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RESEARCH ARTICLE

Microsatellite mapping of genes for branched spike and soft glumes in *Triticum monococcum* L.

Y. Amagai · P. Martinek · N. Watanabe · T. Kuboyama

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Abstract The locus responsible for branched spike in a branched spike mutant of *Triticum monococcum* L. (2n = 2x = 14, A^mA^m genome) and soft glume in *Triticum sinskajae* Filat. et Kurkiev (2n = 2x = 14, A^mA^m genome) were mapped by genotyping F_2 populations using microsatellite markers. Phenotypic analysis in the cross *T. sinskajae* PI 418587/a branched spike mutant KT3-24 confirmed that both characters were under control of a recessive allele at a single locus, and they were linked with 26.6 cM. The branched head in *T. monococcum* (bh^m) locus was located on chromosome $2A^mS$ and the marker *Xgwm122* flanked the bh^m gene distally. Soft glume locus in *T. sinskajae* was allelic to the soft glume (*sog*) locus in mm09, a soft glume mutant of *T. monococcum.* The *sog* locus was linked with *Xwmc644* distally. In the F_2 hybrids of *T. monococcum* #252/PI 418587 and *T. monococcum* KT 3-21/PI 418587, *sog* was linked with *Xgwm71*. The gene *fg* which determines a false glume was also located on chromosome $2A^mS$ and the recombination between *sog* and *fg* (1.6 cM) was obtained in F_2 hybrid of KT 3-21/PI 418587.

Keywords Branched spike · Genetic resource · Mutant · Soft glume · *Triticum monococcum*

Y. Amagai · N. Watanabe (✉) · T. Kuboyama
College of Agriculture, Ibaraki University, 3-21-1 Chuo, Ami, Inashiki, Ibaraki 300-0393, Japan
e-mail: watnb@mx.ibaraki.ac.jp

Y. Amagai
United Graduate School of Agricultural Science, Tokyo University of Agriculture and Technology, 3-5-8 Saiwai, Fuchu, Tokyo 180-8509, Japan

P. Martinek
Agrotest Fyto, Ltd., Havlíčkova 2787, 767 01 Kroměříž, Czech Republic

Introduction

One of the ways to improve wheat yield is to increase grain number per spike and per unit area, and this would be partially depend on spike morphology. The wheat spike is composed of many spikelets arranged to form two opposite rows along the main axis. The spikelet is composed of several florets jointed at the axis alternatively on opposite sides. In normal spike, a single spikelet arises from each rachis node. Wheats with supernumerary spikelet are evidently a genetically heterogeneous group, where more than one spikelet arises per rachis node (Peng et al. 1998; Klindworth et al. 1990a, b). A frequently type of supernumerary spikelet is the branched form of *Triticum turgidum* L. (2n = 4x = 28, genome BBAA) where the extra spikelets grow from secondary spike rachides and are named genuine branching (syn. 'turgidum type of branching'). The genes for this type of branching were mapped earlier (Klindworth et al. 1990a, b). Although the expression of the branched form was modulated by a number of environmental factors (Sharman 1944; Pennell and

Halloran 1983), the branched form was recessive (Pennell and Halloran 1983; Klindworth et al. 1990a; Peng et al. 1998; Martinek and Bednar 2001). In tetraploid wheat, Klindworth et al. (1990a) suggested that branched form was conditioned by a single major gene (*bh*) on chromosome 2A in concert with an unknown number of minor genes. Haque et al. (2012) indicated that the *bh* gene was linked to microsatellite loci on chromosome 2AS. Martinek and Bednar (2001) developed winter hexaploid wheat germplasm characterized by genetically stable multirow spike (*mrs*), which is controlled by a single recessive gene. Dobrovolskaya et al. (2009) mapped the *mrs1* gene on chromosome 2DS using microsatellite markers. The involvement of the homoeologous group 2 chromosomes in the control of branched form has been noted in both tetraploid and hexaploid wheat (Klindworth et al. 1997, 1990a, b; Peng et al. 1998). Muramatsu (2009) presumed that the homoeologous group 2 chromosomes are involved in a genetic system determining the number of spikelets per rachis node in the tribe *Triticeae*.

