line

It was of interest that the rachis of R-61 was brittle, whereas the rachis of recipient parent, Bet Hashita,

Table 1. Segregation for brittle rachis in five F_2 populations

Cross combination	Rachis		χ^2 analysis ($df = 1$)[a] (3:1)
	Brittle	Tough	
KU511/R-61	126	0	–
Bet Hashita/ R-61	77	22	0.407^{NS}
CS/R-61	104	24	2.667^{NS}
CS dT 3DS/R-61	94	32	0.011^{NS}
CS dT 3DL/R-61	112	4[b)]	28.736^{**}

[a]Values for significance at $P = 0.01$; 6.635 ($df = 1$).
[b]$2n = 40$.
**: Significant at $P = 0.01$.

was tough. R-61 was derived from the cross, *T. aestivum* cv. Bet Hashita with an accession of *Ae. tauschii* to introduce a disease resistance gene. The gene for brittle rachis of R-61 was tentatively designated as Br^{61}. The rachis of R-61 breaks at the node above the insertion point of the spikelet, thus creating a wedge-shaped spikelet unit attached to the rachis internode beneath, whereas the rachis of *Ae. tauschii* breaks at the node, thus creating a barrel-shaped spikelet.

As shown in Table 1, the F_2 hybrid of KU511/R-61 did not segregate any plants with tough rachides, indicating that Br^{61} of R-61 was allelic to Br_1 of KU511. The F_2 of Bet Hashita/R-61 segregated in the ratio of 3:1 (brittle:tough). In the F_2 generation from the crosses KU511/R-61 and Bet Hashita/R-61 the only type of rachis disarticulation found was the wedge type in plants showing the brittle trait.

Telosomic mapping of the gene for brittle rachis

The use of ditelosomics to determine the chromosomal arm location of genes depends on identification of the progenies with aberrant segregation. Figure 1 is a schematic illustration showing how chromosome arm location of Br^{61} and the distance of Br^{61} from centromere were determined.

The cross with the parent carrying the gene for brittle rachis should have an excess of the dominant phenotype because the F_1 plant receives only the chromosomes with the dominant allele. For example, if Br^{61} were on CS 3DS, the cross between the CS dT 3DL ($20'' + t''$) and R-61 ($21''$) would produce monotelodisomic ($20'' + t1''$) F_1 plants with a 3D chromosome from R-61 and a chromosome arm 3DL from the CS dT 3DL. These F_1 plants would produce gametes (either male or female) carrying either one monosomic chromosome or one telosomic chromosome. The telosome chromosome will not be transmitted through the male gamete but it will be transmitted by the female gamete. Hence, all F_2 plants will have the brittle rachis phenotype.

The F_2 of crosses of CS/R-61 and CS dT 3DS/R-61 segregated into the ratio of 3:1 (brittle:tough), while the segregation of F_2 progenies CS dT 3DL/R-61 showed a significant excess of plants with brittle rachides, because the telosomic chromosomes were eliminated from the F_2 population. Four segregant plants with tough rachis were nullisomic ($2n = 40; 20''$) and therefore completely lacked 3DS. These results confirmed that the gene for brittle rachis is located on the short arm of chromosome 3D.