Triticum monococcum L. (2n = 2x = 14, genome A^mA^m), commonly known as einkorn wheat, was widely cultivated during the pioneering human farming activities in the Fertile Crescent. Its A^m genome is closely related to the A^u genome of *Triticum urartu* Tumanian ex Gandilyan (2n = 2x = 14, genome A^uA^u), which was the A genome progenitor of the polyploid wheat species. *T. urartu* has been the dominant A genome donor of the most important polyploid wheat species, *T. turgidum* L., *Triticum timopheevii* (Zhuk.) Zhuk. (2n = 4x = 28, genome AAGG), and common wheat *Triticum aestivum* L. (2n = 6x = 42, genome BBAADD). In contrast, *T. monococcum* has only been the A^m genome donor of *Triticum zhukovskyi* Menabde et Ericz. (2n = 6x = 42, genome A^mA^mAAGG) (Dvorak et al. 1993; Dubcovsky et al. 1996; Baum and Bailey 2004). Although the A^m genome is under-represented in hexaploid wheat, the exploitation of genetic diversity in *T. monococcum* and discovery of novel variant alleles may provide opportunities for further wheat genetic improvement (Valkoun 2001). Several orthologous genes are confirmed and mapped in *T. monococcum*. The genes for black glume (*Bg*) and pubescent glume (*Hg*) were located on chromosome $1A^m$ (Dubcovsky et al. 1996; Goncharov et al. 2007; Jing et al. 2007). Singh et al. (2007) located the blue aleurone (*Ba*) gene on chromosome $4A^m$. Morphological mutants in *T. monococcum* were induced by Multani et al. (1992) and Dr. K. Yamashita (http://www.shigen.nig.ac.jp/wheat/komugi/strains/). Kosuge et al. (2011) located the chlorina mutant gene on chromosome $7A^m$ using a Yamashita's mutant. The branched spike mutant was developed Dr. K. Yamashita. *Triticum sinskajae* Filat. et Kurkiev (2n = 2x = 14, genome A^mA^m) was discovered in accession K-20970 of *T. monococcum* during the analysis of the accessions collected in the coastal zones of Turkey by Prof. Zhukovskii (Filatenko and Kurkiev 1975). Filatenko and Kurkiev (1975) believe that *T. sinskajae* is a natural naked mutant of *T. monococcum*. Kuspira et al. (1989) found semi-compact spike and soft glume (free-threshing) of *T. sinskajae* were tightly linked. A false glume (gene symbol, *fg*), a glume-like structure, is located between the glume and lemma of the outer florets of each spikelet. False glume was also closely linked to the gene for soft glume/semi-compact spike. Goncharov et al. (2007) found that fissile inner (flower) glume (gene symbol, *fig*) was linked with semi-compact spike. It seems that fissile inner (flower) glume is a synonym of "false glume". Taenzler et al. (2002) mapped the gene for soft glume (*sog*) of *T. sinskajae* on chromosome $2A^mS$ using AFLP markers. Sood et al. (2009) also mapped the soft glume (*sog*) locus of a soft glume mutant of *T. monococcum* on chromosome $2A^mS$.

Molecular markers involving mapping genes of agricultural importance are widely applied. Numerous polymorphic microsatellite markers have been integrated into a genetic framework map of wheat (Röder et al. 1998a, b; Song et al. 2005; Torada et al. 2006). We applied microsatellite markers to map the genes for branched spikes and soft glumes in *T. monococcum*.

Materials and methods

Five accessions of *T. monococcum* and one accession of *T. sinskajae* were available for the experiment. Heading of *T. monococcum* #252 was early. *T. monococcum* KT 3-24 was a mutant with branched spike developed by Dr. K. Yamashita. *T. monococcum* KT 3-21 has the chlorina phenotype. The spike of *T. monococcum* mm09 has a soft glume and

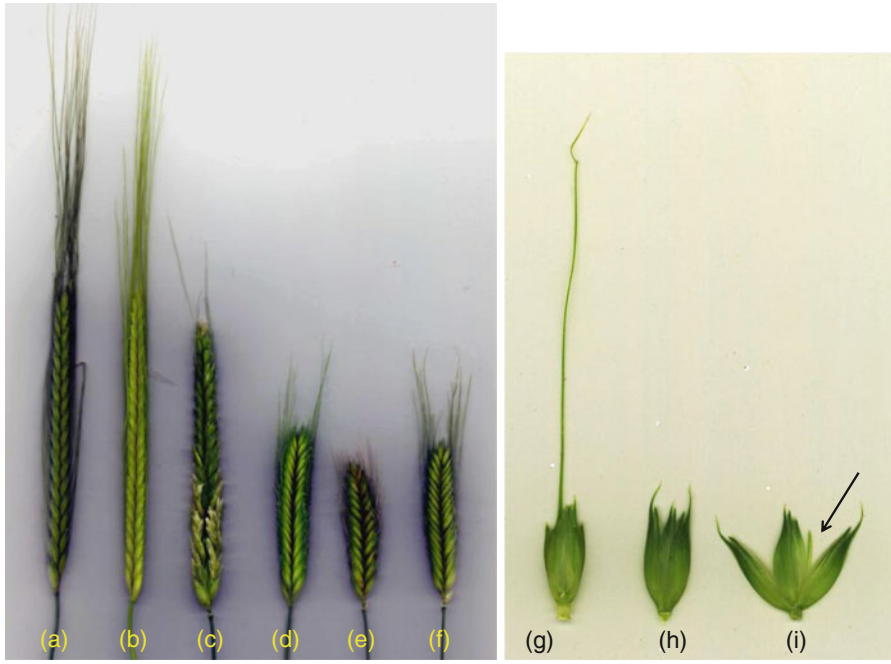

Fig. 1 The spike features of *Triticum monococcum* accessions (left to right; **a** *T. monococcum* #252, **b** *T. monococcum* KT 3-21, **c** *T. monococcum* KT 3-24, **d** *T. sinskajae* PI 418587, **e** *T. monococcum* mm09 and **f** *T. monococcum* PI 584654) and spikelets of **g** *T. monococcum* KT 3-21 and **h**, **i** *T. sinskajae* PI 418587. *Arrow* in spikelet **i** indicates the false glume, a glume-like structure located between the glume and lemma of the outer florets of each spikelet of PI 418587

simultaneously semi-compact spike determined by the gene *sog* located on chromosome $2A^mS$ (Sood et al. 2009). *T. sinskajae* PI 418587 has soft and semi-compact spike. *T. monococcum* PI 584654 is a breeding line with soft spike and semi-compact spike, and is a bulk of equal quantities of seed from 34 F_5 lines selected from the cross, *T. monococcum*/*T. sinskajae* (Vallega 1996). In the present study, we used the progenies of a single spike of PI 584654. Figure 1 shows the spike features of all parental accessions (Fig. 1a–f), and spikelet morphology of KT 3-21 and PI 418587 (Fig. 1g–i).

To construct the linkage map of the genes for branched spike (*bh*), soft glume/semi-compact spike (*sog*) and false glume (*fg*) and to check allelic relationships, we developed seven F_2 hybrids, PI 418587/KT 3-24, PI 584654/KT 3-24, #252/PI 418587, KT 3-21/PI 418587, mm09/#252, mm09/PI 418587 and mm09/PI 854654. The progenies the F_2 recombinants of KT 3-21/PI 418587 were grown to observe in the F_3 generation. All F_2 populations and F_3 progenies were grown in the experimental field at the College of Agriculture, Ibaraki University, Japan.

Microsatellite mapping

Genomic DNA was extracted from seedling leaves from individuals of three F_2 populations, KT 3-24/PI 418587, #252/PI 418587 and KT 3-21/PI 418587, according to Dellaporta et al. (1983). To map the gene, we used wheat microsatellite markers located on chromosome 2A (Röder et al. 1998a, b; Song et al. 2005; Torada et al. 2006). The PCR conditions, electrophoresis of PCR products and detection of amplified fragments were performed according to Kosuge et al. (2008). Multipoint linkage values were calculated using Map Manager QTX (Manly et al. 2001). Minimum LOD scores of 3.0 were used to develop the linkage map. The software calculated genetic distances in centiMorgans (cM) by applying the Kosambi (1944) mapping function.

Results

Table 1 shows the segregation of branched spike, soft/semi-compact spike and false glume in seven F_2

Table 1 Segregation of branched spike, soft glume/semi-compact spike and false glume in seven F_2 hybrids of *T. monococcum*

Cross combination	Spike		Total	χ^2 analysis (3:1)
	Normal	Branched		
(a) Branched spike				
PI 418587/KT 3-24	85	30	115	0.073
PI 584654/KT 3-24	201	72	273	0.274
Cross combination	Glume/spike		Total	χ^2 analysis (3:1)
	Hard/normal	Soft/semi-compact		
(b) Soft/semi-compact spike				
PI 418587/KT 3-24	88	27	115	0.142
PI 584654/KT 3-24	209	64	273	0.353
#252/PI 418587	131	50	181	0.665
KT 3-21/PI 418587	96	26	122	0.885
mm09/#252	104	41	145	0.830
mm09/PI 418587	0	166	166	–
mm09/PI 584654	0	181	181	–
Cross combination	False glume		Total	χ^2 analysis (3:1)
	Absent	Present		
(c) False glume				
KT 3-21/PI 418587	95	27	122	0.536
mm09/PI 418587	0	166	166	–
mm09/PI 584654	0	181	181	–