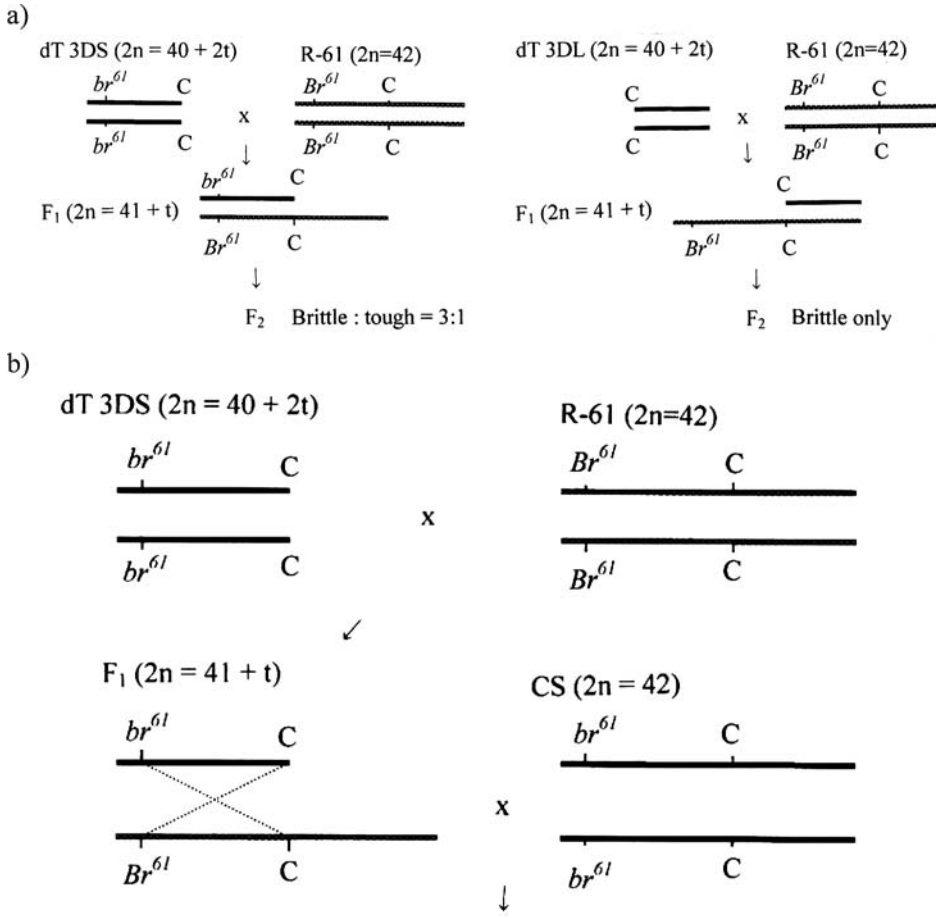
As Br^{61} is located on 3DS, in the monoteldisomic F_1 plant, the gametes with the entire chromosome 3D will have Br^{61} or br^{61}, in a ratio depending on the recombination frequency. The gametes with chromosome 3DS will have either Br^{61} or br^{61}, also depending on recombination frequency. The ratio $Br^{61} : br^{61}$ will be (1-p):p, where p is recombination frequency. In the test cross progenies, the chromosome number of plants is either $2n = 42$ or $2n = 41 + t$ in the ratio 1:1 and segregation for brittle rachis was expected in the ratio 1: 1. Recombinants are the plants with brittle rachis and $2n = 41 + t$, and plants with tough rachis and $42n = 42$. From the progeny of the cross CS dT 3DS/R-61//CS (Table 2), the recombination frequency (p) was calculated as $(17+23)/142 = 0.282$. The standard error (0.038) was calculated as $[(1-p)p/142]^{1/2}$. The recombination frequency was converted to map distance map distance following

$$\text{Kosambi (1944): } x = 25 \log_e [(1 + 2p)/(1 - 2p)] \quad (1)$$

where x is the map distance (cM) corresponding to the recombination frequency, p. The standard error of x was calculated as $100 \times 0.038/(1 - 2p^2)$. The distance of Br^{61} from the centromere was 31.9 ± 4.49 cM.

Comparison of the allelic composition of 3D chromosomes between Bet Hashita and R-61

From the telosomic mapping, Br^{61} was located on the short arm of chromosome 3D. The allelic composition of 3D chromosomes of Bet Hashita and R-61 was analyzed using 24 microsatellite markers specific to chromosome 3D. As shown in Figure 1, the parts of



Gamete type	Genotype	Chromosome number
Non-recombinant	Br^{61}	21
	br^{61}	20 + t
recombinant	Br^{61}	20 + t
	br^{61}	21

Figure 1. Scheme employed to determine arm location of Br^{61} and distance from the centromere (a) If Br^{61} were on CS 3DS, the cross of CS dT 3DL/ R-61 would produce monotelodisomic ($20'' + t1''$) F_1 plants with a 3D chromosome from R-61 and a chromosome arm 3DL from the CS dT 3DL. These F_1 plants would produce gametes (either male or female) carrying either one monosomic chromosome or one telosomic chromosome. The telosome chromosome will not be transmitted through the male gamete but it will be transmitted by the female gamete. Hence, all F_2 plants will have the brittle rachis phenotype. F_2 plants of CS dT 3DS/ R-61 will segregate into the ratio of 3:1 (brittle:tough). (b) When Br^{61} is located on 3DS, in the monoteldisomic F_1 plant, the gametes with the entire chromosome 3D ($n = 21$) and with chromosome 3DS ($n = 20 + t$) will have either Br^{61} or br^{61}, depending on recombination frequency. C indicates the centromere.

the chromosomes carrying Bet Hashita allele are designated in white and the parts of chromosome carrying R-61 alleles are designated in black. The segments of *Ae. tauschii* were introgressed into the short arm of chromosome 3D of R-61, which contains the loci, *Xgwm2*, *Xgdm72* and *Xgwm497*. Watanabe et al. (2005) found that the centromeric markers *Xgdm72* and *Xgwm2* were linked with brittle rachis locus, Br_1 of KU511. The segment of *Ae. tauschii* was also found in the long arm of chromosome 3D of R-61.