We did not record presence/absence of false glume in F_2 plants of #252/PI 418587 and PI 584654/KT 3-24

Note Significant at 5 % level; Value for significance at $p = 0.05$; 3.84 (df = 1)

hybrids. The spike branching phenotype segregated in a ratio of 3 normal: 1 branched in the two F_2 hybrids, PI 418587/KT 3-24 and PI 584654/KT 3-24. For the soft/semi-compact spike, F_2 hybrids of *T. sinskajae* PI 418587/KT 3-24, #252/PI 418587 and KT 3-21/PI 418587 segregated 3 hard/monococcum type: 1 soft/semi-compact type. F_2 hybrids of PI 584654/KT 3-24 also segregated 3 hard/monococcum type: 1 soft/semi-compact type. The F_2 hybrid of mm09/#252 segregated 3 hard/monococcum type: 1 soft/semi-compact type. The F_2 hybrids of mm09/PI 418587 and mm09/PI 584654 did not segregate for spike type indicating that the genes for semi-compact of spike in these parents were allelic. For false glume, the F_2 hybrid of KT 3-21/PI 418587 segregated 3 absent: 1 present. We did not obtain any plants without false glume in the F_2 hybrids of mm09/PI 418587 and mm09/PI 584654, indicating allelic gene conditioned false glume in these parents.

Linkage relationship among branched spike, soft/semi-compact spike and false glume

Table 2 shows the linkage relationship among branched spike, soft/semi-compact spike and false glume in three F_2 hybrids. The F_2 hybrids of PI 418587/KT 3-24 and PI 584654/KT 3-24 indicated the linkage relationships between *sog* and *bh*. The calculated recombination rates were 0.267 and 0.243, respectively. We found three recombinants in the F_2 of KT 3-21/PI 418587. Joint segregation for semi/soft compact spike and false glume was 94 hard/monococcum type without false glume: 2 hard/monococcum type with false glume: 1 soft/semi-compact type without false glume: 25 soft/semi-compact type with false glume, and it did not fit a 9:3:3:1 ratio ($\chi^2 = 88.944$, df = 3, $p < 0.05$). The calculated recombination rate between *sog* and *fg* was 0.026

Table 2 Linkage relationship among branched spike, soft/semi-compact spike and false glume in three F_2 hybrids of *T. monococcum*

Cross combination	Locus		Number of plants with phenotype				χ^2 value		Recombination rate
	A	*B*	*A-B-*	*A-bb*	*aaB-*	*aabb*	9:3:3:1 (df = 3)	Linkage (df = 1)	
PI 418587/KT 3-24	*Bh*	*Sog*	60	25	28	2	6.55	6.34*	0.267
PI 584654/KT 3-24	*Bh*	*Sog*	141	60	68	4	18.07*	17.44*	0.243
KT 3-21/PI 418587	*Sog*	*Fg*	94	2	1	25	88.94*	87.52*	0.026

The recombination rate between two loci was calculated by the maximum likelihood method

* Significant at 5 % level

Note χ^2 value for significance at $p = 0.05$; 3.84 (df = 1) and 7.81 (df = 3)

(Table 2). The genotypes of two recombinants with hard/monococcum type spike and false glume were supposed to be *Sog–fgfg*, whereas the genotype of a recombinant, soft/semi-compact spike plant without false glume, was supposed to be *sogsogFg*. We confirmed the recombined types in F_3 progenies of three recombinants.

Microsatellite mapping of bh^m, *sog* and *fg* genes

It was known that the gene for soft glume (*sog*) was located on the chromosome $2A^mS$ by Taenzler et al. (2002) and Sood et al. (2009). In the F_2 of PI 418587/KT 3-24, 20 polymorphic markers on chromosome $2A^m$ were used to assign the position of the spike branching gene (bh^m, branched head in *T. monococcum*) and soft glume (*sog*). The linkage map was divided into two fragments (Fig. 2). The major fragment indicated the linkage relationships among bh^m, *sog* and markers. The gene bh^m was linked with *Xgwm122* marker distally, whereas *sog* was linked with *Xwmc644*. The map indicated that the genes bh^m and *sog* were located on chromosome $2A^mS$.

According to Sood et al. (2009) and Haque et al. (2012), the *Xgwm71* marker was a pivotal marker franking *sog* and *bh* loci. However, in the cross PI 418587/KT3-24, *Xgwm71* was not polymorphic between parents. Hence, we mapped the *sog* gene further using two F_2 hybrids of #252/PI 418587 and KT 3-21/PI 418587, paying attention to the *Xgwm71* marker franking the *sog* gene. In the F_2 of #252/PI 418587, the *sog* gene was bracketed by the markers *Xgwm558* and *Xgwm71* (Fig. 2) at distances of 5.0 and 5.2 cM respectively. In the F_2 of KT 3-21/PI 418587, the *sog* gene was linked with *Xgwm71* distally, and the distance between *sog* and *Xgwm71* was 15.3 cM.

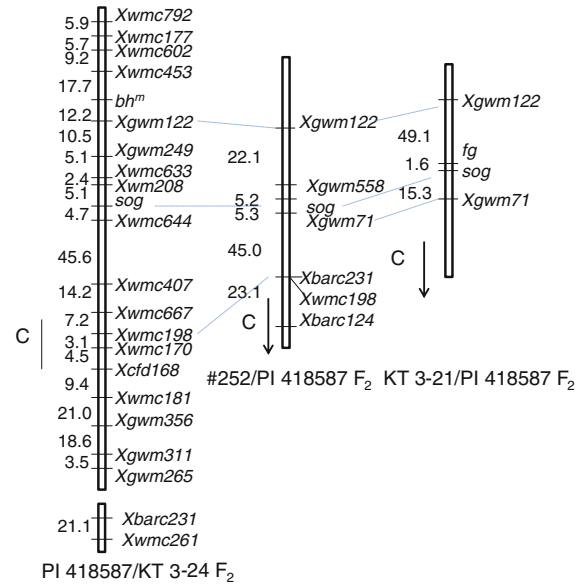

Fig. 2 Linkage maps of chromosome $2A^m$ in the F_2 hybrids of *Triticum monococcum* KT 3-24/*T. sinskajae* PI 418587, *T. monococcum* #252/*T. sinskajae* PI 418587 and *T. monococcum* KT 3-21/*T. sinskajae* PI 418587

Recombination between *sog* and *fg* (1.6 cM) was obtained in the F_2 of KT 3-21/PI 418587.

Discussion

In the present study, the segregation behavior of the branched spike in *T. monococcum* indicated that it is controlled by a single major gene, bh^m. This result coincided with Klindworth et al. (1997) and Haque et al. (2012) in *T. durum.* Shitsukawa et al. (2009) hypothesized that the branched spike phenotype is caused by the transformation of the floret meristem into a spikelet-like meristem. Spike architecture

influences the processes of pollination and seed formation, and thus plays an important role in the determination of grain number in spike. The branched spike allows the formation of more spikelets per spike, thereby increasing the spike sink capacity and can influence then harvest index of the plant. *T. monococcum,* commonly known as einkorn wheat coined from the German expression of 'one grain', generally has one grain per spikelet, *Triticum monococcum* L. subsp. *aegilopoides* (Link) Thell. also has one grain per spikelet. The *thaoudar* type of *T. monococcum* subsp. *aegilopoides* (syn. *Triticum boeoticum* Boiss. subsp. *thaoudar* (Hausskn.) E. Schiem.) and *T. urartu* has two grains per spikelet. It indicated that introduction of bh^m gene concerted with increasing spikelet and floret number in spike is essential for increasing yield potential. Multirow spike has also been considered as a usable donor for increasing the spikelet and seed number per spike (Martinek and Bednar 2001; Dobrovolskaya et al. 2009; Martinek et al. 2011). This is important for enhancing the crop yield potential, since wheat yield is generally thought to be sink-limited (Wang et al. 1998). The development of genetic resources which increase number of reproductive organs is particularly desirable (Miralles and Slafer 2007; Reynolds et al. 2005). It is interesting that Dobrovolskaya et al. (2009) mapped the gene for multirow spike (*mrs1*) on chromosome 2DS. The location of bh^m was found on chromosome $2A^mS$. The similar homoeoallelic position of both genes responsible for supernumerary spikelet expression suggests that these genes may be orthologous loci.

We found that the naturally occurring *sog* mutation in *T. sinskajae* and the artificially induced *sog* mutation in *T. monococcum* were allelic. The *sog* mutation was associated with 'false glume' formation in the mutants. Observation by Kuspira et al. (1989), Goncharov et al. (2007) and the present study indicated mutations occurred in the genomic region of the soft glume-false glume complex. In *T. monococcum,* Multani et al. (1992) induced a liguleless mutant, and Dr. K. Yamashita (http://www.shigen.nig.ac.jp/wheat/komugi/strains/) produced a non-glossy mutant. The liguleless and non-glossy mutants may be useful produce a more precise linkage map of chromosome $2A^m$ because those genes should be orthologous with the *lg* and W^I loci of tetraploid and hexaploid wheat.

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