Table 2. Joint segregation for chromosome number and brittle rachis in the progenies of CS dT 3DS/R-61//CS, associated χ^2 values and map distances

	Rachis		χ^2 analysis	
Chromosome number	Brittle	Tough	Ratio	Value[a)]
			Dihybrid (1:1:1:1)	28.479^{**} $(df = 3)$
42	47	23	Chromosome number (1:1)	0.028^{NS} $(df = 1)$
41 + t	17	55	Rachis (1:1)	1.380^{NS} $(df = 1)$
			Linkage χ^2	27.070^{**} $(df = 1)$

[(a)]Value for significance: 3.84 $(df = 1)$ at $P = 0.054$ and 11.345 $(df = 3)$ at 0.01.
[NS]:Non-significant. Linkage (centromere -Br^{61}): 31.9 ± 4.49 cM.

Microsatellite mapping of genes for brittle rachis

Among the 55 plants of the B_1F_1 population (Bet Hashita*2/R-61), 25 had brittle rachis, and 30 tough rachis. The segregation ratio of brittle rachis fitted the expected 1:1 ratio ($\chi^2 = 0.455$, $df = 1$). Thirteen polymorphic microsatellites were chosen for analysis. No deviations from the expected 1:1 ratio were found, with χ^2 values ranging from 0.018 to 1.473 ($df = 1$). The results of microsatellite mapping of Br^{61} are shown in Figure 2. They showed that the Br^{61} locus is closely linked to *Xgwm2* (27.5 cM) and the centromeric marker *Xgdm72* (25.3 cM) on the short arm of chromosome 3D (Figure 2).

The results of microsatellite mapping of Br^{61} coincided with those obtained by the location using telosomic stocks. The location of Br^{61} was similar to Br_1 whose location was determined by telosomic mapping (Watanabe et al., 2003) and microsatellite mapping (Watanabe et al., 2006). The brittle rachis gene, Br^t of *Ae. tauschi*, which disarticulated as barrel type, also located to the the short arm of chromosome 3D (Watanabe et al., 2005). However, the allelic relationship between *Br1* and Br^t was not well elucidated, because the expression of the brittle rachis gene of *Ae. tauschii* in synthetic hexaploid wheat is not known. We note that the *Br*/*br* gene complex on chromosomes 3A and 3B is epistatic to the gene for brittle rachis of *Ae. tauschii*, because the rachis of the first synthetic hexaploid wheat derived from the cross, *Triticum dicoccoides*/*Ae. tauschii* by McFadden and Sears (1946) disarticulated as wedge type. The rachis of Tetra Canthatch (AABB, $2n = 4x = 28$), which was cytologically extracted from a hexaploid cultivar Canthatch (Kerber, 1964), is tough, whereas the accessions of *Ae. tauschii* are brittle. Five synthetic hexaploid wheat accessions (Tetra Canthatch/*Ae. tauschii*), which were developed by Dr. E. R. Kerber, have tough rachides

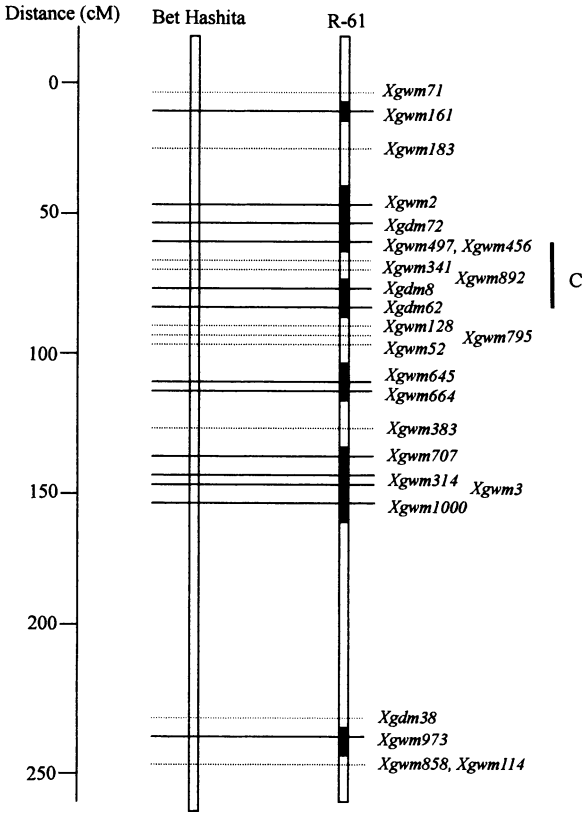


Figure 2. Comparison of the allelic composition of 3D chromosomes of Bet Hashita and R-61. The allelic composition of Bet Hashita and R-61 was analyzed using 25 microsatellite markers specific to chromosome 3D. The parts of the chromosomes carrying Bet Hashita allele are designated in white and the part of chromosome carrying R-61 alleles are designated in black. The markers and the distances on chromosome 3D were provided by Dr. M.S. Röder.

(Watanabe, 1983). All synthetic hexaploid wheat accessions of 'Langdon' durum/*Ae. tauschii* had tough rachides (Xu, *personal communication*). The rachis of the chromosome substitution line, CS-Synthetic wheat DS 3D, where chromosome 3D from Chinese Spring

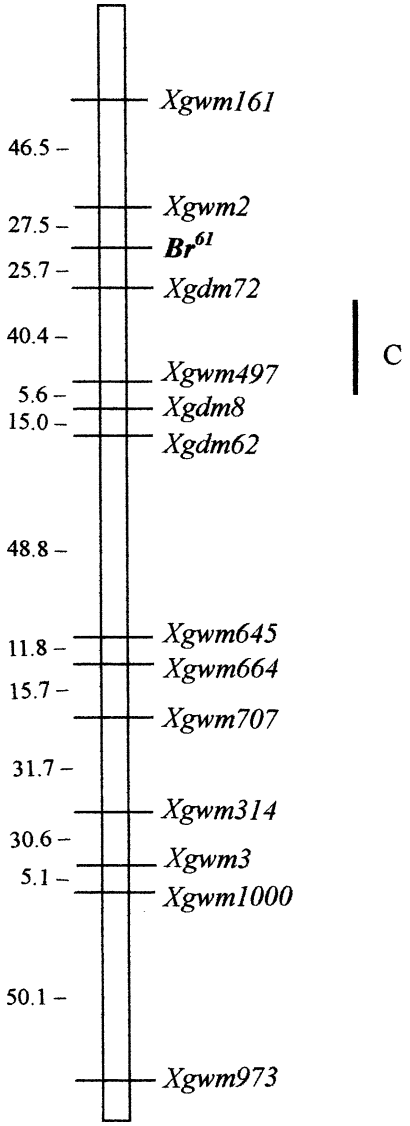


Figure 3. Linkage map of chromosome 3D showing the locations of Br^{61}. Genetic distances are given in centiMorgans (cM). The putative location of centromere is indicated by bar labeled with C.

(CS) was replaced by its equivalent in synthetic wheat by McFadden and Sears (1946), was tough. The brittle rachis of R-61 originating from introgressive hybridization between *T. aestivum* cv. Bet Hashita and *Ae. tauschii* disarticulates as wedge type.

It is of interest if Br^{61} and Br_1 were different alleles at the same locus. It was evident that the recombination around the regions of Br_1 locus and Br^t locus created the wedge type disarticulation of R-61. This suggests that either intralocus recombination at the complex locus determining brittle rachis or recombination of closely linked locus/loci for brittle rachides was responsible for the brittle rachis of R-61. Alternatively, Chen (2001) suggested that some genes modify disarticulation type.

Discrepancy of disarticulation was also found between *Triticum* and its wild relative, *Aegilops speltoides* ($2n = 2x = 14$). The *ligustica/aucheri* spike dimorphism of *Ae. speltoides* (Zohary and Imber, 1963), behaved as allelic variants at a single locus, which was mapped in the centromeric region of chromosome 3S (Luo et al., 2005). The *ligustica* spikes disarticulate into wedge shaped below each spikelet. In the form *aucheri*, the rachis of the spike is tough except for a brittle node at base of spike. The genomic regions of *Br* loci of A, B and D genomes need to be characterized more precisely along with those of *Br* loci of wild relatives.

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